Functional and Floristic Dynamics of Amazonian Forests

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The candidate confirms that the work submitted is her own, except where work which has formed part of jointly-authored publications has been included. The contribution of the candidate and the other authors to this work has been explicitly indicated below. The candidate confirms that appropriate credit has been given within the thesis where reference has been made to the work of others.

Chapter 3

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Abstract

Intact Amazonian forests are often considered to be in a steady-state, where gains in growth and recruitment are offset by losses in mortality and where net carbon accumulation is close to zero. However, permanent plot data have shown that this ecosystem removes ca. 0.4 Pg of carbon per year from the atmosphere, approximately 5% of annual anthropogenic emissions. This thesis tests several competing hypothesized drivers of detected shifts in the structure and dynamics of intact forest, by assessing changes in functional and floristic composition over the last 30 years in over 100 long-term tree monitoring plots distributed across the Amazon. I first show that the majority of species are restricted to wetter conditions, indicating that stronger and more frequent droughts could threaten many species (Chapter 3). I generated an index of water-deficit affiliation for more than 500 genera and 1800 species (Chapter 3), and demonstrated that this index can predict drought-induced mortality in several drought experiments (Chapter 4). Finally, I document how floristic and functional composition of Amazonian forests has shifted over the last 30 years: forests are increasingly dominated by large-statured taxa, and further, large trees are becoming even larger in absolute size (Chapters 5 and 6). However, relative gains in basal area were similar across size classes and canopy status. In addition, recruits are increasingly comprised of dry-affiliated genera, while the mortality of wet-affiliated genera has increased in plots where the dry season has become more intense. Communities are becoming more dry-affiliated, although these changes still lag behind the drying trend. Overall, this thesis shows the potential vulnerability of Amazonian biodiversity to an increase in aridity and supports the hypotheses that a changing climate and increased atmospheric CO_2 are driving changes in Amazonian floristic and functional dynamics.

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Abbreviations

Δm – drought mortality effect

ATDN – Amazon Tree Diversity Network

BCI – Barro Colorado Island

CI – Confidence Interval

CO_2 – Carbon dioxide

CRU – Climate Research Unit

CWD – Cumulative Water Deficit

CWM – Community Weighted Mean

D – Diameter

DGVM – Dynamics Global Vegetation Model

ENSO - El Niño Southern Oscillation

GLMM – Generalized Linear Mixed effect Model

ha – hectare

ITD – Ideal Tree Distribution

m – mortality

MAP – Mean Annual Precipitation

N – Nitrogen

P – Phosphorus

PCG – Precipitation Centre of Gravity

PS – Potential Size

RAINFOR – Red Amazónica de Inventarios Forestales

RMA- Reduced Major Axis regression

SST – Sea Surface Temperature

TFE – Through-fall exclusion experiment

TRMM – Tropical Rainfall Measuring Mission

WD – Wood Density

WDA – Water Deficit Affiliation

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Introduction

Tropical forests are responsible for around one third of atmospheric carbon absorbed via photosynthesis (Zhao and Running, 2010) and hold the majority of the terrestrial biodiversity (ter Steege et al., 2013;Slik et al., 2015). This vital ecosystem have been altered substantially over the last 50 years due to deforestation, defaunation, and changes in atmospheric and climatic conditions (Peres, 2000;Malhi et al., 2008;Hansen et al., 2013;Malhi et al., 2014). Around one half of the world's tropical forest area that existed before humans began significant farming activity has been converted to other land cover types (Wright, 2005). Even the remaining intact forests, such as areas in the heart of the Amazon or in the Congo Basin, have been affected in some scale by anthropogenic activities (Lewis et al., 2009b;Phillips et al., 2009;Malhi et al., 2014).

The increased emissions of fossil carbon have taken carbon dioxide concentrations in the atmosphere from ca. 300 ppm to 400 ppm in the last century (Conway and Tans, 2015), which is likely to have altered tree communities by increasing biomass and turnover rates (Phillips et al., 1994;Baker et al., 2004b;Lewis et al., 2009a). Climate has also been changing, with the increase in CO_2 causing an increase in tropical land surface temperature (IPCC, 2013b;Jiménez-Muñoz et al., 2013;Jiménez-Muñoz et al., 2016) and shifts in precipitation (Hilker et al., 2014;Gloor et al., 2015). In turn these changes in climate are likely to increase tree mortality and possibly cause a decline in forest productivity (Zhao and Running, 2010;Brienen et al., 2015;Feldpausch et al., 2016). However, little is known about the consequences of such changes to the great number of species within tropical forests (Lewis et al., 2009a). In particular, the great biotic complexity of tropical ecosystems increases the difficulty of understanding the consequences of environmental changes on biological communities. The aim of this thesis is to comprehend how tree communities in the remaining ‘intact’ tropical forests are responding to environmental changes in terms of their floristic and functional composition, and, where possible, to use these findings to shed new light on the roles of different mechanisms that may be driving ecological changes in these forests. To achieve my goal I investigate tree inventory records from long-term inventory plots monitored over the last 30 years across the Amazon forest, the largest and most diverse tropical forest on the planet.

In this first chapter I review the environmental conditions of tropical forests, how they have been changing and how tropical forests are expected to respond to these alterations to the environment. From the literature I compile a series of predictions of how environmental changes could affect different aspects of the tropical tree communities based on theory and empirical observations. Then, in Chapter 2, I narrow these predictions down to a few testable hypotheses, i.e. outcomes, expected as a response to the most likely drivers of changes in Amazonian forests dynamics. Most of the effort in my thesis was concentrated on understanding the effects of the increasing moisture stress over Amazonian forests and Chapters 3 and 4 are dedicated to this question. Chapters 5 and 6 focus on functional, floristic and structural dynamics of Amazon forests over the last 30 years.

The structure of all plant communities depends on environmental conditions and the interactions between species which together drive evolutionary and ecological processes (Weiher et al., 1998). The main physical environmental controls on plant species encompass climatic (i.e. temperature and precipitation), geological/edaphic conditions and associated resource availability (i.e. solar radiation, water, CO_2 and nutrients). Species can in turn also modify their environment, and this can be observed in vegetation successional processes at short temporal and spatial scales, or through very long-term evolutionary processes such as the development of tropical forests in the Cretaceous and Tertiary (Boyce and Lee, 2010). The aim of this literature review is to develop an overview of how tropical forests may already be responding to contemporary environmental changes due to human activity, and how they might be expected to change in the future. The scope of such a review is potentially vast, so after briefly assessing the potential environmental drivers of tropical forest change I restrict the review’s focus to potential impacts on tree ecophysiology, community ecology and their relation to ecosystem processes, considering that the trees are the organisms that form the essential matrix of tropical forests.

The two first sections of this chapter provide an overview of the main environmental factors and how they have been changing recently. Tropical forest vegetation is adapted to a warm and wet climate, which often has significant seasonality in terms of precipitation; it also varies spatially and temporally depending on geographical and atmospheric conditions (Malhi and Wright, 2004). In addition, atmospheric characteristics play an important role in plant ecology directly affecting photosynthesis and also through climatic changes (Körner, 2006;Lloyd and Farquhar, 2008). Given that, the first section of this literature review focuses on how natural environmental conditions affect tropical forests. As recent human activity has been profoundly affecting “standard” tropical environmental conditions, the second section analyses the principal recent environmental changes and their potential consequences on the plant community.

Section three presents current ideas around the interaction between tropical forest trees and environment and the responses to environmental changes detected to date. Tropical forests, with few exceptions, are very complex ecosystems, with high species diversity within communities (alpha-diversity), as well as covering a large area and wide environmental range, which contributes to their high species turnover (beta-diversity) and a wide range of ecosystem processes and conditions (Condit et al., 2002). Considering this, I opted to adopt an ecophysiological approach to conceptualising tropical forest ecology. Thus in the third section of this chapter I present an overview starting from the level of the organism discussing how resources and thresholds can affect from individual tropical forest trees all the way to the dynamics of these entire forests. Then, I use this information to link environmental changes and forest plant ecology, by describing the expected and observed plant responses to the environmental changes detected so far.

Section four explores the issue of sample sufficiency to correctly assess the dynamics of these forests (Fisher et al., 2008;Gloor et al., 2009;Espírito-Santo et al., 2014). Finally, section five situates the framework of this thesis by summarizing the current state of understanding of tropical forest ecology in a changing world and highlighting key gaps. This section contains the main aims of the thesis and the questions that led to my research.

Our understanding of the impact of global changes on tropical ecology will evidently depend on what information is available. Apart from the particular characteristics of different locations, there are also large disparities in the quantity and quality of information available from across the biome. Most tropical forest knowledge is based on the Neotropical region (principally from Central America and parts of Amazonia) although even here in many senses what is known is at a very early stage in relation to the complexity and scale of the system. For Africa and Southeast Asia there is often a particular lack of information regarding long-term forest dynamics and climate conditions. For that reason, even while aiming to review the literature on tropical regions across the globe, this chapter, and my thesis, focuses on Neotropical forests, principally Amazonia, which itself represents one-half of the remaining area of humid tropical forests and is the main focus of this thesis.

1.1 Environmental conditions

It is impossible to investigate change without understanding the starting point of a system. For simple phenomena the previous statement might seem too obvious however, regarding complex and dynamic systems, such as tropical forests, comprehending prior conditions is also challenging. In this section I briefly review the main conditions that determine the present tropical forest. I focus on environmental conditions related, directly or indirectly, to change. For instance, soil characteristics or forest history, included here, may not themselves be subject to change on annual or decadal timescales of interest here but they are key to understanding the spatial variability of change.

1.1.1 Climate in tropical rainforests

Tropical rainforests are often found under conditions of extreme warmth, medium to high insolation, and high precipitation (Malhi and Wright, 2004)**.** Warm and wet conditions are mostly a consequence of the position at lower latitudes

(Figure 1.1) where solar radiation (16 GJ y^{-1}) and thus temperature (≈ 25° C) are high and precipitation is abundant (2000 mm y^{-1}) as a result of the behaviour of the inter-tropical convergence zone[1] (ITCZ) (Malhi and Wright, 2004). Whilst some regions are indeed always wet and warm, as central Amazonia in Southern Colombia and Northern Peru (Sombroek, 2001) and the south of the Malay-Thai peninsula (Baltzer et al., 2007), there is a spectrum of climatic conditions where tropical forests can be found (Malhi and Wright, 2004). Temperature varies mostly as a consequence of topography, with higher areas being cooler, such as Central Africa and Andean forests (Malhi and Wright, 2004) (Figure 1). Within lowland rainforests the greatest climatic variation is found in the length and intensity of the annual dry season, which is characterized as a period when evapotranspiration (≈100 mm $month^{-1}$) overpasses precipitation. This period could be as long as seven months and is particularly strong in the Southern Brazilian Amazon, Central America, West Africa and Australia (Sombroek, 2001;Malhi and Wright, 2004). In the south-eastern extreme of the biome, the region of transition between tropical forest and savannah/dry forest, the so called fringes of the Amazon, the length of dry season can be up to seven months (Sombroek, 2001). In general, dry season length decreases towards the north-west of the Basin so that in the foothills of the Andes rainfall is abundant all year round (Figure 1.1). However, a few pockets of dry climate are found along the Western Amazonia, mostly as a consequence of local topography.

In addition to intra-annual variation, natural climatic cycles at inter-annual and multidecadal scales are also important components of climate in the tropics (Malhi and Wright, 2004). These cycles provoke changes in the dry season by causing alterations to the precipitation regime, which can result in extreme dry events over tropical forest regions (Kousky et al., 1984). For example, in Africa variations of the sea surface temperature (SST) of the Tropical Atlantic and the Indian oceans are likely to have caused the Sahel droughts (Shanahan et al.,

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[1] The ITCZ is a low-pressure region that pulls moisture from northern and southern hemispheres to the tropics. The ITCZ tracks the path of the sun shifting to higher latitudes during each hemisphere’s summer, therefore acting as the main driver of rainfall seasonality in the tropical rainforest.

2009;Dai, 2011). The most well-known climatic natural cycle impacting the tropical region is the El Niño Southern Oscillation (ENSO) that presents typically a 3 to 5 year cycle in the SST and atmospheric patterns in the equatorial Pacific Ocean (Kousky et al., 1984;Yoon and Zeng, 2010). ENSO is an important driver of the global temperature inter-annual variability and precipitation fluctuations in the tropical region, with a greater impact on the tropical forests of America and Asia than on most African forests (Malhi and Wright, 2004). For instance, ENSO was partly responsible for the 2010 drought, one of the most extreme events registered in the Amazon forest in the last one hundred years (Marengo et al., 2011). In addition to the El Niño variations of tropical Atlantic SST can also alter climate in the Amazon with the 2005 drought (Marengo et al., 2008;Marengo et al., 2011).

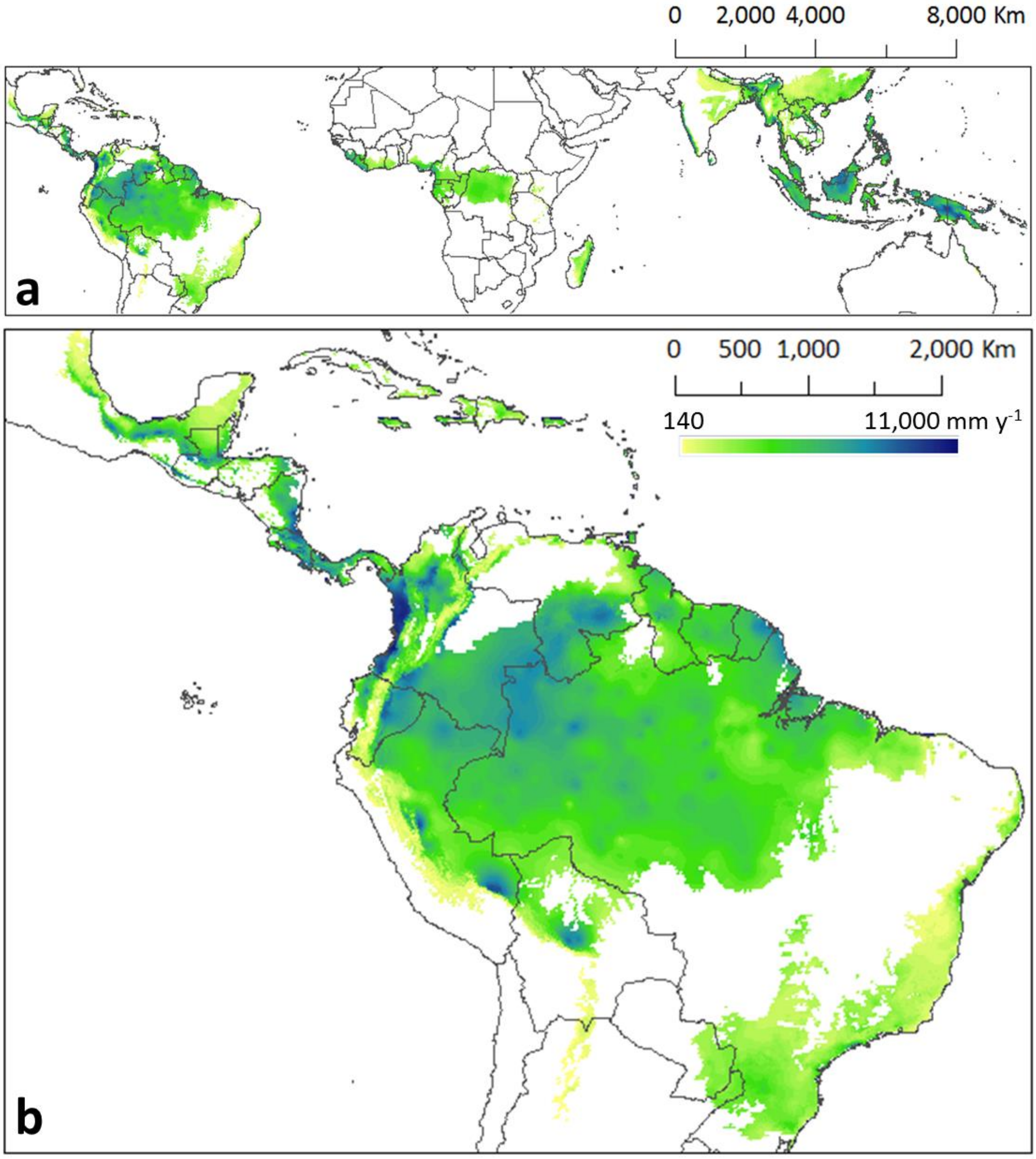


Figure 1.1 – Annual mean precipitation across tropical forests. Mean annual precipitation from the WorldClim database - interpolations of weather station data to a 2.5 minute resolution raster (Hijmans et al., 2005). Precipitation data plotted to for humid tropical biome was delineated following Olson et al. (2001). In (a) distribution of precipitation for tropical forests distributed globally and (b) show the Neotropics in more detail.

Forest and climate feedbacks

Not only is the distribution of tropical forests shaped by climate, but they are also a fundamental component of the water cycle in the tropics (Shukla and Mintz, 1982;Spracklen et al., 2012). Tropical forests influence precipitation pattern from local to continental scale, largely by feeding back rainfall water via evapotranspiration so that the air that passes over tropical forest can have up to twice as much rain as the air that passes over little vegetation (Spracklen et al., 2012). The evapotranspiration of these forest also have a significant cooling effect, which overpasses its potential heating effect due to its higher albedo potential when compared to pasture (Bonan, 2008).

1.1.2 Soil and nutrient availability in tropical forests

It can seem paradoxical that tropical forests, the most productive of biomes, are mostly found on chemically poor soils by the standards of most other ecosystems. The predominant types of soil, covering around 63% of tropical forest, are Oxisols and Ultisols, both characterized by low cation exchange capacity (i.e. weak ability to hold and exchange nutrients), which confers infertility from an agricultural perspective (Vitousek and Sanford, 1986). However, most nutrients in the tropical forest are normally not stored in the soil, but rather in the tree biomass. Therefore this system typically possesses a relatively fast closed nutrient cycle, in which trees supply the forest with nutrients due to litterfall, throughfall and stemflow and the fast decomposition rates and efficient nutrient capture by plants and micro-organisms make them available to return to vegetation (Vitousek and Sanford, 1986).

Amazonian soils have recently been characterized regarding their nutrient availability and physical properties. Soils with high phosphorus and cation exchange capacity are found near the Andes (Quesada et al., 2010), where soils are younger as a consequence of relatively recent sediment deposition from the Andean uplift (Hoorn et al., 2010). More weathered soils which also show more favourable physical properties are found in central and eastern Amazonia (Quesada et al., 2010) over older Pre-Cambrian formations (Hoorn et al., 2010). In general terms, young soils tend to have low nitrogen concentration but high phosphorus and base cations (i.e. calcium, magnesium and potassium) concentrations, originally from the parent material (Townsend et al., 2008). Inceptisols in the Andean region for example, where uplift constantly exposes new substrate (Quesada et al., 2010), are potentially nitrogen limited. Old soils under warm and wet tropical conditions tend to be deeply weathered, presenting a strong phosphorus limitation (Townsend et al., 2008). The ideal balance of nutrients may be found however in intermediate state soils that still retain nutrients from parent material and also nitrogen, provided by atmospheric deposition and N_2 microbial fixation (Townsend et al., 2008). The Northeast/Southwest soil gradient is an important driver of variation in tree community in the Amazon, also influencing its forest dynamic rates (ter Steege et al., 2006;Quesada et al., 2012). The low concentration of phosphorus in Northeast Amazonia is associated with a potential greater dependency of this region on aeolian deposition of phosphorus from desert dust from Africa (Okin et al., 2004) or from fire emissions from adjacent areas (Artaxo et al., 2002).

The two most important nutrients for plant communities are nitrogen and phosphorus. Nitrogen is the most abundant component of the atmosphere (80%), yet is often highly limiting to plant growth. In its atmospheric form, N_2, it is not directly metabolised by plants. Rather, plants need to access it as biological available forms ammonium (NH_3) and nitrite (NO_2^-), which are produced by the mineralization of nitrate (NO_3^-). Input of biologically available N to the system can occur by lightning events, but is mainly due to soil bacteria that fix N_2 in forms available to plants. Therefore young soils tend to be poor in nitrogen, and N in the soil tends to increase with soil formation as a result of microbial fixation. Phosphorus concentration and plant availability is usually low in tropical soils. Soils phosphorus content results from the chemical breakdown of the parent material resulting in a small P concentration in old soils that have been highly weathered. Phosphorus is biologically available as phosphate (PO_4^{-3}), which is not only absorbed by the plants but also by inorganic constituents of tropical soil present in oxisols and ultisols (Vitousek and Sanford, 1986). As well as phosphorus, cations, such as calcium, are also typically scarce in tropical soils as a consequence of weathering and absorption by inorganic constituents of the soil. Poor soil conditions result in a premium on plants to develop other mechanisms to allow them to access nutrients from recalcitrant pools in the soils, including mycorrhizal symbioses which involve trees swapping carbon for phosphorus with their fungal symbionts.

1.2 Physical and Environmental Changes in Tropical Forests

In recent decades environmental changes due to human activity have become important themes in both the scientific and political sphere, as it has become generally accepted that changes in climate and atmospheric conditions are impacting all of Earth's ecosystems. Tropical forests have been affected by a suite of physical, chemical and biological changes (e.g. Redford, 1992;Vitousek et al., 1997;Malhi et al., 2014;Brienen et al., 2015). This section will present evidence concerning contemporary environmental changes due to human activity, providing an overview of how it has affected, and may affect, the forests of the tropics.

1.2.1 Atmospheric changes

Greenhouse gasses

Atmospheric composition has changed in the past centuries as a consequence of the intensification of fossil fuel combustion and land-use change, especially in the last 60 years (Le Quere et al., 2009;Tans, 2009). Greenhouse gases (GHG) have increased considerably since pre-industrial times, with major contributions from the increase in carbon dioxide (CO_2) and methane (CH_4) (IPCC, 2013b). Methane concentrations are now 150% greater than pre-industrial records and values for carbon dioxide have increased by 40% within the same time period, with particularly pronounced growth rates in the last 50 years (IPCC, 2013b). Analyses from air enclosed in ice cores show that pre-industrial levels of CO_2 were around 280 ppm (Etheridge et al., 1996), and measurements have revelled a rapid increase from around 310 ppm in late 1960s to ca. 400 ppm in 2016 (Figure 1.2) (Keeling et al., 1968;Conway and Tans, 2016). The current levels of atmospheric CO_2 have not been reached since ca. 3 Ma during the Pliocene (Seki et al., 2010). These observed changes in the concentrations of GHG have already caused an increase in temperature and potential alterations to the hydrological cycle (IPCC, 2013b).

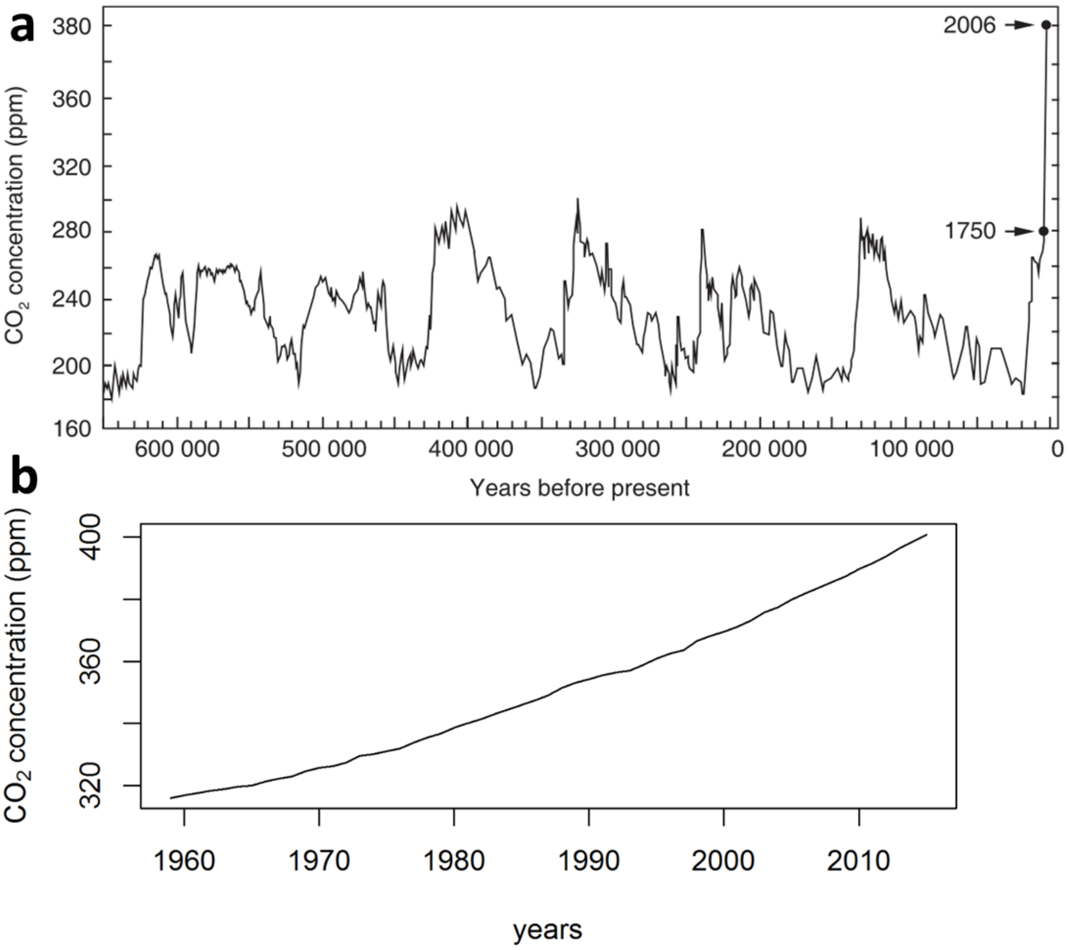


Figure 1.2 – Global trends in atmospheric carbon dioxide. a CO_2 in the last 600 000 years, data from Antarctic ice cores adapted from Körner (2006), which combined data from (Petit et al., 1999) and (Siegenthaler et al., 2005). **b** CO_2 concentrations since 1957 from observations data (Keeling, 2016;Tans, 2016). Note that CO_2 concentrations post industrial revolution are unprecedented during the last 600,000.

Aerosol concentration

Increase in atmospheric pollution, primarily due to fossil fuel combustion, led to consecutive decades of increases in aerosol concentration until the 1980s (Wild et al., 2005). Now the planet has been through a phase of 'global brightening', where aerosol concentrations have been decreasing as a consequence of the adoption of new cleaner technologies that emit less aerosols (Wild et al., 2005). The observed decrease in aerosol concentrations is likely to accelerate the ongoing temperature rise by reducing cloud formation and thus their total albedo effect (Andreae et al., 2005). However, global average trends in anthropogenic aerosol concentrations may not hold for the Amazon. As a consequence of their short lifetime, the anthropogenic aerosols emissions in the last century may have only directly affected the Northern Hemisphere (Carslaw et al., 2010;Spracklen and Rap, 2013), and in contrast to the global pattern, aerosol concentrations in the Amazon have potentially been increasing as a consequence of more frequent forest fires (Oliveira et al., 2007). In addition to the effects on temperature, aerosol concentrations can also influence the hydrological cycle directly. Thus, a direct effect of aerosols on precipitation may invigorate clouds and can lead to an intensification of rainfall (Koren et al., 2012). Indirectly, as the recent decline in aerosols may have accelerated temperature rise, particularly in the Northern Hemisphere, this could have enhanced the North:South tropical Atlantic SST gradient that tends to draw the ITCZ further north, inducing droughts in the Amazon basin (Cox et al., 2008).

Nitrogen deposition

Nitrogen is a fundamental component of organic matter and for the process of photosynthesis. During the last century, deposition of active nitrogen forms as a consequence of agriculture and energy production increased from 15 Tg N y^{-1} to around 160 Tg N y^{-1}, thus surpassing global biological fixation on land (110 Tg N y^{-1}) or in the ocean (140 Tg N y^{-1}) (Galloway et al., 2004;Gruber and Galloway, 2008). This impressive extra amount of N could potentially boost forests globally by modifying the N biogeochemical cycle. However, most N deposition has historically been concentrated in the Northern Hemisphere, predominantly in North America and Europe (Galloway et al., 2008). A considerable acceleration on N deposition in tropical regions occurred only in the last decades, being particularly intense in South East Asia, but also observed in parts of Latin America (Galloway et al., 2008;Austin et al., 2013). Although the change in N deposition has the potential to fertilize tropical forests worldwide, there is no strong evidence of significant N deposition in the largest continuous blocs of tropical forest, such as the core of the Amazon forest.

1.2.2 Changes in climate

Temperature

Temperature has increased globally by around 0.72°C (95% CI 0.49°C to 0.89°C) per decade between 1951 and 2012, mostly as a consequence of an increase in the atmospheric concentration of GHGs (IPCC, 2013b). Long-term climate data in the tropics are extremely scarce, as few climate stations are found in the region (Malhi and Wright, 2004). Information on temperature trends are mostly based on satellite data and interpolations of data from climate stations since the 1970s, which hampers the identification of true long-term trends in temperature at least for some individual localities. The data available shows that temperature in tropical forests has increased by 0.25 °C per decade since the 1970s (Malhi and Wright, 2004). For the Amazon there is an apparent increase by 0.13 °C decade^{-1} between 1979 and 2012, with temperature rising by 0.28 °C decade^{-1} when calculating the trends based on the months of July, August and September (Jiménez-Muñoz et al., 2013). Such a trend has been influenced by thermal anomalies, especially in 2005 and 2010, caused by unusually high sea surface temperatures (SSTs) in the Pacific and Atlantic (Jiménez-Muñoz et al., 2013). In line with the global trend, the temperature rise in the Amazon is expected to continue increasing and is expected to rise by 3 to 6 °C by the end of the century (Zelazowski et al., 2011). Temperatures in 2015 and 2016 have broken the global temperature records (NASA, 2016). In the Amazon these high temperatures occurred together with a strong El Niño drought, which is likely to have caused impacts on the vegetation (Jiménez-Muñoz et al., 2016).

Precipitation

The lack of long-term and well spatially distributed climatological stations also hampers the understanding of precipitation trends in the tropics, which is an even greater challenge than understanding temperature trends, given that precipitation is less spatially autocorrelated than temperature (Wohl et al., 2012). Recent precipitation reconstructions for the Basin have therefore used indirect estimates of rainfall intensity, which may provide large-scale estimates and annual resolution of precipitation at the expense of finer spatial resolution, notably via river discharge data and analyses of palaeoproxies such as tree ring isotopes (Espinoza et al., 2011;Brienen et al., 2012;Coelho et al., 2012;Gloor et al., 2013). Satellite data from the Tropical Rainfall Measuring Mission (TRMM - Huffman et al., 2007) have also made an important contribution to the understanding of precipitation trends since 1998 (e.g. Hilker et al., 2014).

Different data sources show that precipitation seasonality has been increasing, with the wet season becoming wetter, whilst the dry season gets drier (Feng et al., 2013;Hilker et al., 2014;Gloor et al., 2015). This trend is also mirrored by a spatial equivalent, whereby the strengthening of the dry season has been more marked in the drier areas in the southeast of the Amazon, and the intensification of the wet season taking place especially in the very wet Western Amazon (Hilker et al., 2014;Gloor et al., 2015). Furthermore, the dry season seem to be increasing in duration, with the onset of the rainy season being delayed over time (Shukla et al., 1990;Butt et al., 2011;Marengo et al., 2011;Fu et al., 2013).

In addition to these general trends, since the beginning of the century the Amazon has experienced three extreme droughts during the dry season of 2005, 2010 and 2015 (Marengo et al., 2008;Lewis et al., 2011;Marengo et al., 2011;Jiménez-Muñoz et al., 2016). During the 2005 drought, 48% of the Amazon basin experienced a rainfall anomaly (Aragao et al., 2007). The water-deficit during 2005 was 37% stronger than the long-term mean for the Basin (Aragao et al., 2007). This drought was more intense in southwestern Amazonia where the drought intensified the dry season (Marengo et al., 2008). This spatial pattern is characteristic of droughts associated with higher SSTs in the North Atlantic, which weakens the transport of moisture into the Amazon Basin (Marengo et al., 2008;Yoon and Zeng, 2010). In 2010 the drought affected an even larger area (3 million km^2) of the basin when compared to 2005 (1.9 million km^2) and had three epicentres: south-western Amazonia, north-central Bolivia and Mato Grosso in Brazil (Lewis et al., 2011). In contrast to the 2005 event, the 2010 drought started during a weak El Niño and then was intensified due to the high temperatures of the North Atlantic Ocean (Marengo et al., 2011). During 2015 and 2016, a strong El Nino caused wet-dry dipole between southeast and northwest Amazonia, when 13% of the Amazon forest experience drought during the first months of 2016 (Jiménez-Muñoz et al., 2016).

Changes in SSTs are not only the drivers of droughts in Amazonia, but they are also responsible for the observed increase in intra-annual seasonality across the Basin (Cox et al., 2008;Yoon and Zeng, 2010). Warmer SSTs in the North Atlantic are likely to be driving the increase in the length of the dry season (Marengo et al., 2011). This dependence of the Amazonian hydrological cycle on tropical SSTs indicates that in a future warmer climate we can expect further intensification of the seasonality and extreme wet and dry events in Amazonia (Cox et al., 2008;Malhi et al., 2008;Duffy et al., 2015;Gloor et al., 2015;Marengo and Espinoza, 2016).

Another important component of the future of Amazonian climate is the increase in deforested areas. Deforestation results in landscapes with less evapotranspiration capacity, such as crops, pastures or urban areas. In these landscapes the water inputs to the system from precipitation tends to exit mostly via run-off, instead of evapotranspiration (Aragao, 2012;Spracklen et al., 2012). As a consequence, landscape transformation reduces water recycling to the atmosphere, decreasing the air moisture, as well as precipitation rates (Shukla et al., 1990;Spracklen et al., 2012).

1.2.3 Direct anthropogenic impacts

While these large-scale anthropogenic and climatic changes are expected to have widespread ecophysiological and ecological impacts, more direct anthropogenic processes may be almost as pervasive.

Deforestation

Deforestation in the Amazon started to increase effectively since the 1960s, especially stimulated by the Brazilian government through incentives for migration to the Amazon region. Deforestation in the Brazilian Amazon had its peak between 1995 and 2005, when 19,500 km^2 of forest were cleared per year (Nepstad et al., 2009). The following years (2004-2012) were marked by a sharp decline of 82% in the deforestation rates (Nepstad et al., 2009). The drop in the deforestation rates was a result of specific policies to reduce deforestation such as the soy and beef moratorium, and the plans to prevent and control deforestation (e.g. Plano de prevenção e controle do desmatamento na Amazônia Legal - Ministério do Meio Ambiente, 2013), improvement of monitoring via satellite images coupled with more enforcement, and also fluctuations in the global markets for commodities such as soybean, meat and sugar cane (Nepstad et al., 2009;Malhi et al., 2014). However, together with low deforestation rates, there has been an increase in small-scale deforestation (6 – 50 ha), which indicates that the new policies to reduce deforestation are potentially ineffective in reducing small clearings (Rosa et al., 2012). The deforestation trends inside Brazil, moreover, do not reflect what has occurred in several other Amazonian countries, where deforestation has actually increased (Malhi et al., 2014).

Defaunation

Hunting pressure may have been affecting even intact forests as its effects can severely deplete the numbers of important seed dispersers (Redford, 1992). Hunting is a widespread and frequent activity in many if not most tropical forests and bush meat plays an important role as protein source for its residents (Peres and Palacios, 2007). Hunting is estimated to remove an animal biomass of 164,692 tons y^{-1} in the Brazilian Amazon (Peres, 2000). Game hunting affects mostly large animals and particularly seed dispersers, having less impact on seed predators and smaller dispersers (Redford, 1992;Peres and Palacios, 2007). Thereby, this activity can potentially alter the recruitment rates of zoochoric taxa (Chapman and Chapman, 1995), especially those dependent on large dispersers, and thereby cause a shift in floristic composition. Hunting may compromise not only forest biodiversity but also important aspects of its functional composition and carbon cycle as, for example, seed size is positively related to both tree size and wood density (Bello et al., 2015;Peres et al., 2016). Although hunting is a pervasive threat to tropical fauna, and shows to affect tree communities at a local scale (Terborgh et al., 2008) there is as yet no empirical evidence of a widespread impact on Amazonian tree communities.

1.2.4 Previous disturbances

The title ‘intact forest’ used as a convenient shorthand to describe the more remote areas of the Amazon Basin has been contested by those who believe Amazonia to be undergoing late successional recovery after climate-driven disturbances or anthropogenic alteration. This argument has implications on the interpretations of the detected changes in forest dynamics. Importantly, the hypothesis that forests are undergoing late successional recovery, if borne out at large-scale, could negate the interpretation that the increase in biomass observed pan-tropically is primarily driven by atmospheric CO_2 (e.g. Pan et al. 2011) (Wright, 2005;Chave et al., 2008;Muller-Landau, 2009). The two possible causes of continental-wide disturbances are: (1) widespread clearing by pre-Colombian communities, with recovery since, and (2), large historical climate fluctuations having caused tree mortality and forest fires (Wright, 2005). To characterize a major cause of disturbance capable of leading to current late successional recovery across Amazonia, either of these possible causes would have had to have been spatially widespread, taking place in the past 200 to 500 years (Wright, 2005). These disturbances could have affected forests structure, including by potentially introducing new even-aged cohorts, starting a successional process where pioneers will be replaced by shade tolerant trees and stand biomass will increase, whilst the number of trees in the plot decreases as a consequence of self-thinning (Odum, 1969;Connell and Slatyer, 1977;Chave et al., 2008).

The hypothesis that native Amazonian cultures have caused continental-wide disturbances is based on the assumptions that populations were large and have impacted most of the Amazon and collapsed within the last 500 years. The evidence that Amazonia was a ‘cultural parkland’ up to around the 1500s is based on evidence from earthworks left from previous settlements (e.g. Heckenberger et al., 2003), anthropogenic altered soil for agriculture (archaeological dark earth AED or *terra preta*) (e.g. Willis et al., 2004) and from fossil pollen record (e.g. Carson et al., 2014), from which it is possible to tell when an area was deforested to be used for agriculture. The evidence for the occupation of the Amazon before the arrival of Europeans has been increasing, with the Amazon having been considered to be a domesticated landscape occupied by up to 10 million people (Bush and Silman, 2007). These communities would have collapsed, with Amazonian population reducing by 95% as a consequence of diseases from the contact with Europeans (Bush and Silman, 2007). However, these settlements are likely to have been limited in extent and distribution, as *terra preta* soils, although frequent, occupies only a rather small proportion in terms of area (Bush and Silman, 2007;Barlow et al., 2012). Therefore, it is likely that previous occupations of Amazonia where restricted spatially to the proximity of rivers with the vast majority of the Basin remaining largely unmanaged, at least intensively (Bush and Silman, 2007;Barlow et al., 2012).

Extreme climatic events are frequent in Amazonia, however, it is unlikely that climate fluctuations in the last 500 years have caused major Basin wide alterations to the forests (Lewis et al., 2009a). The Amazon droughts on record indeed do cause at least short-scale alterations to forest communities, such as observed in the recent 2005 and 2010 drought events. Arguably, past droughts may have had stronger impacts - for instance, the 1926 El Niño drought was particularly intense, with water deficit being potentially 50% lower than normal and affecting the central-northern Brazilian Amazon and southern Venezuela (Marengo et al., 2008). Regardless of its intensity, it is unlikely though that this drought has been driving most of the increase in biomass observed for the Basin, as the scale of the biomass gain is much larger than the estimated loss by the 1926 drought (Lewis et al., 2009a). It has been hypothesized that climate fluctuations as part of a 200 year cycle in solar radiation could have caused major changes to Amazonian forests (Wright, 2005). However, to date, evidence showing that this cycle has caused major alterations to the vegetation across the Amazon is scarce, and based on a few isolated observations (e.g. Schimmelmann et al., 2003).

1.3 The Ecology of tropical forests in a changing environment

Ecologists used to believe that ecosystems follow a trajectory through ecological succession culminating in stable ecosystems, where net accumulation of biomass is small or close to zero (Odum, 1969). However, as soon as the scientific community started to acknowledge that human activity was causing pervasive alterations to the environmental conditions globally (Keeling et al., 1968;Vitousek et al., 1997), this paradigm of a supposedly homeostasis in ecological systems started to change. For tropical forest ecology this new way of thinking emerged during the 1990s, with a series of papers suggesting that intact forests were in fact acting as a carbon sink (Grace et al., 1995;Lloyd and Farquhar, 1996), increasing in biomass (Phillips et al., 1998) and with an accelerating dynamics (Phillips and Gentry, 1994).

Here, I briefly review how forests would be expected to respond in light of the many recent and anticipated large-scale environmental changes affecting them. I start by reviewing the expectations from an ecophysiological point of view. I then show how the alterations to tropical forests can affect different levels of organization, moving from the tree level to the community and ecosystem levels. This information, combined with the previous sections, leads us towards the generation of the hypotheses to be tested in this thesis.

1.3.1 Ecophysiology

Increase in resources

Deduction based on stoichiometry and on the dependence of photosynthesis on CO_2 leads to the prediction that the increase in CO_2 will increase CO_2 uptake (A) (Lloyd and Farquhar, 1996), as:

$$A = g_s(c_a - c_i) \quad \text{Eq 1.1}$$

where g_s is the stomatal conductance and c_a and c_i are atmospheric and intercellular CO_2 concentrations. The increase in photosynthesis as a consequence of additional atmospheric CO_2 is known as CO_2 fertilization. In theory, photosynthesis should increase continuously with the rise of CO_2 until it is limited by the capacity of the enzyme ribulose 1-5 bisphosphate carboxylase/oxygenase (Rubisco), or by the rate of ribulose 1,5-bisphosphate (RuBP) regeneration (Farquhar et al., 1980). This increase in carbon accumulation have been observed for tropical forests (Grace et al., 1995) and is expected to persist considering that plants will not acclimate to extra CO_2 concentrations (Lloyd and Farquhar, 1996). The increase of leaf-level photosynthesis should translate to growth, after accounting for the carbon lost from respiration:

$$\frac{dM}{dt} = A\,(1 - \varphi). \qquad \text{Eq 1.2}$$

where M is the moles of C in the plant, t is time and φ is the proportion of A lost via respiration (Lloyd and Farquhar, 1996).

Under low light availability carbon assimilation may not be enough to compensate for the carbon lost by respiration (Ehleringer and Björkman, 1977). Thereby, it is under low light availability that the increase in CO_2 is expected to make a greater relative contribution to growth, as shaded plants could shift from being carbon negative to becoming carbon positive (Ehleringer and Björkman, 1977;Würth et al., 1998). Tropical forests are vertically structured with their dense canopies restricting light availability to understorey trees, which could have greater quantum yield and potentially greater relative growth as atmospheric CO_2 increases (Augspurger, 1984;Lewis and Tanner, 2000).

Changes in aerosol concentration can also stimulate carbon accumulation. CO_2 uptake in the understorey can increase with the increase in aerosol concentration (Mercado et al., 2009). In high concentrations the aerosol particles scatter sunlight, increasing the ratio of diffuse to direct radiation; the enhanced levels of diffuse light, which can penetrate deeper below the forest canopy, potentially boosting the photosynthetic rates (Gu et al., 2003). In the central Amazon, when comparing different aerosol concentration concentrations, smoky conditions showed greater carbon uptake, which was mostly likely caused by the increase in diffused light (Doughty et al., 2010). On a larger scale, biomass burning aerosol and thus higher levels of diffuse light is estimated to have increased net primary production across the Amazon Basin (Rap et al., 2015).

It has been argued that N and P limitation could limit or hamper the increase in carbon accumulation based on the ‘Law of the minimum’, which posits that the deficiency or absence of one resource, the limiting factor, will impede increases in growth (for details on the history of the origins of this law attributed to Justus von Liebig see van der Ploeg et al., 1999). Most tropical forests are indeed P limited in terms of productivity (Cleveland et al., 2011;Quesada et al., 2012). However, ecophysiological theory and empirical data and modelling work show that even under low levels of N, CO_2 fertilization can take place (Lloyd and Farquhar, 1996;Finzi et al., 2007;Dybzinski et al., 2015). Tropical trees would also be able to trade C for P with mycorrhizae. Nonetheless, although N concentrations are not expected to impede the increase in C accumulation, under more nutrient-rich soils the CO_2 fertilization is expected to have a greater effect (Curtis and Wang, 1998).

The influx of CO_2 is associated with the loss of water vapour through the stomata – the small pores that allow gas exchange between the leaves and the atmosphere. When the stomata are open, together with the uptake of A (Eq 1.1), water vapour is lost to the atmosphere via transpiration (E):

$$E = 1.6 g_s (v_i - v_a) \qquad \text{Eq 1.3}$$

where v_i and v_a are the ambient and intracellular water vapour pressure respectively. Changes in the concentrations of atmospheric CO_2 can alter the ratio of water loss to carbon gain, known as water-use efficiency (WUE = A/E). Under constant difference between v_i and v_a, WUE should increase with the increase in atmospheric CO_2. This mechanism is particularly important for plants in water-limited environments where the increase in CO_2, and thus the increase in WUE, will in theory allow a reduction in the stomata opening, thus saving water whilst maintaining the same A. There is an increasing body of evidence showing that WUE has been increasing as a response of CO_2, and that it has been contributing to terrestrial carbon accumulation by terrestrial ecosystems (Brienen et al., 2011;Loader et al., 2011;Keenan et al., 2013;Brienen et al., 2016).

Ecophysiological challenges to plants

Water deficit: the effect of droughts

Droughts are known to cause tree mortality and affect growth of trees in various ecosystems (Anderegg et al., 2013), however, the precise physiological mechanisms behind the effect of droughts on trees are still poorly understood, especially for the tropics (Meir et al., 2015a). The three main hypotheses explaining drought-induced mortality are: hydraulic failure, carbon starvation and biotic agent demographics, (McDowell et al., 2008). These were postulated based on empirical knowledge from temperate areas, mostly from a two-species system - the piñon-juniper woodlands - and its relevance for the tropics is still questionable. In the last few years significant effort has been directed to understanding the physiology behind drought induced mortality in the tropics (Engelbrecht et al., 2005;Poorter et al., 2006;Meir et al., 2015b;Rowland et al., 2015).

The hydraulic conductivity from soil to leaf follows Darcy's law (Whitehead, 1998;McDowell et al., 2008):

$$E = K_l \, (\Psi_s - \Psi_l - hp_w g) \qquad \text{Eq 1.4}$$

where E is evapotranspiration, K_l is leaf-specific hydraulic conductance, ψ_s and ψ_l are the soil and leaf hydraulic potentials, h is the tree height, p_w is the water density and g gravity. Thereby following the cohesion tension theory, the water column is pulled by E from soil to leaf. Hydraulic failure occurs when E exceeds the critical E (E_{crit}), so that the water column is broken by air entry, initiating cavitation. At this point K_l will be close to zero. The hydraulic-failure hypothesis predicts that droughts will drive E to surpass E_{crit}, causing cavitation and leading to tree mortality. Results from a drought experiment in the Amazon show that hydraulic failure is an important mechanism of tree mortality (Rowland et al., 2015).

The hypothesis of carbon starvation posits that as a defence mechanism to avoid hydraulic failure trees would close their stomata during periods of strong water deficit (McDowell et al., 2008). With the stomata closed, photosynthetic activity stops and thus under prolonged droughts the carbohydrate reserves used to maintain the plant's metabolism will be depleted, which will lead to eventual death by starvation. During the 2010 drought in the Amazon, photosynthesis indeed seems to have been suppressed(Gatti et al., 2014), which indicates possible carbon starvation leading to tree mortality following the drought period (Doughty et al., 2015). However, whether carbon starvation can drive tree mortality is still debatable, as other studies have not found evidence of carbon starvation (Anderegg et al., 2012;Rowland et al., 2015). Moreover, although information is still scarce, tropical trees seem to have a high concentration of non-structural carbohydrate, which is also apparently high during the dry season and may act as a reserve or 'insurance policy' to cover difficult periods, making actual carbon starvation unlikely (Wurth et al., 2005). The third hypothesis to explain drought-induced mortality, the biotic agent demographics, suggests that droughts will increase the population of pests or pathogens that will then cause tree mortality (McDowell et al., 2008). For the tropics to date there is no strong evidence that biotic attack drives drought-induced tree mortality (Doughty et al., 2015;Rowland et al., 2015).

Temperature

High temperatures may affect photosynthesis through alterations to the activity of important enzymes or by altering electron transportation (Lloyd and Farquhar, 2008). With an increase in temperature the oxygenating reaction of Rubisco increases more than the carboxylating, and photorespiration will be relatively more important than photosynthesis compromising carbon assimilation. However, the effect of temperature on photosynthesis may be offset by the changes in atmospheric CO_2 as under high CO_2 atmospheric concentrations photorespiration/photosynthesis rates may decrease as a result of the high availability of CO_2 as a substrate for Rubisco (Sage and Kubien, 2007;Lloyd and Farquhar, 2008). Additionally, higher temperatures can alter the rate of regeneration of ribose-1,5-biphosphatase (RuBP), an important substrate for photosynthesis. This limitation has been shown to be reversible, even under high temperatures (June et al., 2004). Therefore, it has been argued that direct temperature effects on photosynthesis may not compromise carbon assimilation under elevated CO_2 (Lloyd and Farquhar, 2008).

Temperature extremes are potentially a more important threat to tropical forest trees if they cause irreversible damage to the photosynthetic apparatus (Lloyd and Farquhar, 2008). Above 45 °C of leaf temperature important photosynthetic enzymes and membranes can suffer alteration beyond the threshold (Berry and Bjorkman, 1980). Heat extremes can also cause oxidation and changes in membrane permeability, with potential permanent damage to photosynthesis (Huve et al., 2011). Whether these leaf-level processes will affect canopy level photosynthesis and ecosystem level carbon accumulation is still an open and important question. High temperatures can alter carbon assimilation indirectly, by increasing vapour pressure deficit and influencing stomata conductance, which will cause a physiological drought, where evapotranspiration demand is increased even without a decline in precipitation (Lloyd and Farquhar, 2008;Corlett, 2011).

1.3.2 Changes to forest communities

Whilst ecophysiology provides a basis to understand the effect of environmental changes on tropical forests, a great variation in these responses is expected at different ecological levels of organization. For example, and very relevant for the topic of this species, within a community, species are expected to respond differently to alterations to the environment depending on their characteristics (McGill et al., 2006). If these changes are pervasive, they could lead to biodiversity losses or compromise important ecosystem services, such as carbon accumulation capacity.

Increase in resources

The most simplistic prediction for the increase in resources within tropical forest communities is that all individuals will respond in the same way. Ecological theory in fact can be used to predict more complex responses, which are more likely to reflect reality (Lewis et al., 2009a).

Under conditions of greater resource availability, species composition, specifically the dominance of those individuals that have greater access to light, should increase (Coomes and Grubb, 2000;Coomes et al., 2011). The processes behind this *winner takes all* response are under debate. One explanation for such an outcome would be that more resource-rich environments will drive a shift from below ground competition for resources to competition for light, which is size asymmetric (Coomes et al., 2011;DeMalach et al., 2016). Therefore, under greater resource availability, as competition for light becomes more pronounced, large individuals, which already have disproportionally more access to light, and fast growing taxa that can reach the canopy quickly, will have an advantage over other individuals and taxa (King, 1990;Falster and Westoby, 2003). Moreover, a *winner takes all* response is also predicted by the metabolic scaling theory, which posits that resource use should scale with tree size (Enquist et al., 1998;Enquist et al., 2009). Thereby, larger individuals should have greater dominance in resource-rich areas (Niklas et al., 2003). Regardless of the mechanism driving a *winner takes all* response from the community, it can be expected that large and fast-growing trees will gain following CO_2 fertilization or nitrogen deposition. In one location in central Amazonia, large and fast growing taxa do appear to have been gaining, following the predictions above (Laurance et al., 2004) but there has been no large-scale test of the predictions.

In contrast, from consideration of leaf-level and plant-level ecophysiology, it could instead be argued that higher CO_2 will favour those individuals whose growth is most carbon-limited, i.e. the understorey trees (Körner, 2006;Lloyd and Farquhar, 2008). This prediction is based on the idea that most understorey trees are close to their light compensation point (i.e. where there is insufficient light for photosynthetic activity so that the carbon assimilated is not enough to compensate for the respiratory demand), and so even a small enhancement of carbon fixation would have a relatively large impact on survivorship and on growth (Körner, 2006;Lloyd and Farquhar, 2008). If valid, this mechanism could allow for the survivorship of saplings and seedlings that would otherwise die.

The effect of CO_2 on communities may vary depending on climate. Under high atmospheric vapour pressure, additional CO_2 will increase water-use efficiency and potentially release trees from water-stress. In particular, it could allow taxa to occupy areas where they were previously physiologically limited to occur (Zelazowski et al., 2011). For instance, it has been hypothesised that higher WUE could allow the expansion of the rainforest occupying areas which are currently dry forest or savannahs, as observed by Marimon et al. (2006). Indeed, the increase of WUE in dry areas of the Amazon has been observed for trees (Brienen et al., 2011), however there is still no evidence that it has been driven by compositional changes or biome expansion.

Little is known about changes in community composition following Nitrogen deposition. One could expect that the most Nitrogen limited plants would show a greater advantage, and thus legumes, known to be able to fix Nitrogen via symbiosis with rhizobia, would show a relative decrease in abundance. Observations from Panama and Thailand show that legumes show no change and a slight decrease in the abundance of legumes following a period of N deposition (Hietz et al., 2011).

Ecophysiological challenges

Increase in moisture stress

An increase in moisture stress is likely to present a physiological challenge for tropical trees (Nepstad et al., 2007;Baltzer et al., 2008;da Costa et al., 2010;Rowland et al., 2015). This physiological challenge could increase as a consequence of (1) an increase in the frequency of extreme droughts and/or as a response of the (2) increase in moisture stress. Each of these processes will increase hydraulic stress in different magnitudes and time scales, thus leaving different fingerprints on the forest community. Thus, the increase in the *frequency* of droughts represents more recurrent peaks in hydraulic stress where low precipitation is often associated with high temperatures (Jiménez-Muñoz et al., 2013). This will result in greater evapotranspiration demand, leading soil moisture to fall below the soil moisture threshold where high tree mortality occurs (Meir et al., 2015b). As the larger the tree the greater the changes of embolism, strong droughts are expected to selectively kill large tress via hydraulic failure (McDowell and Allen, 2015). The expected increase in the mortality of large trees following strong droughts have been observed in neotropical inventory plots (Condit et al., 1995;Phillips et al., 2010) and in two drought experiments in the Amazon (Nepstad et al., 2007;da Costa et al., 2010). Thereby, greater moisture stress should shift community composition favouring smaller taxa, with a potential decrease in mean tree size as a consequence of an increase in the mortality of large individuals, which are most likely to die as a consequence of hydraulic failure (Bennett et al., 2015;McDowell and Allen, 2015).

On the other hand, long-term drying trends may bring rather different consequences to the community. Evidence of changes in community composition as a consequence of the pressure of long-term droughts come from two studies (Fauset et al., 2012). These observed a decrease in the abundance of small trees and attributed these patterns to the fact that small trees tend to have shallower roots and thus would not be able to access deeper water reserves in the soil. Moreover, small trees in the understorey are more likely to be close to being carbon negative, thereby could potentially be at greater risk of carbon starvation (Fauset et al., 2012). Greater CO_2 concentrations could also increase the concentration of non-structural carbohydrates (Wong, 1990;Korner and Arnone, 1992), which could make trees more resistant to carbon starvation and allow small trees to survive continued stress of drought year after year.

Regardless of which climatological phenomenon is driving the increase in aridity in the Amazon, it will favour drought-resistant over drought-vulnerable taxa. Following a climate envelope approach (e.g. Peterson et al., 2002;Thuiller et al., 2005) we can expect that taxa distributed over dry areas will tend to gain over wet-restricted ones. Earlier tests of this prediction with tropical seedling experiments did indeed find that drought-induced mortality was greater within wet-restricted tree taxa than for more widely-distributed ones (Baltzer et al., 2007;Engelbrecht et al., 2007). Within tree communities, this predicted shift towards a more dry-affiliated composition has been observed on local scales following droughts in the Western Africa and Central America (Enquist and Enquist, 2011;Feeley et al., 2011a;Fauset et al., 2012).

Temperature

Higher temperatures are expected to have a greater impact on canopy trees, where leaf temperatures, particularly for fully exposed sun leaves, reach higher levels. Further, the more humid microclimate in the understorey should help protect trees from increasing temperature, whilst canopy trees will be exposed to increased vapour pressure deficit caused by higher temperatures.

There is little information on the thermal sensitivity of tropical species. An analysis estimating thermal niches from plant collections shows that tropical species have apparently narrow climatic niches when compare to temperate taxa (Feeley and Silman, 2010). Thereby, if the fundamental niches of tropical species mirror their realized niches, the expected increase in temperature will lead to great biodiversity loss in tropical regions (Feeley and Silman, 2010). Moreover, the same study also observed that temperature niches for tropical species are apparently truncated at the hottest temperatures, which indicates that the actual fundamental niche may expand observed temperatures. Along these lines, a study analysing 12 Amazonian species found that nine of them had Neogene origin, when temperature was much higher than present, indicating that Amazonian taxa could tolerate warmer conditions (Dick et al., 2013). However, this is not the case for other genera, such as *Inga*, an abundant and species rich Amazon genus that has Pleistocene origin and has not endured early high temperatures (Richardson et al., 2001). Whilst the thermal tolerance of most tropical forest taxa are still unknown, this variation in the origin of Amazonian clades indicates a range in their tolerances, and thus leads to the prediction that the composition of communities will shift as a result of global warming.

A potential temperature driven change in floristic composition is supported by long-term studies along altitudinal gradients that show a surprisingly rapid upward movement of taxa. A study in the Colombian Andes show uphill migration of 2 m y^{-1} for adult and 4.9 m y^{-1} for juvenile trees, mostly driven by the mortality of heat sensitive taxa in the lowland areas (Duque et al., 2015). The uphill movement has been documented for other taxa (Chen et al., 2009) and other locations across the tropics (Jump et al., 2012;Morueta-Holme et al., 2015), evidencing the influence of the temperature rise on tropical communities.

Direct human impact

It has been suggested that hunting could change tree composition in tropical forests, as hunting removes important seed dispersers within the community (Peres and Palacios, 2007;Terborgh et al., 2008;Doughty et al., 2016;Osuri et al., 2016;Peres et al., 2016). Therefore, defaunation would lead to dispersal failure of trees dispersed by large mammals and birds (Chapman and Chapman, 1995). It has been shown that zoochoric trees tend to have high wood density and large stature, thus plant with these traits will show reduced abundance following an increase in hunting pressure (Bello et al., 2015;Peres et al., 2016).

Previous disturbances

Structurally intact forests where previous disturbances took place are expected to undergo a late-successional recovery (Chazdon, 2003). During this process the dominance of the late-successional taxa should increase, which will imply an increase in large and high wood density trees (Connell and Slatyer, 1977). As a consequence of self-thinning, mean tree size should also increase with small understorey trees losing (Connell and Slatyer, 1977). Shifts in community composition as expected during late-successional recovery were observed in several plots distributed pan-tropically (Chave et al., 2008) and in some sites in the Amazon (van der Sande et al., 2016).

Increase in lianas

Environmental changes, such as the increase in CO_2, natural disturbances, land-use change and evapotranspirative demand are expected to favour lianas, which will show increased height and growth (Condon et al., 1992;Schnitzer and Bongers, 2011). The increase in lianas will cause alterations to forest communities, as lianas will have a greater impact on slow-growth trees with high wood density (van der Heijden and Phillips, 2009).

1.3.3 Changes to tropical forests structure and dynamics

Increase in resources

An increase in photosynthesis (Grace et al., 1995;Gatti et al., 2014) should result in greater forest net primary production, which will in part be allocated to wood (Malhi et al., 2011). In the form of wood, carbon can endure for centuries as stable chemical forms, which characterize aboveground biomass stocks (Grace, 2014). Long-term measurements from inventory plots show that Neotropical forests have indeed been acting as a carbon sink for at least the last three decades (Phillips et al., 1998;Baker et al., 2004a;Brienen et al., 2015). Together with the increase in forest productivity observed in a mostly overlapping set of plots, there has also been observed an increase in turnover rates, with increased mortality and recruitment in tropical forests worldwide (Phillips and Gentry, 1994). This should also lead to more frequent gap openings, and thus an increase in gap affiliated taxa (Phillips and Gentry, 1994).

The outcomes at the community level in turn may partially determine the path of the forest dynamics (Lewis et al., 2004a). Thus, a *winner takes all* response from the community, with large trees gaining, could lead to a decrease in recruitment and a decrease in stem density, similar to what is expected from self-thinning (Connell and Slatyer, 1977). However, if understorey trees are also gaining from a CO_2 driven release of light-suppression (Lloyd and Farquhar, 2008), then we could expect that recruitment rates and the number of stems will increase over time. The latter outcome might also be predicted by an increase in gap dynamics following a greater tree turnover. In fact, published data from Amazonia do show an increase in recruitment rates in Amazonia, but because stem mortality rates have also increased, there has been little change in the number of stems per unit area (Brienen et al., 2015).

Environmental challenges

Considering the physiological challenge that droughts impose on individual trees and plant communities, it is expected that they would lead to major losses in forest biomass from tree mortality and a decrease in biomass accumulation as a consequence of growth anomalies. Experimental work shows that very strong droughts can reduce forest biomass markedly, sufficient to turn forests from carbon sinks to carbon sources (Nepstad et al., 2007;da Costa et al., 2010). Observations from inventory plots so far lack the extreme treatment imposed by rainfall-excluding experiments, but the natural droughts of 2005 and 2010 led to at least short-term increases in tree mortality and some decline in biomass productivity – with the latter being statistically significant only for 2010 (Phillips et al., 2009;Phillips et al., 2010;Feldpausch et al., 2016). These results are consistent with atmospheric observations made from a limited number of aircraft flights to sample GHGs and carbon monoxide, that for instance show that after accounting for burning, during 2010 the whole Amazon biosphere switched from being a carbon sink, accumulating 0.25 Pg C y^{-1}, to becoming a source of ca. 0.48 Pg y^{-1} (Gatti et al., 2014). In contrast to the fairly strong shorter-term impacts observed in response to Amazonian droughts, a long-term drying trend in part of West Africa seemed to not compromise carbon accumulation capacity due to a shift in species composition (Fauset et al., 2012), implying that, perhaps, over time community diversity in tropical forests may be able to confer substantial resistance to droughts, given enough time for species replacement to occur.

Direct human impact

The increase in hunting may lead to a turnover of species towards small and light wooded trees (Bello et al., 2015;Peres et al., 2016). As the capacity to store biomass is determined by the presence of large, heavy-wooded trees (Fauset et al., 2015), it has been hypothesized that increased hunting pressure will lead to a decrease in forest biomass storage capacity across the Amazon (Bello et al., 2015;Peres et al., 2016).

Previous disturbances

During late successional recovery, as large trees start to dominate, carbon accumulation capacity will increase (Odum, 1969;Chave et al., 2008). As a consequence of self-thinning, recruitment rates and the number of stems are expected to decrease (Lewis et al., 2004b). As the pioneers leave the system, mortality rates should also decrease, and as the system stabilizes over time, stem turnover rates should thus decrease (Lewis et al., 2004b).

Increase in lianas

Lianas make a modest contribution to forest biomass in most locations but are potentially a much more important component of the forest dynamics (Phillips et al., 2005). Lianas reduce the carbon uptake of trees by increasing light competition and switching carbon allocation from wood to leaves (van der Heijden and Phillips, 2009;van der Heijden et al., 2015). Greater abundance of lianas is also known to increase tree mortality and decrease tree recruitment and growth (Schnitzer and Bongers, 2011).

1.4 Sample sufficiency

The dynamics of tropical forest are characterized by frequent disturbances, caused when a tree dies, knocking down many of the trees around and opening a gap that provides light and space for a sudden growth of the trees in the understorey (Chambers et al., 2004). This is an important mechanism that determines forest structure (Farrior et al., 2016). When analysing long-term trends in tropical forests, it is expected that some areas will be undergoing recovery from such natural dynamics (Fisher et al., 2008;Gloor et al., 2009;Lloyd et al., 2009). Gap dynamics can be confound long term trends caused by external drivers, possibly leading to erroneous conclusions on how forests are responding to environmental changes (Feeley et al., 2007). To effectively understand long-term trends in tropical forests, inventory plots should be either large enough or analyses should include a sufficient number of samples so that the effect of gap dynamics is diluted within the sample.

In Central Amazon wind storms can knock out several trees at once, opening forest gaps of up to 3,000 ha (Nelson et al., 1994). If these large-scale mortality events were a major driver of mortality in the Amazon, standard-size inventory plots of ca. 1 ha would fail to capture the mortality process at the landscape-scales (Nelson, 2005;Fisher et al., 2008;Chambers et al., 2009). However, large and intermediate-scale mortality events showed to be responsible for ca. 0.01Pg C y^{-1} of biomass losses and the increase, which is not enough to outweigh the biomass accumulation in the Amazon estimated based on inventory plots (Espírito-Santo et al., 2014).

1.5 Aims and objectives

This chapter reviews the most likely climatic, atmospheric and ecological alterations to be affecting Amazonian forests. Stand level changes across the Amazon have been intensively investigated (Phillips et al., 1998;Baker et al., 2004a;Brienen et al., 2015). Much less attention has been given to changes at the stem level. Several experiments have been conducted aiming to understand the physiological responses of tropical plants to environmental changes (Lovelock et al., 1998;Engelbrecht et al., 2007;Nepstad et al., 2007;da Costa et al., 2010). Based on theory, model exercises have been develop to use information from floristic composition to predict stand-level parameters in the future (Levine et al., 2016;Peres et al., 2016;Sakschewski et al., 2016). However, the few studies actually testing for changes in floristic composition in Amazonian forests are limited in terms of sample size (Laurance et al., 2004;Chave et al., 2008;van der Sande et al., 2016). Understanding the trajectory of Amazonian species over time is a necessary step to project the future of this ecosystem, understanding their resilience to changes in climate in terms of biodiversity and ecosystem services. Moreover, information on shifts in floristic composition can contribute to understanding which drivers are behind the observed stand-level alterations to the Amazonian dynamics and structure (Lewis et al., 2004a).

1.5.1 Aims

The aims of this thesis are to describe recent changes in Amazonian tree communities in terms of their functional and floristic composition and to use this information to help distinguish between different potential drivers of the changing structure and dynamics of Amazon forests.

1.5.2 Objectives

1 Review the most likely drivers of change in Amazonian dynamics.

2 Understand the role of rainfall on determining the floristic structure of neotropical tree communities.

> 2.1 Compile species abundance data from large networks of inventory plots across the Western Neotropics;
>
> 2.2 Identify the bioclimatic space ('affiliation') of each taxon across the Western Neotropics;
>
> 2.3 Investigate the structure of metacommunities across precipitation gradients to understand the importance of moisture deficit as a physiological limitation of species distributions.

3 Validate bioclimatic affiliation as a predictor of drought-induced mortality.

> 3.1 Compile data of taxon-specific drought mortality responses from published experiments and drought observations across the Neotropics;
>
> 3.2 Test for relationships between my newly derived bioclimatic affiliation and drought-induced mortality as revealed from the published literature, for multiple taxa.

4 Assess changes in functional and floristic composition within the Amazon

> 4.1 Calculate trends of climate for each inventory plot;
>
> 4.2 Calculate trends in functional composition and abundance of different taxa over the last decades;
>
> 4.4 Determine the relationship between trends in climate and functional and floristic changes.

5 Assess changes in tree size across the Amazon.

> 5.1 Using information from long-term inventory plots characterize each census in terms of tree size parameters;

  - 5.2 Calculate trends in tree size over time;
  - 5.3 Test for potential influence of tree measurement techniques on long term trends in tree size;
  - 5.4 Investigate possible drivers of tree size trends.

6 Integrate the results of this thesis with information from the literature in order to support or reject the hypothesized drivers of recent changes in Amazonian dynamics.

2

Conceptual Approach and Methods

Abstract

To understand the effects of climate and atmospheric change on tropical forests it is important to go beyond general stand-level parameters and understand the proportional changes in functional and floristic composition. The high complexity of these systems hampers the elaboration of clear and testable hypotheses when assessing changes in community structure and their drivers. I propose using my thesis a hypothesis-testing guide to understand changes in tropical tree communities. This consists of a fingerprinting approach that assesses potential atmospheric, climatic and biological drivers of changes and their predicted effects on different levels of organization. From my review of the literature I can conclude that increases in CO_2 concentrations and a trend towards a drier climate are the most likely factors affecting tropical forest. In my thesis I focus testing for the fingerprints from these main hypotheses, which could tell them apart from other hypothesised drivers (i.e. late successional recovery and hunting pressure). This will allow me to get closer to the understanding of the mechanism behind them by investigating changes among (e.g. mean tree size, tree size distribution) and within-stand (e.g. taxa abundance) across the Amazon. I use macroecological information, from two large data networks of forest inventories, RAINFOR and ATDN, and climate datasets, to test for the predicted effects of these two drivers in Western Amazonian forests. In my thesis describe each taxon in terms of functional traits, and use this information to characterize the plots in terms of the traits' community-weighted mean. I then quantify changes in the abundances of different taxa, which allows me to understand how the whole community has been changing and whether these shifts are related to climatic affiliations. Moving from among to within stand analysis on a macro scale will allow me to provide a better understanding of which are the mechanisms behind the recent changes in tropical forests.

2.1 Introduction

The overall aim of this thesis is to better understand how and why Amazon forests are changing internally in terms of their functional and floristic composition, and to use this information to distinguish between different potential drivers of Amazon dynamics. This requires, firstly, critically reviewing the potential drivers of recent ecological change in Amazonia (see Chapter 1 – Literature Review) and secondly, to identify the most likely drivers of Amazon dynamics and which information is missing in order to allow us to reject some of these hypotheses or to increase the body of evidence that corroborate them (Figure 2.1). In this chapter, I synthesize the information from the literature review and present the analytical approach applied in this thesis to distinguish between the different hypotheses.

Most of the literature on the dynamics of tropical forests has focused on stand-level parameters. For the Amazon, there is a growing body of evidence showing that aboveground biomass has been increasing for at least 30 years (Phillips et al., 1998;Baker et al., 2004a;Brienen et al., 2015). In parallel to these AGB changes, an increase in tree mortality and recruitment has been observed (Phillips et al., 1994;Lewis et al., 2004b), with some studies showing an increase in stem density until the 2000s (Lewis et al., 2004b), and more recent studies suggesting a slight decrease in stem numbers in the last decade (Brienen et al., 2015) and wood productivity significantly increasing over the last 30 years (Brienen et al., 2015). Moreover, this overall trend showed to be affected by the two large Amazonian droughts, where productivity decreases and mortality rates are higher, leading to a decrease in biomass accumulation (Phillips et al., 2009;Lewis et al., 2011;Feldpausch et al., 2016).

Analyses on within-stand attributes across the tropics have shown an advantage to large taxa over time (Laurance et al., 2004;Fauset et al., 2012;van der Sande et al., 2016). There has been a shift observed towards dry-affiliated taxa in Central America (Enquist and Enquist, 2011;Feeley et al., 2011a), Western Amazon (Butt et al., 2014) and Western Africa (Fauset et al., 2012), however there is as yet no completely Amazon-wide evidence of such compositional shift.

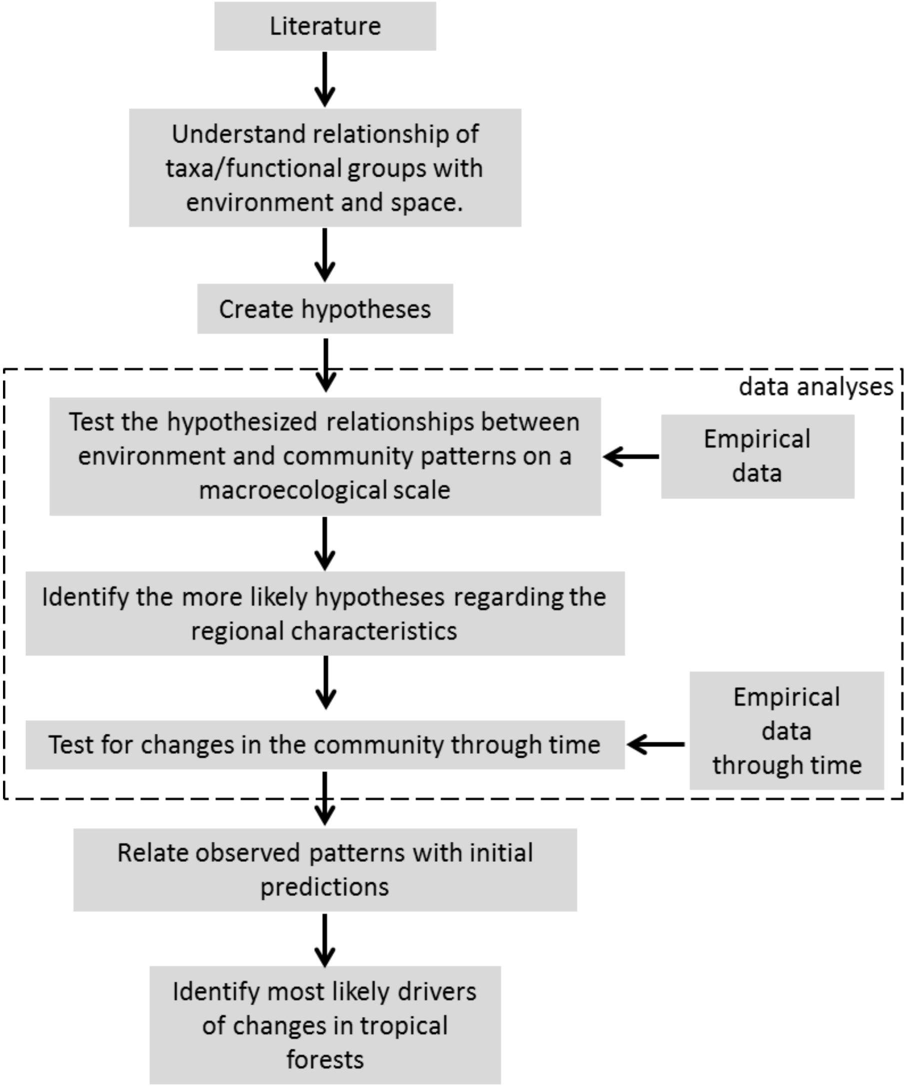


Figure 2.1 - Summary of the conceptual approach to understand the internal changes in tropical forest. Dashed box highlight the steps that depend on data analyses.

2.2 Proposed overall conceptual approach

The key change questions are: “Which kinds of trees may be winning? Which ones may be losing? Where is this happening? and Why?“. To tackle these, acknowledging the complexity of Amazonian forest communities, I propose a multiple working hypothesis approach (Chamberlin, 1890;Elliott and Brook, 2007). This method is based on the idea that a series of hypotheses may be important, thus it aims to find the most likely set of hypothesis that are necessary and sufficient to explain the observed phenomenon. I summarize here important hypotheses on internal changes in tropical forests, discard the unlikely ones, and set out how I propose to use the observations from two large tropical forest networks (RAINFOR and ATDN) to test the set of predictions and get closer to the explanations of recent changes in the Amazon forest.

In Chapter 1 I reviewed the theory on possible physical, chemical and biological drivers of changes in composition and assessed the ecophysiological processes affected by them, as well as the expected ecological outcomes for dynamics (e.g., growth, mortality), structure (e.g., wood density, mean seed size, tree size) and composition (e.g. changes in abundance of moisture-living Arecaceae, changes in the relative basal area of nitrogen-fixing Fabaceae, etc). Table 2.1 summarizes this knowledge and uses it to outline my predictions on how change drivers are likely to affect among and within-stand parameters in the tropical forest. Appendix 2.1 gives brief mechanistic justifications for each prediction, and is designed to be read in conjunction with Table 2.1. For instance, in table 2.1 I predict that droughts preferentially kill big trees and in Appendix 2.1 explain that this is because taller trees are more likely to be vulnerable to embolism.

Table 2.1 – Fingerprints of drivers of change in Amazonia. Each cell shows the predictions for each driver on a certain ecological parameter; **?** shows gaps in current knowledge; **+** represents increases and **–** decreases, in brackets most likely outcomes when there is no strong evidence supporting the prediction or no prediction. To help visualization + outcomes are shown in grey. Drivers divided into climatic, atmospheric and ecological.

	Climatic		
	Precipitation		Temperature
	↑ Dry season intensity	↑ Frequency of droughts	↑ Temperature
Spatial range of impact	Regional	Regional	Regional
Impact correlated with Consequences	gradual and progressive drying	Drier climate	Warmer climate
Mechanism (individual level)			Protein denaturation
Photosynthesis	-	-	-
AGB	-	-	(-)
Stem density	-	-	(-)
Woody Productivity	-	-	-
Mortality	+	+	+
Recruitment	-	-	-
Average size	+	-	-
Large trees	+	-	-
Small Trees	-	+	+
Wood density	-	+	(+)
Zoochoric plants	?	?	?
Anemochoric plants	(+)	(+)	?
Compound leaved	(+)	(+)	?
N-fixing Fabaceae	?	?	?
Palms	?	?	?
Wet-affiliated taxa	-	-	?
Dry affiliated taxa	+	+	?
Light dependent taxa	+	-	?
Shade tolerant taxa	-	+	?
Canopy taxa	+	-	-
Understory taxa	-	+	+
Secundary consequences on other drivers	increase in lianas	increase in lianas	

Table 2.1 – Fingerprints of drivers of change in Amazonia (continuation).

	Atmospheric			
	↑$[CO_2]_{atm}$			
Spatial range of impact	Global			
Impact correlated with Consequences		No stressful condition Resource availability		Under water-stress Drier climate
Mechanism (individual level)	General increase - all community is equally benefited by increase in $[CO_2]_{atm}$	CO_2 Fertilization plants close to light compensation point do better	CO_2 Fertilization winner takes all	Increase of water use efficiency will offset climate stress
Photosynthesis	+	+	+	+
AGB	+	+	+	+
Stem density	+	+	-	+
Woody Productivity	+	+	+	+
Mortality	+	-	+	-
Recruitment	+	+	-	+
Average size	+	-	+	+
Large trees	stable	-	+	+
Small Trees	stable	+	-	-
Wood density	stable	?	-	-
Zoochoric plants	stable	?	?	?
Anemochoric plants	stable	?	?	?
Compound leaved	stable	?	?	?
N-fixing Fabaceae	stable	?	?	?
Palms	stable	?	?	?
Wet-affiliated taxa	stable	?	?	+
Dry affiliated taxa	stable	?	?	-
Light dependent taxa	stable	(+)	?	?
Shade tolerant taxa	stable	(-)	?	?
Canopy taxa	stable	(-)	+	+
Understory taxa	stable	(+)	-	-
Secundary consequences on other drivers	increase in lianas	increase in lianas	increase in lianas	increase in lianas

Table 2.1 – Fingerprints of drivers of change in Amazonia (continuation).

	Atmospheric		**Ecological**	
	N deposition	↑[aerosols]$_{atm}$	Previous disturbances	Hunting pressure
Spatial range of impact	Regional	Regional	Local	Local - forest edges
Impact correlated with	Distance from cities	Dry periods, related with fires		distance from the edge
Consequences		↑ diffuse radiation	Late successional processes	Decrease of seed dispersers and herbivorous
Mechanism (individual level)		↓ self-shading of leaves in the canopy		Limited dispersion of zoochoric taxa
Photosynthesis	(-)	+	stable	stable
AGB	stable	+	+	-
Stem density	(+)	+	-	+
Woody Productivity	stable	+	-	stable
Mortality	?	?	stable	stable
Recruitment	(+)	+	-	stable
Average size	(-)	-	+	-
Large trees	stable	-	+	-
Small Trees	(+)	+	-	+
Wood density		?	+	-
Zoochoric plants	?	?	+	-
Anemochoric plants	?	?	-	+
Compound leaved	?	?	-	?
N-fixing Fabaceae	(stable)	?	-	?
Palms	?	?	?	?
Wet-affiliated taxa	?	?	stable	stable
Dry affiliated taxa	?	?	stable	stable
Light dependent taxa	?	?	-	?
Shade tolerant taxa	?	?	+	?
Canopy taxa	stable	(-)	+	-
Understory taxa	(+)	(+)	+	+
Secundary consequences on other drivers				

2.2.1 Predictions

Each driving process will engender a causative chain that affects plant ecophysiology, whose changes are expected to be imprinted as patterns in the ecological parameters. Here I present below some of these chains of (i) drivers, (ii) ecophysiology and (iii) falsifiable hypothesized ecological impacts at A. among-stand level, B. within-stand level.

Increase in resources

(i) Increasing CO_2, causes
  (ii_a) Growth fertilisation, causes
    (iii_a) **A.** Stand biomass and stand growth rates to rise everywhere, but especially in more nutrient-rich forests.
    B_1. Asymmetric competition increases relative gains by large trees (Coomes et al., 2011), or
    B_2. Plants near to their light compensation point (e.g. smaller, shaded trees) show greater relative gains (Ehleringer and Björkman, 1977;Augspurger, 1984;Lloyd and Farquhar, 2008).
  (ii_b) Increased water-use efficiency, causes
    (iii_b) **A.** Gains in stand growth and biomass everywhere, but especially in drier forests.
    B. Relative gains by taxa restricted to wetter environments.

Decline in resources and/or increase in ecophysiological risks

(i) Increasing drought frequency, causes
  (ii) More risk of xylem embolism, causes
    (iii) **A.** Loss of stand biomass via growth decline and increased mortality, especially in drier forests.
    B_1 Dry-adapted taxa gain relatively, and
    B_2 Tallest trees show greatest losses, through mortality increases and decreases in growth rate.

Biological changes

(i) Hunting pressure, causes

  (ii) Failure of large animal-dispersed taxa to disperse seeds, enhancing density dependent mortality of their seedlings under conspecific adults, which causes

    (iii) **A.** Loss of stand-level biomass, driven by a decline in mean wood-density, especially in forests close to access points.

    B. Small-seeded, light-wooded taxa that are more likely to be wind/bat/small-bird dispersed increase in correlation with hunting pressure (proximity to forest's edges and fragmentation can be used as a proxy), especially when comparing the trees which newly recruit vs. those which die.

Biases in plot selection or inadequate sample size to capture natural disturbance-recovery dynamics

(i) Previous disturbances, causes

  (ii) Natural successional process towards forest maturity, which causes

    (iii) **A_1**. Gains in stand biomass and wood density, and

    A_2. Growth rate of stands to decline as they move towards maximum biomass and competition.

    B_1. Large trees increase in size whereas small trees decline, and

    B_2. Gain in dense-wooded trees, decrease in pioneer species.

2.2.2 Prioritizing hypotheses to be tested

Some of the hypotheses from Table 2.1 are in practice arguably unlikely to be realised at a sufficient scale to be relevant. Here I will develop a simple prioritysetting framework to help determine the predictions that require urgent investigation, in which I evaluate:

(a) Strength of evidence that the process is a real widespread physical, chemical or biological change in Amazonia;
(b) Hypothesized magnitude of ecological and ecophysiological impact on tropical plants and ecosystems;
(c) Focus on outcomes that maximize the discrimination between drivers;
(d) Pragmatic concerns, such as data availability.

Practical example:

One of the possible drivers is the deposition of nitrogen, caused by fires and emissions from urban centres. Responses to additional nitrogen should vary with soil conditions and among N-fixing and non N-fixing species (Hietz et al., 2011). However, enhanced N-deposition is hypothesized to be localized in forests near urban centres, such as in patches of Atlantic Forest near the cities along the Brazilian coast and inland, as well as close to large agricultural forest edges in Amazonia. Since there has been insufficient evidence that N deposition may be affecting “intact” tropical forests on a large scale and over long distances, testing for the effects of this driver will not be a priority here (following criterion a, see above).

2.2.3 Hypotheses testing

Once I have a set of likely explanations I will use empirical data to test their predictions. The validation of a prediction suggests that it may be true; whereas a falsified prediction allows me to eliminate the underlying hypothesis as an important driver of change, reducing the number of possible explanations. In the following paragraphs I outline the specific most credible hypotheses I propose to test in my thesis, as those processes which are most credible in terms of the prioritization criteria (a) and (b) which I outlined above. In table 2.2 below I present a concise overview of the likely hypothesis-testing matrix, based on Table 2.1 and Appendix 2.1.

Table 2.2 – Most likely drivers of change in Amazonian tropical forest and the expected shifts. In brackets are the most likely outcome for the cases where there is not strong evidence supporting the predictions or there is not a known prediction.

	Within-stand predictions						Stand-level predictions				
Hypotheses	Potential size	Precipitation affiliation	Wood density	Mean tree size	Large trees	Small trees	Above-ground biomass	Productivity	Recruitment rate	Mortality	Stem density
Climatic											
Drying trend	(Larger)	Drier	(Higher)	Increase	Increase	Decrease	Decrease	Decrease	Decrease	Increase	?
Increase in frequency of extreme droughts	(Smaller)	Drier	(Higher)	Decrease	Decrease	?	Decrease	Decrease	Decrease	Increase	?
Increase in temperature	Smaller	Drier	Higher	Decrease	Decrease	Increase	Decrease	Decrease	Decrease	Increase	?
Atmospheric											
CO_2 fertilization: Winners take all	Larger	No change	(Lower)	Increase	Increase	Decrease	Increase	Increase		Increase	Decrease
CO_2 fertilization light suppressed do better	(Smaller)	No change	(Higher)	No change		Increase (relatively)	Increase	Increase	Increase	Decrease	Increase
CO_2 increase WUE	Larger	Wetter	(Lower)	Increase	Increase		Increase	Increase	Increase	Decrease	Decrease
Anthropogenic											
Late succession	Larger	No change	Higher	Increase	Increase	Decrease	Increase	Decrease	Decrease		Decrease

2.2.4 Possible hypotheses

(i) Under an increase in resources large individuals are expected to do better as an outcome of the increase in the asymmetric competition for light (Weiner, 1985;Falster and Westoby, 2003) Therefore, I would expect a rise in $[CO_2]_{atm}$ to enhance light limitation and thereby create a stronger pattern of asymmetric competition, and canopy individuals to show the larger net gain rates and mean tree size to increase as a consequence.

(ii) Alternatively, an increase in resources could make a greater difference for plants close to the light compensation point, so that they have a larger relative increase in size (Ehleringer and Björkman, 1977;Augspurger, 1984;Körner, 2006;Lloyd and Farquhar, 2008). Given this assumption, understorey trees, saplings, and even seedlings may be expected to have the greatest relative advantage from an increase in resources and so I would expect the size-frequency distribution to shift towards the smaller size classes, contradicting the previous prediction above.

(iii) The increase in moisture stress should be a physiological challenge for trees in the Amazon (Nepstad et al., 2007;Baltzer et al., 2008;da Costa et al., 2010;Rowland et al., 2015). Thus, dry-affiliated taxa should have an advantage in tolerating longer periods of moisture-stress when compared to wet-affiliated taxa and composition will shift towards a dry-adapted community. In parallel, mean community tree size should decrease as well as the abundance of small statured taxa, which are expected to have shallower roots and thus less access to ground water (Feeley et al., 2011a;Fauset et al., 2012)

(iv) If the increase in the frequency and intensity of big droughts is a major driver of change in forest communities, the mortality of wet-affiliated taxa will increase and communities will shift to become more dry-affiliated. Large trees more likely to die from hydraulic failure, are also expected to increase and community composition should shift towards short-statured taxa (Rowland et al., 2015).

(iv) Disturbances, either natural or anthropogenic, are part of tropical forest dynamics and so it is reasonable to expect some degree of disturbance-recovery in many plot data in intact forests (Clark, 2002;Wright, 2005). The dominance of the late-successional disturbance-recovery processes means that we could expect an increase in high wood density trees and shade tolerant trees (Chave et al., 2008). As a consequence of self-thinning, mean tree size should increase and stem density should decrease over time (Connell and Slatyer, 1977). Growth rates should decline as biomass approaches an asymptotic saturation point (e.g. Chambers et al., 2004).

2.2.5 Selecting the most parsimonious explanations:

Trying to find the simplest and most likely explanation, I aim to eliminate unlikely drivers based on my observations together with information from ecological theory (i.e. fingerprinting framework table 2.1). Under this philosophical approach the premises do not guarantee the conclusions, considering that other unknown factors may be creating the observed patterns, however by eliminating some of the hypothesis I expect to get closer to a set of potential drivers of tropical forest change.

2.3 Review of Amazonia's vegetation data

The study is to be developed at a macroecological scale, using data from forest plots across the Neotropics. This information comes from two major data networks – one primarily floristic (ATDN) and one primarily dynamic (RAINFOR), and smaller floristic tree data sets (Gentry, Ruokolainen and Phillips) described below in Table 2.3.

2.3.1 Amazon Tree Diversity Network (ATDN)

This network of botanists has developed a dataset in which the total number of tree species recorded for more than 1,000 plots of 1 hectare across Amazonia. Each plot is installed in an old-growth forest area, where each tree that has diameter at breast height (dbh, i.e. the diameter of the tree trunk measured at 1.3m height or above any deformity) ≥ 10cm is registered. Outcomes from this database have made major contributions to the understanding of spatial patterns of Amazon tree biodiversity and composition (ter Steege et al., 2003; 2006; 2013).

One limitation of ATDN is that it does not have time scale information – i.e. these are single census datasets-, which obviously restricts studies regarding change. For this thesis ATDN data also have other limitations. One such is that there is no *in situ* information on soil, which implies that to understand the influence of climate on floristic composition I have to isolate the effect of soil variation as far as possible, by working with a relatively geologically homogeneous data set. Thus, I will use data from Western Amazonia and biogeographically similar regions with Andean-type influence in Colombia, Chocó, Central America and dry inter-Andean valleys, where soils show relatively low variation in comparison with the whole basin (Hoorn et al., 2010;Quesada et al., 2010). These soils are, on average, the youngest and more fertile in the Neotropics, mostly strongly influenced by the uplift of the Andes and subsequent deposition. With a low "pedogenic level" they are also less weathered and have received parent material from the Andes (Quesada et al., 2010). I use ca. 367 ATDN plots located in this region and exclude plots located in swamps or white sand, which are local exceptions in this landscape. Another limitation of ATDN data is that data available for analysis simply represents stem numbers per taxon in each plot and do not have the information on basal area (i.e. cross-sectional area of the trunks), which is a better indicator of the relative competitive performance of each taxon in each location.

ATDN data have the advantage of having a large number of sample units across a large area. These data are therefore appropriate to develop some macroecological analyses, such as estimating patterns of diversity (ter Steege et al., 2003) and species dominance across Amazonia (ter Steege et al., 2013), distributions of individual taxon and their relationships with environmental variables (ter Steege et al., 2006). While ATDN does not have data on the full climate range of all taxa, it is the largest data network for Amazon forest vegetation, and therefore the closest to the real distribution of taxa that one can get based on forest inventories. Alternatively, this kind of analysis could be developed using herbarium data, however this would be less appropriate since these data are not collected with the original purpose of supporting ecological studies. As a consequence, the location and the number of individuals sampled per species can be strongly biased by various factors unrelated to ecological importance, such as the difficulty of sampling a certain species, which could include the height of flowering branches or the frequency with which the species flowers. Also, ATDN data provide abundance and absence information, neither of which can be obtained from herbarium data, and are key to understand the relationships of each group with the environment – species will be more abundant under their ideal environmental conditions.

2.3.2 RAINFOR

This network has approximately 400 plots in South America of which more than 300 are in Amazonia. Most of these also contribute to the large ATDN floristic set described above, but in contrast to the ATDN data, these have mostly been revisited every 1 to 5 years and the surviving trees measured again, dead trees noted and new trees with ≥ 10cm diameter included (Oliver Phillips pers. comm.). The recensus of each plot provides information on trends in the forest's growth, mortality, biomass and composition through time. RAINFOR plots have been monitored for an average of more than 10 years each and they mostly have *in situ* soil data (e.g. Quesada et al., 2010;Quesada et al., 2012), important when analysing the potential effects of climatic variables, as explained above. Long-term data potentially allow the direct testing of changes through time, rather than simply modelling environmental affiliations as a function of distribution in space, as permitted by single-census floristic data.

2.3.3 Smaller plots

In addition to ATDN and RAINFOR plots, I will also include three other available groups of single-census smaller plots, contributed by Gentry, Ruokolainen and Phillips, to increase the number of sample units and to cover a larger geographic region, including important dry areas (e.g. Gentry plots in the Amazon fringes, Central America and the Chocó). These plots were mostly installed with the purpose of characterizing in detail the composition of a particular landscape or region. For a rapid, efficient assessment of stand composition (cf. Phillips et al., 2003) they included smaller stems down to 2.5 cm diameter in smaller samples of typically 0.1ha. Most of them have also had soil collected and analysed (see table 2.2 for the description of each cluster of plots).

Table 2.3 – Metadata table of the data set used in this thesis. Some plots are organized in larger groups (e.g. ATDN in which RAINFOR plots are included). Larger groups are shown here in bold, first order of subsets in black and second order of subsets in grey. WA= Western Amazonia; L S Ame = Lowland South America; NWA = North-west Amazonia; SWA = South-west Amazonia. >D is the minimum stem diameter measured in each plot.

Source	Cluster	Geographical extent	Stem information	>D (mm)	N plots	size (ha)	total area (ha)	Monitoring length	% of plots that have soil data	soil variables available	Notes: science
ATDN	**ATDN-WA**	**W A**	**N**	**100**	**350**	**1**	**350**	**Snapshot**	**Few**		
RAINFOR	RA-WA-1c	W A	D, n	100	200	1	200	Snapshot	Some		
RAINFOR	RA-WA-Mc	W A	D, n	100	100	1	100	Mean ca. 12 years	Most		
RAINFOR	RA-LSA-1c	L S Ame.	D, n	100	400	≥1	450	Snapshot	Some		
RAINFOR	RA-LSA-Mc	L S Ame.	D, n	100	280	≥1	250	Mean ca. 12 years	Some		
Gentry	**GE-LSA**	**Lowland Neotropics**	**D, n**	**25**	**75**	**0.1**	**5**	**Snapshot**	**Most**		**Huge climate range of forests (600 – 6,000 mm)**
Gentry	GE-NWA	NW A	D, n	25	10	0.1	1	Snapshot	Yes		All ca 2700-3000mm
Ruokolainen	**RU-NWA**	**NW A**	**D, n**	**25**	**53**	**0.04**	**2.12**	**Snapshot**	**Yes**		**All ca 2700-3000mm**
Phillips	**OP-NWA**	**NW A**	**D**	**25**	**10**	**0.1**	**1**	**Snapshot**	**Yes**		**All ca 2700-3000mm**
Phillips	**OP-SWA**	**SW A**	**D**	**25**	**88**	**0.1**	**8.8**	**Snapshot**	**Yes**		**All ca 2100-2300mm**

2.4 Analytical approach

In this thesis I combine environmental data with ecological information from (1) observations of tree communities and their dynamics assessing inventory plots, (2) drought tolerance using data from drought experiments and (3) functional traits (Figure 2.2). Together, these data allowed me to characterize the Amazon basin in terms of species distributions, climate and trends in functional and floristic composition (Table 2.4) and generate information to understand the drivers behind changes in the dynamics and structure of Amazonian forests.

I firstly, used abundance data (RAINFOR, ATDN, Gentry, Phillips and Ruokolainen plots) across the Western Amazon to investigate the importance of water-deficit on driving the distribution of tree species (Chapter 3). I generated, for each taxon, an index of water-deficit affiliation (WDA), which indicates the most favourable condition along a water-deficit gradient. The capacity of this index to predict drought-tolerance is tested in Chapter 4 using experimental data and observations from a strong drought in a 50 ha plot in Barro Colorado Island. For that, I tested for the correlation between drought-induced mortality in each case-study and WDA.

Then, in Chapter 5, I tested for changes in functional and floristic composition, combining information from 108 RAINFOR long-term tree inventory plots across the Amazon with functional traits (WDA, potential size and wood density). For each census I calculated a value trait community weighted mean (CWM sensu Díaz et al., 1992) and tested how the mean trait for each community changes over time. The different compartments of the community dynamic, i.e. recruitment, basal area gains and losses were also analysed individually. I further assess long-term climate data to calculate trends in cumulative water deficit and then investigate the relationship between these trends and changes in community composition. Floristic trends were assessed by calculating the trends in abundance of each taxa over time, this information allowed me to understand which taxa in particular, if any, are driving the changes in functional composition.

Finally, in Chapter 6, I assessed trends in tree size across the Amazon using information from 194 inventory plots from RAINFOR. For each census I calculated a series of tree-size variables, including mean and median tree size and parameters characterizing the size-frequency distribution. Then I tested for changes in these parameters over time.

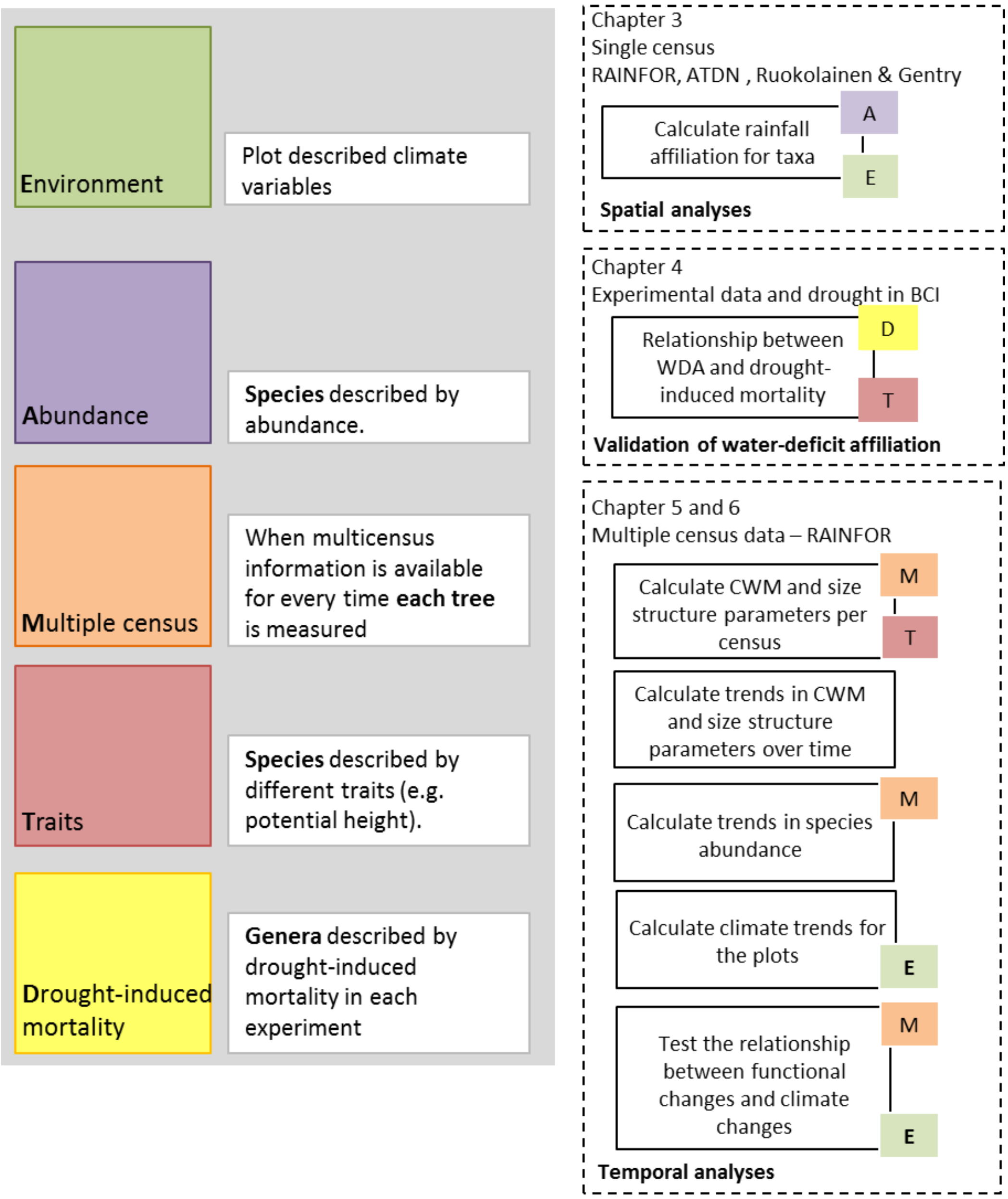


Figure 2.2 - Thesis data organization and summary of the analytical approach. On the left squares represent different data frames in which the data were organized. On the right a summary of the analytical approach including which type of data was used for each analyses (small squares colour coded following the colours in the left panel).

Table 2.4 - Summary of the analytical procedures suggested for my thesis including data to be used, main methods and outcomes. CWM (community weighted mean) is the mean trait value at the community (i.e. plot) level weighted by species abundances (Díaz et al., 1992).

Objective	Describe the study area	Describe taxa based on traits	Verify predictability of water-deficit affiliation (WDA)	Assess functional, floristic and structural changes over time
Data sources	• Assess climate data from WorldClim, TRMM and CRU; • Plot locations from RAINFOR, ATDN (West Amazon), Gentry, Phillips and Ruokolainen plots.	• ATDN (West Amazon), Gentry, Phillips and Ruokolainen plots; • South American RAINFOR plots, pontential size from Fauset et al. (2015) and wood density from Zanne et al. (2010).	• WDA for neotropical genera; • Through-fall exclusion experiments of seedlings and trees; • 1982-83 drought observation in Barro Colorado Island.	• RAINFOR multicensus plots across Amazonia; • Western Amazonian tree rainfall affiliation; • South American tree potential size and wood density.
Methods	• Extract climate variables from datasets to each plot based on their latitude and longitude; • Calculate temporal series of cumulative water-deficit;	• Calculate water-deficit affiliation (WDA) following Feeley et al. (2011b) altitude center of gravity; • Compile potential size and wood density for Amazonian taxa;	• Test for the relationship between WDA and drought-induced mortality;	• Test for changes in within-stand level parameters (WDA, potential size, wood density); • Calculate changes in different taxa abundance; • Test for changes in mean and median tree size and size-distribution parameters over time;
Outcomes	• Information of precipitation for each plot and across the Amazon; • Trends in CWD across the Amazon.	• Western Amazonian tree WDA at genus and family level and species level for most common species; • South American tree potential size at genus and family level and species level for most common species.	• Information on whether WDA can predict tree responses from droughts.	• Functional changes over time across the Amazon; • Changes of abundance for Amazonian genera.

3

Seasonal drought limits tree species across the Neotropics

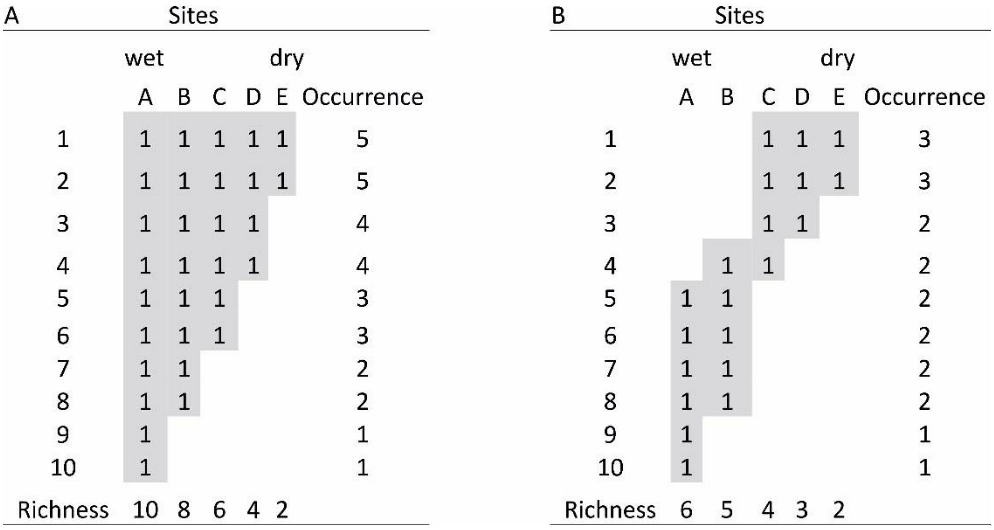
Abstract

Within the tropics, the species richness of tree communities is strongly and positively associated with precipitation. Previous research has suggested that this macroecological pattern is driven by the negative effect of water-stress on the physiological processes of most tree species. This process implies that the range limits of taxa are defined by their ability to occur under dry conditions, and thus in terms of species distributions it predicts a nested pattern of taxa distribution from wet to dry areas. However, this ‘dry-tolerance’ hypothesis has yet to be adequately tested at large spatial and taxonomic scales. Here, using a dataset of 531 inventory plots of closed canopy forest distributed across the Western Neotropics I investigated how precipitation, evaluated both as mean annual precipitation and as the maximum climatological water deficit, influences the distribution of tropical tree species, genera and families. I find that the distributions of tree taxa are indeed nested along precipitation gradients in the western Neotropics. Taxa tolerant to seasonal drought are disproportionally widespread across the precipitation gradient, with most reaching even the wettest climates sampled; however, most taxa analysed are restricted to wet areas. The results suggest that the ‘dry tolerance’ hypothesis has broad applicability in the world’s most species-rich forests. In addition, the large number of species restricted to wetter conditions strongly indicates that an increased frequency of drought could severely threaten biodiversity in this region. Overall, this study establishes a baseline for exploring how tropical forest tree composition may change in response to current and future environmental changes in this region.

3.1 Introduction

A central challenge for ecologists and biogeographers is to understand how climate controls large-scale patterns of diversity and species composition. Climate-related gradients in diversity observed by some of the earliest tropical biogeographers, including the global latitudinal diversity gradient itself (e.g. von Humboldt et al., 1808;Wallace, 1878), are often attributed to the physiological limitations of taxa imposed by climate conditions (e.g. Dobzhansky, 1950). This idea is expressed in the ‘physiological tolerance hypothesis’ (Janzen, 1967;Currie et al., 2004), which posits that species richness varies according to the tolerances of individual species to different climatic conditions. Thus, species able to withstand extreme conditions are expected to be widely distributed over climatic gradients, while intolerant species would be constrained to less physiologically challenging locations and have narrower geographical ranges. An implicit assumption of this hypothesis is that species’ realized niches tend to reflect their fundamental niches, and a key implication of the hypothesis is that past, present, and future distributions of species will tend to track changes in climate (Boucher-Lalonde et al., 2014).

Within the tropics tree diversity varies considerably, possibly as a consequence of variation in water supply (e.g. ter Steege et al., 2003). Water-stress is indeed one of the most important physiological challenges for tropical tree species (Engelbrecht et al., 2007;Brenes-Arguedas et al., 2011), and precipitation gradients correlate with patterns of species richness at macroecological scales (Clinebell et al., 1995;ter Steege et al., 2003). In particular, tree communities in wetter tropical forests tend to have a greater number of species than in drier forests (Gentry, 1988;Clinebell et al., 1995;ter Steege et al., 2003). If this pattern were driven by variation among species in the degree of physiological tolerance to dry conditions, then I would predict that all tropical tree species could occur in wet areas whilst communities at the dry extremes would be made up of a less diverse, drought-tolerant subset. Thus, I would expect a nested pattern of species’ occurrences over precipitation gradients, characterised by widespread dry-tolerant species and small-ranged species restricted to wet environments. In this chapter I refer to this scenario as the dry tolerance hypothesis (Figure 3.1 a).



A

	Sites					
	wet				dry	
	A	B	C	D	E	Occurrence
1	1	1	1	1	1	5
2	1	1	1	1	1	5
3	1	1	1	1		4
4	1	1	1	1		4
5	1	1	1			3
6	1	1	1			3
7	1	1				2
8	1	1				2
9	1					1
10	1					1
Richness	10	8	6	4	2	

B

	Sites					
	wet				dry	
	A	B	C	D	E	Occurrence
1			1	1	1	3
2			1	1	1	3
3			1	1		2
4		1	1			2
5	1	1				2
6	1	1				2
7	1	1				2
8	1	1				2
9	1					1
10	1					1
Richness	6	5	4	3	2	

Figure 3.1 - Two conceptual models of how species' distributions may be arrayed along a precipitation gradient, with presence/absence matrices where rows represent taxa and columns represent communities, ordered from wet to dry. A. Nested pattern expected by the dry tolerance hypothesis. Nestedness (*sensu* Leibold and Mikkelson 2002) is represented by gradual disappearance of taxa along the precipitation gradient from wet to dry. B. Turnover of taxa along the precipitation gradient. This pattern is characterized by the substitution of taxa from site to site, resulting in communities at opposite sides of the precipitation gradient being completely different in composition (Leibold and Mikkelson 2002).

Alternatively, nestedness may not be the predominant pattern for tropical tree metacommunities over precipitation gradients. Multiple studies have documented substantial turnover in floristic composition over precipitation gradients in tropical forests (Pitman et al., 2002;Engelbrecht et al., 2007;Quesada et al., 2012;Condit et al., 2013). This pattern could be driven by a trade-off between shade-tolerance and drought-tolerance (e.g. Markesteijn et al., 2011;Brenes-Arguedas et al., 2013). Whilst drought-tolerant species tend to have a higher capacity for water conductance and CO_2 assimilation under water-limiting conditions, they grow more slowly in the scarce understorey light of wet forests where shade-tolerant species have a competitive advantage (Brenes-Arguedas et al., 2011;Brenes-Arguedas et al., 2013;Gaviria and Engelbrecht, 2015). Drought-tolerant species are also apparently more vulnerable to pest damage in moist areas (Baltzer and Davies, 2012;Spear et al., 2015). Thus, in less physiologically stressful environments, tropical tree species' occurrences could be limited by stronger biotic interactions, both with competitors and natural enemies (MacArthur, 1972;Normand et al., 2009). In a scenario in which both wet and dry limitations to species distributions are equally important, I would expect progressive turnover of species' identities along precipitation gradients (cf. Figure 3.1b), rather than the nested pattern described above.

Both nested and turnover patterns have to some extent been documented in the tropics. A nested pattern has been detected in the Thai-Malay peninsula where widespread species, occurring across both seasonal and aseasonal regions, are more resistant to drought than species restricted to aseasonal areas (Baltzer et al., 2008). Across the Isthmus of Panama, Engelbrecht et al. (2007) found a direct influence of drought sensitivity on species' distributions, whilst light requirements did not significantly limit where species occur, which is consistent with the mechanisms underlying a nested pattern of species distributions. Also in Panama, another experimental study found that pest pressure was similar for species regardless of their distribution along a precipitation gradient (Brenes-Arguedas et al., 2009), indicating that the distributions of taxa that occur in drier forests may not be constrained by pest pressure. However, recent data from the same area show that drought-tolerant species are more likely to die than drought-intolerant taxa when attacked by herbivores or pathogens (Spear et al., 2015). Furthermore, when comparing two sites, an aseasonal (Yasuní; ca. 3200 mm y^{-1} rainfall) and seasonal (Manu; ca. 2300 ca. mm y^{-1}) forest in lowland western Amazonia, Pitman et al. (2002) reported that similar proportion of species were unique to each (Yasuní, 300 exclusive species out of 1017; Manu, 200 out of 693). The presence of a similar and large proportion of species restricted to each site is consistent with species distributions showing a pattern of turnover among sites. While there is thus evidence of both nestedness and turnover in tropical tree species distributions, a comprehensive investigation at large scale is lacking.

There are various approaches to estimate the tolerance of taxa to water-stress. For example, experimental studies of drought imposed on trees provide the clearest indicator of sensitivity to water-stress and provide insight into the ecophysiological mechanisms involved. Yet in the tropics, these are inevitably constrained to a minor proportion of tropical diversity, limited by tiny sample sizes (e.g. Nepstad et al., 2007;da Costa et al., 2010) and practical challenges of achieving any spatial replication and of integrating effects across multiple life stages (e.g. Brenes-Arguedas et al., 2013). By contrast, observational approaches, which consist of mapping species' distributions across precipitation gradients, could potentially indicate the sensitivity of thousands of species to dry or wet conditions (e.g. Slatyer et al., 2013). Fixed-area inventories of local communities from many locations, offer a particular advantage for this kind of study as they avoid the bias towards more charismatic or accessible taxa that affects *ad hoc* plant collection records (Nelson et al., 1990;Sastre and Lobo, 2009). Inventory-based attempts to classify tropical tree taxa by their affiliations to precipitation regimes have already advanced the understanding of species precipitation niches (e.g. Butt et al., 2008;Fauset et al., 2012;Condit et al., 2013), but have been fairly limited in terms of spatial scale, number of sample sites and taxa. In this chapter I apply this inventory-based approach to investigate the macroecological patterns of trees across the world's most species-rich tropical forests, those of the Western Neotropics, an area of 3.5 million km^2 that encompasses Central America and western South America. Because species richness in this region is so high, meaning that individual species' identifications are often challenging, I also explore whether analyses at the genus - or family - level offers a practical alternative for assessing the impacts of water-stress on floristic composition.

I selected the Western Neotropics as the study area for two reasons. First, there is substantial variability in climate at small spatial scales relative to that of the entire region, meaning that associations between precipitation and floristic composition are less likely to be the result of dispersal limitation and potential concomitant spatial autocorrelation in species' distributions. The Andean Cordilleras block atmospheric moisture flow locally, maintaining some areas with very low precipitation levels, whilst enhancing orographic rainfall in adjacent localities (Lenters and Cook, 1995). As a result, there are wetter patches surrounded by drier areas across the region, such as the wet zones in central Bolivia and in South East Peru (Figure 3.2). The inverse is also observed, such as the patches of drier forests south of Tarapoto in central Peru. There is also a general tendency for precipitation to decline away from the equator in both northward and southward directions (Figure 3.2). Secondly, the western Neotropics is a cohesive phylogeographic unit. Western Amazonian forests are floristically more similar to forests in Central America than to those in the Eastern Amazon, despite the greater distances involved and the presence of the world's second highest mountain range dividing Central America from southern Peru (Gentry, 1990). This floristic similarity between the western Amazon and Central American forests is thought to be because: (1) the Andes are young (~25Ma) so represent a recent phytogeographic barrier (Gentry, 1982; 1990), and (2) the soils of moist forests in western Amazonia and Central America are similar, being young, relatively fertile, and often poorly structured, largely as a consequence of the Andean uplift and associated Central American orogeny (Gentry, 1982;Quesada et al., 2010).

Here, I use a unique, extensive forest plot dataset to investigate how precipitation influences the distribution of tree taxa, at different taxonomic levels, across the Western Neotropics. Using 531 tree plots that include 2,570 species, I examine the climatic macroecology of the region's tropical trees. Specifically, I 1) test the dry tolerance hypothesis, which posits that tolerance to dry extremes explains taxa geographic ranges within closed-canopy forests (Figure 3.1a); and 2) quantify the affiliations of taxa to precipitation using available data, in order to assess individual taxon-climate sensitivities and predict how tropical trees may respond to potential future climatic changes.

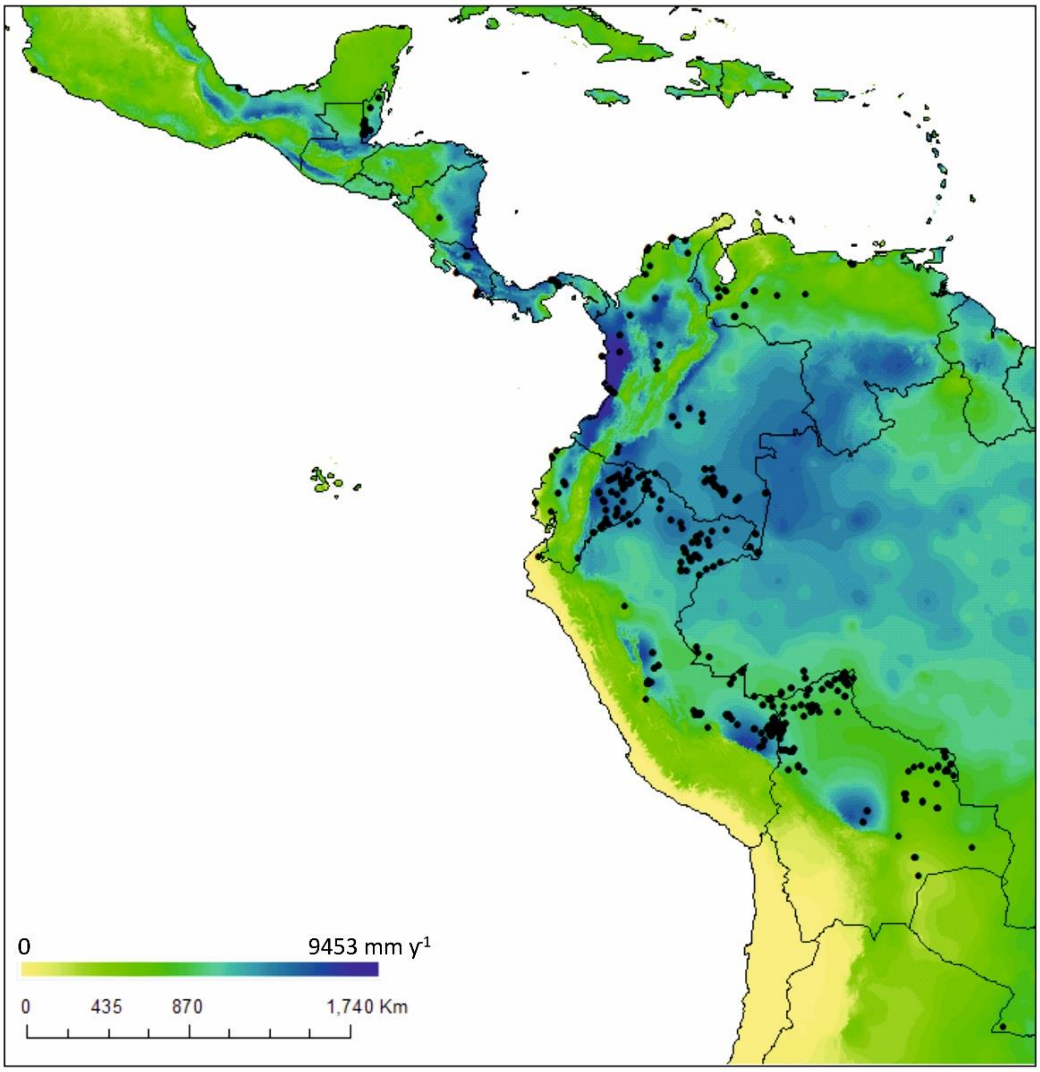


Figure 3.2 - Mean annual precipitation in the Western Neotropics and distribution of the 531 forest inventory plots (black dots) analysed in this study. Precipitation data come from WorldClim (Hijmans et al., 2005). Note the spatial complexity of precipitation patterns within the study area.

3.2 Methods

3.2.1 Precipitation in the Western Neotropics

To investigate the effects of water-stress on the distribution of tropical forest taxa I used the maximum climatological water deficit (CWD) (Chave et al., 2014). This metric represents the sum of water deficit values (i.e. the difference between precipitation and evapotranspiration) over consecutive months when evapotranspiration is greater than precipitation. CWD values were extracted at a 2.5 arc-minute resolution layer, based on interpolations of precipitation measurements from weather stations between 1960 and 1990 and evapotranspiration calculated using the same data (New et al., 2002) (Appendix 3.1). Additionally, I used mean annual precipitation (MAP) from the WorldClim database (Hijmans et al., 2005) to quantify total annual precipitation. MAP values are derived from interpolations of weather station data with monthly records between ca. 1950 and 2000 at a resolution equivalent to ca. 1 km^2. Although these datasets have different grain sizes, the underlying data used in both interpolations have the same spatial scale (Hijmans et al., 2005;Chave et al., 2014).

3.2.2 Vegetation data set

I used data from 531 floristic inventories from three plot networks: ATDN (ter Steege et al., 2003;ter Steege et al., 2013), RAINFOR (Malhi et al., 2002) and Gentry and Phillips plots (Gentry, 1988;Phillips and Miller, 2002;Phillips et al., 2003), distributed throughout the Western Neotropics (Appendix 3.2). Plot areas varied from 0.1 to 5.0 ha. I included all trees with a diameter (D) ≥ 10 cm. The analysis was restricted to lowland *terra firme* forests below 1000 m.a.s.l., excluding all lianas. The RAINFOR and Phillips datasets were downloaded from ForestPlots.net (Lopez-Gonzalez et al., 2009;Lopez-Gonzalez et al., 2011) and the Alwyn H. Gentry Forest Transect Data Set from http://www.mobot.org/mobot/research/gentry/welcome.shtml.

The plots in the dataset provide a largely representative sample of actual precipitation values across all western neotropical lowland forests (Appendix 3.3). However, the dataset only includes 18 plots in very wet environments (above 3500 mm y^{-1}, Figure A3.2), which are largely confined to small pockets on both flanks of the Andes. Because this sampling (3% of all plots) is insufficient to accurately determine species’ occurrences and ranges in the wettest forests, the precipitation and taxa distribution analyses was restricted (see below) to the 513 plots with MAP ≤ 3500 mm y^{-1}.

3.2.3 Analyses

Precipitation and diversity

If water supply broadly limits species' distributions, then community-level diversity should also be controlled by precipitation regime. However, variation in local diversity is nevertheless expected as a consequence of other factors (ter Steege et al., 2003). For example, even under wet precipitation regimes, local edaphic conditions such as extremely porous soils could lead to water stress and lower diversity. Therefore, I fitted a quantile regression (Koenker and Bassett, 1978), describing the role of precipitation in controlling the upper bound of diversity. Diversity was quantified using Fisher's α because this metric is relatively insensitive to variable stem numbers among plots. In addition, to assess whether the correlation between diversity and precipitation is robust to the potential influence of spatial autocorrelation I applied a Partial Mantel test (Fortin and Payette, 2002), computing the relationship between the Euclidian distances of diversity and precipitation, whilst controlling for the effect of geographic distances. Lastly, I also used Kendal's τ non-parametric correlation coefficient to assess the relationship between diversity and precipitation. All diversity analyses were restricted to the 116 1-ha plots that had at least 80% of trees identified to species level.

Metacommunity structure

I used the approach of Leibold and Mikkelson (2002) to test whether the distribution of taxa along the precipitation gradient follows a turnover or nested pattern. The analysis was performed by first sorting the plots within the community matrix by their precipitation regimes. Then I assessed turnover by counting the number of times a taxon replaces another between two climatologically adjacent sites and comparing this value to the average number of replacements found when randomly sorting the matrix 1000 times. More replacements than expected by chance indicate a turnover structure, whilst fewer imply that the metacommunity follows a nested pattern (Presley et al., 2010) as predicted by the dry tolerance hypothesis. This analysis was conducted applying the function *Turnover* from the R package *metacom* (Dallas, 2014).

Precipitation and taxa distribution

To explore the influence of precipitation on taxa distributions firstly, I simply plotted taxa precipitation ranges, i.e. the range of precipitation conditions in which each taxon occurs, to visually inspect the variation of precipitation ranges among taxa. According to the dry tolerance hypothesis, for each taxon the precipitation range size should be positively associated with the driest condition at which it is found, i.e. the more tolerant to dry conditions the taxon is, the larger its climatic span should be. However, the predicted pattern could also arise artefactually if taxa that occur under extreme regimes have on average bigger ranges regardless of whether they are associated to dry or wet conditions. I therefore, secondly, used Kendall's τ coefficient of correlation to explore analytically the relationship between taxon precipitation range and both the driest and wettest CWD values at which each taxon occurs. If the dry tolerance hypothesis holds I expect precipitation range size to be negatively correlated with the driest precipitation condition where each taxon occurs and not correlated with wettest precipitation where each taxon is found.

Thirdly, I compared taxa discovery curves, which represent the cumulative percentage of taxa from the whole metacommunity that occur in each plot when following opposite environmental sampling directions, i.e. from wet to dry and from dry to wet. The dry tolerance hypothesis predicts that wet to dry discovery curves should be steeper initially than dry to wet curves, as wet areas are expected to have more narrow-ranged taxa.

Finally, I examined the loss of taxa from extremely wet and from extremely dry plots over the precipitation gradient. I tested whether tree taxa found at the driest conditions within the sample can tolerate a larger range of precipitation conditions than taxa in the wettest plots. I thus generated taxa loss curves to describe the decay of taxa along the precipitation gradient within the 10% driest plots and the 10% wettest plots.

I compared discovery and loss curves in different directions of the precipitation gradient (i.e. from wet to dry and from dry to wet) against each other and against null models of no influence of precipitation on taxa discovery or loss.

These null models represented the mean and confidence intervals from 1000 taxa discovery and loss curves produced by randomly shuffling the precipitation values attributed to each plot. Taxa recorded in 10 plots or fewer are likely to be under-sampled within the metacommunity and were excluded from the analyses regarding metacommunity structure and taxa distribution.

Taxa precipitation affiliation

To describe the preferred precipitation conditions for each taxon I generated an index of precipitation affiliation, or precipitation centre of gravity (PCG). A similar approach was adopted to that used to estimate the elevation centre of gravity by Chen et al. (2009) (see also Feeley et al., 2011a), which consisted of calculating the mean of precipitation of locations where each taxon occurs in, weighted by the taxon's relative abundance in each community (Equation 1).

$$\text{PCG} = \frac{\sum_1^n P \times Ra}{\sum_1^n Ra} \qquad (1)$$

Where: n = number of plots

P = precipitation

Ra = relative abundance based on number of individuals

The resulting taxon-level PCG values are in units of millimetres per year, the same scale as the precipitation variables: CWD or MAP. The null hypothesis of no influence of precipitation on the distribution of each taxon was adopted by calculating the probability of an observed PCG value being higher than a PCG generated by randomly shuffling the precipitation records among the communities, following Manly (1997) (Appendix 3.4). I also generated an alternative estimator of precipitation affiliation for each taxon by correlating its plot-specific relative abundance and precipitation values using Kendall's τ coefficient of correlation (following Butt et al., 2008). Here, a negative correlation indicates affiliation to dry conditions, whilst a positive correlation indicates affiliation to wet conditions (Appendix 3.6).

PCG values were calculated for each taxon recorded in at least three localities (1818 species, 544 genera and 104 families), and Kendall's τ values were calculated for each taxon recorded in at least 20 localities (525 species, 327 genera and 78 families). I also calculated the proportions of significantly dry- and wet-affiliated taxa. To verify that these proportions were not merely a consequence of the number of taxa assessed, the observed proportions were compared to 999 proportions calculated from random metacommunity structures where taxa abundances were shuffled among plots (Appendix 3.5).

Each analysis was repeated at family, genus and species levels. All analyses were performed for CWD, and precipitation affiliations were also calculated for MAP. Analyses were carried out in R version 3.1.1 (R Core Team, 2014).

3.3 Results

In the Western Neotropics, diversity was negatively related to water-stress at all taxonomic levels, being strongly limited by more extreme negative values of maximum climatological water deficit (CWD) (Figure 3.3). This result remained after accounting for possible spatial autocorrelation (Partial Mantel test significant at $\alpha = 0.05$ for all taxonomic levels: $r = 0.31$ for species; $r = 0.38$ for genera; $r = 0.37$ for families). The large increase in diversity towards the wettest areas was most evident at the species level (around 200-fold), but was also strong at genus (ca. 70-fold) and family levels (ca. 16-fold) (Figure 3.3).

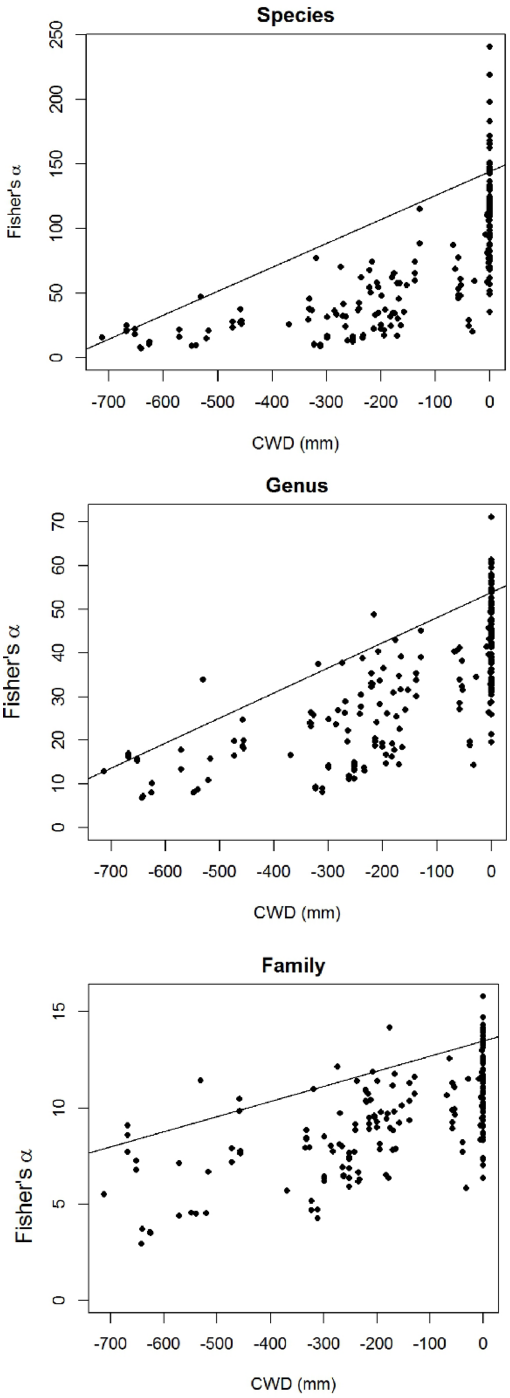


Figure 3.3 - Tree alpha diversity (evaluated with Fisher's alpha parameter) as a function of precipitation, represented by maximum climatological water-deficit (CWD) for 1 ha plots across the Western Neotropics. Solid curves represent the 90% upper quantile regression. Note that more negative values of CWD limit alpha diversity and that the diversity vs. CWD correlation is stronger for finer taxonomic levels – Kendall's $\tau = 0.66$ for species, 0.60 for genus and 0.51 for family level, P values < 0.001.

For all analyses of taxa distributions it was evident that they follow a nested pattern along the water-deficit gradient, as predicted by the dry tolerance hypothesis. Thus, firstly, when investigating metacommunity structure, among any given pair of sites, the number of times a taxon replaced another was significantly lower than expected by chance at all taxonomic levels (Table 3.1). Secondly, compared to all taxa, those able to tolerate the dry extremes were clearly distributed over a wider range of precipitation regimes (Figure 3.4 a-c). This was confirmed by precipitation ranges being very strongly and negatively correlated to the driest condition where each taxon occurs (Kendall's τ = -0.93 for species, -0.96 for genera and -0.99 for families, one-tailed P values < 0.001) and not correlated to the wettest condition of occurrence (Kendall's τ = 0.01 for species, 0.05 for genera and -0.01 for families, P-values > 0.05).

Table 3.1 - Observed and expected turnover of taxa along the precipitation gradient. Turnover was measured by the number of times a taxon replaces another between two sites. Expected values represent the average turnover when randomly sorting the matrix 1000 times. P-values test the null hypothesis that replacement of taxa along the precipitation gradient does not differ from random expectations considering $\alpha = 0.05$. Note that observed taxa turnover is significantly lower than the expected, which indicates that the distributions of taxa follows a nested pattern along the precipitation gradient (Leibold & Mikkelson 2002, Presley et al. 2010).

	Observed turnover	Expected turnover	P
Families	0	755,226	0.01
Genera	2,061	3,529,527	< 0.01
Species	0	25,592,113	< 0.01

Thirdly, nested patterns were evident in most taxa discovery curves, with the floristic composition of dry plots being a subset of wet plots (Figure 3.4 d-f). At species and genus levels, the wet-dry cumulative discovery curves were steeper than the dry-wet curves, indicating more taxa restricted to wet conditions. However, this distinction in the shape of the discovery curves between the directions of the precipitation gradient (wet-dry vs. dry-wet) was much less evident at the family level (Figure 3.4 f). Finally, the loss curve analysis also showed that plots at the wet extremes of the precipitation gradient have many more taxa restricted to wet conditions than expected by chance (Figure 3.4 g-i). Extreme dry plots also had a much greater proportion of species with wide precipitation ranges than the wettest plots, with at least 80% of their species persisting until all but the very wettest forests are reached (Figure 3.4 g – red curve). Again, these patterns were most clearly evident for species and genera.

For the 1818 species, 544 genera and 104 families assessed across the Western Neotropics, I found a large proportion of taxa with significant values for rainfall affiliation (Table 3.2 a, Appendix 3.9, tables A3.9.1, A3.9.2 and A3.9.3). Affiliations to wet conditions were substantially more common than affiliations to dry conditions at all taxonomic levels (Table 3.2 b) (see Appendix 3.5). Anacardiaceae and Rutaceae are examples of the 10 most dry-affiliated families registered in 10 or more localities and Lecythidaceae, Myrsinaceae and Solanaceae are amongst the most wet affiliated families (see Appendix 3.7, Tables A3.7.1 and A3.7.2 for the most wet and dry affiliated taxa). Lastly, the observed patterns persisted when repeating the analyses excluding those species possibly affiliated to locally enhanced water supply (Appendix 3.8).

Table 3.2a. - Number of taxa significantly affiliated to wet or dry precipitation regimes, based on their precipitation centre of gravity (PCG) and Kendall's τ coefficient of correlation between relative abundance and precipitation. Taxa with significant PCG are more dry or wet-affiliated than expected by chance, at α < 0.05. Significant values of Kendall's τ indicate that the probability of observing a correlation between relative abundance and precipitation by chance is lower than 5%. Affiliations calculated for two precipitation variables: maximum climatological water deficit (CWD) and mean annual precipitation (MAP). Values in brackets show the proportions of significant values of precipitation affiliations in relation to the total number of taxa in the analyses. I tested the influence of the sample size on the proportion of significant values by comparing the observed proportion against 1000 random proportions generated by shuffling precipitation values across communities. The null hypothesis that proportions are an artefact of the number of taxa analysed was rejected considering α = 0.001 in all cases (see Appendix 3.5 for details).

	Total	Significant PCG		Total	Significant Kendall's τ	
		CWD	MAP		CWD	MAP
Species	1818	1065 (58%)	615 (34%)	525	426 (81%)	398 (76%)
Genera	544	291 (53%)	236 (43%)	327	259 (79%)	242 (74%)
Families	104	60 (58%)	46 (44%)	78	60 (77%)	59 (76%)

Table 3.2b - As in Table 3.2a, but giving a breakdown by affiliations to wet and dry conditions. As for Table 3.2a the influence of the sample size on the proportion of significant values was assessed by comparing the observed proportion against 1000 random proportions generated by shuffling precipitation values across communities (see Appendix 3.5 for details). P-values test the null hypothesis that proportions are an artefact of the number of taxa.

		Maximum climatological water deficit (mm) (CWD)		Mean annual precipitation (mm) (MAP)	
		dry	wet	dry	wet
Significant PCG	Species	112 (6%)*	953 (52%)*	153 (8%)*	462 (25%)*
	Genera	67 (12%)*	224 (41%)*	94 (17%)*	142 (26%)*
	Families	13 (12%)*	47 (45%)*	18 (17%)*	28 (27%)*
Significant Kendall's τ	Species	59 (11%)*	367 (70%)*	52 (10%)*	346 (66%)*
	Genera	49 (15%)*	210 (64%)*	48 (15%)*	194 (59%)*
	Families	6 (8%)	54 (69%)*	8 (10%)*	51 (65%)*

* P< 0.05

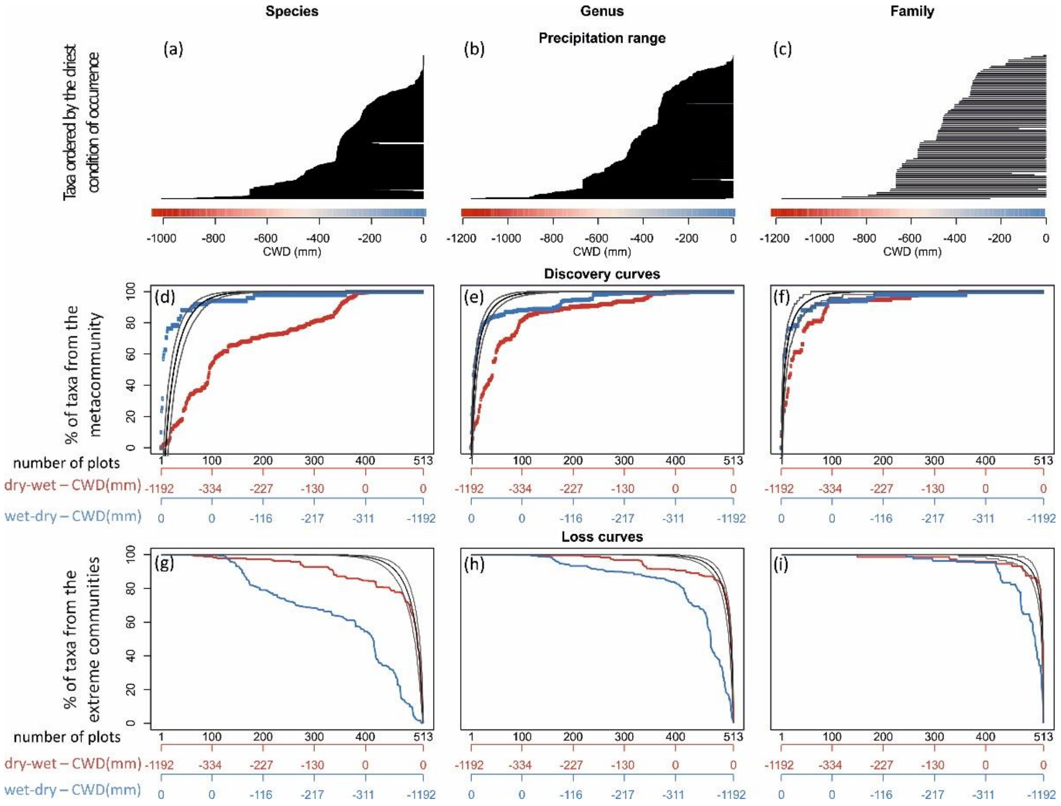


Figure 3.4 - The influence of precipitation on the distribution of taxa in Western neotropics. a-c Range of water-deficit conditions (black horizontal lines) over which each **(a)** species, **(b)** genus, and **(c)** family occurs. The x-axes express the water-deficit gradient in mm of maximum climatological water-deficit (CWD) from dry (red) to wet (blue), while taxa are stacked and ordered along y-axes by the most negative value of CWD of occurrence. **d-f** Discovery curves showing the cumulative percentage (y-axes) of **(d)** species, **(e)** genera, and **(f)** families from the whole region found in each plot when moving along the CWD gradient (x-axes). **g-i** Loss curves giving the percentage of **(g)** species, **(h)** genera, and **(i)** families from the 10% of plots under the most extreme precipitation regimes that drop out when moving to the opposite extreme of the gradient. In d-i x-axes show the number of plots, ordered from wet to dry (blue axis labels and blue curves) and from dry to wet (red axis labels and red curves). Black and grey curves represent respectively, the mean and 95% confidence limits of loss and discovery curves generated by shuffling values of precipitation within the plots 1000 times. Taxa restricted to 10 or fewer localities were excluded from analyses. Note that of the taxa from the 10% driest communities, 86% of species, 91% of genera and 96% of families are also recorded in plots with zero CWD.

3.4 Discussion

The results demonstrate the influence of precipitation gradients on the patterns of diversity and composition for families, genera and species of Neotropical trees. I confirm that community diversity is much higher in wet than in drier forests, being as much as 200-fold greater at the species level (Figure 3.3). Additionally, the analyses indicate that the diversity decline towards more seasonal forests is a consequence of increasingly drier conditions limiting species distributions. To my knowledge this is the first time that the influence of precipitation affiliation has been quantified at the level of individual Amazon tree species.

Water-stress during the dry season, represented here by the climatological water-deficit (CWD), limits tree species distributions across the Western Neotropics (Figure 3.4). In areas with a very negative CWD, forest composition is a subset of those communities that do not suffer water-stress (Figure 3.4). These findings are consistent with results from studies at much smaller scales (Engelbrecht et al., 2007;Baltzer et al., 2008). The physiological challenges in dry areas require species to have specific characteristics in order to recruit and persist. For example, certain species have the capacity to maintain turgor pressure and living tissues under more negative water potentials at the seedling stage, which allow them to obtain water from dry soils (Baltzer et al., 2008;Brenes-Arguedas et al., 2013). At the wet extreme of the gradient, more favourable conditions may allow a wider range of functional strategies to coexist (Spasojevic et al., 2014). Consistent with this, most taxa in the data set occur in the wet areas, with only a small proportion restricted to dry conditions (Figure 3.4). Furthermore, the results indicate that other factors such as pests and pathogens (Spear et al., 2015) or tolerance to shaded environments (Brenes-Arguedas et al., 2013), are much less important in determining the distribution of taxa. In some cases these may restrict the abundance of dry affiliated taxa but generally appear not to limit their occurrence. Geomorphology and dispersal limitation can impact species' distributions, and these drivers likely account for some of the unexplained variation in the relationship between diversity and precipitation shown here (Higgins et al., 2011;Dexter et al., 2012). The scarcity of plots from the very wettest forests (Appendix 3.3, Figure A3.3.2) may also have limited my ability to fully document patterns of species turnover. Nevertheless, this analysis shows that more than 90% of the species occurring in the driest 10% of the neotropical forest samples are also registered in at least one forest with zero mean annual CWD (Figure 3.4 g). It could be argued that such widespread taxa may not necessarily tolerate dry conditions, but instead be sustained by locally enhanced water supply due to particular conditions such as the presence of streams. However, the results were robust even after excluding taxa potentially affiliated to such local water availability (Appendix 3.8). Thus, this findings, together with those from Asian and Central American tropical forests (Baltzer et al., 2008;Brenes-Arguedas et al., 2009), suggest that the limitation of most tree species' distributions by water-stress may represent a general macroecological rule across the tropics. This has obvious parallels to the well-known pattern for temperate forest tree species, for which frost tolerance substantially governs species' geographical ranges (e.g. Pither, 2003;Morin and Lechowicz, 2013).

Affiliations to specific precipitation regimes are strongest at the species level, but climate sensitivity can still be clearly detected with genus-level analyses (Figure 3.4 d-i). The stronger relationship between species and precipitation when compared to other taxonomic levels could be a consequence of a relatively stronger influence of climate on recent diversification. In particular, massive changes in precipitation regimes took place in the Neogene and Quaternary due to Andean uplift and glacial cycles (Hoorn et al., 2010). During this period, global fluctuations in climate and atmospheric CO_2 concentrations, which affect water-use efficiency (Brienen et al., 2011), are thought to have influenced speciation (cf. Richardson et al., 2001 although see Hoorn et al. 2010;Erkens et al., 2007). Climate sensitivity was also clearly evident at the genus level (Figure 3.4), which has relevant practical implications for tropical community and ecosystem ecology. Because of the challenges of achieving sufficient sample size and accurate identification in hyperdiverse tropical forests (Martinez and Phillips, 2000), ecosystem process and community ecological studies in this ecosystem often rely on the simplifying assumption that the genus-level represents a sufficiently functionally-coherent unit to address the question at hand (e.g. Harley et al., 2004;Laurance et al., 2004;Butt et al., 2014). The results suggest that analysis at the genus-level could be used to assess, for instance, the impacts of climate change on diversity, but that nevertheless such impacts would be underestimated without a species-level analysis.

In addition to the physiological tolerance to dry conditions, other, underlying geographical and evolutionary processes could conceivably drive the patterns I observe in this study. These are, notably, (1) a greater extent of wet areas (Terborgh, 1973;Fine, 2001), (2) greater stability of wet areas through time leading to lower extinction rates (Klopfer, 1959;Jansson, 2003;Jablonski et al., 2006), and (3) faster rates of speciation in wet forests (Rohde, 1992;Allen et al., 2002;Jablonski et al., 2006). The first alternative (Rosenzweig, 1992) requires that species-area relationships govern the climate-diversity associations that I find. Within the region, the areas that do not suffer water-stress (i.e. CWD = 0) are where the great majority of the species (90%) can be found (Figure 3.4), yet they occupy a relatively small area (25% of the Western Neotropics and 31% of plots). Thus, the area hypothesis appears unlikely to be driving the precipitation-diversity relationship.

The other two alternative hypotheses could more plausibly be contributing to the patterns observed here. Climate stability is indeed associated with diversity throughout the Neotropics (Morueta-Holme et al., 2013). In contrast with most of the Amazon basin, the lowland forests close to the Andes and in Central America apparently had relatively stable climates, with only moderate changes during the Quaternary/Neogene (Hoorn et al., 2010), which could have reduced extinction rates (Klopfer, 1959;Jablonski et al., 2006). The diversity gradient may also be a consequence of more diverse areas having higher diversification rates (Rohde, 1992;Jansson, 2003;Jablonski et al., 2006). While both lower extinction rates and higher speciation rates in wet forest might contribute to explaining the climate-diversity gradient, their influence does not invalidate the idea that wet-affiliated species are drought-intolerant. Indeed, the mechanisms that might have favoured lower extinction rates in wetter forests are related to the inability of many taxa to survive environmental fluctuations such as droughts. Experiments showing that seedlings of species from wet tropical environments have higher mortality under water-stress than dry-distributed taxa (Engelbrecht et al., 2007;Baltzer et al., 2008;Poorter and Markesteijn, 2008) indicate that water stress can have direct impacts on species survival and distribution. As ever, untangling ecological and historical explanations of patterns of diversity is difficult with data solely on species distributions (Ricklefs, 2004).

Implications for climate change responses

Understanding how floristic composition is distributed along precipitation gradients is critical to better predict outcomes for the rich biodiversity of the region in the face of climatic changes. The observed small precipitation ranges of wet-affiliated taxa (Figure 3.4 a-c) together with the rareness of extremely wet areas (Fig. A3.2) indicate high potential vulnerability to changes in climate. So far, while total precipitation has recently increased in Amazonia (Gloor et al. 2013), much of Amazonia and Central America have also seen an increase in drought frequency, and more generally in the frequency of extreme dry and wet events (Malhi and Wright, 2004;Aguilar et al., 2005;Li et al., 2008;Marengo et al., 2011). These neotropical trends toward similar or greater annual precipitation, but a greater frequency and intensity of dry events, are expected to continue, albeit with important regional differences (IPCC 2013). While elevated atmospheric CO_2 concentrations may alleviate physiological impacts of water-stress on plants by increasing water-use efficiency (Brienen et al., 2011;van der Sleen et al., 2015), warming will have the opposite impact. Temperatures have increased markedly in Amazonia since 1970 (Jiménez-Muñoz et al., 2013) and this trend is highly likely to continue (IPCC, 2013b) so that plants will experience increased water-stress throughout Amazonia (Malhi et al., 2009) with thermally-enhanced dry season water-stress challenging trees even in wetter environments. The restriction of most tree taxa in the Western Neotropics to wetter areas indicates widespread low tolerance to dry conditions and low capacity to acclimate to them. Together with the anticipated climate changes this suggests that floristic composition may change substantially, potentially with the loss of many wet forest specialists and compensatory gains by the fewer, more climatologically-generalist dry tolerant species. While research is clearly needed to track and analyse ecological monitoring sites to examine where and how tropical forest composition responds to anthropogenic climate changes, protecting the remaining ever-wet forests and coherent up-slope migration routes will be essential if most neotropical diversity is to survive into the next century.

4

Biogeographic distributions predict drought tolerances of neotropical tree genera

Abstract

The strength and frequency of droughts over large areas of tropical forests are predicted to increase. Yet little is known about the vulnerability of the vast number of taxa in these ecosystems to moisture stress. I test whether current distributions of tree genera reflect their fundamental physiological tolerances and whether this relationship varies among life history stages. I integrate experimental and observational data on drought-induced mortality across the Neotropics with large-scale bioclimatic distributions of tree genera. These data allowed me to investigate whether the distribution of genera along a water deficit gradient – ‘water deficit affiliation’ (WDA) – can predict their drought-induced mortality in experimental and natural droughts. Kendall’s τ correlation coefficient and standardized major axis regressions were used to explore the relationship between WDA and drought-induced mortality. Bayesian phylogenetic mixed models were developed to investigate whether the strength of this relationship varies among different life history stages and the extent to which it is consistent across studies after controlling for phylogenetic autocorrelation. Genera affiliated to wetter precipitation regimes tend to show higher drought-induced mortality. Tree mortality was higher under natural or artificial drought than non-drought conditions, and the difference between these two treatments became more evident with increasing drought length. This pattern is stronger for adult trees than for saplings.

4.1 Introduction

The future composition and structure of intact tropical forests may be substantially altered by periods of high water stress. In particular, many neotropical forests have recently experienced increased water stress, driven by a decrease in precipitation in some regions, widespread extreme drought events and a general rise in temperature (Malhi and Wright, 2004;Fu et al., 2013;IPCC, 2013a). Total precipitation has declined recently in Central America and in the southern borders of the Amazon (e.g. Feeley et al., 2011a;Hilker et al., 2014). At the same time, the frequency of extreme dry events seem to be increasing, with the 2005 and 2010 droughts affecting much of the Amazon (Lewis et al., 2011;Marengo et al., 2011;Gatti et al., 2014). The dry season has also recently become longer along the southern borders of the Amazon (Fu et al., 2013), and this trend is likely to continue as an outcome of both deforestation (Spracklen et al., 2012) and global climatic changes (Guimberteau et al., 2013;Boisier et al., 2015;Duffy et al., 2015). Such a drying trend may threaten some neotropical tree taxa, potentially including many of the estimated 16,000 tree species in the humid forests of Amazonia alone (ter Steege et al., 2013).

Not all evidence clearly points to a drying Amazon forest. Records of flow discharge from the Amazon River show that total precipitation has likely increased in some locations, particularly in the northwest of the basin and in the wet season (Gloor et al., 2013;Gloor et al., 2015). Additionally, a decrease in water availability does not necessarily translate into stress for plants, if it is insufficient to surpass ecological thresholds (Meir et al., 2015b), or if it is alleviated by increasing water-use efficiency as a consequence of elevated atmospheric CO_2 concentration (Lewis et al., 2004a;Brienen et al., 2011;Huntingford et al., 2013;Roderick et al., 2015;Conway and Tans). Nonetheless, moisture stress experienced by plants also depends in part on temperature, which has been rising since 1970 in the Amazon (Malhi and Wright, 2004;Jiménez-Muñoz et al., 2013;Gloor et al., 2015) and is predicted to keep increasing (IPCC, 2013a). Overall, it appears likely that water stress will progressively affect neotropical forests, even if regional wet-season precipitation increases or some water-use efficiency gains continue. Indeed, stronger water stress may be partly responsible for the observed long-term increase in mortality rates in Amazon trees (Brienen et al., 2015), and is clearly linked to mortality spikes during and after droughts (Condit et al., 1995;Meir and Grace, 2005;Phillips et al., 2009;Doughty et al., 2015).

Given the threat from drier conditions, better understanding of the drought-vulnerability of different tree taxa would improve the predictability of future climate change impacts on tropical forest communities. Macroecological diversity patterns in Amazonian trees and lianas strongly suggest that water supply, particularly the strength of the dry season, is a major constraint on plant survivorship: woody plant diversity is greatest where seasonal moisture deficits are lowest (Clinebell et al., 1995;ter Steege et al., 2003). This implies that many tropical woody taxa are ultimately limited by physiological constraints related to water supply, and thus the occurrence of individual taxa along a water stress gradient may provide proxy information on their vulnerability to droughts. This hypothesis is supported by evidence from experiments testing whether species distributions can predict seedling water deficit tolerances (Engelbrecht et al., 2007;Baltzer et al., 2008;Poorter and Markesteijn, 2008). Nevertheless, such studies were only developed for seedlings under very controlled conditions, where for instance above- and below-ground competition are suppressed; they do not necessarily represent the likely overall drought vulnerability of tropical trees. Additionally, the key taxonomically-controlled functional differences that translate into variations in drought-vulnerability may not be expressed at all by seedlings. As an obvious example, drought resistance is often related to tree size, with taller trees being more vulnerable to drought-induced mortality (Condit et al., 1995;da Costa et al., 2010;Phillips et al., 2010;Bennett et al., 2015). The taller the tree the longer the xylem pathway, thus increasing the chance of hydraulic failure (McDowell et al., 2008;Anderegg et al., 2012;Doughty et al., 2015;Rowland et al., 2015), which is caused by air emboli constraining water conductance along the xylem, leading to tissue desiccation and potentially death (Urli et al., 2013).

As an alternative to the experimental approach, regional and local-scale community compositional studies have also tended to indicate that tropical droughts favour species affiliated to drier environments (Veenendaal and Swaine, 1998;Enquist and Enquist, 2011;Feeley et al., 2011a). These studies assess the relationship between drought vulnerability and species distributions along local or regional water stress gradients. For example, Feeley et al. (2011a) found that species that could tolerate dry conditions along a short precipitation gradient across the Isthmus of Panama tended to have undergone a relative increase in abundance in an inventory plot in Barro Colorado Island, as a response to a long-term increase in aridity. Similar results were observed in Ghana by a study covering 200 km^2 which represents the largest area assessed for this question in the tropics (Veenendaal and Swaine, 1998). A macroecological analysis of taxa distributions and actual adult tree mortality risk has yet to be attempted for the neotropical realm. Such an approach could provide insights into the potential responses of tropical forest taxa to increasing water stress.

The distributions of taxa are commonly used as a tool to predict species response to climate change (e.g. Peterson et al., 2002;Thuiller et al., 2005), without testing whether they reflect physiological tolerances. However, inference of physiological tolerances only from current distributions is uncertain and in particular risks underestimating the breath of a taxon’s fundamental niche. Taxa could have higher tolerances than those observed if these do not capture more extreme climates potentially experienced by lineages in the past (Dick et al., 2013). A mismatch between physiological tolerances and distributions would also occur if vulnerabilities differ among different populations (e.g. Bansal et al., 2015). Furthermore, distributions could be limited by other variables that may co-vary with climate, such as soil characteristics which influence ecosystem structure and dynamics in Amazonia (Quesada et al., 2012). In sum, while ‘climate-envelope’ approaches have been widely used to attempt predictions of future shifts in floristic composition (particularly in the tropics Miles et al., 2004;Blach-Overgaard et al., 2015), it is clearly important to test empirically as far as possible whether large-scale floristic distributions do indeed provide proxy information on measured tolerances to extreme conditions.

In this study I investigate the relationship between the large-scale bioclimatic distribution of taxa and their tolerance to droughts at different life-history stages. I use information on water deficit affiliation (WDA) (Precipitation centre of gravity calculated for cumulative water deficit, PCG CWD from chapter 3), which quantifies the affiliations of taxa to different precipitation conditions. This variable represents the ‘centre of gravity’ of species abundance across a gradient of water deficit by assessing relative abundance in 531 floristic plots of ≈1 ha each distributed across the Western Neotropics (Figure 4.1). To quantify drought-tolerances I assess a series of five experiments and field observations, spanning different life-history stages and distinct regions within the Neotropics (Table 1). These are:

Natural drought – (1) Field records from the most detailed observation of forest responses to a natural drought in the tropics: the measurements from a 50 ha plot at Barro Colorado Island, Panama (hereafter BCI) from the 1982-83 El Niño drought event. This is an extensive census dataset in terms of sample size per taxon, but is unreplicated spatially and lacks a pre-drought baseline (Condit et al., 1995);

Through-fall exclusion experiments (TFE) – The only two TFEs in the Neotropics (Figure 4.1) are the drought experiments in eastern Amazonia at (2) Tapajós (Nepstad et al., 2007) and (3) Caxiuanã (da Costa et al., 2010). TFEs control for other possible factors affecting mortality by the use of non-droughted control plots, but have limited sample size per taxon, have no within-site replication and lack atmospheric drought conditions;

Seedling experiments – Experiments have tested the resistance of seedlings to drought in (4) Panama (Engelbrecht et al., 2007) and (5) Bolivia (Poorter and Markesteijn, 2008). These can provide detailed information on individual mortality, but are restricted in the number of species sampled at each site.

By their nature, experiments in the diverse neotropical forest environment typically are able to only sample very few individuals of any one taxon. For this reason my ability to infer drought-sensitivity of any one taxon from any one experiment is necessarily limited. Further, each experiment has a unique set of environmental and biological conditions, and thus are not perfect replicates of one another. Therefore my approach was to examine as far as possible across all taxa, using the simple bioclimatic distributional index (WDA), and investigate the community-wide responses as a function of WDA in each observation.

I hypothesize that biogeographically wet-affiliated Amazon taxa will be more sensitive to droughts. Thus I expect a positive relationship between taxon WDA and its drought-induced mortality. Additionally, I predict that the length of the drought period will affect tree mortality (McDowell et al., 2008). In the three case studies involving adult trees, BCI, Tapajós and Caxiuanã, the forest suffered similar levels of water deficit (Table 4.1) and similar reduction in soil water potential for Tapajós and Caxiuanã (Meir et al., 2015b), but over very different periods, being 4 months (0.3 years), 4.2 years and 7 years respectively. Thus I anticipated that total mortality in the dry period and the relationship between WDA and drought-induced mortality would increase from BCI to Tapajós to Caxiuanã.

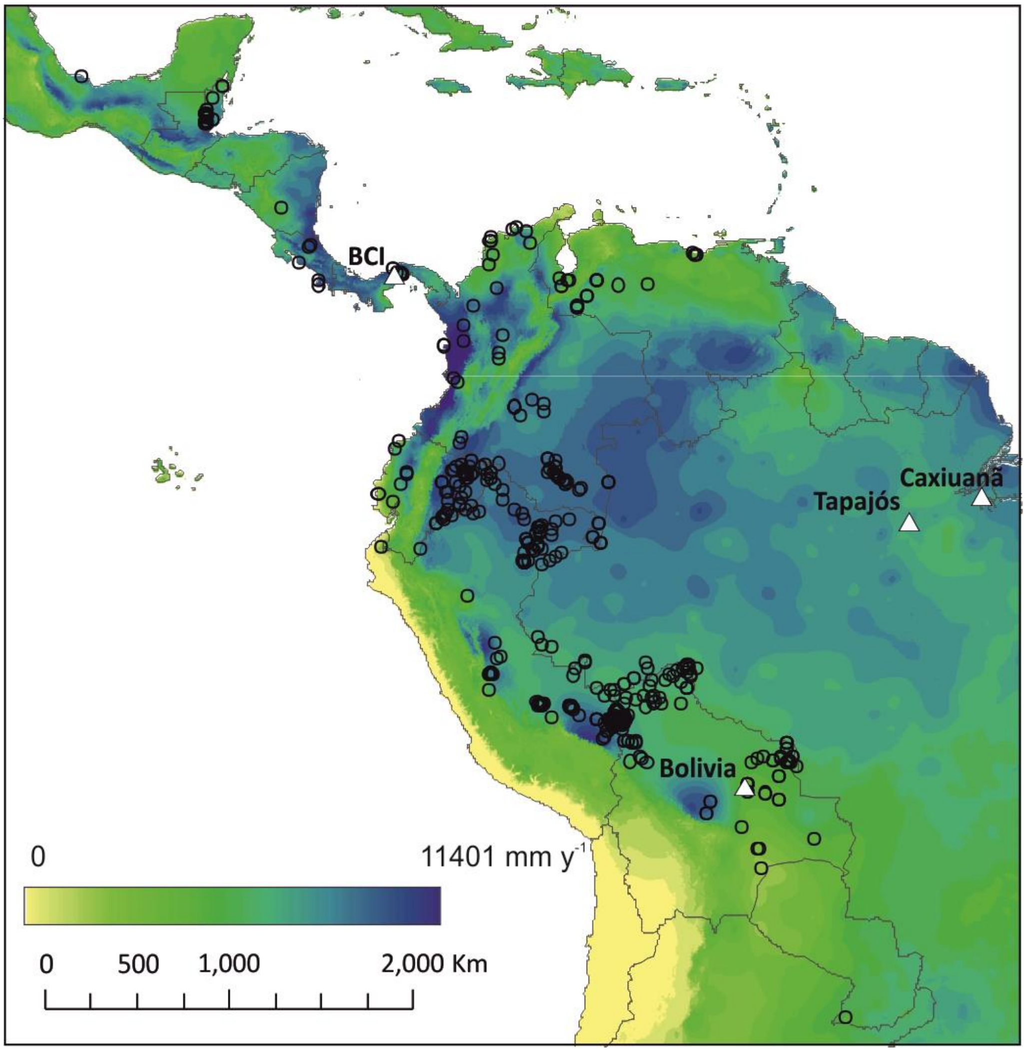


Figure 4.1 - Location of the droughted areas analysed in this study. Triangles represent case studies investigated: two through-fall exclusion experiments in the Brazilian Amazon, Tapajós (Nepstad et al., 2007) and Caxiuanã (da Costa et al.,

2010), field observations from the 1982-83 El Niño drought (Condit et al., 1995) and seedling drought experiments in Panama (BCI) (Engelbrecht et al., 2007) and seedling drought experiments in Bolivia (Poorter and Markesteijn, 2008). Circles show ForestPlots.net (Lopez-Gonzalez et al., 2009;Lopez-Gonzalez et al., 2011) and ATDN (ter Steege et al., 2003) inventory plots used to calculate water deficit affiliation (WDA) (Precipitation centre of gravity calculated for cumulative water deficit, PCG CWD from chapter 3). Patterns within the map represent annual mean precipitation in mm y-1 from WorldClim (Hijmans et al., 2005). Note that case studies are located under different precipitation regimes and that Tapajós and Caxiuanã are more than 2000 km away from the area where WDA was calculated, allowing to explore whether different populations will respond in the same way to droughts.

Table 4.1 - Description of through-fall exclusion experiments and field observations analysed in this study. Ngen represents the number of genera examined in each drought case study; n0 is the number of individuals before the drought in the droughted area. Ddry shows the number of deaths during and after the drought. Life history stage represented by trees (>100 mm diameter), saplings (10 – 99 mm D in BCI and 20 – 99 mm in Tapajós), and seedlings.

Case study	Life stage	Mean annual rainfall ($mm\ y^{-1}$)	% rainfall exclusion	Duration (y)	Area (ha)	N_{gen}	n_0	D_{dry}
Natural drought								
(1) 1982 BCI El Niño drought	trees	2493	59	0.3	50	99	20282	1772 (9%)
(Condit et al., 1995)	saplings					141	213106	17671 (8%)
Through-fall exclusion experiments								
(2) Tapajós (Nepstad et al., 2007)	trees	2024	50	4.2	1	82	311	59 (19%)
	saplings					123	2116	179(8%)
(3) Caxiuanã (da Costa et al., 2010)	trees	2187	50	7	1	74	314	50 (16%)
Seedling experiments								
(4) Panama (Engelbrecht et al., 2007)	seedlings	2493	100	0.4	NA	45	1411	482 (42%)
(5) Bolivia (Poorter and Markesteijn, 2008)	seedlings	1023	100	0.5	NA	31	1440	1440

4.2 Methods

4.2.1 Water deficit affiliation

To characterize genera preferable climatic conditions I use 'water deficit affiliation' (WDA) values that represent the precipitation conditions where the relative abundance of each genera is greatest. This metric is analogous in terms of climate space to the elevation centre of gravity of Chen et al. (2009) and Feeley et al. (2011b). WDA was calculated for individual taxa in Chapter 3 (PCG CWD). Here I use WDA calculated using the cumulative water deficit (CWD) of each site as the input variable. CWD is an estimate of seasonal moisture deficit calculated as the cumulative differences between precipitation and potential evapotranspiration over the dry season (for details on how CWD is calculated see Chave et al., 2014). The more negative the value of CWD the larger the water deficit, thus strongly negative values of WDA indicate affiliations to dry conditions.

For some particular taxa, WDA is not *a priori* expected to accurately reflect a taxon's true moisture affiliation, and these special cases could potentially confound the analysis. Firstly, a very few taxa, notably *Swietenia macrophylla* (mahogany) and *Cedrela odorata* have been nearly exterminated in much of their range, so that current distribution and abundance are unlikely to represent realized precipitation niches. Secondly, and more significantly, for those taxa which are affiliated to locally enhanced water supply ('LEWS') - either through river flooding or with local water supply strongly determined by topography (permanent or seasonal swamps) - the large-scale biogeography of such taxa may be largely decoupled from climate. To identify which Neotropical species are strongly LEWS-affiliated I computed an index based on the Neotropics-wide plot sampling available in ForestPlots.net (Lopez-Gonzalez et al., 2011), which include 881 floristically-identified plots under forests with different intensities of locally enhanced water supply. The abundance per hectare of all genera in each plot was calculated. Plots were classified as being either LEWS (i.e. swamp, floodplain, seasonal floodplain and plots rarely flooded) or non-LEWS (i.e. *terra firme*) plots. For each taxon I calculated the ratio between its abundance in LEWS and non-LEWS plots standardized by the number of plots and plot area. LEWS-affiliated genera, defined as those with such ratios of >1:1, comprised 11% of the 544 genera analysed in chapter 3. The subsequent analyses were performed excluding LEWS-affiliated taxa, and *S. macrophylla* and *C. odorata*.

4.2.2 Experiments and field observation

Information on drought sensitivity was accessed from five studies (Table 4.1): two through-fall exclusion experiments (TFE) conducted in the Brazilian Amazon, at (1) Tapajós (Nepstad et al., 2007) and (2) Caxiuanã (da Costa et al., 2010), (3) one observational study conducted over the 1982 drought in a 50 ha tree inventory plot in Barro Colorado Island in Panama (Condit et al., 1995), hereafter BCI, and the results from two irrigation experiments testing drought sensitivity on transplanted seedlings, in (4) Panama (Engelbrecht et al., 2007) and (5) Bolivia (Poorter and Markesteijn, 2008).

The two through-fall exclusion experiments in the Brazilian Amazon (Tapajós and Caxiuanã) followed similar design but with different through-fall exclusion periods (Table 4.1). The intensity of rainfall exclusion is similar amongst these two experiments (*ca.* 50%) and the BCI field observation (*ca.* 59%). In BCI and Tapajós saplings were also measured (10-99 mm D in BCI and 20-99 mm D in Tapajós). Here I performed the analyses for trees (> 100 mm D) and saplings separately.

Different experiments report drought sensitivity in different ways, e.g. the Bolivia seedling experiments used days of survival whilst the TFEs used mortality. To facilitate the comparison and interpretation of the results I therefore standardized the metric of drought sensitivity across all studies investigated here. For Tapajós, Caxiuanã, BCI, and the Panama seedling experiment, the available data include information on the number of individuals per species exposed to drought and non-drought treatments. This allowed me to apply the same mortality equation to those studies and thus to calculate mortality indices for each taxon in each case study. Here I applied the mortality equation used by Nepstad et al. (2007) and da Costa et al. (2010) (Eq 4.1):

$$m = 1 - \left({}^{n_t}/_{n_0}\right)^{1/t} \qquad \text{Eq. 4.1}$$

Eq.1 estimates the mortality rate of a population given the lapsed time in years, t, the number of stems at the end of the census interval, n_t, and the number of stems in the first measurement, n_0 (Sheil and May, 1996).

In the original study that published the BCI data (Condit et al., 1995), the census interval was obtained from the average of census intervals of each different 20 x 20 m subplot within the 50 ha plot where individuals of each taxon were registered. However, information on the length of census intervals for different subplots is not available in Condit et al. (1995), and thus I use the overall average interval, i.e. 3.9 years for the drought period (1982-1985) and 5.25 years for the non-drought period (1985–1990). This approach generates almost identical mortality rates as those reported in Condit et al. (1995) (see Appendix 4.1). For the other case studies, t was 4.2 years for Tapajós, 7 years for Caxiuanã, and 22 weeks (0.42 years) in the seedling experiment in Panama.

In the experiment in Bolivia, water supply was suppressed for 40 individuals of each species (Poorter and Markesteijn, 2008). The only information available was for t, which in this case was represented as the number of days after irrigation stopped when all 40 individuals of each species had died. Therefore in time t, the number of individuals, n_t, would be 0, and mortality (m) would necessarily be equal to 1 for all species. In order to calculate mortality rate using the data from Poorter and Markesteijn (2008), I assumed that on the day before all individuals were reported as dead, only one individual remained. Thus, I applied Eq. 5.1 at time t-1, where $n_t = 1$ so that different values of mortality rate per species could be assessed. I also scaled the information to the genus level, considering n_0 as the sum of all individuals within congeneric species and t as the maximum t among the species within each genus.

Selecting the appropriate taxonomic unit for analysis is necessarily a compromise between maximising replication within units and the need to address influential degrees of freedom in terms of the number of units. After preliminary exploration of such effects (see Appendix 4.2), I elected to work at the genus level. This helps maximize the characterization of the tree community. For example, among all taxa in Tapajós, 98% of tree genera had information on WDA, but only 57% of tree species appear in both the mortality experiment and the WDA datasets (see Appendix 4.3). Furthermore, the average number of individuals for each genus is naturally larger than for species, providing more confidence when calculating mortality. Taxonomic names from all different data sets were standardized against the Tropicos database using the Taxonomic Name Resolution Service (TNRS, 2014). All analyses were carried out in R version 3.1.2 (R Core Team, 2014).

4.2.3 Controlling for the baseline mortality

Within any forest, stand mortality rates vary, with population dynamics potentially differing from taxon to taxon (e.g. Sheil and May, 1996;Baker et al., 2014). Therefore, before testing the influence of a disturbance or any stressor on mortality rates, it is important to determine each taxon's baseline mortality (i.e. the mortality under standard conditions, which in the through-fall exclusion experiments refers to mortality in the control areas and in BCI to the post-drought interval). Here I estimated a 'drought mortality effect' ($\Delta \mathrm{m}$), or drought anomaly, by simply subtracting the baseline mortality rate from the mortality rate under drought conditions (Eq. 4.2).

$$\Delta \mathrm{m} = \mathrm{m}_{drought} - \mathrm{m}_{non-drought} \qquad \text{Eq. 4.2}$$

The seedling experiment in Bolivia lacked a control treatment, therefore it is not possible to control for baseline mortality, and in this case, analyses were performed using the mortality calculated as described in Eq. 4.1.

4.2.4 Statistical approach

For each case study, I assessed the relationship between drought-induced mortality and climate affiliations. For Caxiuanã, BCI and Tapajós, where the number of stems per genus were in some cases potentially too small to allow accurate estimations of mortality rates, I first investigated the relationship between taxon abundance and the correlation between Δm and WDA (see Appendix 4.2). Here my intention was to select the appropriate sample size (n genera) that would maximize the ability to detect a relationship, given that for many taxa the small sample size (i.e. number of stems per genus) is likely to be highly limiting. For the genera with enough stems, I tested the relationship between Δm and WDA through Kendall's τ coefficient of correlation and standardized major axis regression (SMA) (Legendre and Legendre, 1998) using the R package *smatr* (Warton et al., 2012). One-tail P-values were calculated testing the null hypotheses of non-positive correlation between Δm and WDA.

Next, I combined studies, where appropriate, to test whether a consistent WDA effect was still detectable. This was done in two ways. Firstly, I analysed all four different datasets with controls together (BCI, Tapajós, Caxiuanã and Panama seedling experiment), by standardizing Δm into z-scores within each case study and using Bayesian phylogenetic mixed models to explain Δm. WDA, case study and the interaction between them were included as fixed effects. These models also accounted for non-independence among genera, which is a consequence of their shared phylogenetic history (Felsenstein, 1985;Freckleton et al., 2002). Secondly, just for the two largest data sets, BCI and Tapajós, which included information on trees and saplings, I used Bayesian phylogenetic mixed models as before to understand the influence of WDA on Δm, also here investigating the influence of life stage on this relationship. I include case study, WDA, life stages and the interaction among these factors as fixed effects. For this analysis, values of Δm were transformed to log (Δm + 0.1) to minimise its heteroscedasticity. In both analytical frameworks, use of the Bayesian phylogenetic mixed models allowed me to account for phylogenetic autocorrelation as a random effect. The models were developed using the R package *MCMCglmm* (Hadfield, 2010). To select among models I used the deviance information criteria (DIC), a Bayesian equivalent of the Akaike's Information Criteria (Spiegelhalter et al., 2002). The phylogenetic information was obtained from a phylogeny developed for the genus level by (Dexter and Chave, 2016), which includes 632 Amazonian tree genera.

4.3 Results

Overall, the water deficit affiliation of genera is significantly associated with their tolerance to drought. In each of the case studies, genera WDA was positively correlated to drought-induced mortality when assessed using Kendal's τ, and significantly so in all cases except for the trees in Caxiuanã and the seedling experiment in Panama (Table 4.2). The slopes of the standardized major axis regression are also positive for all case studies, being significant for Tapajós (trees and saplings) and marginally significant for the seedling experiment in Panama and the natural drought in BCI (Figure 4.2a; Table 4.2).

The relationships between water deficit affiliation and drought-induced mortality are maintained even when accounting for the influence of phylogenetic autocorrelation. Thus, the gradient of the WDA effect on Δm is positive when I combine all experiments and control for the effects of both phylogeny and case study, with water deficit affiliation credible intervals not overlapping zero (Table 4.3).

Life history stage also influences genera drought-induced mortality as shown by two analyses. Firstly, in the only TFE in which saplings and trees have been analysed, the ratio of drought:control mortality was four times greater for trees than saplings (see Appendix 4.4 for details). Secondly, after controlling for potentially confounding phylogenetic effects, life stage, case study and WDA and their interactions all featured in the Bayesian phylogenetic mixed models with lowest DIC values, compared with simpler models of drought-induced mortality at BCI and Tapajós, the two sites where both trees and saplings were sampled (Table 4.4).

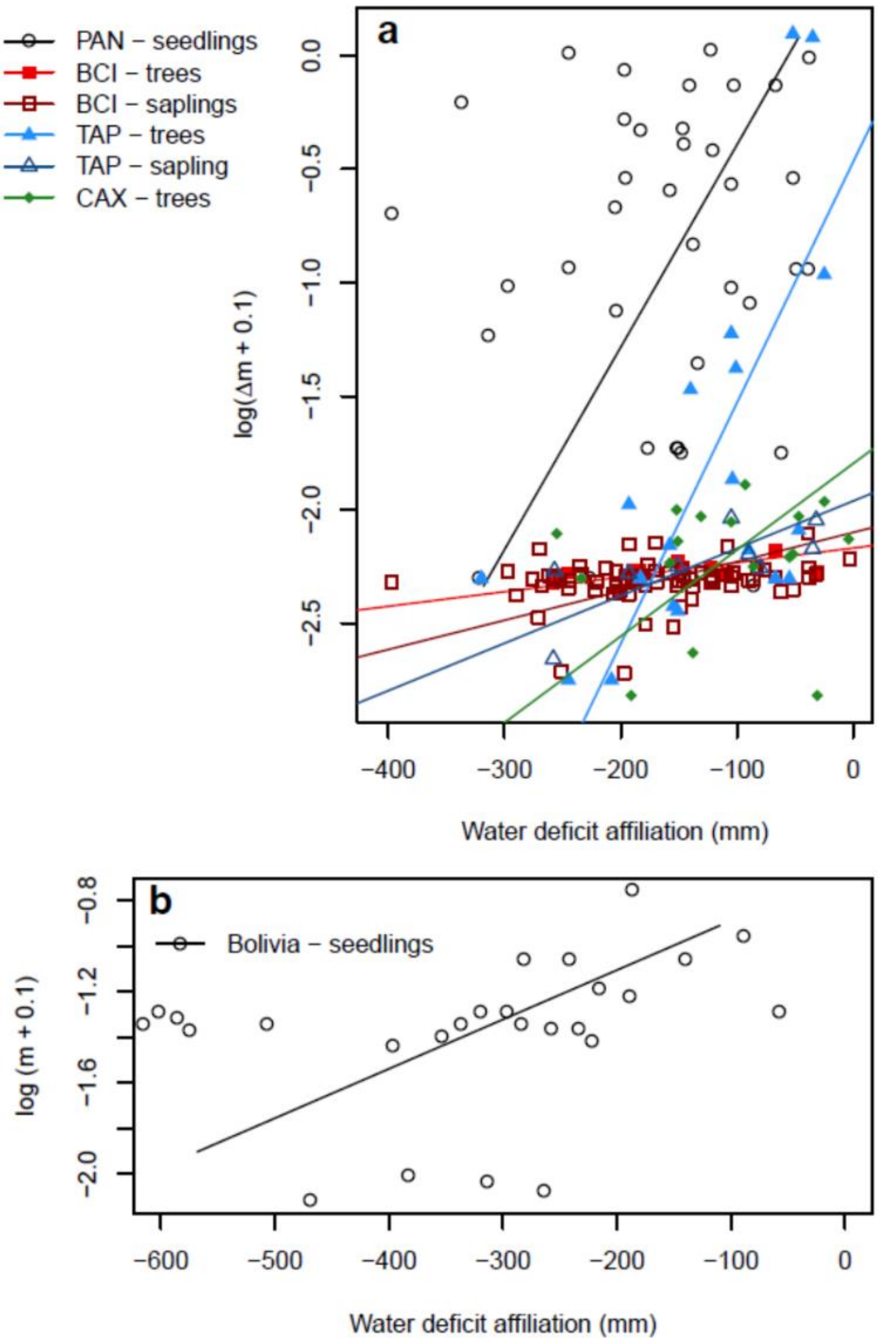


Figure 4.2 - Standardized major axis regression (SMA) between log transformed drought-induced mortality (Δm) and water deficit affiliation (WDA) in different case studies and for different life history stages. a. Two through-fall exclusion experiments in the Brazilian Amazon, Tapajós (Nepstad et al., 2007) and Caxiuanã (da Costa et al., 2010), field observations from the 1982-83 El Niño drought (Condit et al., 1995) and a seedling drought experiment in Panama (Engelbrecht et al., 2007). b. Seedling drought experiment in Bolivia (Poorter and Markesteijn, 2008), where y-axis represents log transformed mortality rates (m) + 0.1 during the drought experiment. Trees include stems over 100 mm diameter. The size range of saplings sampled was 10 – 99 mm D in BCI and 20 – 99 mm in Tapajós. WDA data were extracted from Chapter 3.

Table 4.2 - Relationship between drought mortality (Δm) and water deficit affiliation (WDA) in five droughted locations in the Neotropics. Slope and intercept from standardized major axis regressions (SMA) and Kendall's τ coefficient of correlation ($K\tau$) between Δm and WDA were calculated for the 1982-3 El Niño drought in BCI (Condit et al., 1995), two through-fall exclusion experiments in the Brazilian Amazon, Tapajós (Nepstad et al., 2007) and Caxiuanã (da Costa et al., 2010), and two seedling experiments, one in Panama (Engelbrecht et al., 2007) the other in Bolivia (Poorter and Markesteijn, 2008). For BCI, Tapajós and Caxiuanã the relationship Δm *vs.* WDA was calculated for the subset (Number of genera) that maximizes detectability, including only taxa with the minimum number of stems (Min. number of stem per taxa) needed to permit estimation of mortality for that experiment (see Appendix 4.2 for details). The minimum number of stems per taxa varied depending on the duration of the drought. P-values test (1) whether the slope differs from zero and (2) the null hypothesis of a negative relationship (negative values of $K\tau$) between Δm *vs.* WDA.

Source	Life stage	slope	intercept	$K\tau$	Number of genera	Min. number of stems per taxa
BCI	trees	6 x 10^{-4+}	2.2	0.42*	12	730
	saplings	1 x 10^{-3+}	-2.1	0.13*	74	602
Tapajós	trees	0.01**	-0.5	0.44**	19	8
	saplings	2 x 10^{-3*}	-2	0.61*	9	100
Caxiuanã	trees	4 x 10^{-3}	-1.8	0.16	6	17
Panama	seedlings	9 x 10^{-3+}	0.5	0.05	40	53
Bolivia	seedlings	2 x 10^{-3}	-0.7	0.32*	31	40

+ < 0.1, *P < 0.05; **P < 0.01

Table 4.3 - Relationship between drought-induced mortality (Δm) and water deficit affiliation (WDA) for Neotropical tree genera after accounting for case study and phylogenetic autocorrelation using Bayesian phylogenetic mixed models. The model was fitted for all studies that had a control treatment (i.e. all except Bolivia). Values of Δm were standardized as z-scores for each case study. Lower and upper CI represent respectively the lower and upper 95% credible intervals from the model. The model used an uninformative inverted gamma distribution prior for each parameter, following Hadfield (2010). Posterior distributions were obtained from 260,000 iterations, a burn-in = 60,000, and thinning interval = 200 (Hadfield, 2010). Note that WDA shows a positive relationship with Δm with credible intervals never overlapping zero.

Model	slope	lower CI	upper CI
intercept	0.6	-4 x 10^{-2}	1.1
WDA	3.5 x 10^{-3}	4.5 x 10^{-4}	6.3 x 10^{-3}
case study*			
Caxiuanã	-0.3	-1.3	0.6
Panama	-0.4	-1.3	0.4
Tapajós	0.3	-0.5	1.2
WDA : case study			
Caxiuanã	-1.2 x 10^{-03}	-8.5x10^{-03}	5.6x10^{-03}
Panama	-2.5 x10^{-03}	-6.8x10^{-03}	1.8x10^{-03}
Tapajós	3.4 x 10^{-03}	-2x10^{-03}	8.5x10^{-03}

*Case studies were dummy coded; BCI was coded zero for each variable.

Table 4.4 - Comparison of Bayesian phylogenetic mixed models describing the relationship between drought-induced mortality (Δm) and water deficit affiliation (WDA) for Neotropical tree genera. Models vary in how they account for the influence of case study (Tapajós or Barro Colorado Island) and life-history stage (saplings or trees) and are compared based on deviance information criteria (DIC). Data on Δm were obtained from the Tapajós through-fall exclusion experiment (Nepstad et al., 2007) and from the 1982 El Niño drought in BCI (Condit et al., 1995). WDA values were taken from Chapter 3. Models based on an uninformative prior inverted gamma distribution, following Hadfield (2010). Posterior was obtained after 130, 000 iterations, burn-in = 30 000 and thinning interval = 100 (Hadfield, 2010). Note that the best models are the ones including WDA, case study and life history stage, and their interactions.

Fixed effects	DIC	Δ DIC
WDA + case study + life stage +WDA:case study + WDA:life stage	57	0
WDA + case study + life stage + WDA:case study	62	5
WDA + case study + life stage + WDA:life stage	62	5
WDA + case study + life stage	83	26
WDA + case study	86	29
WDA + life stage	87	30
case study + life stage	88	31
case study	92	36
life stage	93	36
WDA	99	42
1	110	53

4.4 Discussion

I compared the bioclimatic distribution of 115 tree genera along a continental-scale neotropical moisture gradient with drought-induced mortality rates from five experimental or natural drought events across the Neotropics. I found a consistent, positive relationship between the degree of affiliation to climatic water supply and the degree to which droughts enhanced those genera’s mortality. In sum, the analysis shows that (1) drought selectively kills genera that are predominantly found in wetter climates (Figure 4.2; Table 4.2), and therefore that genera distributions in ‘water stress space’ can help predict drought survivorship even after accounting for phylogenetic autocorrelation (Table 4.3); and (2) the relationship between drought-induced mortality and water deficit affiliation was stronger for trees when compared to saplings, evidence of a greater degree of genus-specific drought vulnerability for larger size classes. These findings also, (3), confirm conclusions drawn from previous studies restricted to seedlings and conducted at local to sub-regional scales (Veenendaal and Swaine, 1998;Engelbrecht et al., 2007;Poorter and Markesteijn, 2008;Comita and Engelbrecht, 2009). The comparison of different studies further indicates, (4), that the duration and intensity of droughts, which are generally related to vegetation mortality (McDowell et al., 2008), also determine the strength of specific taxonomic responses (Figure 4.2).

Tree size is an important predictor of drought vulnerability. Large trees tend to be more strongly affected by droughts (Condit et al., 1995;Nepstad et al., 2007;da Costa et al., 2010;Phillips et al., 2010;Bennett et al., 2015;Rowland et al., 2015). Hydraulic failure seems to be the main mechanism of drought-induced mortality among trees (Anderegg et al., 2012;Rowland et al., 2015). The larger the tree the greater the chances of death by hydraulic failure as the vulnerability of xylem tissue to cavitation increases with height (Rowland et al., 2015) and larger trees have their crowns more exposed to high vapour pressure, which may intensify the effect of heat on their exposed crowns (McDowell et al., 2008;McDowell, 2011). The results showed that the climate affiliations of genera are more strongly associated with drought-induced mortality among large trees than among saplings for Tapajós (Figure 4.2; Table 4.2), and that life-history stage and its interaction with WDA are important in explaining drought-induced mortality (Table 4.4). Thus, genera adapted to dry conditions are disproportionately favoured when larger. These findings together suggest that genetically determined traits related to resistance to hydraulic failure - such as wood density, vessel size and vessel density (Preston et al., 2006;Poorter et al., 2010) and the capacity to close stomata during the dry period avoiding water stress (Fisher et al., 2006;McDowell et al., 2008;da Costa et al., 2010;McDowell, 2011) - may provide relatively greater advantage among large trees than among small ones.

Overall, the impact of drought on mortality rates increases with the duration of the drought. Thus drought:control mortality enhancement increased from BCI to Tapajós to Caxiuanã, whether calculated for the total number of individuals or as a mean of mortality per genus (see Appendix 4.4). Nevertheless, for the longest drought (7 years of reduced through-fall in Caxiuanã) climate affiliation loses its power to predict genera mortality. Thus, the slope of relationship between Δm and WDA is steeper for Tapajós (Table 4.2). Therefore, it appears that over very extended periods, the initially drought-resistant taxa also eventually become strongly affected, which translates into higher per-genus mortality and shallower Δm and WDA relationships (Table 4.2; Figure 4.2). Such results indicate that after 7 years of artificial drought most genera have exceeded their moisture deficit tolerance (Meir et al., 2015b). In this case, trees die regardless of their different drought-related traits, represented here by WDA. The implication appears to be that while biodiversity, i.e. the functional and taxonomic diversity found in a community, clearly can provide ecosystem-level resilience to short-term droughts, there exists a threshold of drought intensity and duration beyond which essentially all taxa suffer and therefore compromise central ecosystem services such as carbon storage.

Large datasets are required to detect taxon-specific effects of natural droughts. In the relatively short-lived natural droughts at BCI, significant correlations were only observed at samples of at least 400 stems per genus (see Appendix 4.2). The size of the BCI plot (50 ha) allowed the detection of the effect of natural drought on tree mortality, which emphasizes the substantial data requirements, like those provided by a 19 x 1-ha plot network in Ghana (Fauset et al., 2012) and a 16.3 ha plot in Costa Rica (Enquist and Enquist, 2011), for detecting differences in the response of different taxa to natural droughts. It is also possible that the low drought-induced mortality (and high detectability thresholds) in BCI may in part result from the lack of a real control. The 'control' census here spans from 1985 to 1990, after the drought period (1982-83), and thus is itself not completely independent from the effect of the drought (Condit et al., 1995). Drought disturbances are known to include lagged effects on tropical tree mortality (Phillips et al., 2010;Doughty et al., 2015). Indeed, results from a combination of field observations and controlled experiments suggests that in temperate trees the effect of hydraulic dysfunction may in some cases only be observable years after the drought event (Anderegg et al., 2012). There is also evidence of non-lethal lagged responses in other processes; for example, carbon allocation was still affected two years after a drought (Doughty et al., 2014). It may be that taxonomic driven responses to droughts would be more evident than observed here if pre-drought controls were available in the observational BCI dataset.

I have shown here that the large-scale distribution patterns of tree taxa with respect to climate have predictive value for their physiological vulnerability to moisture stresses. For the first time for neotropical trees, this relationship between physiological tolerances and taxonomic distribution has been demonstrated at a macroecological scale. Of the five experimental and observational drought mortality studies examined, two were located more than 2000 km away from the area where water deficit affiliation was measured. This indicates that different populations within the same taxon - that have likely been geographically distant for a sufficient amount of time to diverge genetically (e.g. Honorio-Coronado et al., 2014) - have conserved ecologically important responses. The fact that the bioclimatic distribution of tree taxa across the Neotropics is indicative of their tolerance to local and experimental droughts also suggests that, to some extent at least, distributions are likely to reflect a significant proportion of their fundamental niches. This is not necessarily always the case, as mismatches between species tolerances and their distributions are often reported in the literature, e.g. when invasive species are registered in areas outside their realized niches (Broennimann et al., 2007;Soberón and Nakamura, 2009;Tingley et al., 2014), when species physiological tolerances are higher in experiments than observed in nature (e.g. Krause et al., 2010;Leuzinger et al., 2011) or when different populations show distinct tolerances (Bansal et al., 2015). However, the results corroborate the central idea behind species distribution modelling, for which current taxonomic distribution is assumed to provide proxy information on physiological tolerances to climatic extremes (e.g. Raxworthy et al., 2003;Thomas et al., 2004). The results indicate that environmental conditions have a fundamental role in determining the relative dominance of neotropical trees at very large biogeographical scales

The analysis suggests that in the lowland Neotropics, droughts are likely to disproportionately impact biogeographically wet-affiliated tree taxa. While this pattern apparently depends on drought duration and life history stage, it is relatively consistent across all studies, indicating the potential for severe natural droughts -

such as occurred in 2005 and 2010 in Amazonia (Marengo et al., 2008;Marengo et al., 2011) - to at least temporarily affect community composition through selective mortality. Any declines in the populations of wet-affiliated genera that may have occurred as a consequence of these drought events may be anticipated to continue if water stress increases as indicated for many Neotropical forests (Dai, 2013;IPCC, 2013a;Boisier et al., 2015;Duffy et al., 2015). I note also that wet-affiliated taxa have on average smaller distributional ranges (Chapter 3, Brenes-Arguedas et al., 2009), and that wetter taxa represent the overwhelming majority of the tree diversity in the Neotropics (Chapter 3, ter Steege et al., 2003). Consequently, if my findings that droughts preferably kill wet-affiliated taxa hold true for the whole Neotropical region, the climate changes anticipated for this century may both alter Neotropical forest composition and endanger much of their high species diversity.

5

Changing composition of Amazonian tree communities

Abstract

Tropical ecosystems everywhere are changing. In Amazonia, even remote, structurally intact forests have experienced increases in aboveground biomass and turnover rates over recent decades. However, it remains poorly known whether or not alterations in forest dynamics are associated with pervasive and similar shifts in species composition. Here I investigated whether the floristic and functional composition of Amazonian forests have recently changed by consistently assessing data from 108 long-term plots distributed across the Amazon, which have been monitored over the last 30 years. Over this period, most plots have experienced an increase in dry season intensity. I analysed changes in three traits hypothesized to respond to different environmental drivers: biogeographic water-deficit affiliation, maximum size, and wood density. For each trait, I computed its community-weighted mean, how it changed over time, and its association with relevant climate trends, across (i) the whole community, (ii) newly recruited stems and (iii) those trees which had died within two consecutive censuses. Plots have become increasingly dominated by large-statured taxa, while dry-affiliated genera became more abundant within the recruits. The mortality of trees with low wood density has marginally increased and the mortality of stems of wet-affiliated genera has increased in plots where the dry season has become more intense. Although communities are becoming more dry-affiliated these changes still lag the drying trend. The observed functional shifts support the hypothesis that climate and increases in resources are driving the changes in Amazonian dynamics.

5.1 Introduction

Structure and dynamics of old-growth tropical forests are shifting (Phillips and Gentry, 1994;Phillips et al., 1998;Baker et al., 2004a;Lewis et al., 2009b;Brienen et al., 2015) and in Amazonia at least, such changes appear to have been underway for several decades (Brienen et al. 2015). Here, in apparently intact forests, both the aboveground biomass and the rate of ecological processes such as growth and recruitment have increased (Brienen et al., 2015). Recent increases in mortality, which may in turn be related to recent droughts, have contributed to a weakening of the biomass carbon sink (Brienen et al., 2015). However, whether such apparently pervasive changes in ecosystem structure and dynamics are also associated with concerted changes in the biodiversity of Amazonian forests remains poorly known. To date, assessments of how tropical tree communities have responded to climatic and atmospheric changes have either been restricted geographically (Laurance et al., 2004;Enquist and Enquist, 2011;Feeley et al., 2011a;Fauset et al., 2012), or based on few locations scattered over larger scales (Chave et al., 2008;Butt et al., 2014;van der Sande et al., 2016) or focused on a single functional trait (Lewis et al., 2009b). Here I analyse long-term floristic records from the largest tree monitoring network in the Neotropics to understand how Amazonian taxa have responded to the last 30 years of environmental change.

During the last few decades, the climate of Amazonia has become more extreme – the dry season length and intensity has increased, whilst precipitation has become more abundant during the wet season (Gloor et al., 2013;Hilker et al., 2014;Gloor et al., 2015;Jiménez-Muñoz et al., 2016). For instance, the two strongest droughts of the last 100 years for the Amazon occurred within a five-year interval in the beginning of the 21st century (Marengo et al., 2008;Marengo et al., 2011). These drought events were widespread across the Amazon (Marengo et al., 2008;Lewis et al., 2011;Marengo et al., 2011) and were combined with a decrease in precipitation which was more intense in the in the south east of the basin (Hilker et al., 2014). In addition to the changes in precipitation, moisture stress is likely to have intensified throughout the whole basin as a consequence of increasing temperatures (Jiménez-Muñoz et al., 2013). The forest was impacted by these fluctuations in climate: tree mortality rates increased during and after drought events (Phillips et al., 2009;Phillips et al., 2010;Feldpausch et al., 2016) with increased losses of biomass, reducing the long-term rate of net carbon accumulation in Amazonian forests (Brienen et al., 2015).

The consequences of a drier climate on Amazonian tree communities remains poorly understood. The drought-impacts studied so far reflect ecophysiological and ecological processes that respond to climate drivers over relatively short time-scales (e.g., cavitation, autotrophic respiration, plant growth, wood productivity) (Nepstad et al., 2007;Phillips et al., 2010;Rowland et al., 2015;Feldpausch et al., 2016). Longer-term processes, particularly changes in floristic composition driven by differential recruitment and mortality due to drought events, could greatly moderate or accentuate the impacts of these short-term responses, but these have been less extensively studied because of the shortage of appropriate long-term datasets. For instance, by assessing the *in situ* multi-decadal responses of tree communities it should be possible to test whether forest composition has tracked local climate changes or not (sensu Loarie et al., 2009). Observations of drought impacts in Ghana (Fauset et al., 2012) and a recent modelling exercise (Levine et al., 2016;Sakschewski et al., 2016) suggest that floristic compositional shifts could protect some of the carbon sequestration and storage services provided by tropical forests in the face of long-term droughts. Regardless of whether or not tropical droughts' impacts on the carbon cycle are ameliorated by changes in functional composition, widespread pervasive changes in taxonomic composition of trees would very likely have implications for Amazonian biota. Additionally, such floristic shifts could potentially add new strands of evidence to our attempts to deduce the key drivers of the recent ecosystem changes in terms of biomass and dynamics already documented from many localities in Amazonia (Lewis et al., 2004a).

Interpreting the potential shifts in floristic composition and linking them with the predicted drivers is particularly challenging considering the high diversity of tropical forests. A widely applied strategy to understand floristic changes and their drivers is to use a suite of functional traits to describe how communities change over time (McGill et al., 2006;Violle et al., 2014). Two largely orthogonal trait axes have been shown to capture significant information on the lifespan and carbon function of tropical tree species, which may have value in addressing these questions. One axis is the life-history trade-off between growth and mortality (Wright et al., 2004), for which wood density has been shown to be a good proxy for tropical forest tree species (Chave et al., 2009;Poorter et al., 2010;Coelho de Souza et al., in review). The other axis is related to potential size (Falster and Westoby, 2005;Coelho de Souza et al., in review). Drought could have differentiated impacts along each of these axes. Most notably, large and light-wooded trees may be at greatest risk, as these are the most likely to suffer from hydraulic failure due to cavitation (McDowell and Allen, 2015). Hydraulic failure has been shown experimentally to be a driver of drought-induced mortality in Amazonia (Rowland et al., 2015). Indeed large trees have been the most affected in exclusion experiments in tropical and temperate regions (da Costa et al., 2010;McDowell and Allen, 2015;Rowland et al., 2015), and by tropical drought events (Phillips et al., 2010;Bennett et al., 2015). If the recent extreme Amazonian droughts have affected floristic composition, we might therefore expect to see a decrease in the abundance of large and light-wooded taxa (Table 5.1). Conversely, several observations from tropical tree inventories show in fact a decline of small understorey taxa associated with the long-term increase in water-stress (e.g. Condit et al., 1996;Enquist and Enquist, 2011;Feeley et al., 2011a;Fauset et al., 2012). Thus, it has also been hypothesized that small taxa with shallower roots would be more vulnerable than large deep-rooted trees under long-term drying trends, which might reduce soil water but not to an extent that compromises canopy trees (Condit et al., 1996;Fauset et al., 2012). Indeed, across Amazonia there is an indication that wetter areas may have more densely populated understoreys (Malhi et al., 2002). Alternatively, changes in precipitation regimes may not necessarily drive shifts in tree size, but other environmental changes, such as the on-going increase in atmospheric carbon dioxide, may lead to such changes (Enquist et al., 1999;Laurance, 2004;Enquist et al., 2009;Coomes et al., 2011).

Given the uncertainty about how different tree sizes are expected to respond to drying, information on species distributions along precipitation gradients may provide a more direct way to test for the effects of drought on floristic composition. The distributions of tree taxa have been shown to be a valuable proxy for drought tolerance in observations and experiments (chapter 4, Engelbrecht et al., 2007;Baltzer and Davies, 2012;Butt et al., 2014). This type of biogeographical information has been widely used to understand changes in floristic composition in tropical forests (Enquist and Enquist, 2011;Feeley et al., 2011a;Fauset et al., 2012). For instance, the increase in moisture stress has apparently favoured dry-tolerant taxa in Ghana (Fauset et al., 2012) and at two locations in Central America (Enquist and Enquist, 2011;Feeley et al., 2011a). If drought is increasingly affecting Amazonian forests, we might therefore expect concerted shifts in the biogeographic composition of tree communities across Amazonia towards a more dry-affiliated composition.

Overall, while considerable interest has focussed on the atmospheric and climatic changes, particularly drought, other environmental changes may be important. Conceivably one or more of these could have pervasive impacts on mature forests across the basin to rival or exceed any climate impacts. It is beyond the scope of this chapter to account for all such possible effects, but a detailed description of every possible driver is given in chapters 1 and 2 (see Table 2.1 - Chapter 2). As well as describing the changes in floristic composition within the Amazon basin, I use this information to test between different hypotheses about the potential drivers of shifts in forest dynamics. In addition to the hypothesis of environmental drivers, here I focus on the late successional hypothesis, the leading alternative hypothesis for non-atmospheric drivers of pervasive changes in tropical tree communities. A number of studies have suggested that the increase in carbon accumulation capacity observed within tropical forests in Amazonia and Africa may be a consequence of plots containing late-successional forest (e.g. Clark, 2002;Chave et al., 2008;Muller-Landau, 2009). If so, we expect to observe not only an increase in the potential size of trees but also an increase in community-level mean wood density due to declines in pioneers and gains in late successional taxa (Chave et al., 2008;van der Sande et al., 2016). Of course, if disturbance-recovery has widespread tree-compositional impacts it could partly obscure (or conceivably magnify) any putative impacts of climatic and atmospheric changes. Importantly however, each such driver leads to a different multi-trait set of predictions, and so if any one driver has a dominant impact it should be visible in the unique ‘fingerprint’ within Amazonian communities (Lewis et al., 2004a). Thus, for example, a widespread increase in potential tree size might implicate either disturbance-recovery or increasing carbon dioxide (e.g. Laurance et al., 2004), but a simultaneous increase in wood density would imply that the former dominates (Chambers et al., 2004;Chave et al., 2008).

Here, I aim to quantify the potential shifts to date in the floristic composition of Amazonian tree communities at the genus level, and test the hypothesis that recent climatic drying has already impacted the composition of Amazonian forests. Additionally, I assess whether possible compositional changes are consistent with other potential drivers of change, such as the increase in atmospheric CO_2 and previous disturbance. The dataset consists of 108 tree inventory plots monitored between 1985 and as recently as 2015, across intact closed-canopy moist forests in lowland Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guyana, Peru, and Venezuela (Figure 5.1). To better understand the dynamics of these forests I investigate trends within the overall community, the recruits and the trees that died, and the growth that occurred within each census interval (Figure 5.2). Based on predictions from physiological theory and experimental studies, I expect increases in dry season intensity to shift floristic composition towards genera with potentially large statured trees, and higher wood density (McDowell and Allen, 2015;Rowland et al., 2015). Alternatively, based on field observations of shifts in floristic composition I expect that a long-term increase in moisture stress may favour small statured genera adapted to dry conditions. Overall, by analysing compositional responses along these tree orthogonal trait axes: growth (via wood density) size and bioclimatic distribution (Appendix 5.1), I aim to shed light on the possible effects of recent climate shifts on Amazonian floristic composition, as well as help to parse out the effects of climatic and atmospheric changes from other potential drivers of change in the forest's dynamics.

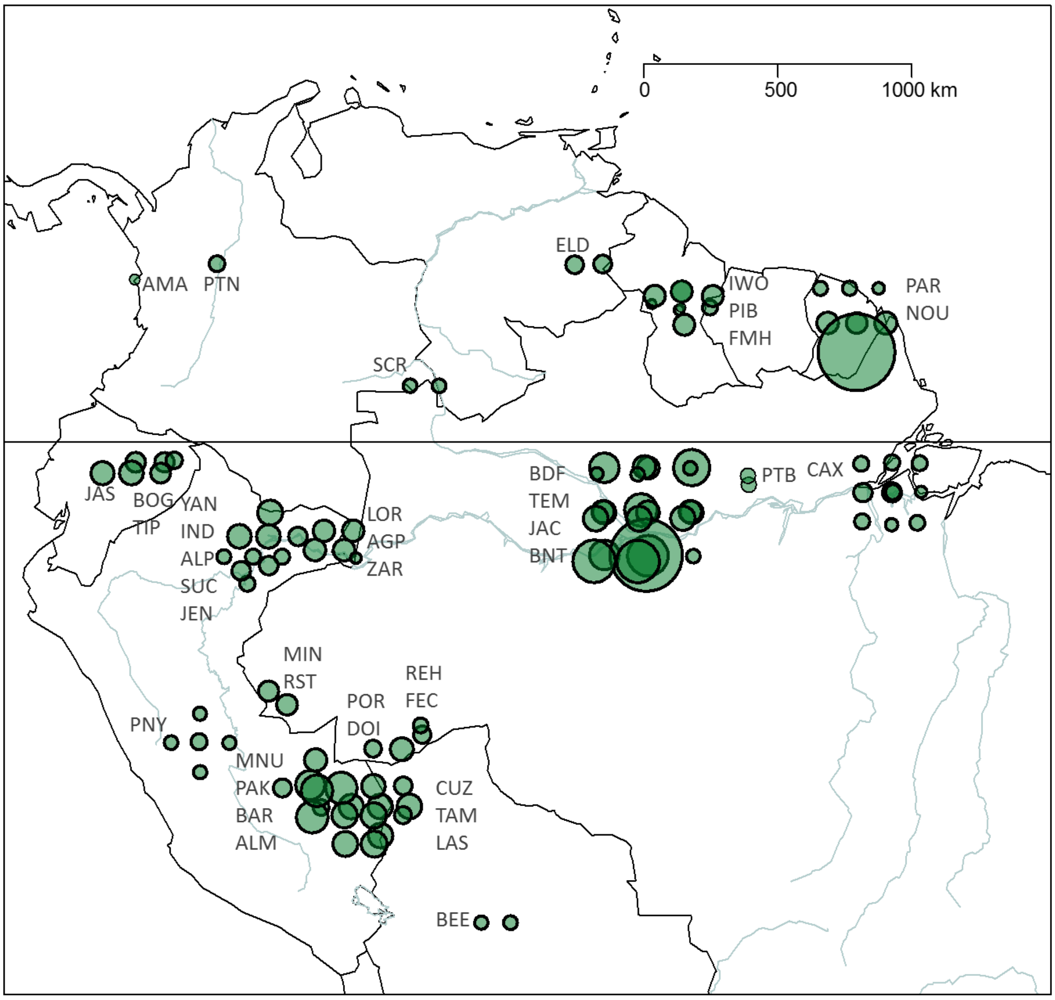


Figure 5.1 – Sample effort in the analyses. Circles represent 108 tree inventory plots across the Amazon used in this chapter. The area of each circle represents the sample effort per plot as square root of plot area * monitoring period. The locations of overlapping plots have been adjusted to allow visibility.

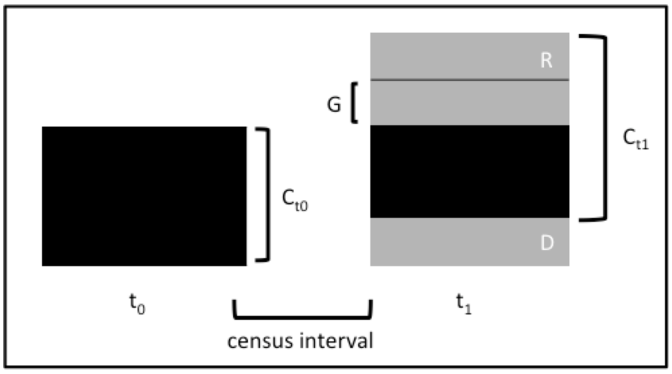


Figure 5.2 – Schematic model representing the different components of forest dynamics. The box on the left represents an inventory plot of a forest community at the first census (C_{t0}), whilst the box on the right shows the community at the second census (C_{t1}). After the census interval recruits (R), i.e. the trees that attained 10 cm of diameter within the census interval, will now be part of the community analysed. Other trees will have died (D) thus leaving the community, also called *losses* throughout the chapter. Finally, the trees from C_{t0} which survive through the census interval are expected to grow (G). Thus, the basal area of the community at $C_{t1} = C_{t0} + G_{t1} + R_{t1} - D_{t1}$. In this chapter I am interested in what is driving the net flux ($= G_{t1} + R_{t1} - D_{t1}$) and to investigate that I look at the characteristics and identity of genera in each of these compartments of the forest dynamics over time. The diagram represents the dynamics in basal area terms, but similar logic can be applied for stem-based analyses that investigate shifts in the identity of individuals recruiting and dying over time. Note that in this case I am not interested in the growth of trees surviving from t_0 to t_1, and so the net flux will be represented as $R_{t1} - D_{t1}$.

5.2 Methods

5.2.1 Climate data

To investigate the influence of climate on forest dynamics I calculated temporal trends in cumulative water deficit (Aragao et al., 2007;Malhi et al., 2009) for each plot. CWD represents the accumulated water deficit (WD), i.e., the difference between precipitation (P) and evapotranspiration (E) within each year:

$$CWD = \sum_{n=1}^{12} WD \qquad \text{Eq (1)}$$

If $WD_{n-1} - E + P_n < 0$;

then $WD_n = WD_{n-1} - E + P_n$;

else $WD_n = 0$

where n = the months within a year. In other words, CWD is an annual measure of the length and intensity of dry season. The calculation of CWD should not necessarily follow the calendar year, as for tropical forests in the northern hemisphere the annual dry season typically spans two calendar years. Thus, the starting point, i.e. when n = 1, was defined climatologically as the wettest month in 1985, the first year in the time series, rather than the first month of the calendar year.

In addition to annual CWD, I also computed the intensity of the most extreme dry season between two consecutive censuses, hereafter termed CWDi. This metric represents a measure of maximum environmental disruption between two censuses, i.e. the most negative value of annual CWD between each successive pair of censuses, following Feldpausch et al. (2016). Only complete years were considered for this calculation. For the first censuses of each plot the CWDi was calculated as the most negative CWD values within the 3-year period preceding that census. This time window is equivalent to the average census interval within the data (2.8 years).

To verify whether the trends observed were consistent with other sources of climate data, I calculated CWD using precipitation based on both satellite and ground based datasets. Satellite precipitation data were obtained from the Tropical Rainfall Measuring Mission (TRMM - Huffman et al., 2007) at 0.25^{o} spatial resolution between 1998 and 2010. Ground-based precipitation data were extracted from the Climatic Research Unit (CRU), at 0.5^{o} spatial resolution from 1985 to 2015 (Harris et al., 2014). Evapotranspiration data used in CRU and TRMM based CWD were obtained from CRU at 0.5^{o} spatial resolution (Harris et al., 2014), calculated based on the Penman–Monteith equation (Allen et al., 1994). Precipitation and evapotranspiration data were combined and annual CWD was estimated based using both precipitation sources. CWD values from census intervals from CRU and TRMM data are reasonably well-correlated (R^2 = 0.87; P <0.0001 - see Appendix 5.2 for more detail), so for my main analyses I used the ground-based data from CRU to estimate CWD as this covers the whole time window of the floristic analyses.

5.2.2 Field observations and forest dynamics

I investigate the trends in functional and floristic composition of tree communities by analysing long-term data collected by colleagues from permanent tree inventory plots in the Amazon and adjacent lowland forests (Figure 5.1). Information from 108 South American forest plots from the RAINFOR network (Malhi et al., 2002) was accessed via the ForestPlots.net repository (Lopez-Gonzalez et al., 2011). All plots are lowland (< 1000 m.a.s.l), *terra firme,* moist (i.e. where mean CWD is less negative than -300 mm y^{-1}) forests. Plots have been monitored regularly and throughout the period of the two most intense dry seasons (2005, 2010). I excluded plots where the floristic dynamics for different census intervals could not be compared due to extreme discrepancies between interval lengths, i.e. census intervals longer than 10 years followed by census intervals shorter than one year. The analyses are restricted only to plots with more than 80% of tree stems identified to the genus level, all lianas and non-woody standing plants (*Phenakospermum*) were also excluded.

Each long-term plot has been established and monitored following a standardized protocol (Phillips et al., 2016). Methodological details are given elsewhere (Brienen et al., 2015); in brief, when each plot is installed all trees $\geq$10 cm diameter (D) at 1.3 m (or above-buttress) are tagged, identified to the species level, have their D measured, and the point of measurement marked and recorded. Plots have been re-censused on average every 2.8 years and at every census trees previously recorded are re-measured. The new recruits, i.e. trees that attain 10 cm when the plot is revisited, are tagged, measured and identified and notes are taken about the individuals that died within the interval between censuses.

5.2.3 Traits

I describe Amazonian tree genera in terms of three basic traits hypothesized to respond to drivers of change:

- **Potential Size (cm):** estimated by Fauset et al. (2015), as the 95th percentile of the distribution of trees’ D, derived from 530 inventory plots within the Amazon basin.

- **Water deficit affiliation (WDA) (mm):** derived from relative abundances across 513 inventory plots distributed along a large gradient of CWD across the Western Neotropics (see Chapter 3). Species affiliated to dry conditions show the most negative values of WDA, whilst the most wet-affiliated species have values of WDA approaching or equal to zero.
- **Wood density (g cm^{-3}):** values were extracted from the Wood Density Database (Chave et al., 2009;Zanne et al., 2010).

Trait values were then assigned to each individual tree based on their genus. Given the high tree diversity of Amazonia, trait values were missing for some taxa (e.g. WDA was missing for 10% of the genera and 1% of the families); when genus-level trait data were not available I used the mean trait values from their respective families (Baker et al., 2004b;Flores and Coomes, 2011). A small number of individuals belong to families for which no trait information was available, 4% of the trees in the case of WDA, and for these I used the average trait value of the community in that census. For those stems not identified to family level (3% of all stems) I applied the mean trait for all dicot individuals of the plot-census during which the tree was recorded. To test the hypothesis deduced from previous work that the traits analysed here (WDA, PS and WD) are orthogonal trait axes for Amazonian trees, I used ordinary least squared (OLS) regression to test for the relationship among these traits (Appendix 5.1).

Then, to obtain a census-level value for each of the 3 traits I scaled the genus-level traits to the community level by calculating the community weighted mean (CWM sensu Diaz et al., 2007) for each trait in each census. CWM was calculated for the whole community and for each component of forest dynamics, i.e. the recruits (new trees that reach the 10 cm D cut-off after each census interval), the basal area gain of those trees that survived the census interval, and those trees that died within each census interval, hereafter losses (Figure 5.2). For each of the 754 censuses across 108 plots, the CWM of each of these components was calculated as the mean trait value across the genera of the community, weighted by (1) the number of stems and (2) the total basal area occupied by each genus.

5.2.4 Analytical approach

I investigated changes in functional (mean potential size, water deficit affiliation and wood density) and floristic composition (the relative abundance of individuals of each taxa) by assessing trends over time of these parameters for each plot and scaling up to the basin level.

Trends in functional composition

Functional trends were quantified as: (1) bootstrapped mean and 95% CI linear slopes of the community weighted mean (CWM) as a function of time across all plots; (2) generalized linear mixed effect model (GLMM) of CWM as a function of time using function *lmer* from the R package *lme4* (Bates et al., 2014). Whilst the first approach provides information of overall trends across the basin, the second approach gives an idea about the trend within the whole period (1985-2015), accounting for potential switches in which plots are analysed over different time windows along the 30-year period. The GLMM is potentially a more powerful analytical technique, however the bootstrapped mean of linear slopes provides a confirmation of the results where the uncertainty estimate is derived using a non-parametric approach.

The bootstrapped mean was calculated from plot-level linear slopes of CWM (i.e. mean plot level traits) in each census (j) as a function of time:

$$\mathrm{CWM}_j \sim \text{census date}_j \qquad \text{(Eq 5.1)}$$

Then, the weighted mean and the 95% CI of the slopes from Eq 5.1 across all plots was estimated using non-parametric bootstrapping by randomly resampling values of the plot-level rate of change across all plots 10,000 times (Feeley et al., 2011a;Fauset et al., 2012). Plot area and monitoring period are expected to affect the variance of plot-level trends from a general mean trend as smaller plots and those monitored for shorter periods are more likely to be affected by stochastic phenomena, e.g. tree fall (Lewis et al., 2009b), and measurement error. Thus, sampling effort, i.e. the square root of plot area times monitoring period, was used as a weight to calculate Amazon-level weighted means (Lewis et al., 2009b;Brienen et al., 2015) (Appendix 5.3).

The GLMM follows the same logic of the previous analyses with CWM as a linear function of time:

$$\mathrm{CWM}_{ij} \sim (\beta_1 + \mathrm{a}_i) + \ (\beta_2 + b_i\ ) * \ \text{census date}_{ij} \ + \ \varepsilon_{ij} \qquad \text{(Eq 5.2)}$$

where CWM in plot *i* and census *j* is a function of the date when the census took place (census date). Here the census date is used as a fixed effect and the random components of the model are the slopes (a) and intercept (b) for each plot and the overall residuals (ε_{ij}). The slope and intercept of each plot were included as random effects considering that the variation in the initial trait value (represented by the plot intercept) and in the intensity of change (represented by the plot slope) can differ across plots. In this analysis I applied the same weighting procedure as for the bootstrapped mean, i.e. each data point in the model was weighted by sampling effort.

The influence of climate on functional composition

To explore the potential impact of climate changes on functional change, I tested whether changes in community are related to changes in climate. First I calculated the trend in CWD and CWDi over the inventory period for each plot. I then used Kendall's τ coefficient to test for the correlation between linear slopes of CWM (composition) and CWD (climate) for each plot. Then, for the cases where the correlation was significant, I applied a reduced major axis (RMA) of trends in CWM as a function of trends in CWD to further probe the strength of any relationship. RMA minimizes sums of squares in both axes simultaneously (Legendre and Legendre, 1998;Warton et al., 2012), and is adopted here because of the uncertainty associated with using the CRU rainfall measurements to estimate actual plot-level climate.

Trends in floristic composition

To understand which taxonomic groups are the main actors in any functional shifts, I investigated taxon-specific changes in relative abundance and tested for their correlation with the traits of each taxon. To calculate these trends in abundance, I followed the same procedure applied to analyse CWM changes as described above, i.e. bootstrapped mean and GLMM, but here using the relative abundance of each taxon as a response variable. For this approach Eq 5.1 was modified as:

$$\mathrm{RA}_j \sim \text{census date}_j \quad \text{(Eq 5.3)}$$

where RA is the relative abundance of a taxon. I then use the GLMM approach by modifying Eq. 5.2 to:

$$\mathrm{RA}_{ij} \sim (\beta_1 + \mathrm{a}_i) + (\beta_2 + b_i) * \text{census date}_{ij} + \varepsilon_{ij} \qquad \text{(Eq 5.4)}$$

An Amazon-wide slope using each of the methods was calculated for each taxon. The same weights applied in the CWM analyses were used here.

Next, I investigated which genera contribute the most to those significant functional changes that were detected. When trends in functional composition were significantly different from zero (see *Trends in functional composition* for details) I estimated Kendall's τ coefficient of correlation between Amazon-wide slopes (either calculated for the whole community, recruits or losses) for each genus and their trait values (WDA, WD or PS). To guarantee that the trends in abundance are estimated with reasonable levels of uncertainty, I restricted the investigation of the trends in abundance vs. traits relationship to only include genera with more than 100 stems for the 'whole community' analyses. The analyses on recruits and losses were constrained only to genera with more than 50 stems within these components of the community dynamics.

5.3 Results

5.3.1 Climate trends

Our plots have on average experienced a strengthening of the dry season. The plot-level annual cumulative water deficit (CWD) became more negative by on average -1.1 mm y^{-1} (95% CI = -1.3, -0.9) since 1985 (Figure 5.3). This represents an intensification in dry season moisture deficits of 12% per decade, compared to an initial average CWD among plots of -89 mm in 1985.

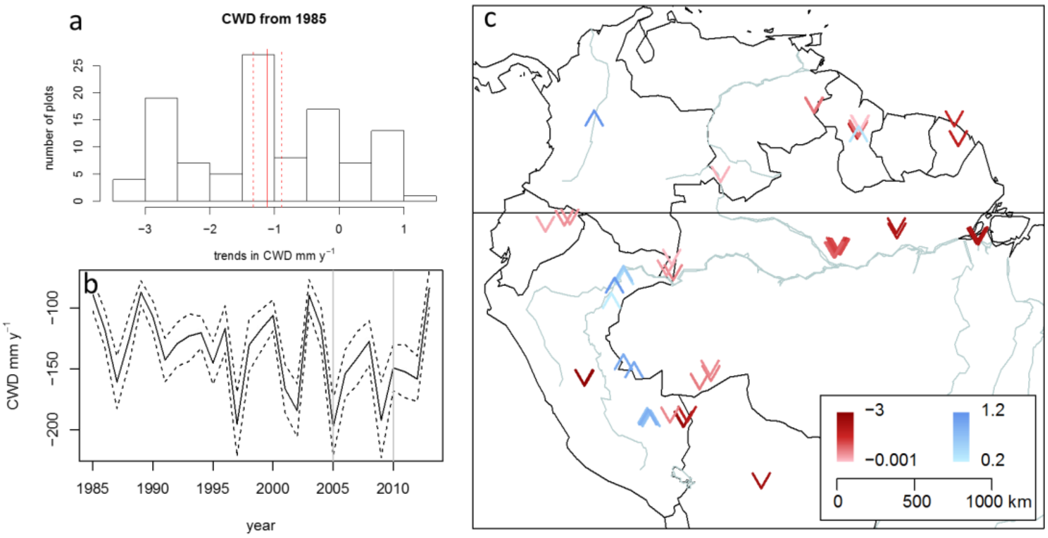


Figure 5.3 – Annual changes in cumulative water deficit (CWD) at the inventory plots across the Amazon basin. Trends in CWD **(a)** are shown as annual linear trends per plot between 1985 and 2014. Mean change and 95% confidence intervals (red lines and dashed red lines) were calculated from 10,000 weighted mean trend values obtained from a bootstrap procedure of resampling with replacement of the trends in CWD from all plots; plot trends were weighted by the squared root of the plot area. Note that for most plots the climate has shifted towards more negative CWD values. **(b)** Mean annual CWD and 95% CI from resampling among all plots, note lower CWD values at 2005 and 2010. **(c)** Map shows trends for each individual plot. Arrows facing down (in red) represent locations where CWD has become more negative over time, i.e. dry season has become more intense. Arrows facing up (blue) represent more positive values of CWD, which means that moisture stress has decreased, the intensity of the colors represents the strength of the climate trend. Note the difference in scale between drying and wetting trends color bars.

5.3.2 Trends in functional composition

The three traits analysed here - water deficit affiliation (WDA), potential size (PS) and wood density (WD) – represent essentially orthogonal axes describing Amazonian tree genera (Appendix 5.1). No significant relationship was found between these traits when compared pairwise WDA vs. PS ($R^2 = 8 \times 10^{-3}$) WDA vs. WD ($R^2 = 5 \times 10^{-4}$) and WD vs. PS ($R^2 = 2 \times 10^{-3}$).

Mean functional changes at the whole community across the Amazon have been small indicating substantial inertia in terms of floristic composition. There has however been a significant increase in the PS of the communities: the CWM PS when weighted by basal area increased by 0.03 cm y^{-1} (95% CI = 0.02, 0.05 cm y^{-1}), meaning that plots have been progressively occupied by larger statured genera (Table 5.2). No significant change in CWM PS was observed for the stem-based analyses (Table 5.1). This holds regardless of the analytical technique, i.e. bootstrapped means or GLMM (Appendix 5.5). There was no significant trend in CWM calculated for water deficit affiliation or wood density at the community level, either for stem or for basal area-based analyses (Table 5.1; Table 5.2).

The fluxes into and out of the tree community provide a more detailed view on the changes than the whole community analyses. Here, although no significant trend was observed in terms of PS either of stem or basal area-based values, there has been a significant decrease in WDA within the recruits in terms of stem density, i.e. dry-affiliated genera have become more abundant for this segment of the community (Table 5.1; Figure 5.4). No significant trend in WDA was observed within the trees that died during the monitoring period. Wood density did not change significantly within the recruits, on a stems or basal area basis. However, WD slightly decreased within the losses for basal area -1×10^{-3} g cm^3 y^{-1}. This trend was not consistent among analytical techniques, i.e. it was significant for the GLMM analyses at $\alpha = 0.05$, but only weakly so for bootstrapped mean: -1×10^{-3} g cm^3 y^{-1} (90% CI = -2×10^{-3}, -1×10^{-5} g cm^3 y^{-1}) (Appendix 5.5). Importantly, the magnitude of the changes observed for WDA are greater than the changes detected for the other traits (Figure 5.4).

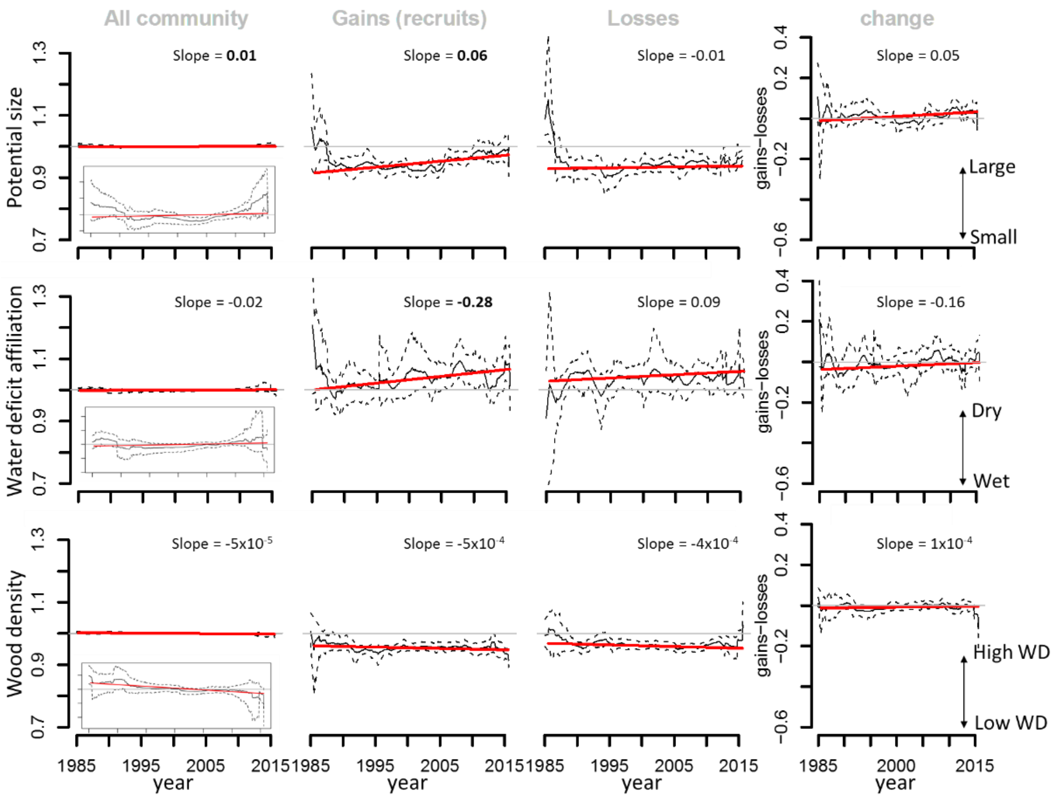


Figure 5.4 – Trends in plot level traits between 1985 and 2015 across Amazonia. The y-axes show community weighted mean (CWM) trends in water deficit affiliation (WDA), potential size (PS) and wood density (WD) at genus level, all standardized with respect to the whole plot population. Graphs show CWM trends for: the whole community (box showing a zoomed-in version of the graph), recruits and losses. Graphs on the right of the panel (Change) show the trends in the difference between gains and losses. Black lines show standardized mean census level trait, which can be influenced by some switching of plots through time. Red lines show generalized linear mixed models (GLMM), accounting for the difference between plots as a random effect, each point is weighted by the square root of plot area x the time which each plot was monitored for. Slope values for GLMM are shown in each graph - these are not standardized by plot population and are shown at a different scale for each trait, with the slopes that differ from zero at α = 0.1 in bold. Note that as a consequence of the standardization in the graphs WDA > 1 indicate communities more dry affiliated than average plot WDA, whilst WDA < 1 represent communities more wet affiliated than average. Additionally, the slopes show opposite direction from what is observed in the graphs.

Table 5.1 – Mean linear slopes in stem-based functional composition across the Amazon. For each trait, the bootstrap mean annual changes in community weighted mean (CWM) weighted by the squared root of plot size x monitoring period. Brackets contain 95 % confidence intervals. CWM calculated for: water deficit affiliation (WDA), potential size (PS) and wood density (WD). The analyses were repeated for recruits, dead trees and the difference between recruits and dead trees (net fluxes). Significant trends are in bold, i.e. where CIs do not overlap zero.

Community	Potential size (cm y^{-1})	Water Deficit affiliation (mm y^{-1})	Wood Density (g cm^{-3} y^{-1})
Whole community	0.01(-0.001|0.01)	-0.01(-0.06|0.03)	-5x10^{-5} (-1x10^{-4} | 4x10^{-5})
Gains (recruits)	0.01 (-0.03 | 0.2)	**-0.5 (-1 | -0.1)**	-5x10^{-4} (-2x10^{-3} | 1x10^{-3})
Losses	0.01 (-0.01 | 0.2)	-0.1 (-0.7 | 0.3)	8x10^{-5} (-9x10^{-4} | 1x10^{-3})
Net fluxes	-0.03 (-0.2| 0.1)	-0.5 (-1 | 0.1)	-7x10^{-4} (-2x10^{-3} | 8x10^{-4})

Table 5.2 – Mean linear slopes in basal area-based functional composition across the Amazon. As Table 5.1 but showing the results for basal area.

Community	Potential size (cm y^{-1})	Water Deficit affiliation (mm y^{-1})	Wood Density (g cm^{-3} y^{-1})
All community	**0.03(0.02|0.05)**	0.01 (-0.05 | 0.06)	1x10^{-5}(-8 x10^{-5}| 1x10^{-4})
Gains (basal area)	0.003(-0.06|0.06)	0.1 (-0.1|0.3)	-3x10^{-4}(-1 x10^{-3}| 1x10^{-4})
Gains (recruits)	0.06(-0.1|0.2)	-0.1 (-0.8|0.6)	-2x10^{-4}(-2 x10^{-3}| 2 x10^{-3})
Losses	0.1 (-0.07|0.3)	-0.4 (-1.3|0.4)	-1x10^{-3} (-3x10^{-3}| 2x10^{-4})
Net fluxes	-0.09 (-0.3|0.1)	0.5 (-0.4|1.5)	1x10^{-3} (-5x10^{-4}| 3x10^{-3})

5.3.3 The influence of climate on functional composition

Analyses testing whether plot-level climate drives floristic changes showed a significant relationship between trends in the intensity of extreme dry events (CWDi) and trends in the losses and fluxes of basal area-based WDA (Figure 5.5). In other words, the mortality of large wet-affiliated trees has increased in plots where the most extreme dry season within a census interval has intensified. There was no significant correlation between trends in climate and trends in community weighted mean of other traits (Appendix 5.6).

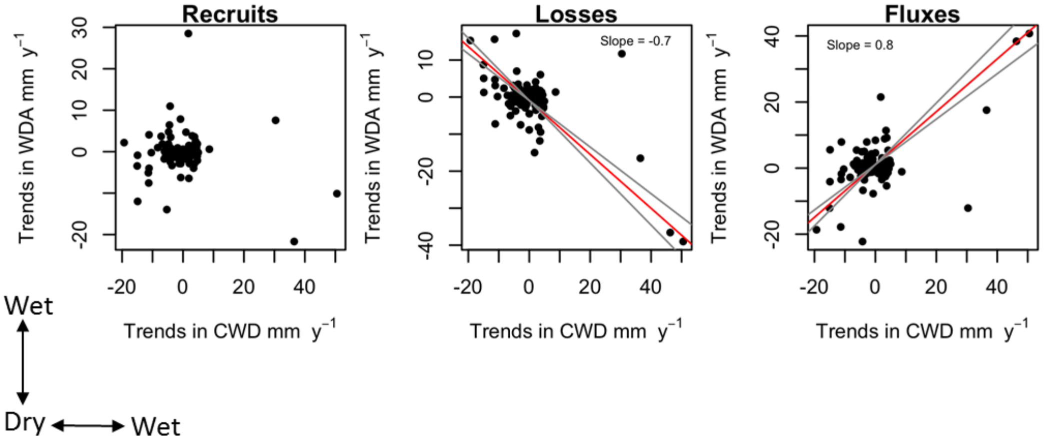


Figure 5.5 – Relationship between trends in climate and composition. The y-axes represent plot linear slope of basal area-based community weighted mean of water deficit affiliation (WDA) per year and x-axes show the trends in most extreme dry season within a census interval (CWDi). Red lines represent the reduced major axis regression and slopes are shown in the figure. Note that changes in basal area-based WDA losses and fluxes (recruits–losses) are correlated to changes in climate (Kendall $\tau = -0.2$; $P < 0.01$ and 0.13; $P < 0.05$ respectively), i.e. stronger drying trends favour the mortality of wet-affiliated taxa. Correlations are not driven by outliers (Kendall $\tau = -0.1$; $P < 0.05$ when excluding outliers with wetting trend > 30 mm y^{-1} for losses, Kendall $\tau = 0.1$; $P=0.1$ for fluxes). Trends in recruits are not correlated to trends in climate: Kendall $\tau = 0.03$; $P = 0.6$.

5.3.4 Floristic trends

The floristic changes represented by the linear trends in abundance for individual taxa are generally consistent with the functional changes observed. There has been a notable increase in the relative abundance of the dry-affiliated genera *Euterpe*, *Pradosia* and *Pseudolmedia*, together with sharp decreases for the wet-affiliated *Iriartea*, *Micrandra*, *Aniba* and *Mezilaurus*. Some large-statured taxa have increased significantly, such as *Eschweilera*, *Qualea*, *Osteophloeum* and *Mora*. A decrease in smaller-statured taxa, such as *Myrcia* is also observed (Appendix 5.7).

Analysing the taxonomic shifts, it is possible to identify which genera contribute to overall changes in functional composition when these changes were observed (i.e. PS in basal area terms for the whole community, WDA stem density for recruits, and WD for losses in basal area terms). The correlation between taxa PS and their trends in basal area was significant (Kendall $\tau = 0.2$; P-value < 0.01) and driven by an increase in some emergent and canopy genera such as *Bertholletia* and *Eschweilera,* and a decrease in some sub-canopy and understorey genera such as *Iriartea* and *Rinorea* (Figure 5.6). The decrease in WDA within the recruits is also explained by changes in floristic composition (Kendall $\tau = -0.14$; $P < 0.05$), e.g. by a decline in the recruitment of new stems of wet affiliated genera such as *Eschweilera*, *Licania* and *Iriartea* and an increase in recruitment for dry affiliates such as *Trema* (Figure 5.6). It was not possible to identify the main genera behind the changes in wood density within the losses, as genus-level floristic shifts were not associated with decrease in WD basal area losses (Kendall $\tau = -0.07$; $P=0.3$). This is consistent with the weak temporal trends detected for WD basal area losses.

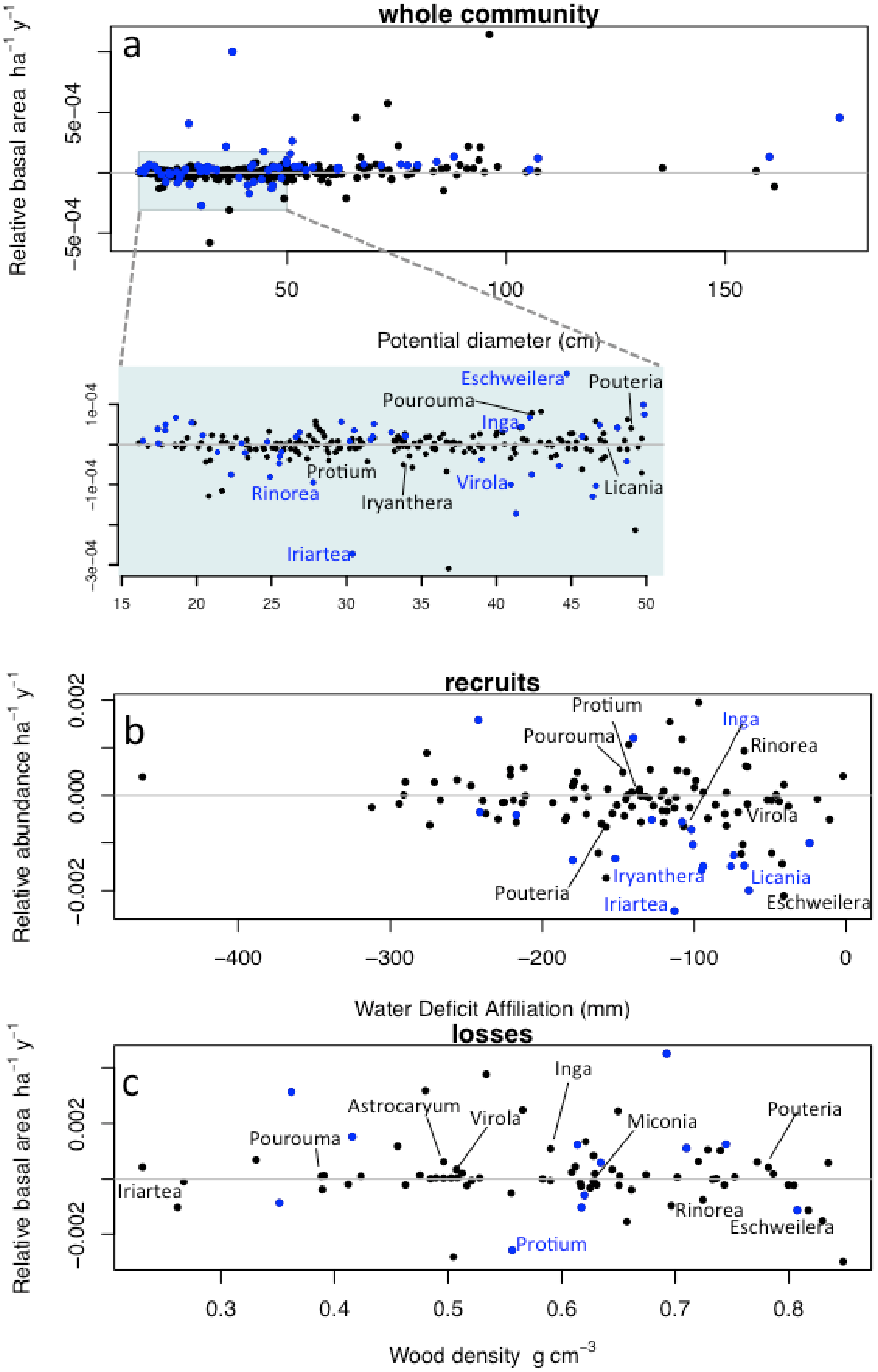


Figure 5.6 – Floristic changes behind the significant functional shifts. The y-axes represent mean linear slopes of plot level genera relative abundance or basal area as a function of time, weighted by the square root of plot area and monitoring period. Zero is represented by grey horizontal lines. The x-axes represent genus-level traits. (a) Trends in relative basal area for different genera within the whole community vs. potential size (cm), with blue box to allow visualization of most dominant genera; (b) Trends in relative abundance of stems for different genera within the recruits vs. water deficit affiliation (mm); (c) Trends in relative basal area for different genera within the losses vs. wood density (g cm^{-3}). In blue the genera where confidence intervals do not overlap zero. Names of the 10 most abundant genera in number of stems within each compartment of the community dynamics are displayed in the graphs.

5.4 Discussion

I detected a consistent intensification of the seasonal drought across the majority of permanent monitoring plots in Amazonia. This climate trend coincides with floristic changes in the inventory plots, which are consistent with the hypothesized effects of drying on forest communities (Table 5.3). Across 108 Amazonian inventory plots analysed over the last 30 years, recruits have become more dry-affiliated and the mortality of wet-affiliated trees has increased in the areas where the drying trend was stronger, suggesting a direct effect of climate change on functional composition. Also, potentially consistent with expectations from a drying climate, mortality of the large light-wooded trees has very slightly increased. However, the basal area of larger-statured genera increased, which contradicts drought-driven expectations but agrees with predictions from increased resources as a driver of changes. Nevertheless, these shifts in potential size and wood density are of a smaller magnitude compared to the shifts in water deficit affiliation, again supporting a drought-driven change in functional composition (Figure 5.5). Although the expected shifts in water deficit affiliation were not observed among the standing community, I find evidence of changes in WDA within the recruits (Figure 5.4), which is consistent with the inertia in the composition of Amazonian forests communities. Moreover, the shift towards dry-affiliated taxa within the recruits indicates that a climate-driven change in composition is underway.

Droughts have contributed to an increase in the mortality of large trees in the Amazon (Phillips et al., 2009), but – somewhat surprisingly – the results here show a slight increase in the basal area of large-statured trees within the Basin. These results contradict some expectations of drought-driven compositional shifts; larger trees are predicted to be more vulnerable to embolism, and thus more likely to die from hydraulic failure under droughts (Bennett et al., 2015;McDowell and Allen, 2015;Rowland et al., 2015). However, smaller-statured genera may have shallower roots relative to larger-statured genera, and thus may in practice be more vulnerable to projected drying (Wright, 1992;Condit et al., 1996;Fauset et al., 2012). To date, information on rooting depth is still very restricted for tropical forest taxa, which limits our ability to conclude that this is the mechanism driving the increase in larger-statured taxa observed here. Most likely, the increase in PS indicates that the effect of the drying trend has been insufficient to suppress the increasing dominance of these taxa. Indeed, the hypothesized shift towards smaller-statured genera as a consequence of droughts is largely based on experiments where water availability is suppressed by 50% continuously for several years (Nepstad et al., 2007;da Costa et al., 2010), a much stronger drought than observed in the Amazon. In sum it appears that the observed short-term increase in mortality of large trees as a consequence of the 2005 drought (Phillips et al., 2009;Phillips et al., 2010) has been insufficient to counter a longer-term tendency to increased basal area of large-statured taxa.

The observed shift toward larger taxa agrees with a hypothesised widespread recovery from disturbance (Wright, 2005;Chave et al., 2008). Successional recovery in tropical forests is characterised by a shift from pioneers to mature forest species, which would drive a concomitant increase in stand-level wood density (Connell and Slatyer, 1977;Chave et al., 2008;Lewis et al., 2009a). In contrast, the 108 Amazonian inventory plots analysed here show no significant shift in wood density, either in the whole community, or perhaps more importantly, among the recruits (Table 5.2). Arguably, the wood density data used here (Zanne et al., 2010) may be a crude tool when compared to the other two traits. Wood density is known to vary considerably across a continental scale and genus-level averages used here may not precisely represent WD in the plots (Patino et al., 2009;Baraloto et al., 2010), thus the WD results should be interpreted with caution. Nevertheless, when testing the late successional hypothesis, wood density is used to distinguish between late successional and pioneer trees, and this distinction should be able to be captured by genus-level WD values. The WD results demonstrated no evidence that this late successional substitution of taxa is happening, as the WD of the recruits was no greater than the WD of the losses - shown by the negative intercept of fluxes (recruits – losses): -0.01 g cm^{-3} (Figure 5.4; Appendix 5.5). It is also noteworthy that the relative change in WDA and PS are of greater magnitude than any putative wood density change (Figure 5.4), so the failure to detect statistically or biologically significant changes in wood density is unlikely to be due to any lack of statistical power.

Larger trees are anticipated to gain disproportionately with additional resources (Enquist et al., 1999;Enquist et al., 2009;Coomes et al., 2011) (see chapter 1 for details), such as increases in atmospheric CO_2 which has risen by ca. 5 % per decade since the 1980s (Conway and Tans, 2016). Thus, the observed greater abundance of larger-statured genera over time indicates that forest dynamics could also be driven by atmospheric changes. Indeed the increase in CWM PS in basal area terms but not in stem number follows the expectation that large trees will benefit under elevated CO_2 (Lewis et al., 2004a). Therefore, although further investigation is needed to confirm this hypothesis, the results do not allow me to reject elevated atmospheric CO_2 as a driver of the dynamics of Amazonian forests. If this holds true, it could lead to changes in community structure, especially as higher CO_2 concentration may change actual tree size throughout the whole community. Moreover, functional changes are only one part of the processes that have been occurring in the Amazon. In the last three decades Amazonian intact forests have been shown to be increasing in above ground biomass, growth, mortality and recruitment, which provides further information to infer the most likely drivers of Amazonian communities (Phillips and Gentry, 1994;Phillips et al., 1998;Brienen et al., 2015). For example, late succession while leading to an increase in large-statured trees and above ground biomass, also involves a slowing of growth and recruitment (Chambers et al., 2004), contrary to the long-term plot observations (Brienen et al., 2015).

There has been considerable concern regarding the ecosystem impacts of widespread removal of large-bodied frugivores. In particular, it has been repeatedly suggested that hunting will or may have already altered tree composition in tropical forests (e.g. Peres and Palacios, 2007;Terborgh et al., 2008;Doughty et al., 2016;Osuri et al., 2016;Peres et al., 2016) via dispersal failure of zoochoric trees (Chapman and Chapman, 1995). These tend to have high wood density and large stature, so a recruitment failure is predicted to lead to a reduction in the prevalence of both of these traits and thus in Amazonian biomass (Bello et al., 2015;Peres et al., 2016). This study was designed to understand floristic dynamics in intact Amazonian forests and not to evaluate the effects of hunting pressure, which is likely to more strongly affect areas adjacent to rural communities, roads and river

(Peres and Lake, 2003). However, the increase in potential size and the lack of any change in wood density (Figure 5.4) contradict expectations of the hunting hypothesis as a driver of community composition change in intact forests, which, again, does not rule out the possibility of hunting pressure causing shifts in composition in particular locations where this activity is stronger.

It is not surprising that the identities of the new trees and dead trees recorded during the monitoring period provide a more sensitive metric of floristic change than the whole community analyses. In Amazonia, recruitment and mortality of trees $\geq$10 cm D averaged 9 trees per hectare per year between 1985 and 2010 (Brienen et al. 2015). In the data used here mean stem density is 520 trees per hectare and mean plot-monitoring length is 14 years, so that by the final census the accumulated turnover of stems is ≈ 24% of the initial population. Thus, we should expect *a priori* that whole community-level composition would be only weakly affected by changes over the measurement period, instead largely reflecting legacy effects of recruitment and mortality processes occurring decades prior to the onset of monitoring period (Davis, 1989). By extension, given a population half-life of >50 years in many Amazonian forests (Galbraith et al., 2013), we may have to monitor for at least as long to detect half the floristic community change 'committed' due to recent climate changes. In summary, the data are consistent **both** with the hypothesis that tropical forest composition responds dynamically to climate changes (dry-affiliated taxa increasingly favoured as recruits, moist-affiliated taxa increasingly likely to die), **and** with the expectation that communities dominated by long-lived organisms may substantially lag behind environmental changes, at least initially (Davis, 1989;Perry et al., 2005;Lenoir et al., 2008).

Table 5.3 - Fingerprinting drivers of changes in Amazonia. Expected changes for the different drivers (as in Table 2.2 - chapter 2) and trends observed over the last 30 years in the Amazon. In brackets the most likely outcome for the cases where there is not strong evidence supporting the predictions or there are no known predictions.

	Potential Size	Water Deficit Affiliation	Wood density
Hypotheses			
Drying trend	(Larger ?)	Drier	(Higher ?)
Increase in frequency of extreme droughts	(Smaller ?)	Drier	(Higher?)
CO_2 fertilization: Winners take all	Larger	No change	(Lower ?)
CO_2 fertilization light suppressed do better	(Smaller ?)	No change	(Higher ?)
CO_2 increase WUE	(?)	Wetter	(Lower ?)
Hunting	Smaller	No change	Lower
Late succession	Larger	No change	Higher
Observation			
	Larger	Drier (recruits)	No change

The composition of Amazonian tree communities showed to be lagging the changes in climate. Across the Amazon forest plots have been undergoing an average drying trend of -1.1 mm y^{-1} CWD (Figure 5.3). The mean trend in water-deficit affiliation for the whole community is, however, two orders of magnitude smaller (-0.01 mm y^{-1}) with confidence intervals overlapping zero. This is evidence of the inertia of a system integrated by long-lived organisms and raises concerns about whether forests will be able to track climate. On the other hand, the net fluxes, i.e. recruits - deaths, seem to be responding to the trends in precipitation (-0.5 mm y^{-1}, Table 5.1), indicating a certain resilience of the system. However, the change within fluxes is not happening at the same pace as the changes in climate, showing that Amazonian communities may not respond to drying trends at the same speed as the forests in Western Africa (Fauset et al., 2012). Thereby it is still uncertain whether the speed of climate change will allow the hypothesized rearrangement of species to cope with climate and protect ecosystem services (Sakschewski et al., 2016).

This study provides the first Amazon-wide picture of functional and floristic dynamics over the last 30 years. My approach to examine community-level change has been to combine a set of orthogonal bioclimatic and structural descriptors for 606 genera, using a long-term dataset of forest community dynamics that spans 108 plots. The data shows that recent droughts and the increasing drying trend have left a fingerprint on the tree communities of the Amazon. Such changes were only observed when analysing the recruits and dead trees, emphasizing the inertia of long-lived communities to changes in climate. However, models predict a strengthening of the dry season over the Amazon (Joetzjer et al., 2013;Boisier et al., 2015), and an increase in water-stress as a consequence of temperature rise (Pokhrel et al., 2014). The results presented here show although shifts towards dry-affiliated Amazonian communities are both possible and are currently underway, the trends in floristic composition are still lagging the trends in climate. Such floristic shifts would increase the tolerance of Amazon tree communities to future droughts, however they could have important consequences for Amazonian biodiversity, as the majority of Amazonian tree taxa are wet-affiliated (chapter 3). Alterations to the abundance of these taxa will potentially compromise important biotic interactions, threatening other trophic levels dependent on wet-affiliated trees.

6

Tree-size dynamics in the Amazon: winners take most but not all

Abstract

In recent decades atmospheric CO_2 concentrations have surpassed levels not seen for millennia, but the consequences of this for biological systems are still unclear. Trees are expected to increase in size stimulated by greater photosynthetic rates. Large trees may be best placed to take advantage of the increase in resources as a consequence of the asymmetric competition for light. Alternatively, light-suppressed stems could gain a relative advantage as a result of improved carbon balance in trees close to the light compensation point. To test these two hypotheses I analysed 30 years of tree inventory data across 194 Amazonian mature forest plots and found that trees have become larger over time. Mean tree size significantly increased, with basal area increasing by 152 $mm^2\ y^{-1}$ (95% CI 114; 193) and the smallest 50% increasing by 41 mm y^{-1} (95% CI 27; 57). Thus, larger trees are gaining in dominance. However, whilst larger trees had greater absolute increases, the relative gain in basal area was similar regardless of size classes or canopy status. This evidence is consistent with a resource-driven boost for larger trees, but also a reduction in suppression among smaller trees.

6.1 Introduction

Within the past 50 years, atmospheric CO_2 concentration, a resource fundamental to photosynthesis, has increased from 300 ppm to 400 ppm (Conway and Tans, 2016). Higher CO_2 concentrations stimulate plant growth rate (Lloyd and Farquhar, 1996) and is the most parsimonious and likely driver of the observed increase in aboveground biomass in tropical forests (Lewis et al., 2009a;Pan et al., 2011;Brienen et al., 2015). Although the impacts of CO_2 on tropical tree communities has been widely debated, less attention has been given to the potential impacts of increased resources on forest structure. Some ecological theory predicts a *winner takes all* response for the increase in resources, where larger individuals obtain disproportionate amounts of resources, outcompeting smaller individuals (Enquist et al., 1998;Falster and Westoby, 2003;Coomes et al., 2011). Alternatively, the additional CO_2 could favour the individuals most suppressed by any resource, allowing for their growth and survival (Ehleringer and Björkman, 1977;Lloyd and Farquhar, 2008). In this chapter I explore these two apparently contrasting predictions using 30 years of forest inventory plot data from across the Amazon.

Large trees are –almost by definition– stronger competitors in forests (Enquist et al., 1998;Falster and Westoby, 2003). Tree size provides such an advantage that to reach the canopy, trees invest large amounts of carbon in vertical stems (Dybzinski et al., 2015), which in return allows them to disproportionally accumulate more biomass (Stephenson et al., 2014). The competition between different size classes is mostly size-asymmetric (Schwinning and Weiner, 1998), with larger individuals able to exploit greater amounts of resources, both above- and below-ground. Size increases light interception and photosynthesis, which boosts individuals' relative fitness by making light unavailable to small trees (Weiner, 1985;Falster and Westoby, 2003). The more resource-rich the area, the greater the advantage of large trees, either due to size scaling with the capacity to use resources (Niklas et al., 2003), or because when resources are not a limiting factor, competition for light becomes even more important (Weiner, 1985;Muller-Landau et al., 2006;Coomes et al., 2011;DeMalach et al., 2016). Following this logic, at higher CO_2 levels we would predict a *winner takes all* response, where the largest trees in the canopy are disproportionally benefited (Dybzinski et al., 2015). As a consequence, the structure of the size-class distribution is expected to shift, with more trees observed within the largest size-classes. Thus, mean tree size would also increase.

Alternatively, higher CO_2 levels will not necessarily favour the best competitors, but rather the individuals whose growth is most carbon-limited – the understorey trees (Lloyd and Farquhar, 2008). This hypothesis is based on the assumption that the proportion of carbon fixed per proton absorbed (quantum yield) depends on atmospheric CO_2 concentration (Ehleringer and Björkman, 1977). Greater CO_2 concentrations favour photosynthesis over photorespiration, as CO_2 competes with oxygen as substrates in the Rubisco (Ehleringer and Björkman, 1977). In tropical forests light is an important limiting factor for tree growth (King, 1994). The lack of light in the understorey is so strong that understorey trees live close to their light compensation point, i.e. on the edge between positive and negative carbon balance (Augspurger, 1984;Lewis and Tanner, 2000). Therefore a small increase in CO_2 can potentially take understorey stems away from negative carbon balance by reducing photorespiration and stimulating photosynthesis, so that the growth of understorey trees increases and in some cases trees that would otherwise have died, survive (Würth et al., 1998). If these predictions are correct, a *winner takes all* response is unlikely, rather, higher CO_2 levels should act to weaken the effects of the asymmetric competition for light. More specifically, changes in growth on a relative basis will be larger in smaller stems, towards infinity when a tree in deep shade lives when growing under high CO_2, when otherwise it would have died.

Given sufficient length and geographical coverage of standardized observations, these hypotheses can in principle be tested by analysing changes of simple size structure parameters, such as the mean and median tree size of a forest stand of trees. Greater mean tree size over time could indicate that either all trees in the community or a specific group (e.g. large or small trees) have gained in size. An increase in median tree size on the other hand is an indication that smaller trees have become larger. Following this logic, an increase in the mean but no change in the median would represent an advantage only for the largest trees as predicted by the *winner takes all* hypothesis. Additionally, a disproportionate increase within the larger taxa will modify communities' overall size-class distributions, which would be detected by shifts in the scaling exponent (α), that describes the community frequency distribution curve (Enquist and Niklas, 2001;Niklas et al., 2003;Clauset et al., 2009;Enquist et al., 2009). Typical *winner takes all* responses will also be captured by traditional metrics of inequality, such as the Gini coefficient (Sen, 1973). If few large trees grow disproportionally more when compared to the whole community, the inequality in the distribution of the area occupied by trees in a plot increases. On the other hand, if higher CO_2 levels alleviate growth suppression on understorey trees, I expect the tree size of understorey trees to increase, and the plot area to be more equally distributed among stems. Importantly, these two hypotheses are not necessarily mutually exclusive, therefore under higher atmospheric [CO_2] large trees could gain more in absolute terms, even whilst understorey trees experience higher relative growth and survival (Würth et al., 1998;Lloyd and Farquhar, 2008).

The increase in asymmetric competition also occurs under constant resource availability as a consequence of late successional recovery. As succession advances self-thinning takes place, with the number of stems dropping whilst space is occupied by fewer, but larger stems, leading to an increase in mean tree size (Connell and Slatyer, 1977). Indeed, it has been hypothesized that Amazonian intact forests would actually be undergoing late successional recovery from past disturbances, either attributed to early occupation of Amazonian forests by pre-Colombian civilizations (Heckenberger et al., 2003;Bush and Silman, 2007;but see Barlow et al., 2012;Clement et al., 2015), or by previous natural disturbances (Wright, 2005;Feeley et al., 2007). However, as a consequence of the successional processes, self-thinning will necessarily happen together with a floristic turnover from lighter-wooded pioneers to denser-wooded late successional species (Connell and Slatyer, 1977). Under CO_2 fertilization such compositional turnover is not expected and, if anything, light-wood density taxa are predicted to gain over time (Lovelock et al., 1998), which is the opposite to what is expected during late succession (Lewis et al., 2009a). Therefore, by assessing changes in wood density over time, it is possible to distinguish between these two possible drivers of asymmetric competition.

My goal in this chapter is to describe the dynamics of tree size structure in the Amazon over the last 30 years, using this information to help understand the potential influence of higher CO_2 concentrations on forest structure. Therefore I test the increasing asymmetric competition and suppressed understorey hypotheses by computing whether changes in structural parameters - mean and median tree size - have changed over time, including differing size classes, and canopy versus understorey trees, the size frequency distribution of trees within plots and the distribution of area occupied by individual trees in a plot (Gini coefficient).

6.2 Methods

6.2.1 Vegetation data set

To describe temporal trends of tree stand structure across lowland (< 1000 m.a.s.l) tropical South American moist *terra firme* forests I selected all long-term permanent tree monitoring plots meeting these criteria from the RAINFOR network (Malhi et al., 2002) assessed via the ForestPlots.net repository (Lopez-Gonzalez et al., 2011). These 194 plots had an average size of 1.2 ha (range 0.4 to 12 ha). Plots were monitored for, on average, 13 years (range 2 to 30 years). All trees ≥ 10 cm diameter were marked, measured and mapped following a standardized protocol (Phillips et al., 2016). Further methodological details are given in Chapter 5 and have been published elsewhere (Brienen et al., 2015). Lianas and coarse herbs (*Phenakospermum*) were excluded from the analyses.

One complexity when monitoring tropical trees is that they may have buttresses or deformities that can extend above the standard point of measurement (POM, 1.3 m) during the monitoring period. When there is any deformity compromising the cylindrical shape of the trunk at 1.3 m, such as buttresses, the POM is placed at higher parts of the trunk, above any deformities where the trunk is cylindrical (Sheil, 1995;Phillips et al., 2016). Over time if buttresses or deformities occasionally further develop, the POM must be raised so that growth is not erroneously inflated. Such changes lead to discontinuities in growth data for individual trees. To deal with this, I use a sequence of the mean D estimated between the first and last POM across the monitoring period, a solution reported in several previous studies (Lewis et al., 2009b;Talbot et al., 2014;Brienen et al., 2015). In appendix 6.1, I show that the trends reported in the results are not an artefact of the procedure I employ to address the non-continuity of some POMs on some trees.

6.2.2 Size structure

To investigate the trends in tree size across the Amazon I characterize each census regarding its size-structure by: (1) its mean and median basal area; (2) the Gini Coefficient of inequality; (3) the scaling exponent (α), an allometric parameter that describes the community frequency distribution curve as a power-law $N_i = D_i^{-\alpha}$, where N_i is the number of individuals in a size class D_i (Enquist and Niklas, 2001;Niklas et al., 2003); (4) the mean basal area of each of three size classes, < 200 mm, 200-399 mm and ≥ 400 mm D, and (5) the mean basal area of overstorey and understorey trees.

The Gini coefficient used to quantify inequality is derived from the Lorenz curve (Sen, 1973), which in forest ecology is used to describe the distribution of the total area of a plot occupied by trees (Weiner, 1985). It represents the area between a hypothetical line where all individuals occupy the same area in a plot and the Lorenz curve, which is the cumulative proportion of area occupied by each tree as a function of the cumulative proportion of the number of trees. Thereby if all individuals occupy the same area, Gini is equal to 0, whilst a total unequal situation will be represented by Gini = 1 (Weiner, 1985). I calculated the Gini coefficient in each census using the package *ineq* for R (Zeileis, 2014).

The scaling parameter (α) from the size-distribution curve for each census was obtained from the best-fitted power-law distribution estimated based on Clauset et al. (2009). This method consists of estimating the minimum diameter (Dmin) above which the power-law best fits, so that α can be estimated by fitting a power-law from that point. The goodness of fit of the power-law is quantified using Kolmogorov-Smirnov (KS) statistics. The standard deviation around Dmin is quantified using non-parametric bootstrap by estimating Dmin for 1000 random distribution curves generated from the data (Clauset et al., 2009).

Power-law curves could fit any data. Therefore I tested for the hypothesis that size-frequency curves actually follow a power-law distribution by using the approach described by Clauset et al. (2009). I (1) generated samples with the same size of the original data that are known to follow a power-law (synthetic data sets sensu Clauset et al., 2009). Then I (2) fitted a power law for each of the synthetic data sets and (3) using KS statistics I calculated the distances of each synthetic dataset from the model. Finally, I (4) tested whether the distance between the empirical data and the power-law falls within 90% of the distances between the synthetic data and the power-law. For this procedure, 2,500 synthetic data sets were generated.

If large trees are gaining as predicted by the *winners take all* hypothesis, it should be expressed that α will decrease, i.e. power-law curves showing a shallower slope (Niklas et al., 2003). Frequency-distribution curves were calculated for every census of the 160 plots within the data with area equal to 1 ha.

6.2.3 Canopy status

I classified each tree by their canopy status (overstorey or understorey) using the Ideal Tree Distribution (ITD) model (Purves et al., 2007). This model places the trees in the overstorey or understorey stratum based on height and crown area. Trees are ordered from the tallest to shortest and the crown areas of the trees are summed cumulatively until this equals the ground area. These trees are classified as in the overstorey layer. Those trees shorter than the smallest tree in the overstorey layer are considered to be in the understorey. The model is based on the assumptions that: (1) the total crown area of each canopy layer is less than or equal to the ground area; (2) trees are sufficiently plastic so there should be no unused space in each canopy layer; and (3) consequentially, tree height defines which tree will be in the canopy. More details of this model can be found elsewhere (Purves et al., 2007;Purves et al., 2008;Bohlman and Pacala, 2012).

In the absence of height and crown area of each tree I estimated the height for each tree in the data in each census using regional allometric equations from Feldpausch et al. (2011). Crown area was estimated using the allometric equation from Poorter et al. (2006):

$$\text{crown area} = \exp\left[-1.853 + 1.888 \ln(\text{height})\right] \qquad \text{Eq. 6.1}$$

I adopted the conservative approach of considering the crown area of palms to be zero, based on the assumption that palms provide little shade when compared to other taxa and considering that they follow different crown allometry when compared to trees (Goodman et al., 2013). This approach avoids exposed trees being classified erroneously as understorey trees. The model was applied at the census level, and tree height and crown area were calculated for each tree in each census so that within the monitoring period, as trees grow in D and trees recruit and die, tree canopy status could change from understorey to overstorey and vice-versa.

Canopies of tropical forests are often irregular as a consequence of gap dynamics (Bohlman and Pacala, 2012). To account for this patchiness in the canopy it is recommended that the model should be applied at the subplot scale (Bohlman and Pacala, 2012). Thus, tree canopy status within plots was classified at the ≈ 400 m^2 subplot scale, for which subplot information was available for 106 plots plus four plots with similar subplot size (385 m^2; 450 m^2, 416 m^2 and 416 m^2). The size of the subplots used here is within the optimum plot size for predicting canopy status according to comparisons between the ITD model and ground-based and satellite data in Central America (Bohlman and Pacala, 2012).

6.2.4 Wood density

I obtained information on wood density from the Wood Density Database (Chave et al., 2009;Zanne et al., 2010). These values were assigned to each tree based on the mean wood density of the species. When species-level wood density was not available or the tree was not identified to the species level, the mean wood density of the respective genus or family was applied to the tree (Baker et al., 2004b;Flores and Coomes, 2011). If no wood density was available for a specific family or if the stem was not identified to the family level, the mean wood density of all dicots of the plot was applied to that tree instead (Lewis et al., 2009b;Brienen et al., 2015).

6.2.5 Analytical approach

I investigated mean linear trends of different size-structure parameters across the Amazon Basin: mean tree basal area, median tree basal area and Gini coefficient, scaling exponent (α), mean tree basal area within each size class and for canopy status. First, the linear trends for the individual plots were calculated as the linear slope of an ordinary least squares regression (OLS) of the size-structure parameters as a function of time (the date when the census took place). Then to test whether the overall pan-Amazonian slopes differ from zero, bootstrapped mean and 95% CI were obtained by randomly resampling values of plot-level trends, with replacement, across all plots 10,000 times (Feeley et al., 2011a;Fauset et al., 2012). These analyses were repeated in relative terms, where size-parameters were divided by the size-parameter in the first census. I weighted plots by the square root of plot area times the monitoring period, to reduce the influence of potential stochastic changes, which are most likely to affect small plots and plots monitored during short monitoring periods (Lewis et al., 2009b;Brienen et al., 2015).

6.2.6 Testing for alternative drivers of change in tree size

Aiming to falsify the hypothesis that alternative mechanisms may lead to an increase in asymmetric competition, I analysed the influence of trends in stem density on changes in mean basal area and investigated the association between trends in tree size and trends in wood density.

To analyse whether the changes in mean tree size are a consequence of reductions in stem density, thus not actually reflecting an increase in size, I estimated the trends in the number of stems for the whole stand and for each of the size classes and canopy status. The trends in mean tree size were then calculated as described above, but (1) using the number of stems in the first census as a denominator and (2) using initial basal area as numerator in each census. Keeping stem density or basal area constant allows me to understand which of the two has a greater contribution to the variation in mean tree size.

I then tested whether changes in tree size are a consequence of forest recovery. First, I tested for the relationship between the trends in mean wood density and mean tree size per plot using an OLS regression and the Kendall's τ coefficient of correlation, under the assumption that if plots are experiencing a successional process, an increase in tree size will be accompanied by an increase in wood density. Second, I investigated whether changes in mean tree size are widespread, stronger at or restricted to plots with smaller mean basal area, where supposedly it is more likely that the forest would be undergoing recovery. This was done by fitting an OLS regression considering the trends in basal area as function of initial basal area.

6.3 Results

6.3.1 Trends in tree-size across the Amazon

Trees are getting bigger across the whole domain of lowland South American forests sampled here (Figure 6.1). In terms of cross-sectional area, mean tree size has increased at a rate of 152 $mm^2\ y^{-1}$ (95% CI 114; 193), which represents a 3% gain per decade in relation to their initial size which averaged 47,835 mm^2 (95% CI 46,315; 49,399). The increase is also observed for median tree size (i.e. bottom 50% smallest trees) at a rate of 41 $mm^2\ y^{-1}$ (95% CI 24; 57), or 2% per decade considering initial median of 21,705 (95% CI 21,237; 22,197).

Larger trees gained more in absolute terms: the increase in mean tree size was more than three times the increase in the median tree size (Figure 6.2; Table 6.1), resulting in a greater inequality between large and small trees across the Amazon. This is confirmed by a significant increase in the inequality as measured by the Gini coefficient of $5\text{x}10^{-4}$ (95% CI 3 $\text{x}10^{-4}$; 7 x 10^{-4}), or 1 % per decade (Figure 6.2; Figure 6.3).

The disproportional gain by large trees caused shifts in the tree-size class distribution, with scaling exponent (α) decreasing by 2% per decade, resulting in shallower power-law curves (Table 6.1, Figure 6.2, Figure 6.4 shows an example for one plot). The power-law explained the distribution of the data significantly for the majority of the censuses (58 %) and was fitted above a minimum diameter averaging (229 mm).

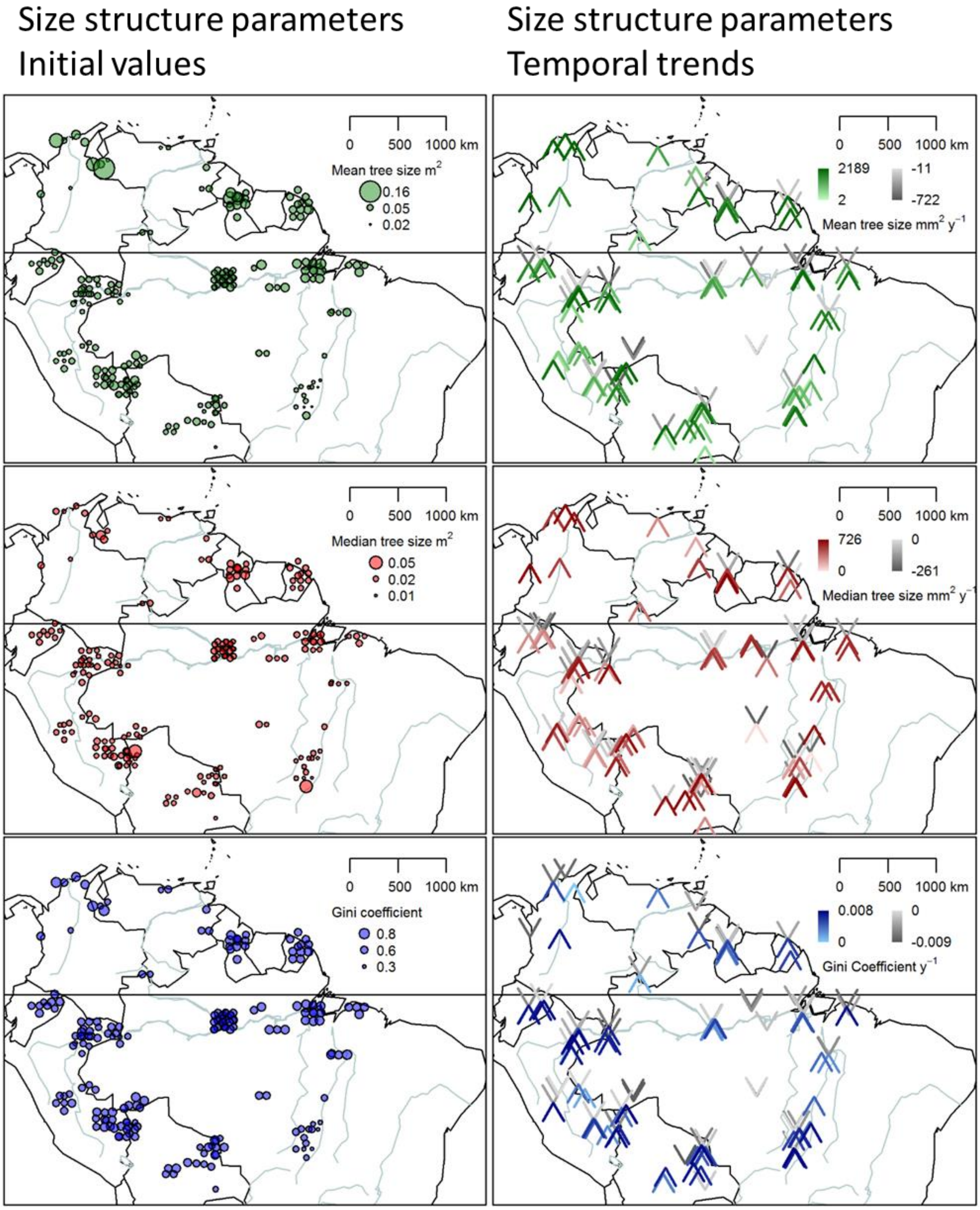


Figure 6.1 – Spatial distribution and trends of mean and median tree size and Gini coefficient across Amazonian tree inventory plots. Structure analyses uses 200 plots in 79 sites, dynamic analyses uses the subset of these which have at least 2 years of monitoring (mean 13 y^{-1}) since 1985 (194 plots, 74 sites). Note that the increase in each of these parameters is observed across the whole basin.

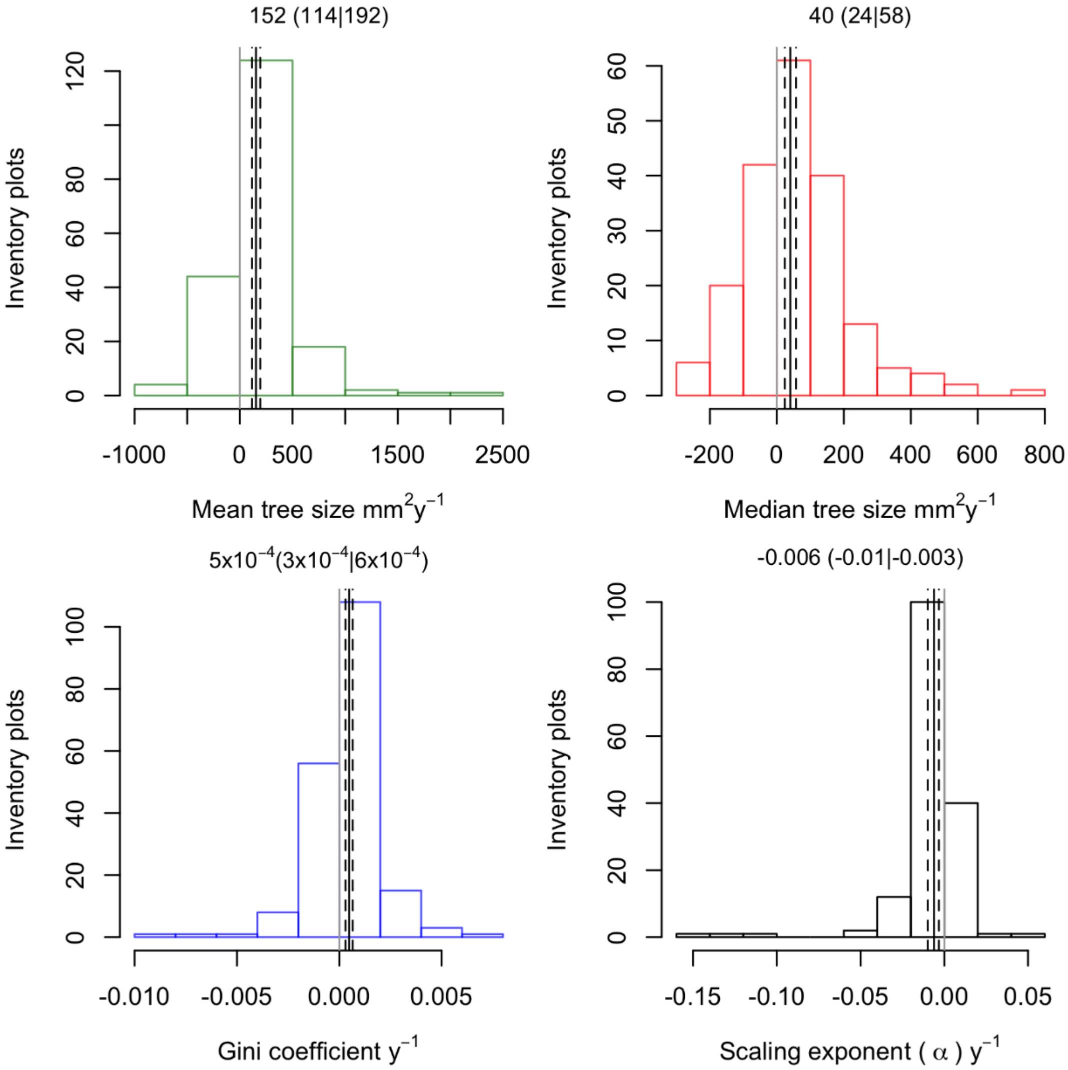


Figure 6.2 - Histograms of linear slopes for size structure parameters in 194 inventory plots across tropical South American mature forests. Trends in mean, median, Gini coefficient of tree basal area in each plot and the scaling exponent α. Black vertical lines represent overall bootstrapped mean (solid lines) and 95% CI (dashed lines). Mean trend and 95% CI (in brackets) are shown on the top of the figure.

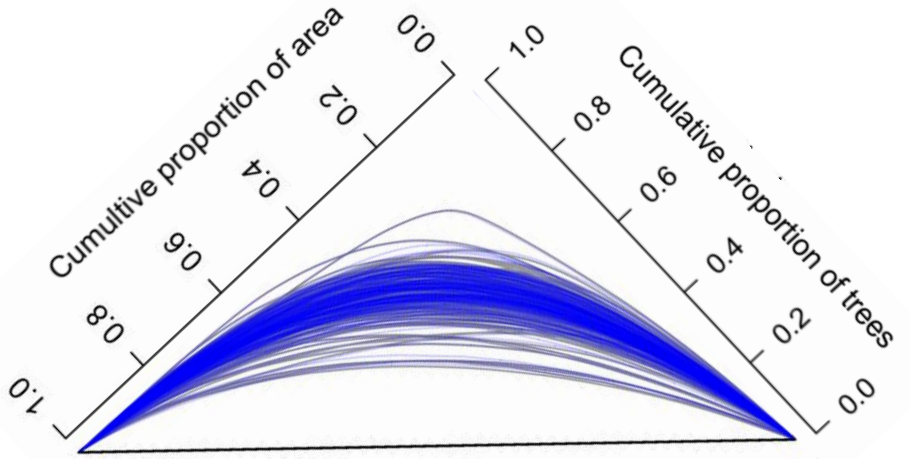


Figure 6.3 - Lorenz curves of inequality for each plot in the initial (grey) and final (blue) censuses. Black line represents hypothetical situation where all trees occupy the same space.

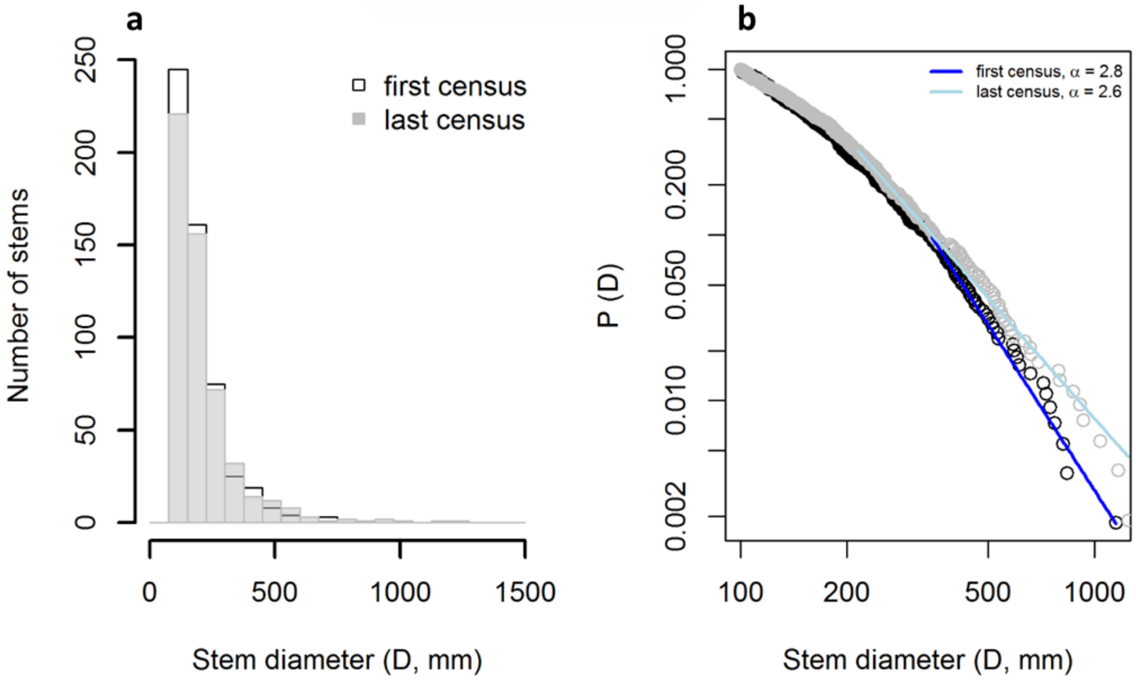


Figure 6.4 – Example of shifts in tree size-frequency distribution in one Amazonian inventory plot (Tambopata 05). (a) Size-frequency distribution for the first census (white) and last census (grey). (b) Cumulative distribution functions and fitted power law for first (black dots and dark blue line) and last (grey dots and light blue line).

Table 6.1 - Trends in tree size across the Amazon basin. Bootstrapped mean and 95% CI (in brackets) of tree size parameters. Note that the parameters indicate significant increases in size class and increases in inequality, although in relative terms different size classes and canopy status increase by the same rate.

	Mean (t_0)	Absolute trend	Relative trend (%)	N (plots)
Mean (mm^2)	47,831 (46,349|49,412)	152 (114|192)	0.3 (0.3|0.4)	194
Median (mm^2)	21,706 (21,244|22,197)	41 (24|58)	0.2 (0.1|0.3)	194
Total basal area (m^2)	45 (32|63)	0.1 (0.05|0.2)	0.3 (0.2|0.4)	194
Tree size distribution				
Gini Coefficient	0.57 (0.56|0.57)	5×10^{-4} (3×10^{-4}| 7×10^{-4})	0.09 (0.06|0.13)	194
Scaling exponent (α)	2.7(2.6|2.7)	-0.006 (-0.01|-0.003)	-0.2 (-0.3|-0.1)	160
Size classes				
< 200 mm	15,607(15,525|15,689)	14 (8|20)	0.09 (0.05|0.13)	194
200 - 399 mm	59,690(59,241|60,123)	19(-5|44)	0.03(-0.01|0.08)	194
≥ 400 mm	258,514(251,258|265,907)	467 (254|673)	0.2 (0.1|0.3)	194
Canopy status				
Overstorey	82,075(75,036|89,887)	249(108|396)	0.4 (0.2|0.6)	110
Understorey	19,960(18,663|21,345)	62 (35|90)	0.3 (0.2|0.5)	110

Table 6.2 – Trends in stem density across the Amazon basin. As table 6.1 but for stem density.

Stem density	Mean (t_0)	Absolute trend
Total n. of stems	932(678|1253)	-0.2 (-0.8|0.4)
N. stems < 200 mm	584(430|782)	-0.4 (-0.8|0.1)
N. stems 200 - 399 mm	273(198|367)	-0.1 (-0.4|0.2)
N. stems ≥ 400 mm	76(51|109)	0.2 (0.1|0.4)
Overstorey	603(345|959)	-0.1(-0.6|0.5)
Understorey	305(273|336)	-1.5(-2.3|-0.6)

6.3.2 Winners are taking most but not all

Despite the increase in inequality within the communities, the increase in tree size was observed across the whole community (Table 6.1). Mean tree size increased significantly for the smallest (< 200 mm D) and largest (≥ 400 mm D) size classes, and also increased for both understorey and overstorey trees (Table 6.1; Figure 6.5), with gains being significantly greater for larger size classes and canopy trees (Table 6.1; Figure 6.5; Appendix 6.2). However, when calculated on a relative basis, the increase in size of light-supressed trees was of the same order of magnitude as the canopy trees exposed to light. The change in mean tree size did not differ between trees < 200 mm D and larger size classes (Table 6.1; Appendix 6.2) or between overstorey and understorey trees (Figure 6.5; Table 6.1).

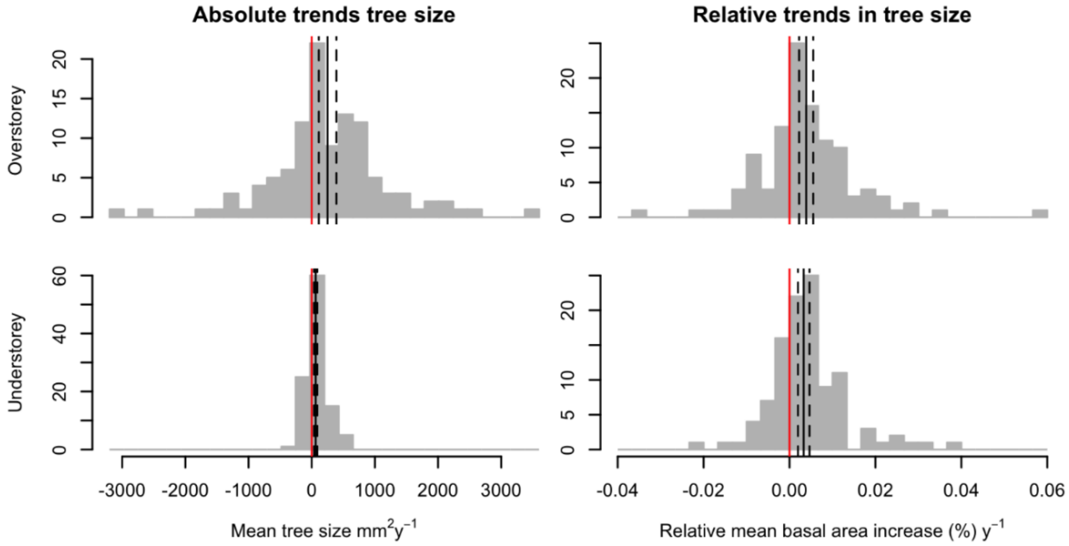


Figure 6.5 - Histograms of linear slopes of absolute and relative change in mean tree size in Amazon plots as a function of time within canopy. Comparison between trends in tree size within different canopy stratum. Black solid line and dashed lines represent bootstrapped mean and 95% CI, zero is shown by the red line. Canopy stratum was defined using the Ideal Tree Distribution (ITD) model (Purves et al., 2007). Note that trends in tree size for overstorey and understorey differ in absolute but not in relative terms.

6.3.3 Alternative drivers of change in tree size

For the overall community, the number of stems did not change significantly over time (Table 6.2). There were trends towards fewer small and/or understorey stems and more large/overstorey trees, but these were only occasionally significant (Table 6.2).

The trends in basal area were more important than stem density in determining the increase in mean tree size. After controlling for any change in stem density, the gain in mean tree size did not differ significantly from the actual trends in mean size observed for the 194 plots (115 mm^2 y^{-1} 95% CI 75; 154); whilst when keeping basal area constant the trends were significantly smaller (50 mm^2 y^{-1} 95% CI 9; 94) than the actual trends in mean tree size (Figure 6.2; Figure 6.6; Table 6.1).

No significant relationship was found between the increase in mean tree size and trends in wood density (Figure 6.7) (R^2 = 0.004 P=0.4; Kendall's τ = 0.01; P= 0.8). Finally, while tree size increased across the Amazon, wood density changes were evenly distributed around a zero mean (95% CI -4.8×10^{-5}; 1.2×10^{-4}). Additionally, the increase in mean tree size was observed even in forests with the highest mean tree size, which was shown by the trend in tree size not being dependant on the initial mean tree size for each plot (R^2 = 0.01, P-value = 0.2) (Figure 6.7).

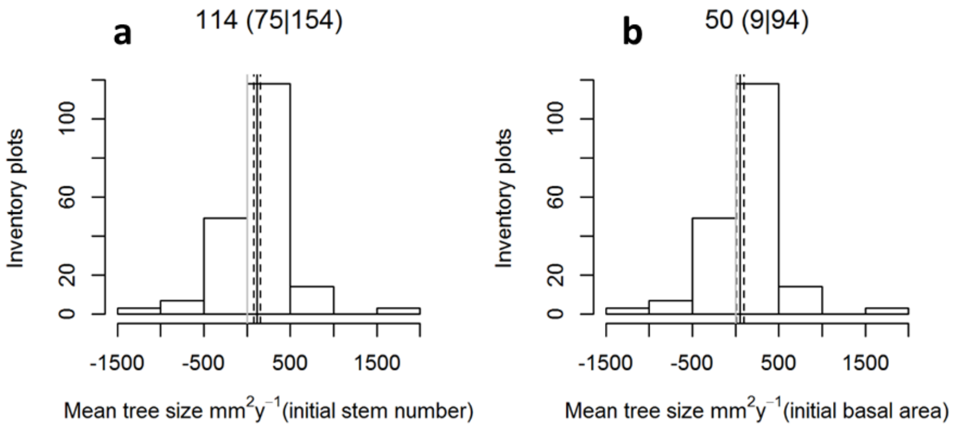


Figure 6.6 - Histogram of linear trends in mean tree size when controlling for change in stem number. Linear trends are estimated for the plot from mean tree size calculated by (a) maintaining the denominator (i.e. number of trees) constant as the number of trees in the first census and by (b) controlling for changes in basal area by using the initial basal area of each plot as a numerator. Bootstrapped mean and 95% CI are shown in black solid

and dashed lines respectively. Note that trends in tree size persist after controlling for potential decreases in stem density, but are significantly smaller when keeping basal area constant.

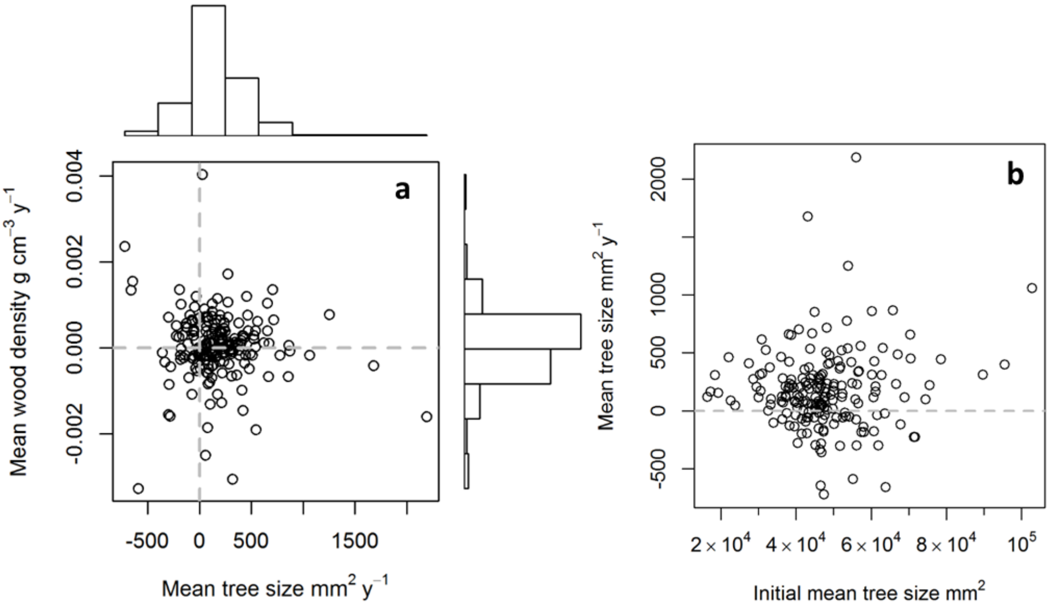


Figure 6.7 - Testing for the drivers of asymmetric competition. (a) Relationship between annual change in mean tree size and annual change in wood density $R^2 = 0.004$ P=0.4; Kendall's tau = 0.01; P= 0.8. If forests were under late successional recovery, an increase in mean tree size would be associated with an increase in wood density. Note that whilst mean tree size increases in the majority of plots, wood density changes are distributed around a zero mean: 3.5x10^{-5} g cm^3 y^{-1} (95% CI -4.8 x10^{-5}; 1.2x10^{-4}). **(b)** Relationship between mean initial tree basal area and trends in mean tree size per year. Note that the increase in tree size was observed regardless of the initial mean basal area (R^2 = 0.01, P-value = 0.2).

6.4 Discussion

Here I show an increase in mean tree size, measured as a change in tree basal area across the Amazon within the last 30 years. The increase in size was observed throughout the whole tree community, however, large and overstorey trees showed greater absolute gain in size than small and understorey trees. As a consequence, the inequality between large and small trees also increased, with a larger proportion of total area being occupied by large trees. Surprisingly, despite the greater absolute increase in tree size within large trees, in relative terms the mean tree size of large and small trees has increased at the same rate. These results are consistent with both: a hypothesised resource driven boost benefitting larger trees and increasing asymmetric competition, and the idea that the growth suppression among smaller trees has been alleviated, as a consequence of elevated CO_2.

Ecological theory predicts that under greater resource availability the competition for light becomes more important and large trees should have an advantage (Coomes and Grubb, 2000;Coomes et al., 2011). Confirming the predictions from the *winner takes all* hypothesis I observed that the general increase in tree size across the Amazon is mainly driven by largest trees gaining (Figure 6.2; Table 6.1). The disproportionate increase within large trees caused a shift in the size-frequency distribution curves, which have become shallower, with the scaling exponent (α) decreasing in most plots (Table 6.1; Example Figure 6.4), and an increase in the inequality between the area occupied by large and small trees, as shown by the increase in the Gini coefficient (Table 6.1; Figure 6.2). This indicates that greater resource availability has been increasing aboveground competition. The findings are consistent with recent evidence that growth does not stop at large sizes (Stephenson et al., 2014) and evidences the importance of height during ecological competition (King, 1990;Falster and Westoby, 2003)

The increase in asymmetric competition observed here does not characterize late successional recovery. Whilst the absolute mean tree size of the population increased over time, wood density (Figure 6.7) did not show significant changes, indicating that a substitution of pioneer to late-successional taxa (Chave et al., 2008) is not observed across the basin. Moreover, if increases in mean tree size were a consequence of late succession, we would expect the trend to be stronger in plots where basal area is smaller. This was not shown by the data, which demonstrate no relationship between mean tree size and the increase in tree size (Figure 6.7). However, it is not possible to reject the hypothesis that there may be some influence of succession on the data, as (1) overall mean tree size increase, although not significant, is weaker when controlling for the change in stem density; and (2) in some plots the increase in tree size is associated with an increase in wood density; and (3) stem density declined in the understorey trees and increased in the largest trees (>400 mm D). Indeed, gap openings are important components of tropical forest dynamics (Farrior et al., 2016) so some plots for some of the time are expected to be recovering from such disturbances (Espírito-Santo et al., 2014).

Therefore, the results presented here imply that CO_2 fertilisation is the most parsimonious explanation of the results, and recovery from a past Amazon-wide disturbance event is very unlikely to be a major driver of changes in tree size across the Amazon.

The winner takes all hypothesis is not sufficient to explain the trends in size across the Amazon. Although large trees increased the most in absolute terms, in relative terms the increase in tree size did not differ between the largest and the smallest size classes or between canopy strata (Figure 6.5; Appendix 6.2; Table 6.1). If increasing asymmetric competition for light alone were driving structural changes, then the suppression on understorey trees should also intensify (Weiner, 1985), and small size classes would not show changes in mean size. The observed relative gains within smaller and understorey trees can be explained by predictions from ecophysiology that posits that additional atmospheric CO_2 will tend to alleviate suppression of understorey trees, releasing them from a negative carbon balance (Valle et al., 1985;Long and Drake, 1991;Körner, 2006;Lloyd and Farquhar, 2008). Such suppression release as a consequence of greater CO_2 concentrations has been observed in experiments (Wong and Dunin, 1987;Würth et al., 1998;Granados and Korner, 2002). However, to my knowledge, this is the first time that evidence of this mechanism is demonstrated within forest stands. Therefore this evidence supports the hypothesis that greater atmospheric [CO_2] increases carbon uptake in tropical forests (Lewis et al., 2009b;Brienen et al., 2015). In line with the potential suppression release within small understorey trees, previous studies reported an increase in recruitment rates across the Amazon (Phillips and Gentry, 1994;Brienen et al., 2015), suggesting that the alleviation of light suppression may also be occurring for smaller trees (< 10 cm D).

The results shown here match the expectations from the hypothesis that increased CO_2 is an important driver of biomass dynamics (Lewis et al., 2004a;Lloyd and Farquhar, 2008;Lewis et al., 2009b), emphasizing the capacity of the Amazon intact forest to accumulate carbon. The findings also show the influence of higher CO_2 concentrations over the ecology of tropical forests. These results are consistent with the findings from chapter 5 that show that large taxa have been gaining over time. Furthermore, the results evidence that the sink activity of Amazonian forests is mainly driven by the increase in size of the largest trees.

7

Synthesis and Conclusions

7.1 Research synthesis

This thesis investigated the impact of recent environmental changes on the functional and floristic composition of Amazonian tree communities. My main aim was to describe functional and floristic changes across the Amazon and to distinguish between the influences of various potential drivers of these changes, e.g. the increase in atmospheric CO_2 concentration, the increase in moisture stress, the rise in temperature and the increase in hunting pressure or previous disturbances.

The first two analytical chapters of my thesis were dedicated to understanding the influence of the lack of moisture on species distribution, so that I could investigate how it influences communities through time. The results from spatial analyses showed that, whilst 52% of the species in the Western Amazon are significantly associated to wet conditions, only 6% are significantly linked to dry conditions.

Overall, the results presented in this thesis showed that over the past 30 years Amazonian tree communities have changed in terms of functional and floristic composition and also in terms of their structure. The abundance of large and dry-affiliated taxa has increased. At the same time that the forest had changed floristically, it had also shifted in terms of structure, with mean tree size increasing over time and large trees having a disproportionate advantage over smaller trees. However, small understorey trees still demonstrated a positive and significant increase in size, which in relative terms did not differ from the increase observed in large trees. These findings indicate that water-stress and increases in resources are together the most likely drivers of the changes in Amazonian dynamics. Combining the results from the spatial and temporal analyses allow us to conclude that the detected shift in the community favouring dry-affiliated taxa could lead to the extinction of small ranged wet-affiliated species.

In the following paragraphs I summarize the main findings of each analytical chapter and how they contributed to achieve the aims of this thesis.

7.1.1 The majority of the Neotropical tree taxa are restricted to wet areas

To understand the influence of the increasing drying trend on community composition of Amazonian forests I first investigated the influence of precipitation on neotropical forest taxa across space. I assessed data from 531 inventory plots of closed canopy forest distributed across the Western Neotropics. The results showed that the distributions of tree taxa are nested along the precipitation gradient. Thus, whilst dry-tolerant taxa are disproportionally widespread across the precipitation gradient, with most reaching even the wettest climates sampled, 52% of the species are restricted to extremely wet areas, which never suffer water deficit. This pattern highlights the importance of climate controlling the distribution of tree taxa in the world’s most species-rich forests. The large number of species restricted to wetter conditions strongly indicates that an increased frequency or intensity of drought could severely threaten biodiversity in this region.

Considering the influence of precipitation on the distribution of tropical taxa I developed an index of water-deficit affiliation (WDA). This index combined information on species occurrence and abundance along different precipitation conditions and was used to characterize the climatic niche of 1818 species, 544 genera and 104 families. The WDA represents the most favourable precipitation condition where each taxon can be found.

7.1.2 Biogeographical distribution predicts drought-induced mortality

Understanding how neotropical forests will respond to changes in climate is a significant challenge when considering the high taxonomic diversity in this ecosystem. The effects of climate on forest communities could be relatively easily assessed if information on drought-tolerance of these many taxa could be summarized in a single variable. Thus, I tested whether the distribution of genera along a water deficit gradient – ‘water deficit affiliation’ (WDA), developed in chapter 3 - could predict drought-induced mortality of neotropical taxa in experimental and natural droughts. For these analyses I compiled all drought experiments available in the literature for neotropical rainforests and from a large plot with extremely detailed drought observations. The analyses showed that genera affiliated to wetter precipitation regimes biogeographically, tended to show higher drought-induced mortality. Tree mortality was higher under natural or artificial drought than in the non-drought controls, and the difference between these two treatments became more evident with increasing drought length. This pattern was consistent across the experiments regardless of their geographical location, which indicates that different populations within the same taxon are likely to respond similarly to changes in climate. These results indicate that WDA has a predictive value and therefore is a valuable tool, not only to assess the effect of previous droughts to Amazon communities, but also to potentially help to predict the impacts of forecast future droughts on tropical forests.

7.1.3 Floristic composition follows changes in climate in the Amazon

I investigated whether the floristic and functional composition of Amazonian forests are changing across the Amazon over the last 30 years, a period when dry season intensity has increased throughout the basin. I used information from 108 plots, the largest sample size used to assess this question to date. The results showed that, firstly, during this period, Amazon communities have become increasingly dominated by large-statured taxa, while dry affiliated genera became increasingly prevalent among the recruits. Also, the mortality of trees with low wood density marginally increased. The mortality of stems of wet-affiliated genera increased in those plots where the intensification of the dry season was stronger. The observed functional shifts were consistent with subtle climate and resource-driven compositional responses already occurring in Amazonian communities. I showed further that Amazonian communities are lagging behind the changes in climate, with no change detected for the whole community in terms of climate affiliation, and the increase in dry-affiliated recruits occurring slower (-0.5 mm y^{-1}) than the shifts in climate (-1.1 mm y^{-1}). Thereby, although the shifts within the recruits indicate a potential resilience of these forests to changes in climate, the pace on which it is occurring demonstrate the systems inertia. Moreover, if the shifts towards a dry-affiliated communities - as detected by the shifts in the recruits - persists we may witness the extinction of wet-affiliated taxa.

7.1.4 Changes in size-structure follow the predictions expected under increasing CO_2

The increase in atmospheric CO_2 is expected to affect the size structure of tropical forest communities by: (1) stimulating tree growth so that mean tree size will increase and large trees will have a greater absolute advantage, as a consequence of the asymmetric competition for light; (2) releasing some understorey stems from light-suppression, allowing them to gain in biomass and basal area relative to their initial size. I tested for these predictions by analysing 30 years of tree inventory data across 194 Amazonian plots. The results confirmed both predictions. Mean basal area per tree increased by 152 $mm^2\ y^{-1}$ (95% CI 114; 193), and with the size of the smallest 50% also increased, but more slowly by 41 mm y^{-1} (95% CI 27; 57), which represents an absolute advantage for larger trees. At the same time, whilst large trees clearly had the greater absolute increase in size, the relative increase in size was similar for small and large canopy size classes, and for understorey and canopy trees. These results are consistent with the hypothesis that the increase in atmospheric CO_2 concentration is driving the dynamics of forest communities via two apparently contradictory mechanisms, i.e. both by increasing asymmetric competition for light, favouring large trees, whilst also releasing small understorey trees from light-suppression.

7.2 Fingerprinting drivers of forest dynamics in the Amazon

One of the main objectives of this thesis was to use information on the dynamics in functional and floristic composition to distinguish between different drivers of changes in the dynamics of Amazonian forests and more specifically the increase in aboveground biomass (Table 2.1 Chapter 2). The results from chapters 5 and 6 can be used in the fingerprinting approach. However, to distinguish between the contributions of different drivers, it is important to integrate the results from the floristic analyses developed in this thesis with recent findings from the literature on other aspects of the forest dynamics (Table 7.1).

7.2.1 The results provide support for the CO_2 fertilization hypothesis

The increase in resources is expected to stimulate photosynthesis and accelerate growth (Lloyd and Farquhar, 2008;Malhi et al., 2011;Huntingford et al., 2013). The results presented in this thesis are consistent with the expectations that would occur under an increase in resources. Mean tree size increased and both large trees and large taxa had a greater advantage. Small trees, some of which are expected to be close to their light compensation point, have been apparently released from light-suppression, as they show an increase in size and there is greater biomass of understorey trees now than in the 1980s. The evidence observed here is consistent with evidence from the analyses of forest dynamics at the stand level found in the literature (Table 2.1, 2.2 and 7.1). Aboveground biomass has repeatedly shown to be increasing across the Amazon (Phillips et al., 1998;Baker et al., 2004a;Brienen et al., 2015), as has wood productivity (Brienen et al., 2015), both of which are expected responses to an overall increased in resources for plant growth. Furthermore, both mortality and recruitment rates have been increasing over time in Amazonia for at least 30 years (Brienen et al., 2015) the stem dynamics (turnover) confirming the observations that forest turnover have been increasing in tropical forests (Phillips and Gentry, 1994).

7.2.2 Climate is likely to be driving changes in Amazonian communities

The detected changes in community composition are consistent with the hypothesis that changes in the precipitation regimes are affecting forest dynamics. I showed the trend towards increased dry season intensity to be affecting the inventory plots analysed within the Amazon. Consistent with the observations of changes in climate, the analyses of floristic composition showed an increase in dry-affiliated recruits across Amazonia (Chapter 5). Furthermore, in the areas where the intensification of the dry season was stronger, an increase in the mortality of wet-affiliated trees was detected (Chapter 5). Both observations confirmed that the increasing drying trend is likely to be causing changes to Amazonian communities.

These trends were expected from the observation that only a subset of taxa was found in dry areas – with most of the Amazon taxa not present in the drier, more seasonal forest communities - which indicates that drier conditions probably exert real physiological limits on the majority of neotropical tree taxa (Chapter 3). The impact of droughts on tropical forests has further support in the literature. Observations have shown that tree mortality increases following drought periods in the Amazon (Phillips et al., 2010;Brienen et al., 2015;Feldpausch et al., 2016). Productivity has also been shown to decline during drought periods (Gatti et al., 2014), so that biomass gain tends to turn negative for a few months (Phillips et al., 2009;Feldpausch et al., 2016). These observations are also supported by through-fall exclusion experiments in the Amazon (Nepstad et al., 2007;da Costa et al., 2010).

7.2.3 Late succession hypothesis is unlikely to be a major driver of changes in Amazonia

If forests are going through late succession, we expect a recovery towards an original higher biomass state (Odum, 1969;Wright, 2005). This process of net biomass gain should be combined with a floristic turnover from fast-growing pioneers to slow-growing shade tolerant species (Connell and Slatyer, 1977). Such substitution and intensified competition for space, light and other resources will imply in an increase in wood density, a decrease in the wood productivity of the stand, a decrease in recruitment and a decrease in tree mortality as the forest stand approaches slower, mature-phase conditions (Lewis et al., 2004a). However, these predictions go against evidence from the Amazon. Firstly, although some of the potential signatures of late succession have been observed in this thesis - notably the increase in mean tree size (Chapter 6) and the increase in abundance of large taxa (Chapter 5) -, there is no overall trend in wood density within Amazonian communities (Chapter 5), which indicates no floristic substitution from pioneer to shade-tolerant taxa. Secondly, I showed that the increase in size, although dominated by larger trees, is not exclusive to them, and that in relative terms the increase within smaller and understorey trees and size-classes is similar to the increase in size observed within the large and canopy trees (Chapter 6). Finally, stand-level analyses showed increases both in stand productivity and in stem recruitment across the Basin (Phillips and Gentry, 1994;Brienen et al., 2015), in contrast to expectations of late-successional self-thinning stand approaching maximum height competition (Chambers et al., 2004).

A related alternative hypothesis is that forest plots are not able to capture mortality across the Basin (Fisher et al., 2008;Chambers et al., 2013) and Amazonian forests could be actually recovering from disturbances caused by gap dynamics (van der Sande et al., 2016). However, large scale disturbances are rare and showed to be unlikely to be driving changes in forest dynamics (Gloor et al., 2009;Espírito-Santo et al., 2014). Moreover, analyses using inventory plots have detected an increase in the mortality across the Basin (Brienen et al., 2015), which would not be expected if the areas sampled were recovering from disturbances.

Therefore, by combining the results presented in this thesis with earlier observations made of pattern and trend in stand-level dynamics, I conclude that the late successional hypothesis is unlikely to be a major driver of changes in the Amazonian forests.

7.2.4 There is no evidence that hunting is affecting the composition of intact Amazonian forest tree communities

Recent simulations have indicated that hunting could lead to a biomass collapse in tropical forests with the elimination of large, high wood-density trees which have zoochoric seeds (Bello et al., 2015;Peres et al., 2016). Although this thesis was not designed to address this question, the analyses here were certainly adequate to test whether any of these processes have yet had a notable impact on Amazon forest tree communities. The results did not show the expected increase in low-wood density and smaller trees as predicted by the hunting hypothesis (Chapter 5). This evidence is consistent with the literature on Amazonian dynamics that shows structurally-intact forests as a carbon sink not losing biomass (Brienen et al., 2015). However, although hunting is shown not to have major impacts on the structure of intact forests in the Amazon, the results here do not rule out the importance of hunting on disturbed forests or areas closer to anthropogenic edges (Peres and Lake, 2003). Thereby, the effects of hunting could occur in a much larger time scale than the other drivers assessed here.

4.2.5 Synthesis of the fingerprinting approach

Considering the large spatial extent and the complexity of the system studied, it is unlikely that a single, isolated mechanism would be able to explain the processes observed across the whole Amazon. Most likely, the dynamics of the Amazon should be a consequence of several processes, where each of the hypothesized drivers may be playing a role together with possibly other unknown factors. Thereby, whilst all competing hypothesis are likely to have some degree of influence on the forests dynamics, following the philosophy of the multiple-working hypothesis (Chamberlin, 1890;Elliott and Brook, 2007), the fingerprinting approach intends to get closer to the most parsimonious set hypotheses, explaining the changes observed in Amazonian forests. For instance, the forests studied in this thesis could have been disturbed at some point in its history, however the results presented here in combination with studies at the stand-level are not consistent with the disturbance hypothesis being a basin-wide driver of change (Table 7.1). The combination of environmental data and the temporal patterns observed across the basin presented in this thesis and in previous research allow me to conclude that the increase in atmospheric CO_2 and the increase in aridity are both sufficient and necessary to explain the observed alterations in the ecology of the Amazon.

Table 7.1 - Fingerprinting drivers of changes in Amazonia updated with the results from this thesis. As in Table 2.2 - Chapter 2, trends observed in this thesis, in red (within-stand), and reported in the literature (stand-level). In brackets the most likely outcomes when there is not strong evidence supporting the predictions or not known prediction. In bold the matching observations. OBS column show the number of predictions matching observations. AGB = above-ground biomass; PS = potential size; WDA = water deficit affiliation; WD = wood density.

	Chapter 5			Chapter 6			Stand-level studies					
Hypotheses	PS	WDA	WD	Mean tree size	Large trees	Small trees	AGB	Productivity	Recruitment rate	Mortality	Stem density	OBS
Climatic												
Drying trend	**(Larger)**	**Drier**	(Higher)	**Increase**	**Increase**	Decrease	Decrease	Decrease	Decrease	**Increase**	?	~5
Increase in frequency of extreme droughts	(Smaller)	**Drier**	(Higher)	Decrease	Decrease	?	Decrease	Decrease	Decrease	**Increase**	?	2
Increase in temperature	Smaller	**Drier**	Higher	Decrease	Decrease	**Increase**	Decrease	Decrease	Decrease	**Increase**	?	~3
Atmospheric												
CO_2 fertilization: Winners take all	**Larger**	No change	(Lower)	**Increase**	**Increase**	Decrease	**Increase**	**Increase**		**Increase**	Decrease	6
CO_2 fertilization light suppressed do better	(Smaller)	No change	(Higher)	No change		**Increase (relatively)**	**Increase**	**Increase**	**Increase**	Decrease	**Increase**	5
CO_2 increase WUE	**Larger**	Wetter	(Lower)	**Increase**	**Increase**		**Increase**	**Increase**	**Increase**	Decrease	Decrease	6
Anthropogenic												
Hunting	Smaller	No change	Lower	Decrease	Decrease	**Increase**	Decrease	No change	**Increase**		**Increase**	3
Late succession	**Larger**	No change	Higher	**Increase**	**Increase**	Decrease	**Increase**	Decrease	Decrease		Decrease	4
Observation	**Larger**	**Drier (recruits)**	**No change**	**Increase**	**Increase**	**Increase**	Increase	Increase	Increase	Increase	Increase	

7.3 Research implications

I showed that only a very low proportion of Amazon tree taxa are dry-affiliated (Chapter 3) and that those that are wet-affiliated occur in a very small range of precipitation conditions. This result highlights the importance of the wettest forests in the Amazon and the Andes. These forests are the most tree species rich forests in the world (Phillips and Miller, 2002) and an important biodiversity hotspot for several taxonomic groups (Myers et al., 2000;Ceballos and Ehrlich, 2006;Finer et al., 2008). The findings of this thesis demonstrates that they also play a central role in the conservation of thousands of taxa constrained to the extremely wet conditions of this region (Chapter 3). Despite its great importance for biodiversity, this area is threatened by oil and gas extraction (Finer et al., 2008;Lessmann et al., 2016). The results of this thesis urge for the conservation of the Western Amazon as an important biodiversity hotspot and a unique habitat for a great number of Amazonian taxa.

In addition, the Western Amazon may be an important *refugia* under future environmental conditions. In Chapter 4 I showed that the biogeographical distribution of taxa mirrors their tolerance to drought events. Such observations indicate that forest in different locations of the Neotropics may respond in a similar way to an increase in water stress, with biogeographically dry-affiliated taxa gaining in abundance when compared to those that are wet-affiliated. So far, increasing drying caused an increase in the recruitment of dry-affiliated taxa, whilst in the areas where climate has become drier, the mortality of wet-affiliated taxa has increased. Thus, if this trend continues, wet-affiliated taxa would need to find *refugia* in wet areas of the Amazon. The most obvious *refugia* are the extremely wet areas in the Western Amazonia or areas at higher altitudes where the water-stress is alleviated by lower temperatures. These *refugia* are expected to be found mostly in Andean countries, where deforestation has been increasing as a consequence of pressure from gas and oil extraction (Asner et al., 2013;Lessmann et al., 2016). As national boundaries do not determine the boundaries of ecosystems, international agreements should be implemented to guarantee forest corridors that allow a potential migration of taxa to *refugia*. Indeed, there are some ecological corridors across the Amazon, for instance the Vilcabamba-Amboró that links biological reserves between Peru and Bolivia (Bennett and Mulongoy, 2006). However there is little information on how effective the existent corridors have been at actually protecting the biodiversity.

It was evident from the results in Chapter 5 that the responses of different taxa to changes in climate are likely to be extremely variable. Even taxa relatively similar in ecological terms and phylogenetically close, such as the palms *Euterpe* and *Iriartera,* show apparently opposite responses to the changes in climate (Figure 5.6 – chapter 5). To date, dynamic global vegetation models still represent tropical forests as only one functional group, which is expected to respond in the same way to variations in the environment (Huntingford et al., 2013). The results presented here urge for the implementation of a more realistic representation of tropical forests within these models so that we can better predict the responses of these forests under future scenarios (e.g. Sakschewski et al., 2016).

The results of this thesis contributed to the understanding of the drivers of biomass dynamics in the tropics. I showed that climatic changes and atmospheric CO_2 concentrations are together necessary and sufficient drivers of functional and floristic changes and therefore should play an important role in the biomass dynamics of tropical forests. Understanding the drivers behind the changes in forest dynamics has important implications in the understanding of the global carbon cycle and to the role of tropical forest as a global carbon sink. Tropical forests store ≈ 55% of the terrestrial carbon (Pan et al., 2011) and understanding the drivers of carbon dynamics in these forests is essential to predict the future of the terrestrial carbon stocks (Huntingford et al., 2013). The fact that forest dynamics are driven by higher CO_2 concentrations indicate a potential continuity for this stimulus as opposed to an expected pause if late succession was the main driver of plot-level observations (Wright, 2005). The influence of climate on forest dynamics could yet compromise the carbon accumulation capacity of these forests, especially with the increased mortality of wet-affiliated taxa. In Ghana, taxa turnover showed to protect carbon stocks (Fauset et al., 2012). In the Amazon, changes towards dry-affiliated taxa show to lag behind changes in climate (Chapter 5), which indicates that these forests may be less resilient than African forests.

7.4 Future research directions

In this thesis I assessed information from inventory plots across the whole Amazon to analyse potential shifts in functional and floristic composition. This methodological approach has the strength of sampling a large area across various environmental conditions, which allowed me to assess the trends in floristic composition for the Amazon. This type of information is unique and of extreme importance to the understanding of forest communities. However, the results presented here should be linked with more mechanistic approaches and physiological information allowing the prediction of the future of tropical communities.

This thesis focused on changes in floristic composition of intact lowland Amazonian communities. Although similar processes are expected to be driving tropical rainforests elsewhere (Lewis et al., 2009b), the dynamics of tropical forests differ among continents and floristic composition plays an important role on this variation (Banin et al., 2014). Research on floristic dynamics on a macroecological scale is needed outside the Amazon to identify the trajectories of biodiversity across the tropics. This kind of research is particularly challenging as it requires high-quality long term data with precise measurements and identification of the species. More researchers should be trained in the challenging task of identifying tropical species.

Within the Neotropics the challenge is to improve sampling and continue monitoring the plots currently installed. The sample size in this study was the largest yet used for a compositional analyses in terms of number of plots assessed. However, the analyses would still have benefited from more plots in sampling gaps, such as the Central Amazon. Sampling should also be intensified in different edaphic conditions. I restricted my analyses to *terra firme* forest, however, it is still unknown if and how other types of forests, such as communities in white sand and swampy areas are also shifting, and whether the changes vary across different types of forests. I noted that these areas are relatively poorly sampled, even when integrating the two largest data networks on Amazonian inventory plots. There is also missing information from the wettest areas of the Amazon. Combining ATDN and RAINFOR, only 18 plots are found under precipitation regimes higher than 3500 mm of annual rainfall in the Western Neotropics. Further research should try to focus on improving the sampling within these extremely wet forests, such as the Chocó in Colombia, the wet extreme in the Western Neotropical precipitation gradient.

I described Amazonian taxa regarding their affiliation to climate based on their distribution and abundance and I showed that climate affiliation is a valuable indicator of drought-tolerance. From these findings it would be interesting to understand the physiological mechanisms behind the climatic affiliations, i.e. which physiological characteristics provide the tolerance to dry conditions and whether these are the same for all dry-affiliated taxa. The next step to develop a more refined predictive formula for anticipating taxon-based impacts of climate change would be to collect data of more mechanistic traits, such as non-structural carbohydrates and hydraulic conductivity, which can tell us how different taxa deal with water-deficit. There has been a large collective effort to understand, for example, the mechanisms behind drought-induced mortality (e.g. Rowland et al., 2015), however so far we only know mechanistic details of a small proportion of the great number of species within the Amazon (e.g. da Costa et al., 2010) and this is based mostly on experimental work at only two sites. Potentially, focusing on clades along the climate affiliation spectrum, by investigating the difference in terms of physiological traits between dry and wet affiliated, could help to solve this problem.

Linked to the mechanistic understanding, it will be interesting to understand the evolution of these affiliations. For instance, in my analyses I observed that most Magnolidaes, a basal angiosperm clade, were restricted to wet conditions, which could indicate that the tolerance to dry environments is a recent adaptation. Remarkably, the fact that the great majority of groups are wet-exclusive indicates that dry-tolerance among tropical forest taxa is a relatively rare phenomenon. However, we still do not know how conserved this tolerance is within the phylogeny.

More detailed understanding of the dynamics of tropical forests will allow the improvement of models predicting the future of these ecosystems. The bridge between process-based models and functional biodiversity has only started to be built (Fyllas et al., 2014;Sakschewski et al., 2015;Sakschewski et al., 2016). The recently released Lund-Potsdam-Jena managed Lands with Flexible Individual Traits (LPJmL-FIT Sakschewski et al., 2015), predicted an Amazonian forest in Ecuador to be resilient to climate in terms of biomass when accounting for the turnover of functional composition. However, empirical data on the turnover of Amazonian species are scarce. This thesis contributes to increase the understanding of floristic dynamics, for instance, in Chapter 5 I showed the tempo of the functional and floristic turnover, which is a key parameter on these models. Thereby, future research should focus on implementing the current models using empirical data on forest dynamics, some of which was produced here.

7.5 Final remarks

In this thesis I showed the changes in functional and floristic composition in the last 30 years across lowland Amazonian forests. The characterization of species bioclimatic niches showed the vulnerability of most Amazonian taxa to moisture deficit. Analysing the actual shifts in Amazonian communities revealed that communities are shifting, with recruits becoming more dry affiliated and the mortality of wet-affiliated trees increasing, particularly where the drying trend was stronger. However, the detected turnover of species is so far lagging behind the changes in climate. The results showed a significant increase in mean tree size dominated by the increase in size of the largest trees, which mirrors the prediction from increased asymmetric competition. The increase in CO_2 concentrations is likely to have released small trees from light suppression, as these also showed a significant increase in size, in relative terms. The shifts detected are consistent with the hypothesized effects of increased atmospheric CO_2 concentrations and a stronger drying, and do not agree with late-successional recovery as a main drivers of Amazonian dynamics. The findings demonstrate that the Amazon may be resilient as dry-tolerant species may replace the most vulnerable ones. However, a future drying trend may eventually cause the extinction of the majority of Amazonian tree taxa which are shown here to be affiliated to wet conditions. This thesis advances our understanding on the ecology of tropical forests, by being the largest attempt to characterize changes in functional and floristic composition in the tropics. The results presented here showed the vulnerability of Amazonian biodiversity to changes in climate and should be applied to improve the process-based models.

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Appendices

Appendix 2.1 – Fingerprinting table (see table supplement 2.1 located in the back cover folder)

Appendix 3.1 Climatological water deficit (CWD)

To better estimate the water-stress within the Western Neotropics we used the maximum climatological water deficit (CWD) as a precipitation variable. CWD is the sum of water deficit (i.e. when precipitation is lower than evapotranspiration) values over consecutive months when the forest experiences water-deficit. Here we use the mean of the annual maximum values of CWD to characterize each plot. This variable was modified from the CWD of Aragao et al. (2007) and Malhi et al. (2009) by Chave et al. (2014) to account for local evapotranspiration. Values of local evapotranspiration were estimated by FAO (Allen et al., 2002) using the Penman-Monteith equation, rather than simply assuming 100 mm month^{-1} evapotranspiration for the whole area as was done by Aragao et al. (2007). The Penman-Monteith equation accounts for temperature, wind speed, relative humidity and solar radiation, and therefore may be expected to yield more precise estimates of water deficit. Chave et al. (2014) also modified the metric to account for a single dry season, i.e. including only the months where precipitation is lower than evapotranspiration.

Appendix 3.2 – Selection of sample units and data management

Our analyses were restricted to lowland *terra firme* forests to limit the effect of other possible variables on the forest's response to precipitation. Plots over 1000 m.a.s.l. were excluded from the analyses, as at higher altitudes temperature and consequently the atmospheric evapotranspiration demand are lower. Thus, at higher altitudes the reduced temperature mitigates the effects of low precipitation levels on tree physiology. In addition we excluded plots: (1) on the quartz-rich soils of white sand forests, as they exhibit low water holding capacity which intensifies the effects of dry periods for trees; (2) swamps and; (3) floodplain plots, where water-supply is locally enhanced. Areas that are very rarely flooded were included in the analyses provided that forests were mature, i.e. they included a normal gap-regeneration structural mosaic and had not suffered recent anthropogenic or stand-initiating disturbance.

Considering that different mechanisms may drive the distribution of trees and lianas, we focused our analyses only on free-standing stems. Also, following the conventions established for Gentry-plot sampling (e.g. Phillips and Miller, 2002), we include all species that have self-supporting stems > 10 cm diameter. This includes all emergent, canopy and understory trees, and a small number of large shrubs, coarse overgrown herbs (e.g., *Phenakospermum* in the Streliziaceae) and scrambling plants capable of self-support (e.g., *Salacia* in the Celastraceae).

We combined data from ForestPlots.net and ATDN data networks. ForestPlots.net (Lopez-Gonzalez et al., 2009;Lopez-Gonzalez et al., 2011) maintains a standardized data structure including stem size, while ATDN data lack stem size information. All data were imported into R version 3.1.1 (R Core Team, 2014), a metadata file was created with information from both plot sources (i.e. ForestPlots.net and ATDN) and checked for overlaps between different sources or plots with coinciding plot codes. ATDN data were accessed in May 2013 and ForestPlots.net data were last downloaded in December 2014.

Species names were checked and corrected following the Tropicos database using the Taxonomic Name Resolution Service (Boyle et al., 2013). Taxonomic standardization is not an easy task, nevertheless within our team there has been a substantial effort towards standardizing identifications. Thus, (1) intensive collection of species vouchers is an important part of RAINFOR field campaigns, as it was for Gentry, and for Phillips and ATDN collaborators; (2) cross-checking among plots is facilitated by the fact that ForestPlots.net includes online vouchers, with ca. 70% of plots in this study with vouchers available online to be checked by collaborators from different regions; and (3) where possible we have ensured the same botanist has visited multiple plots and herbaria to standardize identification. For instance, Abel Monteagudo, botanist co-author of this paper has participated in more than 200 field campaigns in Ecuador, Peru, Brazil, and Bolivia.

Table A3.2 a – Description of data sets used in this study. Plots are organized into larger groups (e.g. ATDN in which some RAINFOR plots are included). Larger groups are shown here in bold of which the subsequent non-bolded rows are subsets. WA= Western Amazonia; NWA = North-west Amazonia; SWA = South-west Amazonia; n = number of trees, D = measurement of diameter

Source	Geographical extent	Stem information	N plots	size (ha)
ATDN	**WA**	**n**	**272**	**1**
RAINFOR	WA	D, n	98	1
ForestPlots	**Lowland Neotropics**	**D, n**	**185**	**0.1-5**
RAINFOR	Lowland Neotropics	D, n	92	0.1-5
Phillips	NWA	D, n	07	0.1
Phillips	SWA	D, n	86	0.1
Gentry	**Lowland Neotropics**	**D, n**	**74**	**0.1**

Table A3.2 b – Total number of plots per sampling method. Columns represent plot size in hectares and rows indicate the method of sampling: (n) number of trees (D) measurement of diameter.

	0.1	0.2 - 0.48	0.5 - 0.9	1	1.2-5	**Total**
n	2	20	12	137	3	**174**
n,D	175	21	7	146	8	**357**
Total	**177**	**41**	**19**	**283**	**11**	**531**

Appendix 3.3 - Preliminary data exploration

We compared precipitation in the inventory plots analysed in this study with precipitation across all lowland forests in the Western Neotropics, testing whether our dataset provides a good sample of actual precipitation values for the whole area. For this, we created a mask delimiting the area referred to here as the Western Neotropics (Fig. A3.3.1). This mask combines information on potential neotropical forest from Hansen et al. (2003) and lowland areas (i.e. below 1000m of altitude). Elevation values were extracted from Jarvis et al. (2008). Additionally, we excluded the Guyana and Brazilian shields (based on layers from Feldpausch et al. (2011)) due to their strong geomorphological distinctiveness. Having delimited the area, we used GIS tools to obtain information on precipitation from every 1 km^2 within the Western Neotropics and performed t-tests comparing precipitation values within this area to precipitation in the sample used in this study.

Our sample represents well the variation in total precipitation along the Western Neotropics (Table A3.3). The mean and median of dry season intensity in our samples differ only slightly and insignificantly from the values for the whole Western neotropical forests (Table A3.3). For all precipitation variables the frequency of sample units and total area sampled along the precipitation gradient matches with the distribution of precipitation over the whole area (Fig. A3.3.2).

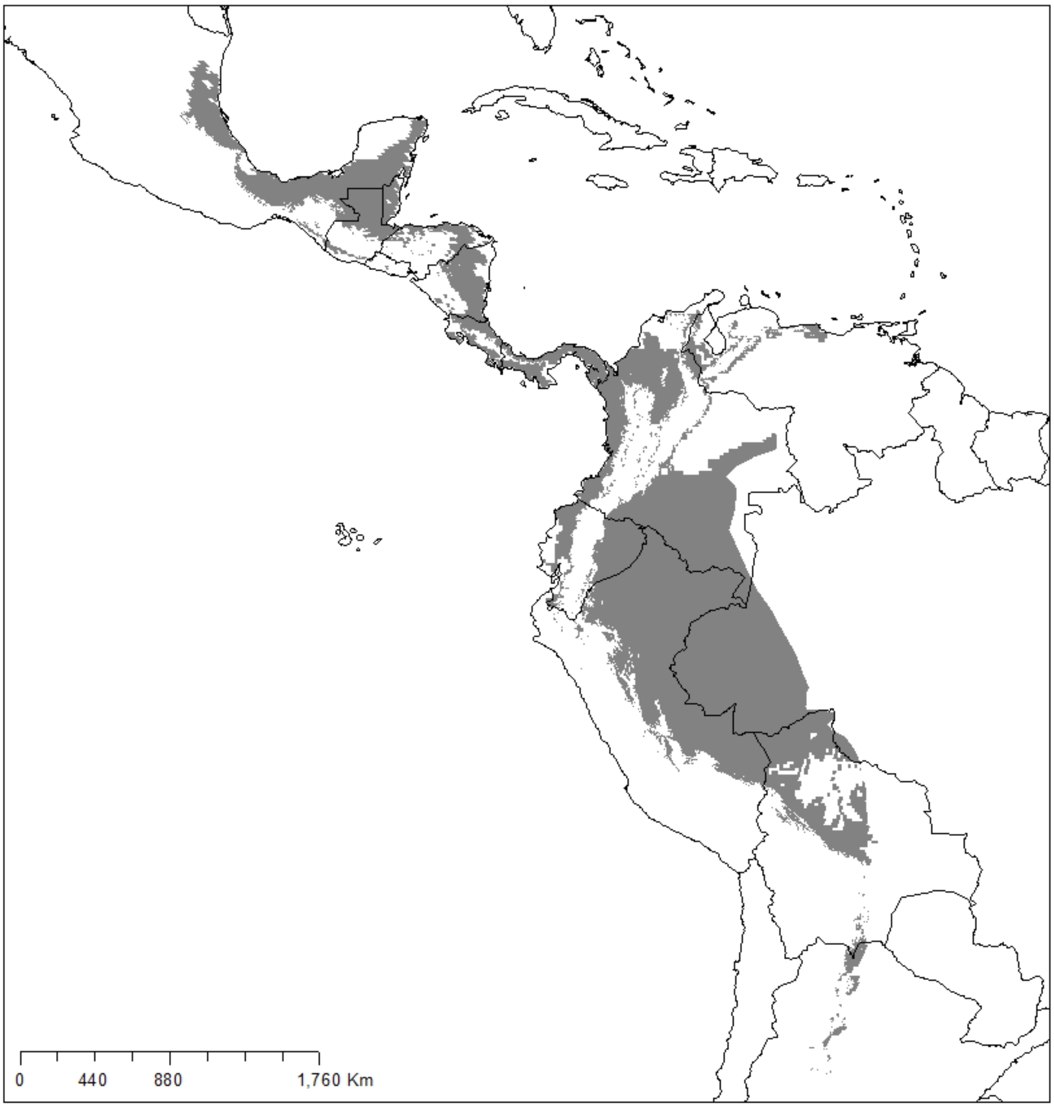


Figure A3.1 – Area used to test accuracy of sample units in representing variation of precipitation (grey). Mask sets the limits of Western lowland moist neotropical forests below 1000 m.a.s.l. based on Jarvis et al. (2008). Information of tropical forest area was obtained from Hansen et al., (2003). Areas from the Brazilian and Guiana shields were excluded based on Feldpausch et al. (2011).

Table A3.3 – Climate variables within entire lowland forested Western Neotropics and within the sample units used in this study. Mean, median and coefficient of variation of four precipitation variables and four temperature variables across Western neotropical forests and within the inventory plots calculated based on the number of sample units and for sample units weighted by their sizes. Precipitation variables represent (1) averages of values of precipitation in millimetres or temperature in degrees celsius between 1950-2000 from WorldClim (Hijmans et al., 2005) and (2) annual mean climatological water deficit from Chave *et al.* (2014).

	Western Neotropics			Sample units			Sample units weighted by size		
	Mean	Median	c.v.	Mean	Median	c.v.	Mean	Median	c.v.
Climatological water deficit	-169	-114	-1.10	-199	-180	-1.11	-169	-129	-1.18
Annual Rainfall	2379	2372	0.36	2323	2287	0.34	2401	2544	0.31
Precipitation of the driest month	81	60	0.82	84	58	0.79	92	71	0.74
Precipitation of the driest quarter	285	225	0.74	287	207	0.74	315	233	0.69
Annual Mean Temperature	26	26	0.05	25	25	0.05	25	25	0.05
Max Temperature of Warmest Month	32	32	0.04	32	32	0.04	32	32	0.04
Mean Temperature of Driest Quarter	25	25	0.08	25	25	0.07	25	25	0.07
Mean Temperature of Warmest Quarter	26	26	0.04	26	26	0.04	26	26	0.04

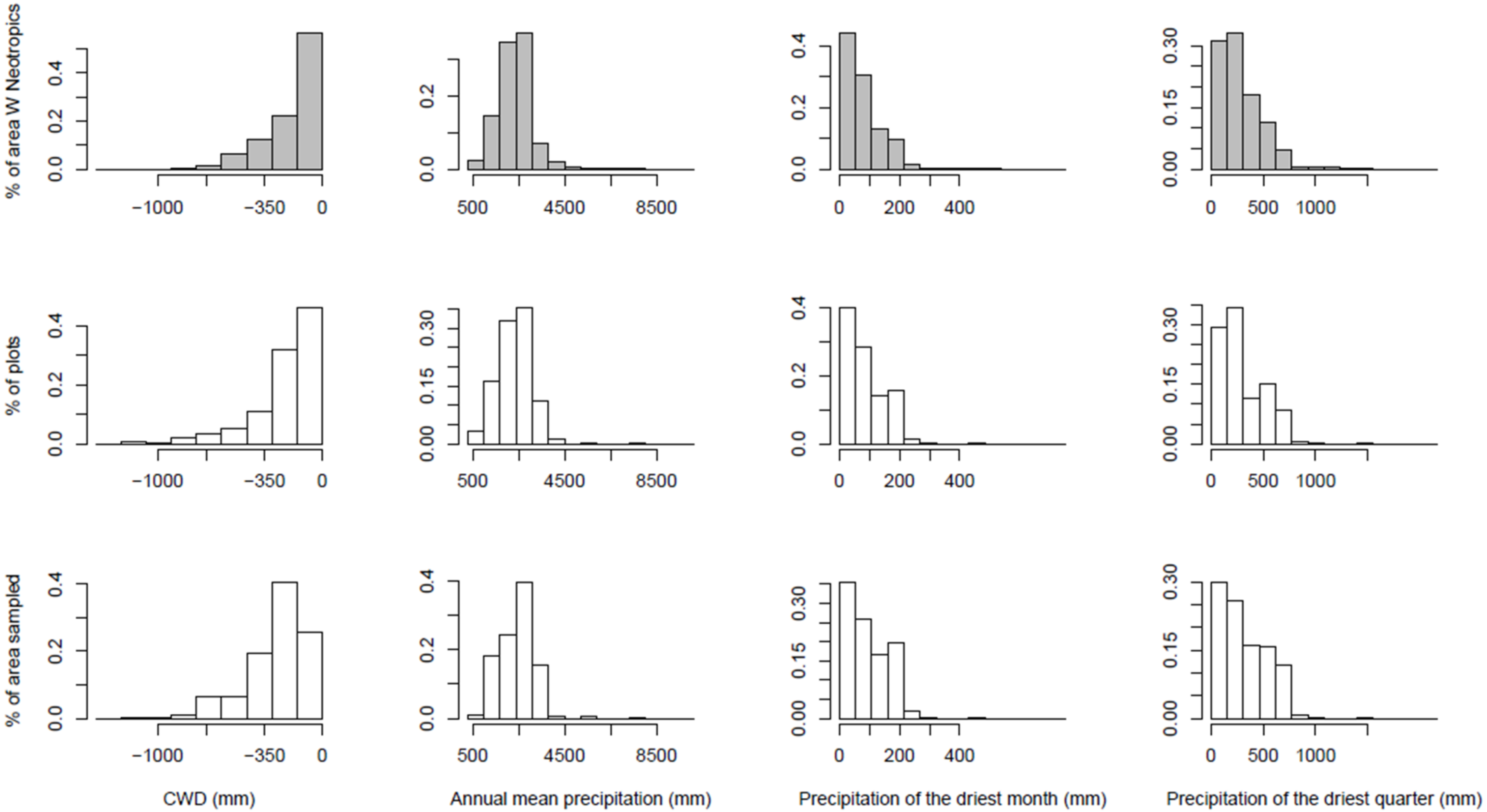


Figure A3.2 – Precipitation variables across the moist lowland western neotropical forests (grey) and within the 531 plots used here (white). The y-axes of the histograms represent either the proportion of: cells within the mask for the whole Western Neotropics (grey); plots in our sample; plots weighted by the area within each plot in which different precipitation regimes occur. The x-axes represent precipitation variables, from dry (left) to wet (right). Maximum climatological water deficit was extracted from Chave *et al.* (2014), other variables based on 1950-2000 means from WorldClim (Hijmans, et al. 2005).

Appendix 3.4 - Testing values of precipitation affiliation

For each taxon we tested the null hypothesis that the observed values of precipitation affiliation (here precipitation centre of gravity, PCG) would not differ from PCG values calculated when the communities are placed randomly along the precipitation gradient. We (1) generated 999 null PCG values for each taxon by shuffling the precipitation values among the communities, and (2) calculated the probability of the observed PCG being higher than the PCG calculated using random values of precipitation, following Manly (1997). This process generated a distribution of two-tailed P values where a small value (<0.025) indicates that the taxon is significantly dry-affiliated. Generalist taxa, not affiliated to any particular precipitation condition, may have PCG values indistinguishable from random (probability between 0.025 and 0.975). Wet-affiliated taxa have a high proportion (>0.975) of random values lower than the observed PCG (Figure A4). Precipitation affiliations and P-values for individual taxa are available in Appendix 9.

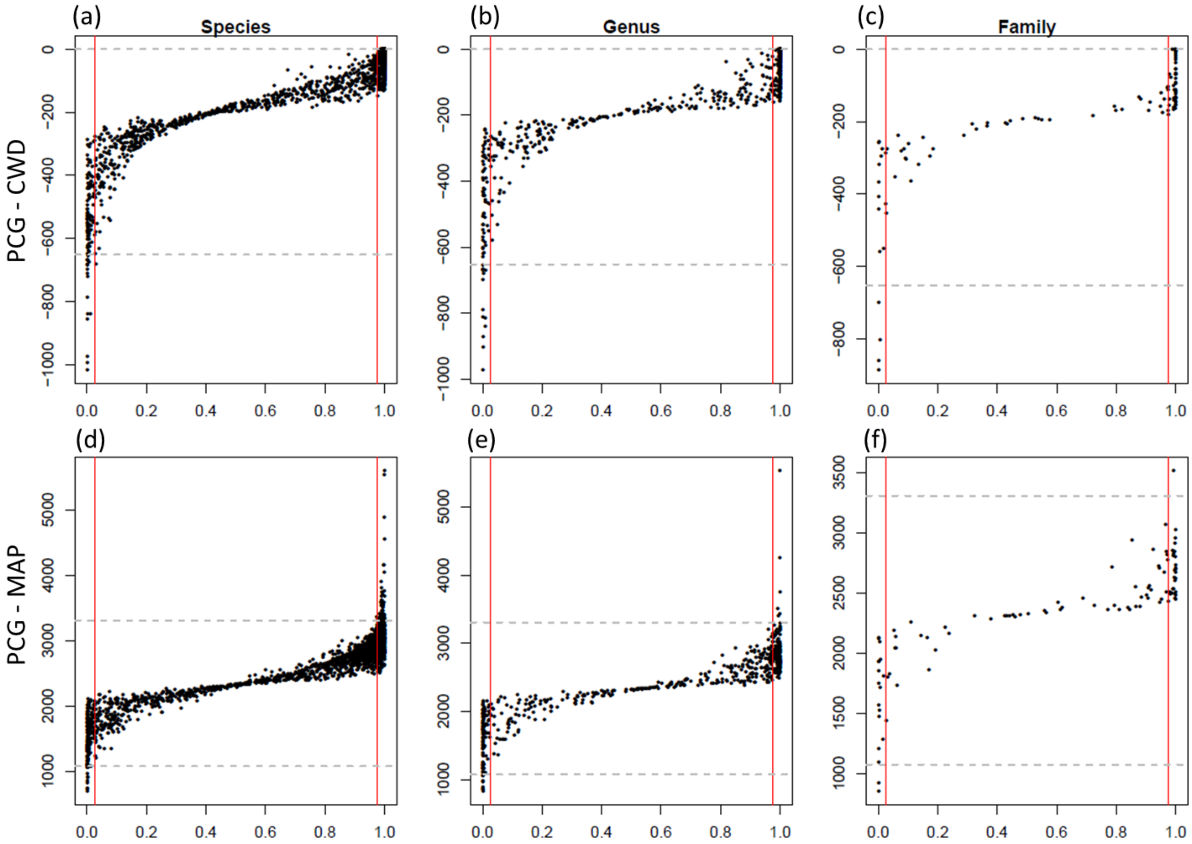


Figure A3.4 Precipitation centre of gravity (PCG) and their probability of happening by chance for each tree taxon in the Western Neotropics. Observed PCG (y-axes) plotted against the probability of random PCG values being lower than the observed value (x-axes). Probabilities on the x-axes were calculated by shuffling precipitation values among the communities. Red vertical lines represent 5% confidence limits. Grey dashed horizontal lines delimit the 5% driest (bottom) and 5% wettest (top) observed PCG values. Precipitation variables represent: maximum climatological water deficit in millimetres (CWD) from Chave et al. (2014) and annual mean precipitation in millimetres (MAP) from the WorldClim database using records between 1950 and 2000 (Hijmans, et al. 2005).

Appendix 3.5 - Testing proportions of significant precipitation affiliation

We calculated the proportion of significant values of precipitation centre of gravity (PCG) for each taxonomic level and each precipitation variable (Table 2 in main text). To explore if this proportion is an artefact of the number of observations we created null metacommunities with the same number of species and calculated the probability of finding the same proportion of significant values of PCG as found in our data. The null metacommunities were generated by randomizing the abundances of taxa among plots while maintaining taxa total frequency using the *permatfull* function implemented in the R package *vegan* (Jari Oksanen et al., 2013). For each null community we then generated PCG values, and their corresponding significance values following the procedures described in Appendix 3.4. This procedure was repeated 999 times resulting in 999 proportions of significant PCG values. Finally, we calculated the chance of the observed proportion of significant PCG being equal to proportions calculated for random communities with the same structure, following Manly (1997). We repeated this procedure at all taxonomic levels, for both techniques used to calculate precipitation affiliation (PCG and Kendall's τ) and for both precipitation variables used here (CWD and MAP).

Appendix 3.6 – Abundance of the most frequent taxa along the precipitation gradient

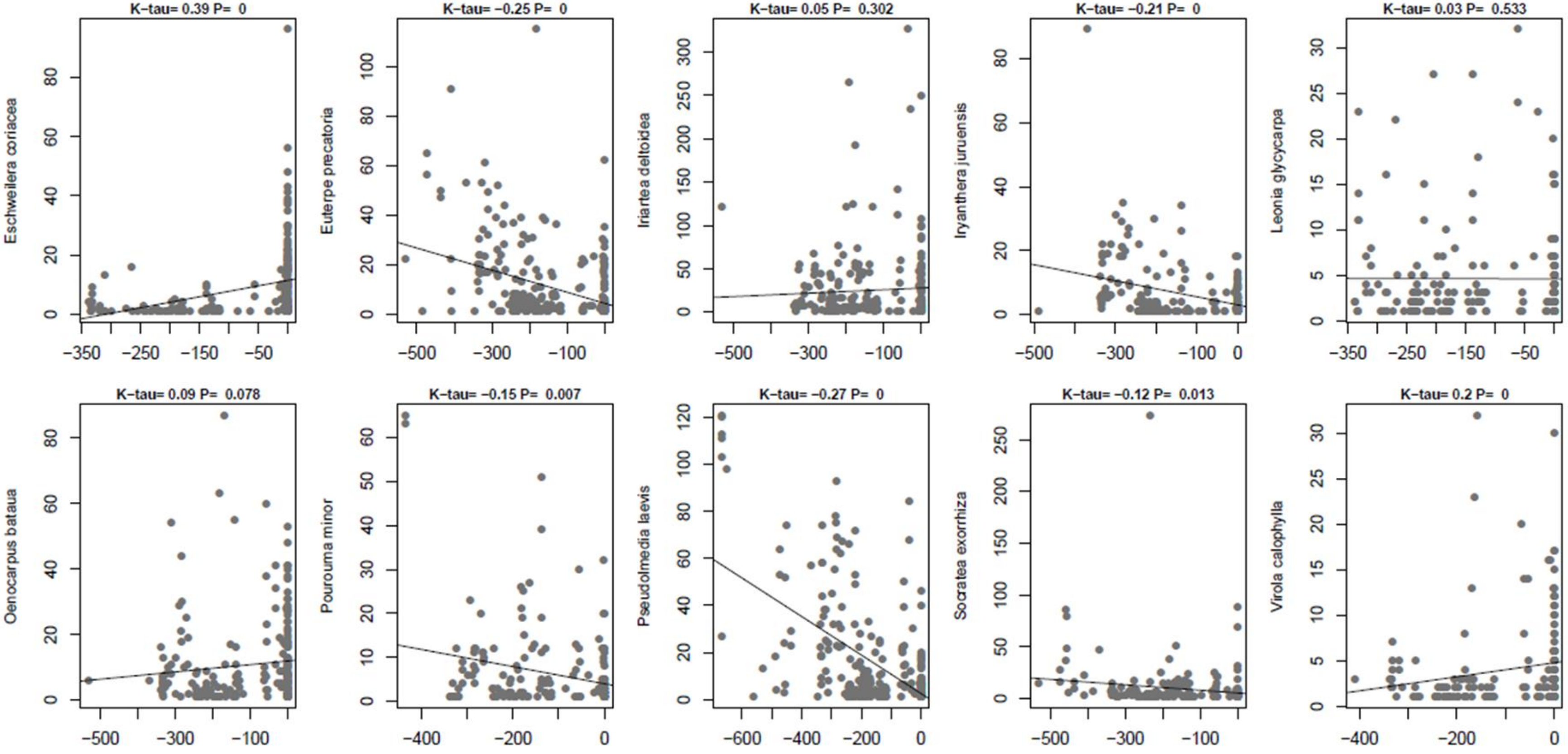


Figure A3.6.1 Abundance of the 10 most frequent species within the Western Neotropics along the precipitation gradient. The x-axes show values of climatological water deficit (CWD) and y-axes show abundance of each species. Black lines represent the linear regression between CWD and abundance. Values of Kendall’s τ coefficient of correlation and the P value testing the null hypothesis of no relationship between the two variables are presented above each graph.

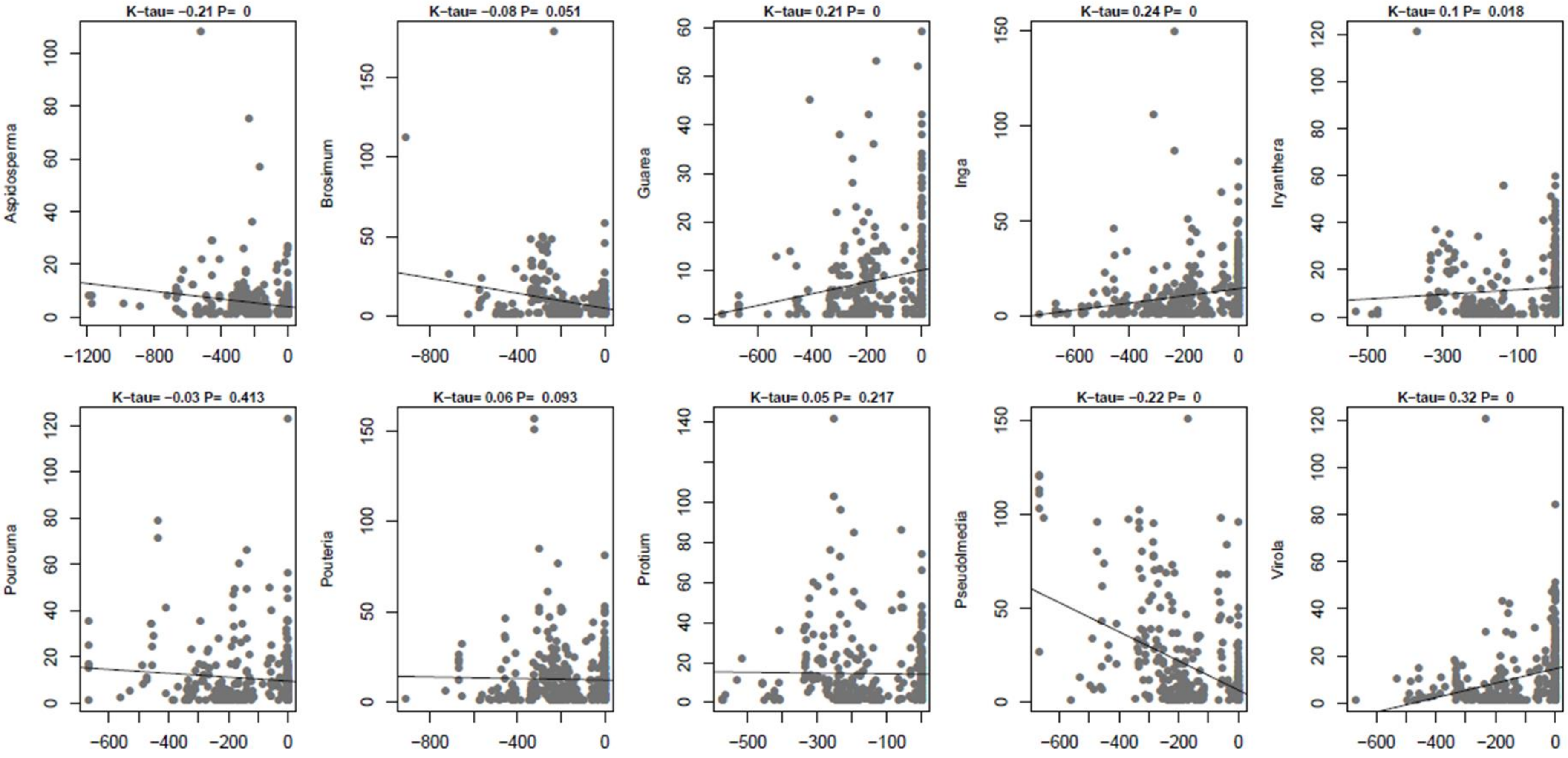


Figure A3.6.2 Abundance of the 10 most frequent genera within the Western Neotropics along the precipitation gradient. The x-axes show values of climatological water deficit (CWD) and y-axes show abundance of each genus. Black lines represent the linear regression between CWD and abundance. Values of Kendall’s τ coefficient of correlation and the P value testing the null hypothesis of no relationship between the two variables are presented above each graph.

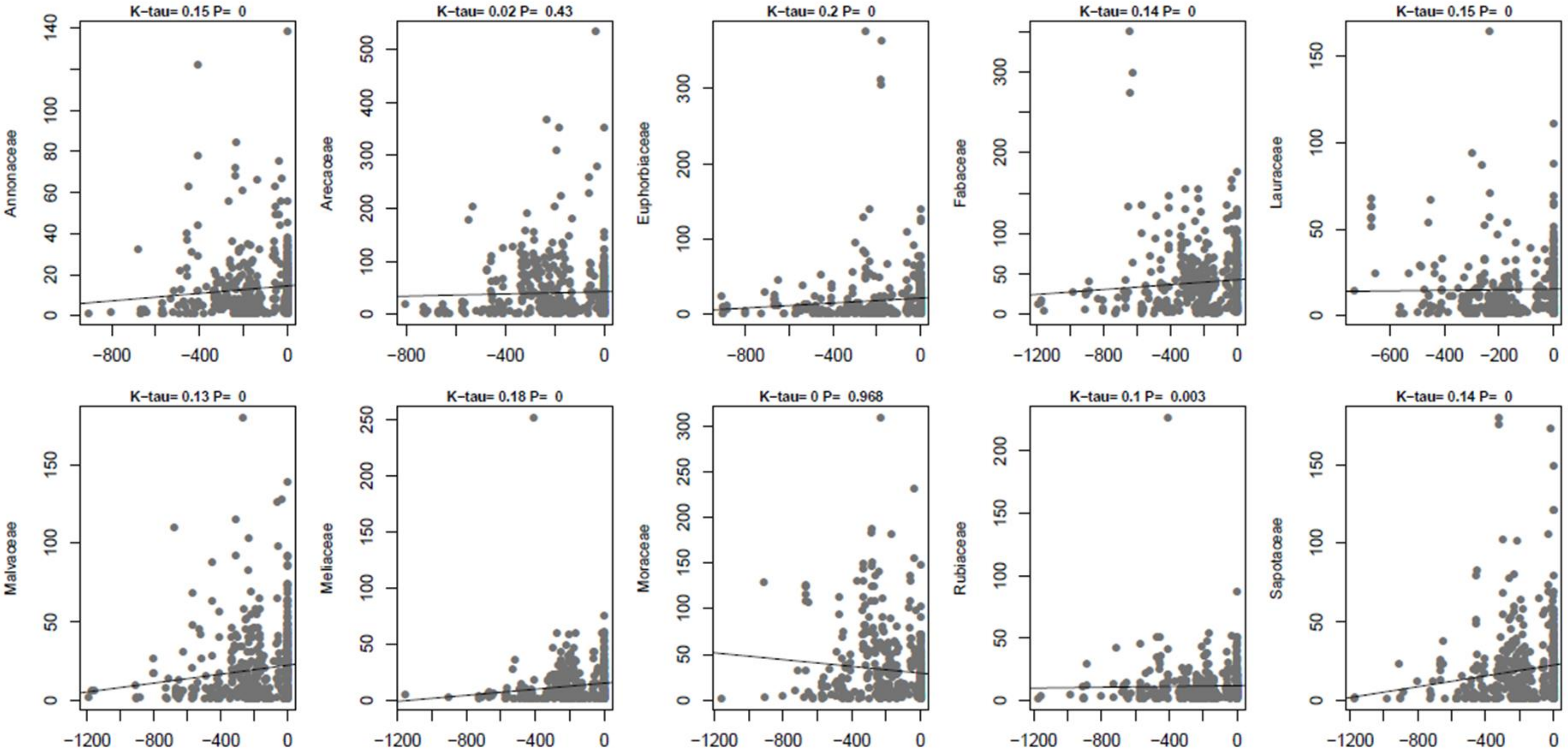


Figure A3.6.3 Abundance of the 10 most frequent families within the Western Neotropics along the precipitation gradient. The x-axes show values of climatological water deficit (CWD) and y-axes show abundance of each family. Black lines represent the linear regression between CWD and abundance. Values of Kendall's τ coefficient of correlation and the P value testing the null hypothesis of no relationship between the two variables are presented above each graph.

Appendix 3.7

Table A3.7.1 Precipitation centres of gravity (PCG) of the ten most extremely dry affiliated families, genera and species occurring in ten or more localities each. PCG calculated using two different precipitation variables climatological water deficit from Chave *et al.* (2014), annual mean precipitation based on 1950-2000 records from WorldClim (Hijmans et al., 2005).

Climatological water deficit		Annual mean precipitation	
Families			
Cactaceae	-886	Cactaceae	853
Oleaceae	-801	Oleaceae	1286
Styracaceae	-441	Acanthaceae	1473
Acanthaceae	-427	Phytolaccaceae	1524
Capparaceae	-408	Styracaceae	1566
Ulmaceae	-366	Lythraceae	1712
Combretaceae	-319	Capparaceae	1751
Rutaceae	-296	Asteraceae	1814
Rhamnaceae	-287	Ulmaceae	1853
Anacardiaceae	-274	Rutaceae	1933
Genera			
Chionanthus	-815	*Poincianella*	1112
Cynophalla	-670	*Acosmium*	1157
Poincianella	-653	*Cynophalla*	1160
Caesalpinia	-629	*Sweetia*	1163
Acosmium	-621	*Geissanthus*	1179
Sweetia	-616	*Centrolobium*	1202
Centrolobium	-603	*Anadenanthera*	1250
Geissanthus	-603	*Chionanthus*	1297
Anadenanthera	-571	*Samanea*	1348
Samanea	-551	*Combretum*	1352
Species			
Piptadenia viridiflora	-654	*Piptadenia viridiflora*	1100
Acosmium cardenasii	-625	*Acosmium cardenasii*	1149
Sweetia fruticosa	-616	*Sweetia fruticosa*	1164
Cochlospermum vitifolium	-604	*Geissanthus ambigua*	1179
Geissanthus ambigua	-603	*Poeppigia procera*	1231
Poeppigia procera	-592	*Anadenanthera colubrina*	1236
Ceiba speciosa	-584	*Ceiba speciosa*	1307
Tabebuia chrysantha	-576	*Aspidosperma cylindrocarpon*	1309
Anadenanthera colubrina	-575	*Ampelocera ruizii*	1316
Aspidosperma cylindrocarpon	-556	*Cariniana estrellensis*	1323

Table A3.7.2 Precipitation centres of gravity (PCG) of the ten most extremely wet affiliated families, genera and species occurring in ten or more localities each. PCG calculated using two different precipitation variables climatological water deficit from Chave *et al.* (2014), annual mean precipitation based on 1950-2000 records from WorldClim (Hijmans et al., 2005).

Climatological water deficit		Annual mean precipitation	
Families			
Anisophylleaceae	-4	Cardiopteridaceae	3027
Myrsinaceae	-6	Solanaceae	2955
Lepidobotryaceae	-7	Stemonuraceae	2910
Theaceae	-13	Hypericaceae	2848
Stemonuraceae	-17	Rhizophoraceae	2842
Cardiopteridaceae	-23	Tapisciaceae	2825
Tapisciaceae	-29	Calophyllaceae	2811
Caryocaraceae	-37	Clusiaceae	2800
Solanaceae	-54	Caryocaraceae	2729
Lecythidaceae	-56	Lecythidaceae	2710
Genera			
Ophiocaryon	0	*Tessmannianthus*	4251
Tetrastylidium	0	*Ardisia*	3750
Heterostemon	0	*Ryania*	3425
Hippotis	0	*Gloeospermum*	3405
Lorostemon	0	*Phragmotheca*	3298
Monopteryx	0	*Cynometra*	3251
Mucoa	0	*Brownea*	3239
Patinoa	0	*Wettinia*	3223
Phragmotheca	0	*Anaxagorea*	3210
Tessmannianthus	0	*Tetrathylacium*	3206
Species			
Sloanea laxiflora	0	*Endlicheria dysodantha*	3737
Sloanea synandra	0	*Macrolobium archeri*	3680
Tetrorchidium macrophyllum	0	*Matisia lomensis*	3608
Tocoyena williamsii	0	*Chrysophyllum manaosense*	3553
Trichilia laxipaniculata	0	*Vochysia grandis*	3452
Vantanea parviflora	0	*Protium guianense*	3416
Vantanea spichigeri	0	*Phragmotheca mammosa*	3399
Virola divergens	0	*Ficus piresiana*	3379
Virola obovata	0	*Pouteria multiflora*	3348
Vochysia grandis	0	*Tovomita weddelliana*	3348

Appendix 3.8

To investigate whether the observed pattern is not biased by locally enhanced water supply (LEWS), we repeated the analyses excluding the species possibly affiliated to LEWS. These taxa are expected to be affiliated to either river flooding or with local topographically-determined water supply (swamps), whether permanent or seasonal. Thus the large-scale biogeography of such taxa may be expected to be largely decoupled from climate. There is no systematic information available on the variation of water availability within plots, but we do have access to plots which sample hydromorphic habitats such as seasonal floodplains.

To identify which Neotropical species are strongly LEWS-affiliated we computed an index based on the Neotropics-wide plot sampling available in ForestPlots.net (Lopez-Gonzalez, et al. 2011). The abundance per hectare of all species in each of the 881 floristically-identified plots in the Neotropics was calculated. Plots were classified as being ‘LEWS’ or ‘non-LEWS’, such as plots on floodplains and terra firme respectively. For each taxon we calculated the ratio between its abundance in LEWS and non-LEWS plots standardized by the number of plots in each of the groups.

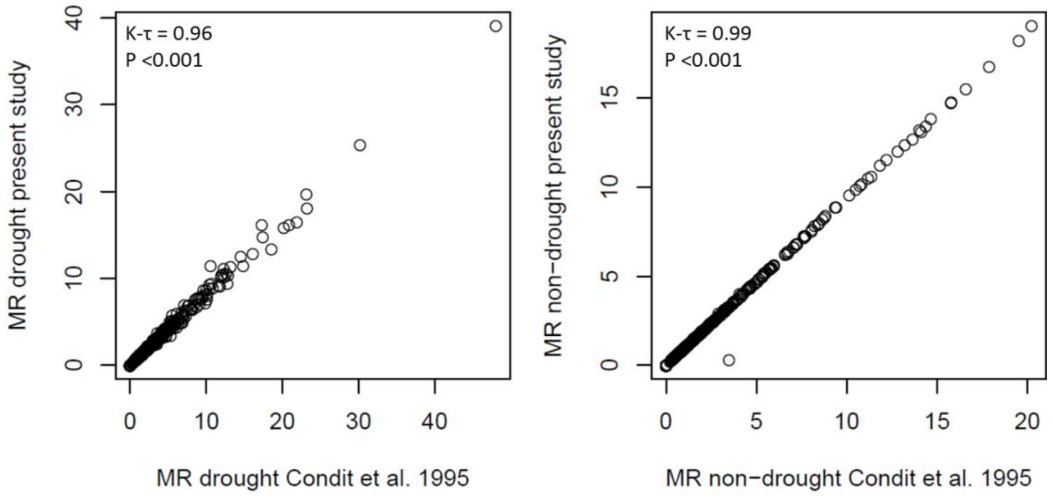
Results excluding LEWS-affiliated taxa show the same pattern as when using the whole dataset. When LEWS affiliated taxa are excluded, the correlation between precipitation range and the minimum CWD was much stronger than the correlation between range and the wettest condition of occurrence, for all taxonomic levels (Table A3.8).

Table A3.8 Kendall's τ coefficient of correlation between precipitation ranges and maximum and minimum CWD values where each taxon occurs. P-values test the null hypotheses of none-negative correlation between precipitation range and CWD min (first column) and none-positive correlation between precipitation range and maximum CWD (second column), α = 0.05.

	Precipitation range vs. min CWD	Precipitation range vs. max CWD
Species	-1*	0
Genera	-1*	-0.02
Families	-1*	-0.02

* P < 0.05

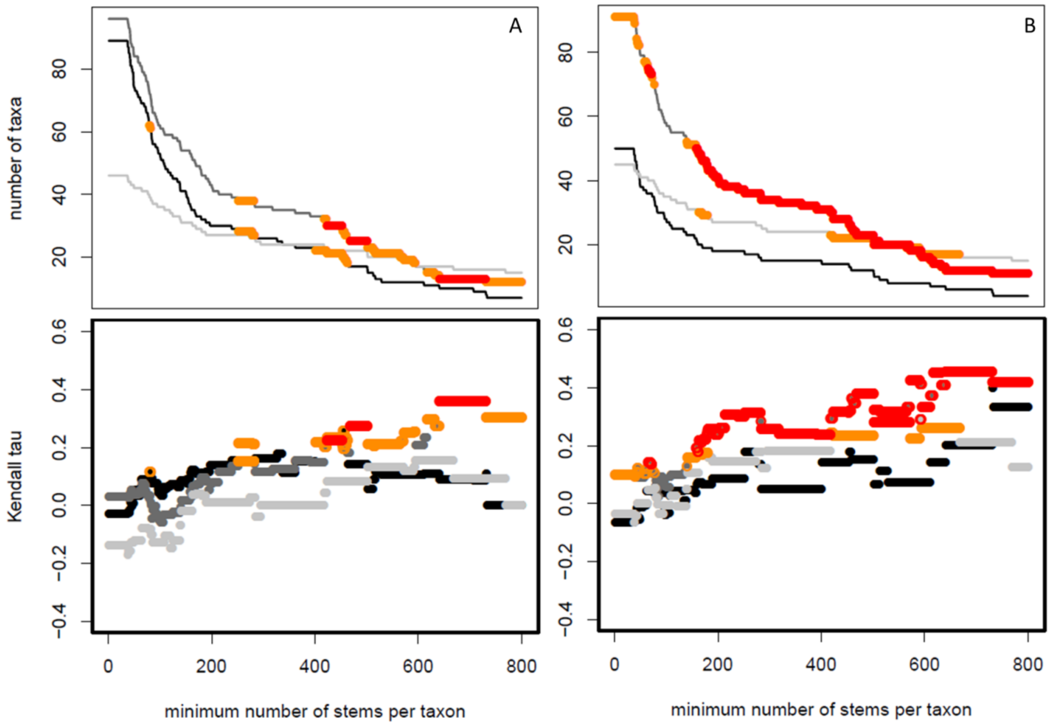
Appendix 4.1. Correlation between mortality rates in Condit et al. (1995) **and as calculated in this study.** The x-axes show mortality rates (MR) as calculated by Condit et al. (1995) and the y-axes represent mortality rates as calculated in this study. Left graph shows mortality rates at the drought period (1982-85) and the right graph mortality rates in the control period (1985 – 1990).



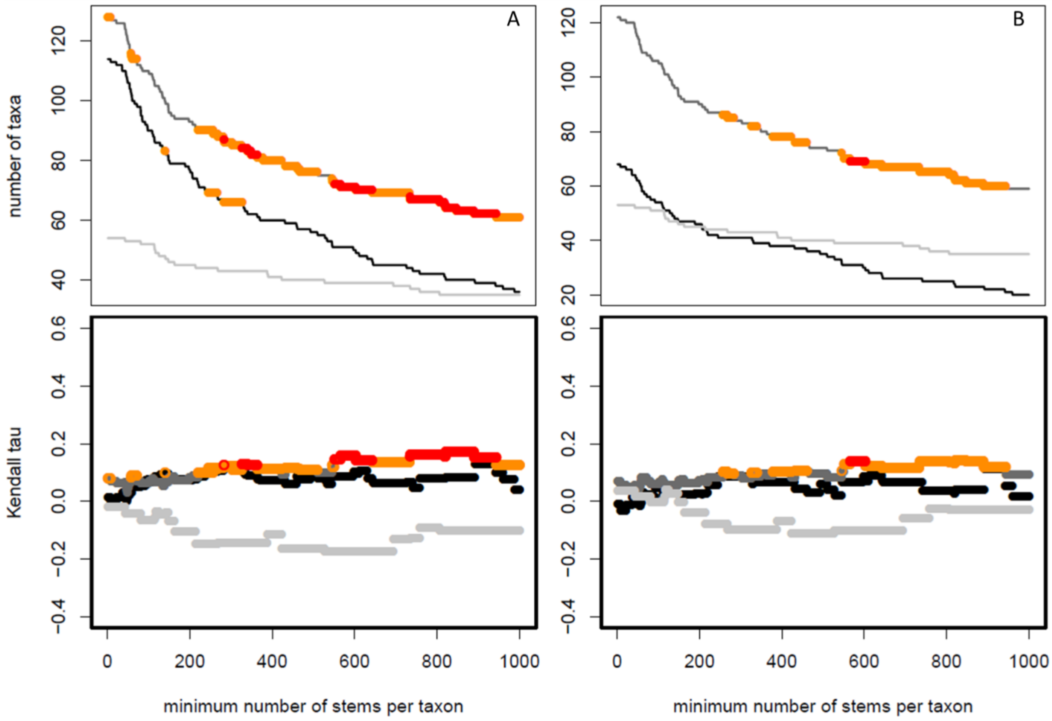
Appendix 4.2 Accounting for the effect of sample size on the correlation between drought-induced mortality (Δm) and water deficit affiliation (WDA).

To assess the impact of (small) sample sizes of individual taxa on confounding our mortality rates estimates (Δm) vs. WDA values, we performed a series of exploratory analyses using all available data from BCI, Caxiuanã and Tapajós. We calculated these correlations for different subsamples, varying the minimum number of stems per taxon required for the taxon to be included in each subsample (Figures A4.3.1 to A4.3.5). This gives information on how the number of stems observed per taxon and the number of taxa analysed in each study case can, together, affect the correlation statistics between drought tolerance and WDA for Tapajós, Caxiuanã and BCI.

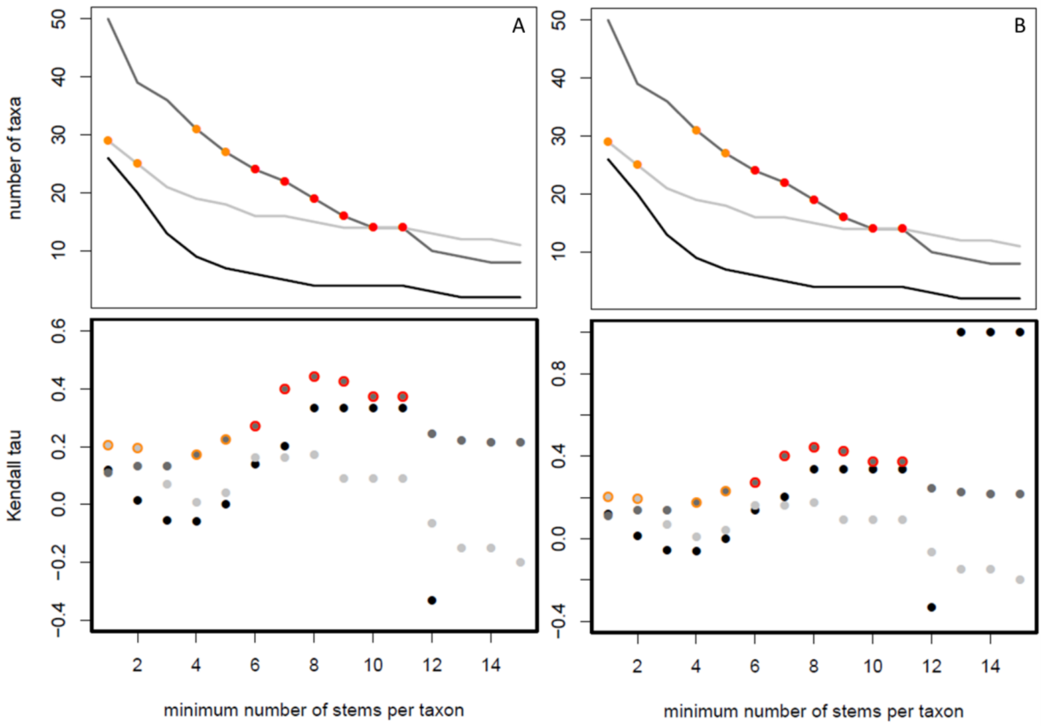
When analysing the influence of the number of stems in the correlation, values of Kendall τ tend to clearly increase as the analyses become progressively restricted to only the best sampled taxa (Figures A4.3.1 to S3.5). However, as the sample size in terms of number of taxa inevitably declines when these criteria are heightened, the P-values for evaluating the hypothesis of association between Δm and WDA tend to be minimal at intermediate number of taxa. This happens as a consequence of the statistical power available to test the hypothesis being maximal when the number of taxa with an adequate number of individuals to estimate mortality accurately is sufficient to test for the relationship between Δm and WDA. We use the subset that maximizes the correlation between Δm and WDA.



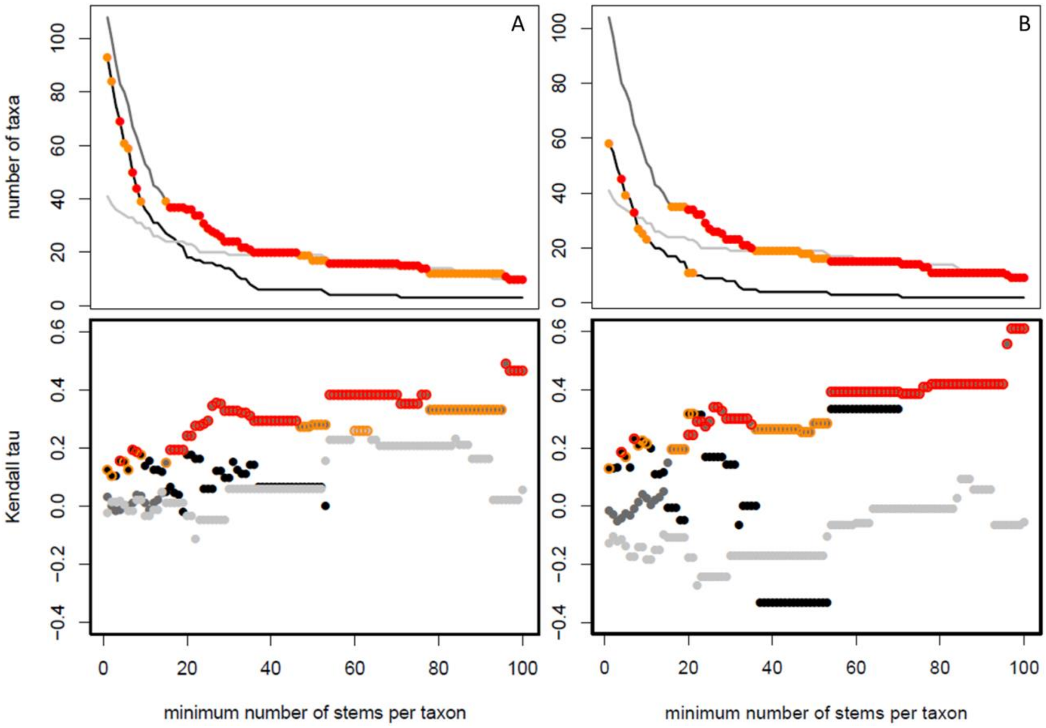
Figures A4.2.1 – Influence of sample sizes on correlation between drought-induced mortality (Δm) and water deficit affiliation (WDA) of trees > 100 mm D as a consequence of the 1982-83 drought in BCI (Condit et al., 1995). Here we present values of Kendall's τ coefficient of correlation between Δm and WDA and the P value of each correlation for various subsamples from the original data differing in the minimum number of stems per taxa. The subsamples are ordered by the minimum number of stems per taxa, moving from 1 to 800, along each x-axis. The top graphs show the number of taxa within each subsample. The bottom graphs show values of Kendall's τ coefficient of correlation between Δm and WDA for each subsample. Black dots represent analyses performed at the species, dark grey at the genus and light grey at the family level. The two graphs on the left show analyses including all taxa whilst the graphs on the right show results for excluding taxa affiliated to locally enhanced water supply areas. P values test the null hypothesis of no positive relationship between Δm and WDA, considering α = 0.1 (orange dots) and α = 0.05 (red dots).



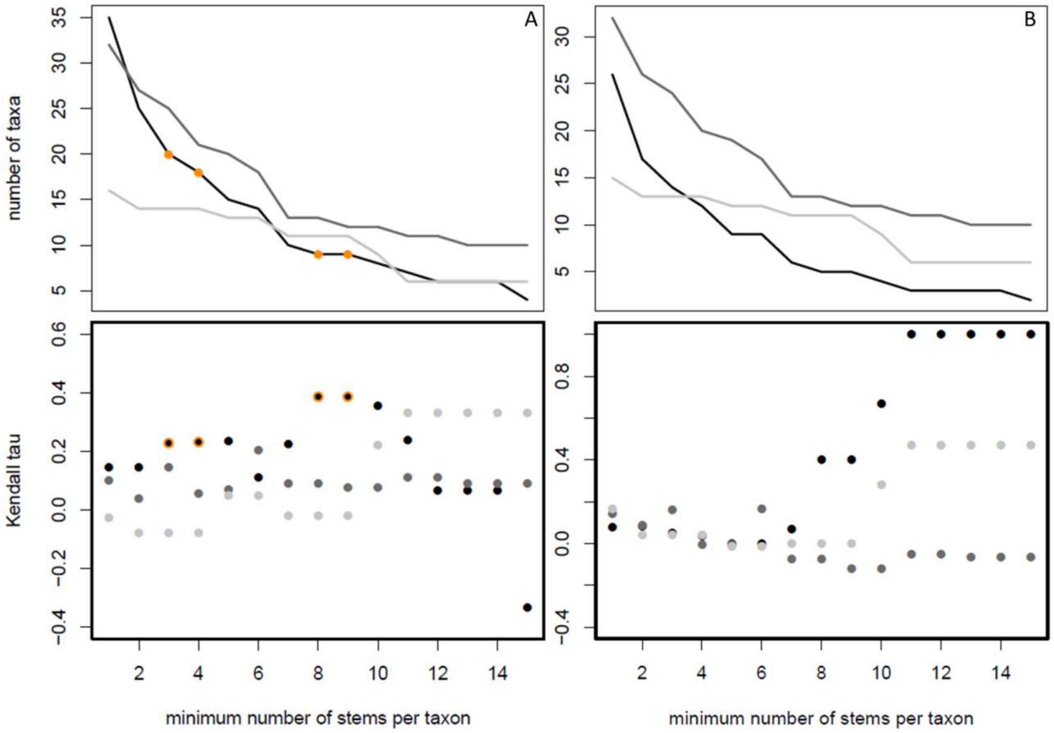
Figures A4.2.2 – Influence of sample sizes on correlation between drought-induced mortality (Δm) and water deficit affiliation (WDA) of saplings 10 mm – 99 mm D as a consequence of the 1982-83 drought in BCI (Condit et al., 1995). Here we present values of Kendall's τ coefficient of correlation between Δm and WDA and the P value of each correlation for various subsamples from the original data differing in the minimum number of stems per taxa. The subsamples are ordered by the minimum number of stems per taxa, moving from 1 to 1000 along each x-axis. The top graphs show the number of taxa within each subsample. The bottom graphs show values of Kendall's τ coefficient of correlation between Δm and WDA for each subsample. Black dots represent analyses performed at the species, dark grey at the genus and light grey at the family level. The two graphs on the left show analyses including all taxa whilst the graphs on the right show results for excluding taxa affiliated to locally enhanced water supply areas. P values test the null hypothesis of no positive relationship between Δm and WDA, considering α = 0.1 (orange dots) and α = 0.05 (red dots).



Figures A4.2.3 Influence of sample sizes on correlation between drought-induced mortality effect (Δm) and precipitation affiliation for trees > 100 mm D in the Tapajós drought experiment (Nepstad et al., 2007). Here we present values of Kendall's τ coefficient of correlation between Δm and WDA and the P value of each correlation for various subsamples from the original data differing in the minimum number of stems per taxa. The subsamples are ordered by the minimum number of stems per taxa, moving from 1 to 14 along each x-axis. The top graphs show the number of taxa within each subsample. The bottom graphs show values of Kendall's τ coefficient of correlation between Δm and WDA for each subsample. Black dots represent analyses performed at the species, dark grey at the genus and light grey at the family level. The two graphs on the left show analyses including all taxa whilst the graphs on the right show results for excluding taxa affiliated to locally enhanced water supply areas. P values test the null hypothesis of no positive relationship between Δm and WDA, considering α = 0.1 (orange dots) and α = 0.05 (red dots).



Figures A4.2.4 Influence of sample sizes on correlation between drought-induced mortality effect (Δm) and precipitation affiliation for saplings (20 – 99 mm D) in Tapajós drought experiment (Nepstad et al., 2007). Here we present values of Kendall's τ coefficient of correlation between Δm and WDA and the P value of each correlation for various subsamples from the original data differing in the minimum number of stems per taxa. The subsamples are ordered by the minimum number of stems per taxa, moving from 1 to 100 along each x-axis. The top graphs show the number of taxa within each subsample. The bottom graphs show values of Kendall's τ coefficient of correlation between Δm and WDA for each subsample. Black dots represent analyses performed at the species, dark grey at the genus and light grey at the family level. The two graphs on the left show analyses including all taxa whilst the graphs on the right show results for excluding taxa affiliated to locally enhanced water supply areas. P values test the null hypothesis of no positive relationship between Δm and WDA, considering α = 0.1 (orange dots) and α = 0.05 (red dots).



Figures A4.2.5 - Influence of sample sizes on the correlation between drought-induced mortality effect (Δm) and precipitation affiliation for trees (>10cm D) in the Caxiuanã drought experiment (da Costa et al., 2010). Here we present values of Kendall's τ coefficient of correlation between Δm and WDA and the P value of each correlation for various subsamples from the original data differing in the minimum number of stems per taxa. The subsamples are ordered by the minimum number of stems per taxa, moving from 1 to 1000 along each x-axis. The top graphs show the number of taxa within each subsample. The bottom graphs show values of Kendall's τ coefficient of correlation between Δm and WDA for each subsample. Black dots represent analyses performed at the species, dark grey at the genus and light grey at the family level. The two graphs on the left show analyses including all taxa whilst the graphs on the right show results for excluding taxa affiliated to locally enhanced water supply areas. P values test the null hypothesis of no positive relationship between Δm and WDA, considering α = 0.1 (orange dots) and α = 0.05 (red dots).

Appendix 4.3 Number and proportions of taxa from original studies analysed. Number of taxa in the original study represents the number of taxa occurring in both drought and control observation. The number of taxa from the original case studies that had information on WDA are shown also as a percentage of the number of taxa in the original study in brackets. Values are shown for all taxa and for a subset excluding taxa affiliated with areas of locally enhanced water supply (LEWS).

Source	Taxonomic level	Number of taxa in original study	Number taxa with information on WDA	
			All taxa (%)	Excluding LEWS affiliated (%)
BCI trees	Species	132	89 (67)	50 (38)
	Genera	99	96 (97)	91 (92)
	Families	46	46 (100)	45 (98)
Tapajós trees	Species	70	40 (57)	26 (37)
	Genera	53	52 (98)	50 (94)
	Families	29	29(100)	29 (100)
Caxiuanã	Species	63	35 (55)	26 (41)
	Genera	36	32 (89)	32 (89)
	Families	16	16 (100)	15 (94)
BCI saplings	Species	203	116 (57)	68 (33)
	Genera	143	130 (90)	124 (87)
	Families	54	54 (100)	53 (98)
Tapajós saplings	Species	202	100 (49)	64 (32)
	Genera	119	114 (96)	110 (92)
	Families	43	43 (100)	43 (100)
Poorter & Markesteijn (2008)	Species	36	30 (83)	18 (50)
	Genera	31	29 (93)	26 (84)
	Families	18	18(100)	17(94)
Engelbrecht et al. (2007)	Species	48	29 (60)	16 (33)
	Genera	45	41 (91)	40 (88)
	Families	29	29(100)	29(100)

Appendix 4.4 Mortality rates at drought and control observations for trees and saplings in the different case studies calculated for individuals and genus levels. Means were calculated considering the genera that occur in both, control and droughted areas. Values in brackets represent standard deviations. Mortality rates are calculated for BCI, the 1982-3 El Niño drought in Barro Colorado Island in Panama (Condit et al., 1995) and two through-fall exclusion experiments in the Brazilian Amazon, Tapajós (TAP, Nepstad et al., 2007) and Caxiuanã (CAX, da Costa et al., 2010).

		$m_{control}$	$m_{\mathrm{droughted}}$	$m_{\mathrm{droughted}}$ / $m_{control}$	$\Delta(m_{\mathrm{droughted}} - m_{control})$
mean *m* all individuals					
Trees	CAX	0.8	2.4	2.9	1.6
	TAP	1.9	5.3	2.8	3.4
	BCI	2.0	2.3	1.2	0.3
Saplings	TAP	1.9	2.2	1.8	0.3
	BCI	2.2	2.2	1	-0.1
mean *m* per genus					
Trees	all observations	4.8 (8)	7 (20)	3.2	4.8
	CAX	0.8 (2)	10.1 (27)	13.4	9.4 (27)
	TAP	2.7 (14)	13.1 (29)	4.8	10.4 (33)
	BCI	2.4 (3)	2.6 (2)	1	0.1 (1)
Saplings					
	TAP	3.7 (16)	4.5 (16)	1.2	0.8 (19)
	BCI	3.4 (4)	3.6 (4)	1.1	0.2 (2)

Appendix 5

All analyses of chapter 5 were repeated using an inclusive dataset, which I call *Extended Amazonia* (Figure A.1). It consists of 176 plots, including those analysed here plus plots in the border of the Amazon where mean CWD is more negative than -300 mm y^{-1} and those which were not monitored throughout 2005 and 2010. The results for the *Extended Amazonia* are similar to the results found the using the most restricted data. However, as my intention was to understand the effect of droughts over Amazonian communities the results using Extended Amazonia are omitted from the main text and can be found in the Appendices. To distinguish between these two datasets in the appendix I called the data used in chapter 5 as *Core Amazonia*.

Appendix 5.1 - Orthogonal Amazonian tree traits

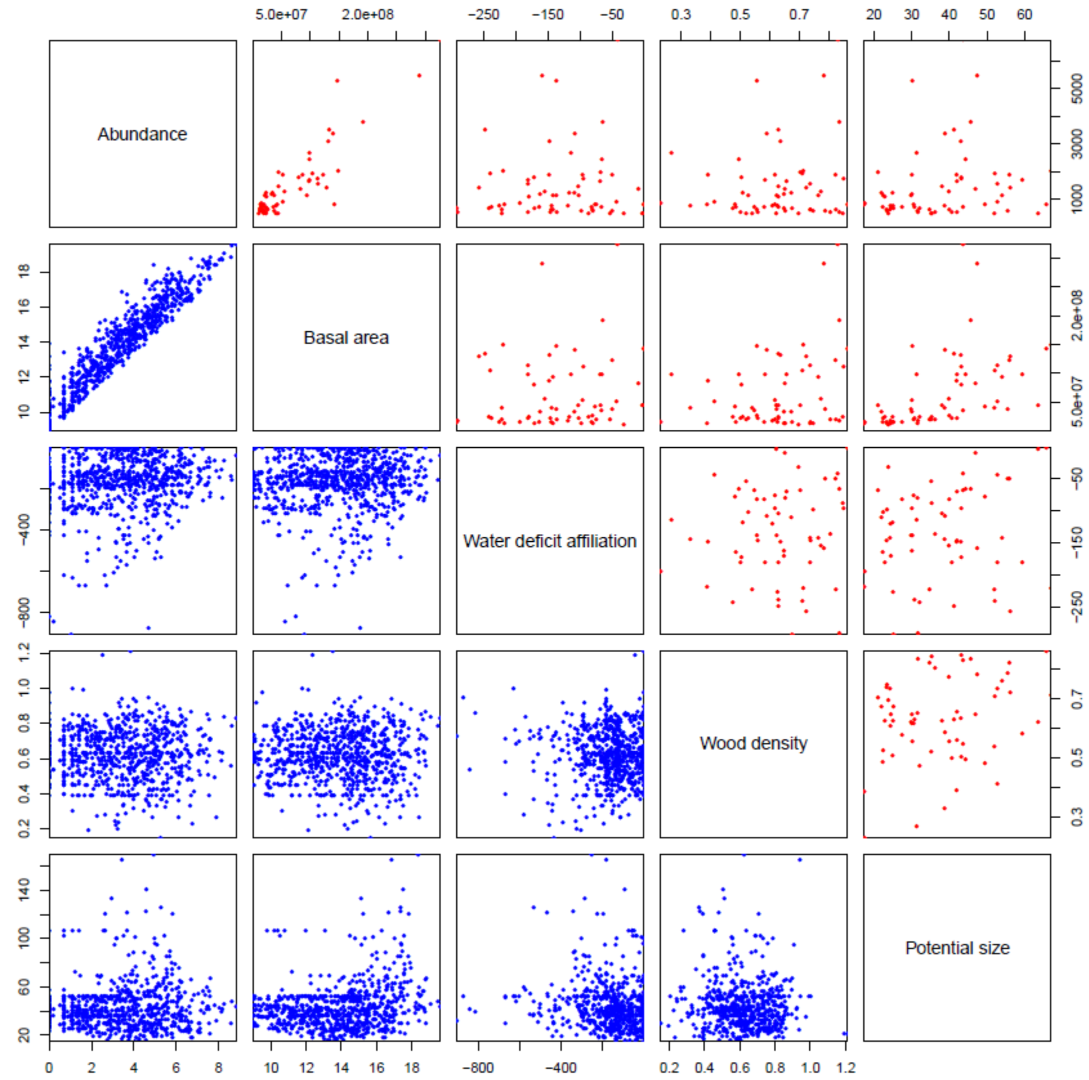


Figure A5.1 - Relationship between genus-level traits and dominance. In blue on the lower panels graphs show relationship including 759 genera from *Extended Amazonia* dataset. Top graphs, in red, show the relationships for the 51 genera with more than 500 individuals across the plots analysed here. For the analyses including all taxa, bottom half of the figure in blue, I used the natural logarithmic of abundance and basal area instead of raw values. Water deficit affiliation values were calculated in chapter 3, wood density was obtained from the Wood Density Database (Chave et al., 2009;Zanne et al., 2010), and potential size from Fauset et al. (2015).

Appendix 5.2 Trends in climatological water deficit across Amazonian plots

Climatological water deficit (CWD) is calculated from precipitation and evapotranspiration data. There are two major sources of information of precipitation for the Amazon basin: ground-based data from weather stations or satellite-based data from the Tropical Rainfall Measuring Mission (TRMM - Huffman et al., 2007). Data from weather stations are interpolated at 0.5° resolution by the climatological research unit (CRU - Harris et al., 2014) are available from 1901 to 2013. Evapotranspiration is calculated using the Penman–Monteith equation (Allen et al., 1994) using absolute values of temperature from CRU data.

Whilst ground-based data are available for a longer period of time, the number of weather stations within the Amazon can compromise the quality of these data. Thereby, I verify the plot-level yearly values of CWD calculated using only CRU data against CWD using precipitation data from TRMM. For these analyses I used plot from the *Extended Amazonia* dataset.

Results

CWD values based on CRU and TRMM tend to agree overall ($R^2 = 0.8$, $P<0.0001$) (Figure A5.2.1). When comparing the overall slope from 1985 for the Basin from bootstrapped mean and 95% CI of individual slopes, both CRU and TRMM show a decrease in CWD, with TRMM showing slight higher values: CRU -1.08 (-1.2; -0.9) and TRMM -1.5 (95% CI -2; -1).

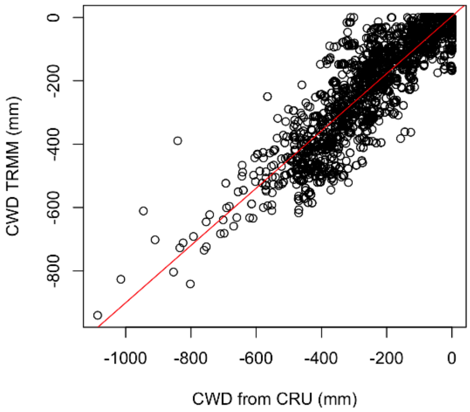


Figure A5.2.1 – Relationship between CRU and TRMM-based CWD values. Black dots show annually CWD values between 1998 and 2013 for each of the 176 plots analysed here. Red line represents a linear regression ($R^2 = 0.8$, $P < 0.0001$).

The two datasets also show differences on how trends in CWD are distributed across space, especially for South East Amazon (Figure A5.2.2), which is not included in the main analyses, i.e. *Core Amazonia*. Overall CRU-based CWD showed similar results from TRMM-based values and the major difference in the direction of trends for some plots seems to be related to the time window analysed, when the same time window is analysed (1998-2013) both dataset show very similar trends for the Basin: TRMM -1.5 (95% CI -2; -1); CRU -0.7 (-1.07; -0.4). Thereby, I used CRU-data in the analyses, as it spans over the same time window of the vegetation dataset.

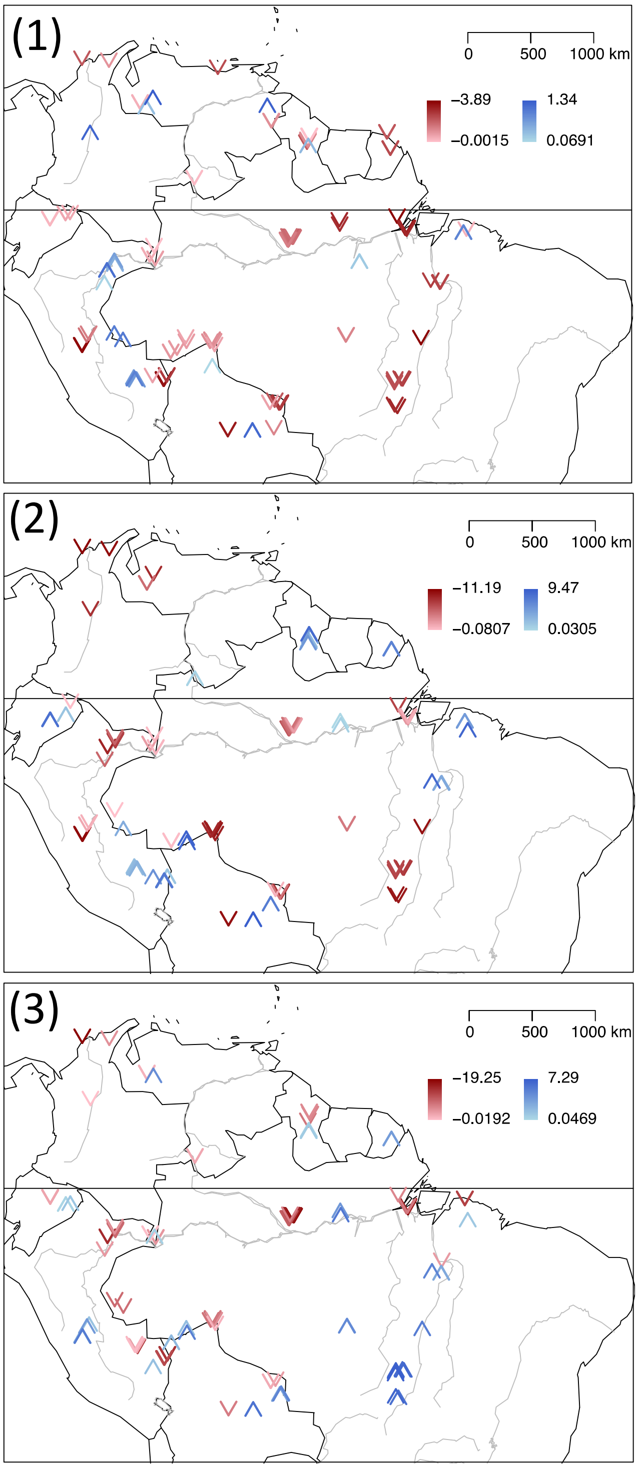


Figure A5.2.2 – Spatial pattern of CWD across the plots analysed here for (1) CRU-based CWD from 1985; (2) from 1998 and (3) TRMM-based CWD from 1998. The direction and colour of the arrows represent the direction of the trend (red, negative and blue positive), whilst the intensity of the colour shows the trend's intensity. Note that the scale of the trend is similar for TRMM and CRU from 1998 and the direction of the trend varies mostly in South East Amazonia, which is in not included in the analyses in the main text.

Appendix 5.3 - Accounting for heterogeneity in the variance of the residuals in GLMM models

I empirically tested for the effect of sample effort on the variance of individual data points from overall trends, following Lewis et al. (2009b). Plot area and monitoring period are expected to affect the plot-level trends as forest stands monitored over shorter periods or smaller areas are more likely to be affected by stochastic phenomena, such as tree falls. The variance of the residuals was higher among smaller plots and shorter interval periods (Figure A5.3.1). To control for the observed variance in the residuals I weighted the data points by squared root of area x monitoring period, as in Brienen et al. (2015).

When including the weights in the models their fit improved overall (Table A5.3.1). Although slightly different weights would be most indicated to control for the heterogeneity among the residuals in particular models (e.g. models considering the whole community for the Core Amazon data, Table A5.3.1), I opted to apply the same weighting procedure for all models allowing for comparison across the results. It is important to note that when including the weights direction or magnitude of the slopes of the models did not change (Table A5.3.2).

Table A5.3.1 Difference in AIC of models with and without weights for stem-based analyses. Note that for most cases this difference is positive, i.e. that the weighted models have overall lower AIC values meaning that they have a better fit to the data.

		Water deficit affiliation (mm y^{-1})	Potential size (cm y^{-1})	Wood Density (g cm^{-3} y^{-1})
Extended Amazonia	All community	155	133	166
	Recruits	-8	59	28
	Losses	50	68	56
Core Amazon	All community	-75	13	-46
	Recruits	40	48	20
	Losses	34	67	34

Table A5.3.2 Slopes from stem-based models where no weights were included 'n/w' and models where weights 'w' were applied. Note that the slopes differ only slightly between plots including or not weights.

		Water deficit affiliation (mm y^{-1})		Potential size (cm y^{-1})		Wood Density (g cm^{-3} y^{-1})	
		n/w	w	n/w	w	n/w	w
Extended Amazonia	All community	-0.15	-0.15	-3x10^{-3}	-4x10^{-3}	-2x10^{-4}	-2x10^{-4}
	Recruits	-0.40	-0.42	0.05	0.05	-2 x10^{-4}	-3x10^{-4}
	Losses	0.10	0.08	-0.05	-0.05	-5x10-^{4}	-5x10-^{4}
Core Amazon	All community	-0.01	-0.01	0.02	0.01	5 x10^{-5}	3x10^{-5}
	Recruits	-0.28	-0.30	0.06	0.05	-5 x10^{-4}	-5x10^{-4}
	Losses	0.08	0.05	-0.02	-0.03	-5 x10^{-4}	-5x10^{-4}

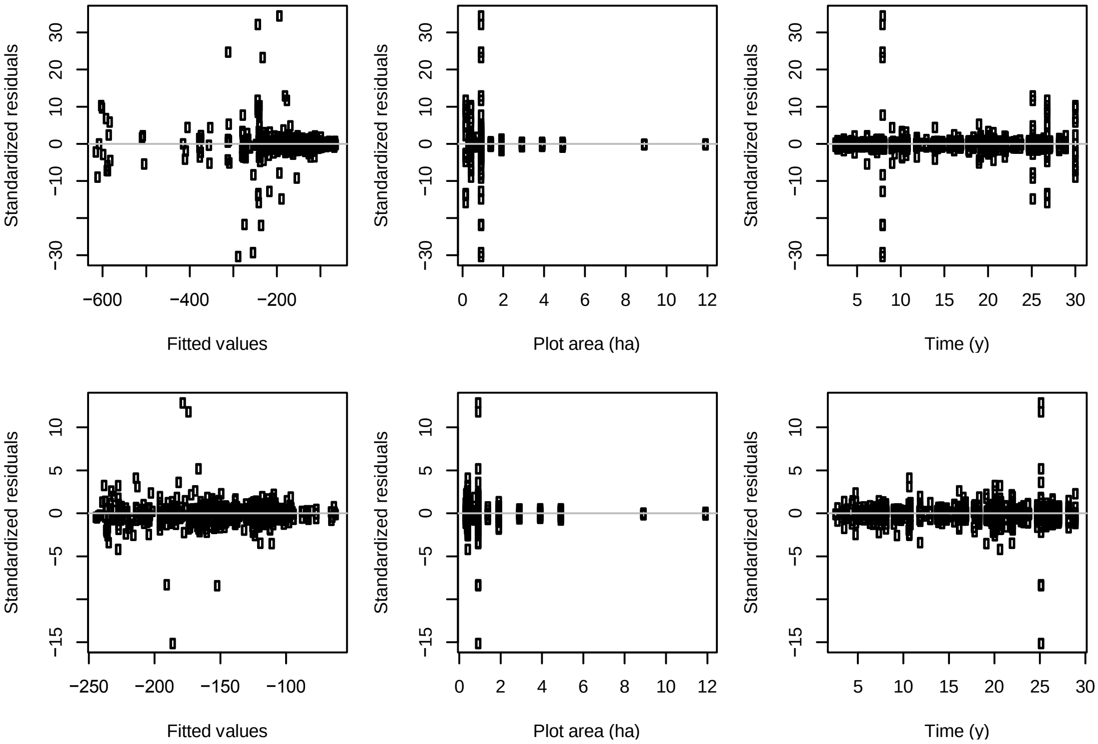


Figure A5.3.1 Residuals versus fitted values, plot area and time of monitoring. The residuals shown here are from two of the GLMM models studied in this chapter: CWM based on WDA from the whole community level using Extended Amazonia data set (top graphs); the same response variable as for the top graphs but for Core Amazonia data set (bottom graphs). The residuals of these two models illustrate the variance of the residuals for the other models (e.g. recruits, losses and other traits). Note the influence of area and time on the variance of the residuals.

Appendix 5.4 - Trends in functional composition for Extended Amazonia

Table A5.4.1 – Mean linear slopes in individual-based functional composition across the Amazon. For each trait, the bootstrap mean annual changes in community weighted mean (CWM) weighted by the squared root of plot size x monitoring period. In brackets: 95% confidence intervals. CWM was calculated for: water deficit affiliation (WDA), potential size (PS) and wood density (WD). The analyses were repeated for recruits, dead trees and the difference between recruits and dead trees (net fluxes). In bold significant trends, i.e. where CIs do not overlap zero.

Community	Water Deficit affiliation (mm y^{-1})	Potential size (cm y^{-1})	Wood Density (g cm^{-3} y^{-1})
Whole community	-0.01(-0.3|0.01)	-0.003(-0.03|0.01)	$-2x10^{-4}$ ($-6x10^{-4}$ | $5x10^{-5}$)
Gains (recruits)	**-0.9(-1.6 | -0.02)**	0.08 (-0.05 | 0.2)	$8x10^{-4}$ ($-9x10^{-4}$ | $3x10^{-3}$)
Losses	-0.01 (-0.9 | 0.7)	-0.06 (-0.02 | 0.06)	$-9x10^{-4}$ ($-3x10^{-3}$ | $5x10^{-4}$)
Net fluxes	-1.5 (-4 | 0.2)	0.15 (-0.2| 0.3)	$4x10^{-4}$ ($-3x10^{-3}$ | $3x10^{-3}$)

Table A5.4.2 – Basal area-based annual plot level trends in functional composition across the Amazon basin. As table A5.4.1 but at for basal area-based analyses.

Community	Water Deficit affiliation (mm y^{-1})	Potential size (cm y^{-1})	Wood Density (g cm^{-3} y^{-1})
All community	-0.04 (-0.14 | 0.03)	**0.03 (0.01|0.05)**	$-5x10^{-5}$(-2 $x10^{-4}$| 6 $x10^{-5}$)
Gains (basal area)	-0.11 (-0.30|0.07)	$3x10^{-3}$(-0.06|0.06)	$-2x10^{-4}$(-7 $x10^{-4}$| 2 $x10^{-4}$)
Gains (recruits)	-0.62 (-1.46|0.14)	0.09(-0.08|0.26)	$2x10^{-3}$(-4 $x10^{-4}$| 4 $x10^{-3}$)
Losses	0.35 (-0.57|1.3)	-0.13 (-0.45|0.15)	$-2x10^{-3}$ ($-4x10^{-3}$| $3x10^{-4}$)
Net fluxes	-0.48(-1.46|0.48)	0.15 (-0.12|0.47)	$2x10^{-3}$ ($-4x10^{-4}$| $4x10^{-3}$)

Appendix 5.5 - Results from the GLMM

Table A5.5.1 – Annual plot level trends in functional composition across the Core Amazonia dataset. Intercept, slope, and percentage change per year (in brackets), of plot-level water deficit affiliation, potential size and wood density between 1985 and 2015. Trends were calculated by fitting a generalized linear mixed model (GLMM) to a time-series of census level community-weighted mean for each trait. The models consider plot as a random effect and were weighted by the square root of both the plot area and the time interval that each plot was monitored for. The analyses were repeated for recruits, losses and the difference between recruits and losses (net fluxes). In bold slopes that significantly differ from zero, considering $\alpha = 0.05$.

		Abundance		Basal Area	
Trait	Community	Intercept	Slope	Intercept	Slope
Water Deficit Affiliation (mm y^{-1})	All community	-126	-0.02(-0.01)	-136	0.01(0.004)
	Gains (growth)			-138	0.06(0.04)
	Gains (recruits)	-126	-0.3 (-0.2)+	-128	-0.3 (-0.2)
	Losses	-130	-0.09 (-0.07)	-132	-0.2 (-0.2)
	Net fluxes	5	-0.2 (-3)	-3	0.09 (3.5)
Potential size (cm y^{-1})	All community	42	0.01 (0.02)+	**51**	**0.03(0.07)**
	Gains (growth)			53	0.02 (0.04)
	Gains (recruits)	39	0.06 (0.15)+	39	0.06 (0.1)+
	Losses	39	-0.01 (-0.02)	43	0.09 (0.2)
	Net fluxes	-0.3	0.05 (15)	9	-0.04 (-0.4)
Wood Density (g cm^{-3} y^{-1})	All community	0.64	5 x10^{-5} (-0.07)	0.64	2 x10^{-5} (0.003)
	Gains (growth)			0.64	3 x10^{-5} (0.004)
	Gains (recruits)	0.62	-5 x10^{-4} (-0.09)+	0.61	-5 x10^{-4} (-0.07)+
	Losses	0.62	-4 x10^{-4} (-0.07)+	0.64	**-1 x10^{-3} (-0.2)**
	Net fluxes	-0.01	1 x10^{-4} (1.8)	0.01	**8 x10^{-4} (6)**

Table A5.2 – As table A5.1 but for Extended Amazonia dataset.

		Abundance		Basal area	
Trait	Community	Intercept	Slope	Intercept	Slope
Water Deficit Affiliation	All community	-151	-0.15 (-0.09)	-160	-0.1 (-0.04)
	Gains (growth)			-162	-0.01(-0.005)
(mm y^{-1})	Gains (recruits)	-147	-0.41 (-0.3)+	-149	-0.4(-0.3)
	Losses	-157	0.10 (0.06)	-162	0.1(-0.06)
	Net fluxes	5	-0.19 (-4)	6	-0.4 (-7)
Potential size	All community	42	-0.004 (-0.008)	**52**	**0.02 (0.05)**
	Gains (growth)			54	0.01 (0.02)
(cm y^{-1})	Gains (recruits)	39	0.05 (0.12) +	39	0.05 (0.1)
	Losses	41	-0.05 (-0.13) +	45	-0.03 (-0.06)
	Net fluxes	-1	**0.10 (8)**	8	0.01 (0.2)
Wood Density	All community	0.64	-2 x10^{-4} (-0.04)	0.64	-3 x10^{-5} (-0.01)
	Gains (growth)			0.63	4 x10^{-5} (-0.01)
(g cm^{-3} y^{-1})	Gains (recruits)	0.61	-2 x10^{-4} (-0.03)	0.60	-3 x10^{-4} (-0.05)
	Losses	0.62	-8 x10^{-4} (-0.13)	**0.62**	**-9 x10^{-4} (-0.14)**
	Net fluxes	-0.01	5 x10^{-4} (4)	0.02	5 x10^{-4} (3)

Appendix 5.6 - Relationship between trends in climate and functional composition

Table A5.6.1 Relationship between trends in climate and composition of the tree mortality for the Core data set. Slope from reduced major axis regression (RMA slope) and Kendall's τ coefficient of correlation between linear slopes of community weighted mean (CWM) and the linear slopes in cumulative water deficit within each census interval. CWM trends are calculated for: water deficit affiliation, potential size and wood density. In bold correlations that differ from zero considering $\alpha=0.05$ when testing the null hypothesis of no relationship between changes in climate and changes in functional composition. Note that the null hypothesis in rejected only for basal area-based losses and fluxes of water deficit affiliation, meaning large wet affiliated trees tend to die more in areas where the trend for climate to become drier is stronger.

		Abundance		Basal area	
Trait	Community	RMA slope	Kendall τ	RMA slope	Kendall τ
Water Deficit	Gains (recruits)	-0.43	0.01	-0.57	0.03
Affiliation	Losses	-0.48	-0.04	**-0.73**	**-0.17**
(mm y^{-1})	Net fluxes	0.60	0.05	**0.80**	**0.13**
Potential size	Gains (recruits)	-0.08	0.03	-0.09	-0.001
(cm y^{-1})	Losses	-0.08	0.08	-0.15	0.02
	Net fluxes	-0.13	0.07	0.16	-0.01
Wood Density	Gains (recruits)	0.001	-0.04	0.001	0.02
(g cm^{-3} y^{-1})	Losses	-0.001	-0.13	-0.001	0.02
	Net fluxes	0.001	0.02	0.001	-0.02

Appendix 6.1 The influence of measurement technique on basal area estimations

The method used to assess a trees' diameter (D) across time can potentially influence results in terms of tree size change. Conventionally, tree growth is assessed based on the diameter of the tree trunk at 1.3 m above the ground (diameter at breast height - DBH), assuming the trunk is cylindrical at the point of measurement (POM). However, this is often not the case for tropical trees that commonly have buttresses or deformities extending above the 1.3 m standard POM. For those trees with irregular trunks, the POM is instead placed in higher areas of the trunk, above any deformities where the trunk is cylindrical (Sheil, 1995). Buttresses often move upwards during a trees' lifespan, which implies that the POM sometimes has to be shifted towards higher parts of the trunk in advance in order to measure tree growth over long periods of monitoring (Sheil, 1995). Various approximations have been developed to estimate growth of those trees that had their POM changed (e.g. Cushman et al., 2014;Talbot et al., 2014).

In this chapter, for those trees that had the POM changed during the monitoring period, I use the mean between the diameter (D) where the old POM is recorded (D_{POMold}) and the D at the new POM (D_{POMnew}), so called $D_{POMmean}$ (Talbot et al. 2014). For every census the diameter sequences of D_{POMold} and D_{POMnew} are calculated based on the actual measured D and on estimations based on the ratio between D_{POMold} : D_{POMnew}. This method has the advantage of creating a continuous growth sequence for each individual tree, regardless of POM changes, and of using the actual measured taper of that tree to create such a sequence. $D_{POMmean}$ has been used in previous studies, where it was found to lead to results consistent with those from other D estimation techniques (Lewis et al., 2009b;Talbot et al., 2014;Brienen et al., 2015). However, because a trees' circumference tends to decrease with height as a result of taper, it is conceivable that the tendency of this method to adjust POMs down the tree stem for later censuses and adjust them up for earlier censuses may still lead to some overestimation of stand level growth rates.

Information from the tree taper is also often used to estimate D (Cushman et al., 2014). This technique consists of estimating the D at 1.3 m based on

$D_{POMactual}$, the POM height and the taper parameter, which quantifies the decay in D from 1.3 to $D_{POMactual}$ (e.g. Metcalf et al., 2009). However, the taper parameter can vary considerably across species and the lack of species-specific taper parameters for tropical trees hampers a more widespread application of D estimations based on tree taper (Cushman et al., 2014).

To verify for possible bias in $D_{POMmean}$ one could use $D_{POMactual}$, i.e. the D where it was measured regardless of POM changes. However, $D_{POMactual}$ always underestimates the growth of stems with POM changes, since the D drops when POM is moved up the tree as a consequence of tree taper, creating discontinuous growth sequences (Phillips et al., 2002). POM changes are applied in advance of deformations reaching within 30 cm of the POM, thus another alternative is $D_{POMactual-1}$, i.e. estimation of D where D_{POMold} is applied for censuses up to, and including, the census when the new POM is first recorded, and D_{POMnew} is applied from the census where the POM change took place. The most highly conservative D estimation would be $D_{POMconst}$, that applies for each tree that had a POM change the mean growth rate of its size class in that plot (gr) during the first census interval calculated based on all Eudicots that did not have POM changes. For monocots and tree ferns with POM changes D_{POMnew} is applied. To estimate $D_{POMconst}$ the growth rate is calculated for each plot in one of three size classes (100-199mm, 200-399mm, $\geq$400mm D). Thus, $D_{POMconst} = D_{t1} + gr * (t_2 - t_1)$ and when $D_{t1} + gr*(t_2 - t_1) >$ D of next size class, the gr of the next size class should be used.

Trends in plot mean POM over time are good indicators of whether there has been any bias in the measurement towards under or overestimating growth. An increase in mean POM height would either indicate that the field team has been conservative in estimating basal area increments and POM changes have been applied often, or that in fact there has been a real increase in the size or number of large buttressed trees which would have high POMs. Another way to assess potential biases in trend in mean tree size as a consequence of the measurement techniques is to investigate the trends in mean basal area-weighted POM height. An increase in basal area weighted POM shows that the POM has been placed higher, especially for large trees. Basal-area weighted POM dynamics are a closer indication of whether trees are being measured around the buttresses as it gives less weight to the fluctuation of small trees from census to census, and is expected to be most insightful when evaluating whether POM change protocols might be affecting stand-level basal area and biomass analyses.

Analyses

Investigating potential changes in mean POM height

I investigate potential bias in tree size estimation caused by shifts in POM. I assessed the trends in mean POM height, diameter weighted mean POM, and basal area weighted mean POM through time in terms of time elapsed (all plots with at least 2 censuses) and in terms of censuses number (plots with at least 5 censuses).

For each plot I calculated the linear slopes of mean and weighted mean POM as a function of time (years or number of censuses). The mean and the 95% CI of all plots weighted by plot sample effort (i.e. squared root of monitoring time x area for year-based analyses and squared root of plot area for census-based analyses) were estimated using non-parametric bootstrapping by randomly resampling values of plot-level mean change across all plots 10,000 times. This analysis was repeated using different ways to estimate basal area, i.e. $D_{POMactual}$, $D_{POMmean}$, $D_{POMactual-1}$ and $D_{POMconst}$.

Comparing results across different D estimation techniques

In order to assess whether $D_{POMmean}$ is in fact a robust D estimation to assess changes in mean tree size I also conducted two alternative analyses: (1) repeated the core analyses using $D_{POMactual}$ and (2) calculated mean tree size using a taper parameter to estimate D. I applied a general taper function:

$$d = D * e^{-b(h-1.3)} \qquad \text{Eq. 1}$$

where d is the diameter at height h, D is the diameter when POM = 1.3 and b is the taper parameter (Metcalf et al., 2009;Cushman et al., 2014). As species-specific b are not available I used a general taper parameter for all trees, which is calculated for each tree based on d and h following Cushman et al. (2014):

$$\log(b) = -2.4368 - 0.3566 * \log(d) + 0.3093 * \log(h). \qquad \text{Eq. 2}$$

The taper correction was applied to all trees that had a POM different than 1.3 m.

The analyses in this appendix, with exception to the repetition of the core analyses using $D_{POMactual}$, were developed using the plots with POM information available for at least 80% of the stems: 113 plots were used to calculate D based on taper function and for the year basis analyses of POM height and 65 plots were used for census basis analyses of POM height.

Results

Investigating potential changes in mean POM height

The analysed trends in POM for different D estimation techniques show that field measurements have progressively moved higher in the trunk to avoid measurements around the buttresses. Thus field teams have either progressively become more conservative in their interpretations of the need to avoid deformities, or trees have generally become larger and more buttressed, or both. Mean POM for $D_{POMactual}$ and $D_{POMactual-1}$ increased when giving the same weight to all trees or when calculating POM weighted by D or basal area (Table A6.1.2 and A6.1.3). The POM used for $D_{POMmean}$ and $D_{POMconst}$ tends to decrease when the same weight was applied to all individuals, or not to change when POM was weighted by tree basal area (Table A6.1.2 and A6. 1.3; Figure A6.1.3).

Comparing results across different D estimation techniques

The main patterns of tree size observed using $D_{POMmean}$ (Table6.1 - main text) persisted when using the more conservative $D_{POMactual}$ (Table A6.1.1). $D_{POMactual}$ underestimates growth as the POM moves up the trunk, which happens more frequently for large trees. However, I still found an increase in mean tree size within the largest size class (≥ 400 mm). The non-significant trend in tree size among overstorey trees is explained by the underestimation of tree size change among large trees when using $D_{POMactual}$.

The increase in mean tree size across the Amazon was more pronounced when calculated using D estimated from the taper function which was 189 mm y^{-1} (95% CI 139; 242) (Figure A6.1.1), this does not differ from mean tree size calculated for the same dataset using $D_{POMmean}$ 174 mm y^{-1} (95% CI 127; 222). The relative increase also did not differ when calculating trends in mean tree size using taper-corrected D (0.45% - 95% CI: 0.34, 0.56) or when using $D_{POMmean}$ (0.42% - 95% CI: 0.32, 0.54).

In addition to the analyses above I used the taper model to calculate the change in D given the shift in mean POM height. For that I applied the taper function to the average Amazonian tree to estimate which would be the trend in mean tree size considering that $D_{POMmean}$ decreases by on average 1 mm y^{-1}. Within the data used here, mean initial POM was 1417 mm, initial D 206 mm, D increment 0.32 mm y^{-1}. Considering mean monitoring length of 15 years the final $D_{POMmean}$ would be 210.8 mm. When applying the taper function, the final D would be 211.5 considering the final POM of 1402 based on the POM decay estimated from the data. This implies a basal area increase of 105 mm^2 y^{-1} or 0.3 % y^{-1}, which is within the CI of the proportional trend estimated for $D_{POMmean}$ for the same dataset and for the more complete dataset used in the main text of the chapter.

Table A6.1.1 – Trends in tree size in forests across the Amazon basin using $D_{POMactual}$ to estimate basal area. Bootstrapped mean and 95% CI (in brackets) for trends in tree size for different group of trees and tree size parameters. Note that none of the estimated trends differ significantly from the trends calculated using $D_{POMmean}$ (Table 6.1 - main text).

	Absolute trend		N of plots
Mean	94 (57|134)	0.2 (0.1| 0.3)	194
Median	30 (12|48)	0.2 (0.1|0.2)	194
Tree size distribution			
Gini Coefficient	$3x10^{-4}$($8x10^{-5}$|$4x10^{-4}$)	0.05(0.02|0.08)	194
Scaling exponent (α)	$-2x10^{-3}$($-2x10^{-4}$|$-4x10^{-3}$)	-0.1 (-0.2|0.04)	160
Allometric constant (β)	-0.6 (-1.2 | -0.1)	-0.1 (-0.3|0.04)	160
Size classes			
< 200 mm	13 (7|19)	0.09 (0.05|0.12)	194
200 - 399 mm	13(-12|38)	0.02(-0.02|0.07)	194
≥ 400 mm	324(107|535)	0.1 (0.1|0.2)	194
Canopy status			
Understorey	46(21|73)	0.3(0.1|0.4)	110
Overstorey	115(-20|251)	0.2(0.1|0.4)	110

Table A6.1.2 - Mean and 95 % CI annual trends in plot level mean POM, diameter weighted mean POM and basal area weighted POM for different diameter (D) estimation techniques across 113 Amazonian plots with at least 2 censuses and 80% of the trees with POM height recorded. $D_{POMactual}$ = actual D of the tree as measured at each point in time. $D_{actual-1}$ = D where the POM was initially recorded is applied for all censuses up to and including the census at which the new POM is first recorded, and D at new POM for all analyses from the census when the POM change took place. $D_{POMmean}$ = mean diameter value where the POM was recorded initially and the diameter at the new POM. $D_{POMconst}$ = applies the mean growth rate of the plot during the first census interval forwards. Mean trends and CI were weighted by plot sample effort (squared root of plot area x monitoring period).

	Mean (mm y^{-1})	2.5% CI	97.5% CI
POM height			
$D_{POMactual}$	3	2	4
$D_{POMactual-1}$	2	1	3
$D_{POMmean}$	-1	-1	-1
$D_{POMconst}$	-1	-1	-1
Diameter weighted POM height			
$D_{POMactual}$	5	4	7
$D_{POMactual-1}$	4	2	5
$D_{POMmean}$	-1	-2	-1
$D_{POMconst}$	-2	-2	-1
Basal area weighted POM height			
$D_{POMactual}$	9	7	12
$D_{POMactual-1}$	6	4	9
$D_{POMmean}$	-1	-2	0
$D_{POMconst}$	-2	-3	-1

Table A6.1.3 - Mean and 95 % CI trends per census of mean POM, diameter weighted mean POM and basal area weighted POM for different diameter (D) estimation techniques across 65 Amazonian plots. As table A6.1.2 but at a census basis for all plots with at least 5 censuses.

	Mean (mm census^{-1})	2.5% CI	97.5% CI
POM			
$D_{POMactual}$	6	1	10
$D_{POMactual-1}$	3	-2	6
$D_{POMmean}$	-3	-3	-2
$D_{POMconst}$	-3	-4	-2
Diameter weighted POM			
$D_{POMactual}$	13	6	19
$D_{POMactual-1}$	7	1	13
$D_{POMmean}$	-2	-4	0
$D_{POMconst}$	-4	-6	-2
Basal area weighted POM			
$D_{POMactual}$	26	15	37
$D_{POMactual-1}$	17	7	27
$D_{POMmean}$	1	-4	6
$D_{POMconst}$	-3	-8	1

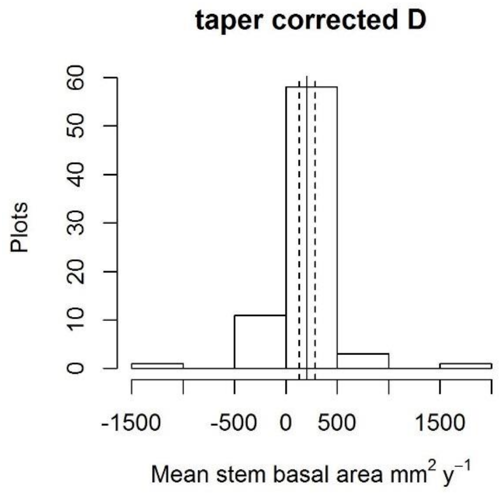


Figure A6.1.1 – Distribution of trends in mean stem basal area per plot using D estimations from the taper function.

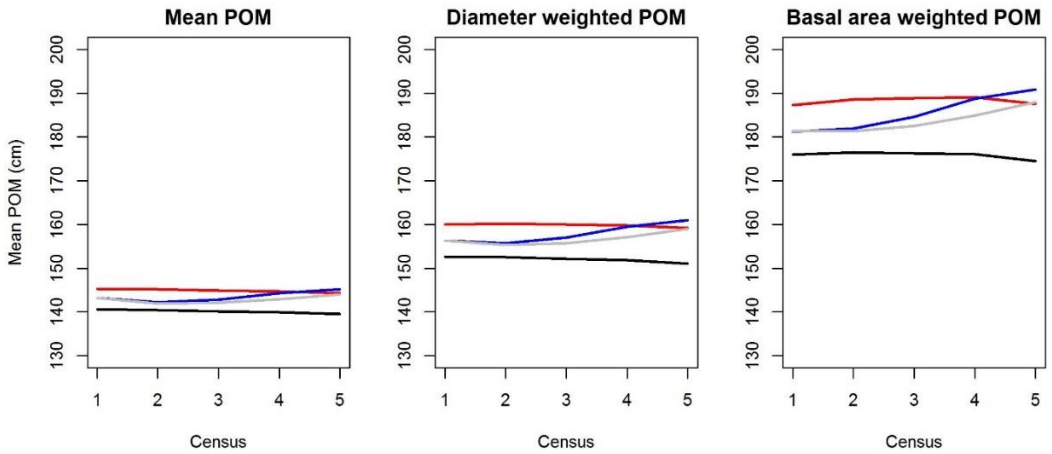


Figure A6.1.2 – Trends in mean, diameter weighed mean and basal area weighed mean POM across censuses for 65 inventory plots in the Amazon Basin. Plots had at least 5 census and 80% of trees with POM height recorded. Different colours represent POM applied to calculate different D estimation techniques: $D_{POMactual}$ (blue), $D_{POMactual-1}$ (grey), $D_{POMmean}$ (red) and $D_{POMconst}$ (black).

Appendix 6.2

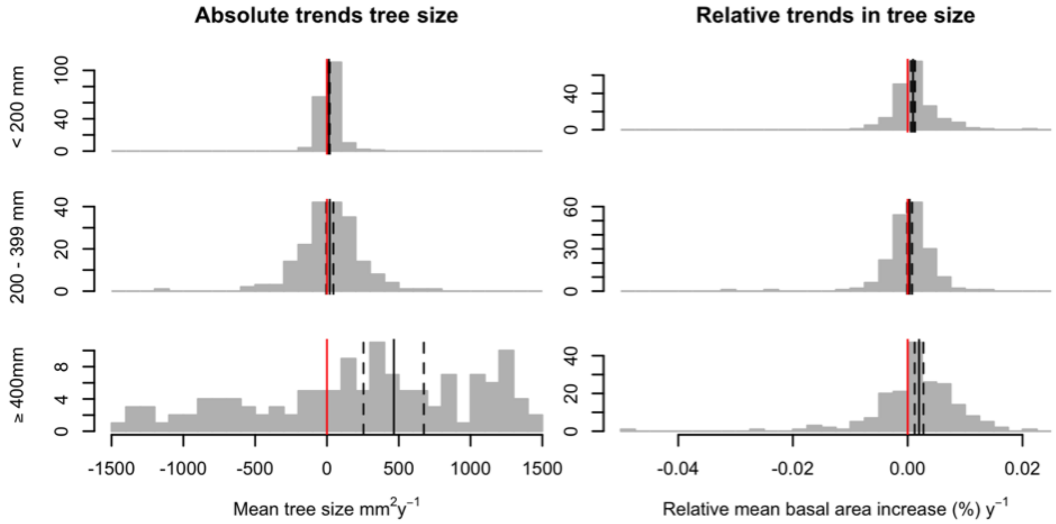


Figure A6.2.1 Histograms of linear slopes of absolute and relative change in tree size in Amazon plots as a function of time within tree size classes. Comparison between trends in tree size within different size classes (<200 mm; 200 - 399 mm and ≥ 400 mm D). Black solid line and dashed lines represent bootstrapped mean and 95% CI, zero is shown by the red line. To help visualization of trends in absolute terms, plots that show trends < -1500 mm y^{-1} or > 1500 mm y^{-1} are omitted from the graph (59 plots ≥ 400 mm D; 1 plot 200-399 mm D). Note that although the increase in tree size is more evident within large trees (≥ 400 mm D) in absolute terms, the trends in size are similar in relative terms regardless of the size class.