Patterns and processes in tropical forests: an analysis of forest structure and function from long-term permanent plots in Venezuela, Northern South America

Emilio Javier Vilanova Torre

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Reading Committee:

Gregory J. Ettl, Chair
Ernesto Alvarado
Jonathan Bakker

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Abstract

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Emilio Vilanova

Chair of the Supervisory Committee:
Professor Gregory Ettl
School of Environmental and Forest Sciences

The differential responses of trees to climate and resource gradients, coupled with historical and current disturbances affect forest dynamics and creates complex landscape patterns in forest assemblages and structures. Long-term data collected from a wide range of forest conditions provides an excellent opportunity to examine the underlying processes behind these patterns, which ultimately drive variations in species diversity, aboveground carbon stocks and forest dynamics in general. In addition, long-term data contains valuable information on the potential effects that climate change may have for terrestrial ecosystems. Thus, management policies, including conservation and restoration might be largely benefited from the results of this type of research. This study is based on long-term data collected from tree populations in different forest-types with contrasting environmental conditions in Venezuela, Northern South America. The *Instituto de Investigaciones para el Desarrollo Forestal* (INDEFOR) affiliated to Universidad de Los Andes in Mérida-Venezuela, maintains the longest running monitoring plots in mature forests anywhere in Latin America and perhaps the tropics, including some sites that were established more than half a century ago. Since 2004, I have been part of four field campaigns (2004, 2009, 2012, 2016) to continue the monitoring of these sites. The information collected is now part of a larger network of similar sites under the umbrella of the Amazon Forest Inventory Network (RAINFOR project) where data has been stored and curated into the Forestplots platform to serve the global scientific community with relevant information from multiple tropical sites in Asia, Africa and South America. Three main studies compose this dissertation project,

all connected through a common theme with a special focus on stem turnover, growth, productivity, and carbon cycle. This dissertation broadly tried to answer the following questions:

- ✓ What are the patterns of tree turnover (i.e. recruitment and mortality) across different forest types?
- ✓ What are the factors controlling Woody productivity (AGWP) across a diverse environmental gradient?
- ✓ What are the relationships between turnover, productivity and aboveground biomass (AGB)?
- ✓ Have turnover rates and AGWP changed over the last three to four decades?
- ✓ What are the principal causal mechanisms behind the observed trends in turnover rates and AGWP?
- ✓ How predictable are these processes using species functional traits?

Part 1: Data from 50 long-term permanent plots from across Venezuelan forests was used to describe the patterns of stem turnover, aboveground biomass (AGB) and woody productivity (AGWP) over contrasting tropical ecological conditions, and the relationships between them and potential climatic drivers. I used a principal component analysis coupled with linear and mixed effects models to analyze the relationship between climate, forest structure and stem dynamics. Two major axes aligned with orthogonal temperature and moisture gradients effectively described more than 90% of the environmental variability in the dataset. Average turnover was 1.91 ± 0.10 % year^{-1} with mortality and recruitment being almost identical, and close to average rates for other mature tropical forests. Nevertheless, dynamic rates were significantly different ($p < 0.001$) among regions, with the lowland forests in Western alluvial plains being the most dynamic, while Guiana Shield forests are showing the lowest turnover rates. A weak positive relationship between AGB and AWGP was found with Guiana Shield forests having, on average, the highest values for both variables (204.8 ± 14.3 Mg C ha^{-1} and 3.27 ± 0.27 Mg C ha^{-1} year^{-1}), but AGB was much more strongly and negatively related to stem turnover. Moisture was a fundamental driver of turnover, with longer dry seasons apparently favoring greater rates of tree turnover and thus lower biomass. Regional variation in AGWP among Venezuelan forests strongly reflects resource availability, with greatest AGWP when both precipitation and temperatures are high. Overall, forests in wet, low elevation sites with low turnover, stored the greatest amounts of biomass carbon. While faster dynamics are closely associated with lower carbon storage, turnover rates and woody productivity were weakly correlated, indicating that stem dynamics and carbon dynamics might be decoupled from one another.

Part 2: Long-term data from 44 plots was used to analyze the temporal dynamics of stem turnover (i.e. mortality and recruitment), aboveground biomass (AGB) and woody productivity (AGWP) across different ecological regions in Venezuela over the last four decades. By means of generalized additive models to analyze temporal trends and linear models to test for a significant change in slopes, I found that 21 plots had a positive slope for recruitment rates (average slope 0.02 % year^{-1}, $p < 0.001$), while 32 plots showed a positive slope of mortality over time (average slope 0.02 % year^{-1}, $p < 0.001$). Regardless of region, elevation, soil fertility or climate seasonality, the increase in tree mortality was highly significant ($p < 0.001$). A significant increase in the amount of biomass from dead trees (average $\mathrm{AGB}_{\mathrm{loss}}$ slope = 0.02 Mg C ha^{-1} year^{-2}, $p < 0.001$) was also found combined with a modest but steady increase in AGWP (average AGWP slope = 0.02 Mg C ha^{-1} year^{-2}, $p < 0.001$). Although a decline in AGB change was found, the magnitude was not sufficient to significantly affect the forest carbon sink (average slope for net AGB change = - 0.003 Mg C ha^{-1} year^{-2}, $p < 0.117$). Using generalized mixed effects models, I detected that for the monitoring period of each plot, competition factors appears to be more relevant explaining observed trends in recruitment rates, while climate, particularly the steady and significant increase in mean annual temperatures was largely responsible for the increase in mortality rates. There was a clear regional effect with each driver contributing in different proportions to the observed trends in turnover, AGWP and net biomass change. The results of this study highlight the importance of including stand development and competition factors to improve our understanding of forest dynamics over time. This study can be used as an input for other more complex models aiming the analysis of effects of climate change on forest ecosystems in the tropics.

Part 3: The objectives of this study were: 1) to describe the functional trait space in two contrasting tropical environmental settings in Venezuela; 2) analyze the relationships between relative growth rates (RGRs) and the average traits values for different tree species; 3) analyze the potential links between the community weighted means (CWMs) of traits with four main response variables at the community scale: rates of recruitment (*r*) and mortality (*m*), aboveground carbon (AGB) and woody

productivity (AGWP). For this, I employed a principal component analysis combined with linear mixed models and data from 10 functional leaf and stem-level traits that are known to be important attributes of tree species. Additionally, four functional diversity indexes, soil nutrient content and chemistry, along with plot stem density were included into the analysis as potential predictors. I used data from long-term permanent sample plots in two contrasting mature forest sites in western Venezuela. I test the existence of a *slow–fast continuum* where lowland and fertile forests would be generally dominated by acquisitive traits (e.g. high Specific Leaf Area – SLA) influencing a much faster dynamics and higher productivity, while high-elevation forests can be better described in terms of conservative traits (e.g. high leaf mass per area - LMA) driving lower turnover rates and productivity but a higher AGB. Results show that both sites are noticeably different ($p < 0.001$) with regards to their structure, dynamics and function, with lowland forests having higher annual recruitment (2.67 ± 0.55 % year^{-1} – Mean ± Standard deviation), mortality (3.09 ± 0.63 % year^{-1}), and AGWP (2.95 ± 0.63 Mg C ha^{-1} year^{-1}), but overall lower AGB (130.99 ± 44.71 Mg C ha^{-1}) when compared to montane forests (r = 2.06 ± 0.26 % year^{-1}; m = 1.59 ± 0.21 % year^{-1}; AGWP = 2.39 ± 0.36 Mg C ha^{-1} year^{-1}; AGB = 178.49 ± 27.95 Mg C ha^{-1}). The species' traits in montane forests were mostly associated with adaptation to high soil moisture, greater shade tolerance and thus lower growth rates (e.g. high leaf thickness, high LMA, low foliar nutrient content), whereas for lowland species, traits were more associated with higher resource availability (e.g. high SLA, high nutrient concentration in leaves). I found that different CWMs of traits have effects over different responses with CWM of leaf nitrogen simultaneously involved in all of the studied response variables. Yet, functional traits were more important when predicting AGB and AGWP compared to stem turnover highlighting the importance of other factors such as soil fertility and environmental conditions when studying stand dynamics.

Venezuela is one of the most biologically diverse countries on earth. Yet, a high proportion of its ecosystems, especially forests, are threatened by deforestation and degradation that may compromise the services these areas currently provide while enhancing climate change through the emissions of carbon. The findings of this project represent a body of knowledge regarding the ecology and dynamics of different forest-types, some of which seem to be already experiencing the effects of increasing temperatures resulting in higher rates of tree mortality and a reduction in productivity. However, in some cases, these areas are not only still acting as carbon sinks mitigating

the effects of climate change, but they also constitute large reservoirs of carbon and habitat for biodiversity making them highly important for a sustainable future. I strongly believe that the results presented in this dissertation project may have important connections and implications to initiatives such as reducing carbon emissions from deforestation and forest degradation, sustainable forest (or land) management for timber and nontimber forest products and increasing forest cover by forest landscape restoration. In addition, each chapter in this dissertation contains information that can help improving decision making processes at different levels regarding current state of Venezuelan forests. Finally, I see the results and conclusions of my research as important elements for a better future of Venezuelan tropical forests, its research community and overall the country.

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Successfully completing this research would never have been possible without the amazing guidance and help from Prof. Oliver Phillips from the University of Leeds. Since our first exchange when I started collaborating with the RAINFOR project back in 2004, and up to today I have learned a lot about tropical forests ecology from him, but more importantly I learned the unique value of networking and collaboration to build solid partnerships that can foster scientific research. I sincerely thank him for the insightful comments and encouragement during this whole process. Being part of his research group, even for a short period of time, was an important experience during my PhD as well.

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Collaboration and networking are two major aspects of my career as a scientist. I am a firm believer that connecting, both professionally and personally, with other scientists with diverse way of thinking is an important component of science. For this reason, I especially want to thank Geertje van der Heijden from University of Nottingham. When we met in 2009, I never expected to collaborate so closely with her, and she have been fundamental in accomplishing this goal with insightful comments and sound scientific advice.

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To all…

Thank you!

DEDICATION

To Venezuela, my beloved country

I want to dedicate this research project to all the academic staff, students, alumni, technicians and all hard workers of Venezuelan universities and research institutions who keep on doing work in science, education and culture, while pursuing freedom in the darkest moment of our contemporary history. I pray for better times to come for our country, but I am sure that with their work, strength and resilience building a better country for all will be much easier.

DATA ACCESSIBILITY

Individual tree-level data from every plot used in this project can be accessed through the forestplots.net portal. All relevant data are within the chapters and its Supporting Information. Data used in Chapter 2 is part of a data package at Dryad DOI: https://datadryad.org/stash/dataset/doi:10.5061/dryad.nf57p95.

ETHICS STATEMENT

This project was carried out in strict accordance with correspondent Venezuelan legislation. Every plot census was done after obtaining the required permits in those cases needed for access protected areas or collecting plant material.

Mature forests in the Venezuelan Andes region

Photo: Emilio Vilanova

CHAPTER 1

INTRODUCTION

CHAPTER 1. INTRODUCTION.

AN OVERVIEW ON THE STRUCTURE, FUNCTION AND DYNAMICS OF TROPICAL FORESTS

Forests in their multiple forms and types are the dominant terrestrial ecosystem on Earth, covering about one third of the globe's land area (FAO, 2018). Forests represent a fundamental component of world's carbon cycle, are the habitat for biodiversity and are important for the provision of a myriad of services from which people depends for their livelihoods. Distributed over different environmental and latitudinal gradients, forest ecosystems account for at least 75% of global terrestrial productivity (GPP) (Beer et al., 2010), with tropical forests (TFs) being disproportionally relevant compared to forests in the temperate or boreal region. For instance, it has been estimated that from the approximately ~1700 Pg[1] of carbon contained in global forests, tropical forests represents about ~1000 Pg (Bonan, 2008), or close to a third of the carbon held in the atmosphere (Mitchard, 2018; Quéré et al., 2016).

The geographical pattern of increasing species diversity from the poles to the equator is one of the most pervasive features of life on Earth (Brown, 2014) making TFs a unique region. Within the different biological expressions of TFs, woody plant diversity exhibits a prominent latitudinal gradient, especially in the Americas, with species diversity reaching a peak in the Neotropics (Dick & Pennington, 2019). For example, TFs worldwide can harbor between 40,000 and ~53,000 tree species (with diameters ≥10 cm) with almost half probably located in the Neotropics (Slik et al., 2015), from which the Amazon region is the richest area with an estimated number of close to 16,000 tree species (ter Steege et al., 2013; ter Steege et al., 2016). This feature of TFs can be better appreciated when compared to other biomes. For example, in 5000 m^2 (1/2 of an hectare) plots in Barro Colorado, Panama, as many as 263 tree species (dbh ≥10 cm) can be found in contrast to 17 species in a temperature forests like the H.J Andrew Forest in Oregon, USA (Brown, 2014). The hypotheses to explain these high levels of diversity are abundant (Dick & Pennington, 2019; Hill & Hill, 2001), but recent studies have found that a combination of resource availability, mostly through high

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[1] A Petagram of carbon (Pg), also known as a Gigaton (Gt), is equal to 10^15 grams or one billion tones. A ton, also known as a metric ton, is equal to one thousand kilograms (1,000 kg).

temperatures (Brown, 2014), and specialized interactions among plants and their natural enemies involving a conspecific negative density dependence (LaManna et al., 2017) are two of the most relevant drivers of species diversity in TFs. While these levels of biodiversity are often cited almost exclusively for lowland forests, a much higher diversity is found in the mountains of the tropical Andes, including outstanding levels of species endemism (Rahbek et al., 2019).

White and Picket (1985) described the concept of disturbance as any relative discrete event that disrupts the ecosystem, community, or population structure and changes resources, substrate availability or the physical environment. Tropical forests, like all ecosystems, are subjected to a diverse set of natural and anthropogenic **disturbances** that varies in type, frequency, duration and intensity. However, from the perspective of natural disturbances, that is, events caused by normal environmental fluctuations or destructive events, tree-fall gaps are by far the most documented form of natural perturbation in tropical forests (Brokaw, 1982; Denslow, 1987; Whitmore, 1989) (Figure 1). Moreover, the creation of gaps is an essential part of the “Intermediate Disturbance Hypothesis” (IDH) (Connell, 1978), one of the first major non-equilibrium theories to explain the maintenance of species diversity in tropical forests (Chazdon, 2014; Schnitzer, Mascaro, & Carson, 2008). The IDH has been part of a large and intense debate over its validity (Fox, 2013; Sheil & Burslem, 2003, 2013), and in practice few studies have been capable of testing the hypothesis of an intermediate disturbance regime acting as a force for maintaining species diversity in the tropics. For instance, it has been argued that the main postulate of Connell´s theory was largely focused on large-scale and less frequent disturbances such as windstorms, ignoring small-scale forces such as gaps that are considered essential in the forest growth cycle (Chazdon, 2014).

Characteristics of the disturbance regime in combination with environmental conditions are largely responsible for the **dynamics and structure** found in tropical forests. Differences in disturbance regimes are linked to pronounced differences in forest dynamics, structure, and composition within and across tropical regions (Chazdon, 2014). Elements such as type of disturbance, at least in an initial stage, duration, and intensity greatly influences the characteristics of the stand development (i.e. succession) process after disturbance (Guariguata & Ostertag, 2001; White & Pickett, 1985).

a) b) c)

Figure 1. Three different disturbance examples common in tropical forests: a) an aerial view of a mature stand in the Guiana Shield region showing the diverse composition and structure of TFs with small gaps naturally created by trees or branches falling; b) Industrial logging is an important driver of anthropogenic disturbances in many TFs, here depicted an industrial logging operation in Eastern Venezuela; c) Agricultural-driven disturbance in the Western Plains of Venezuela. All photos by Emilio Vilanova.

Despite the likelihood of multiple successional pathways that characterize the process of forest recovery (Chazdon, 2014), in the absence of significant disturbance or environmental changes, it has been widely assumed that mature plant assemblages experience little net change in living mass through time, where the rate of gain of new plant mass (i.e. **recruitment**) is closely matched by the rate of loss of plant mass to death (i.e. **mortality**) (Stephenson & van Mantgem, 2005). Under this hypothesis, natural, mature forests would be considered as self-maintaining systems, that is, in accordance with local processes of mortality, growth and regeneration, lost trees are continually replaced with new recruits and the forest vegetation continues in a dynamic equilibrium or steady-state (Swaine, Lieberman, & Putz, 1987) (Figure 2).

One of the main reasons to study the characteristics of turnover patterns is that often the dynamics of recruitment and mortality also determines the dynamics of productivity or carbon absorption, at least at larger scales (Stephenson & van Mantgem, 2005). In fact, it has been recently shown that the spatial distribution of aboveground biomass and carbon across Amazonian forests is largely influenced by the rates of tree mortality (Johnson et al., 2016), which are a response of many other associated biotic and abiotic factors such as tree growth rates (Chao et al., 2008), soil fertility and soil structure (Quesada et al., 2012), and the length of dry season or water stress levels (Vilanova et al., 2018). Given these connections, carbon-rich forests have been typically found in less dynamic conditions or where turnover rates (i.e. the average between mortality and recruitment *sensu* Phillips & Gentry, 1994) are low. In the neotropics, these areas are often located in the Eastern portion of the Amazon and the Guiana Shield (Avitabile et al., 2016; Johnson et al., 2016; Malhi et al., 2006; Mitchard et al., 2014). **In chapter 2 of this dissertation, I analyze these variables (i.e. turnover rates, aboveground biomass – AGB, and aboveground woody productivity – AGWP) in the context of different forest types in northern South America to study the relationships between them and with a series of environmental factors that could help explain existing regional differences and to better understand potential response of tropical forests to climate change.**

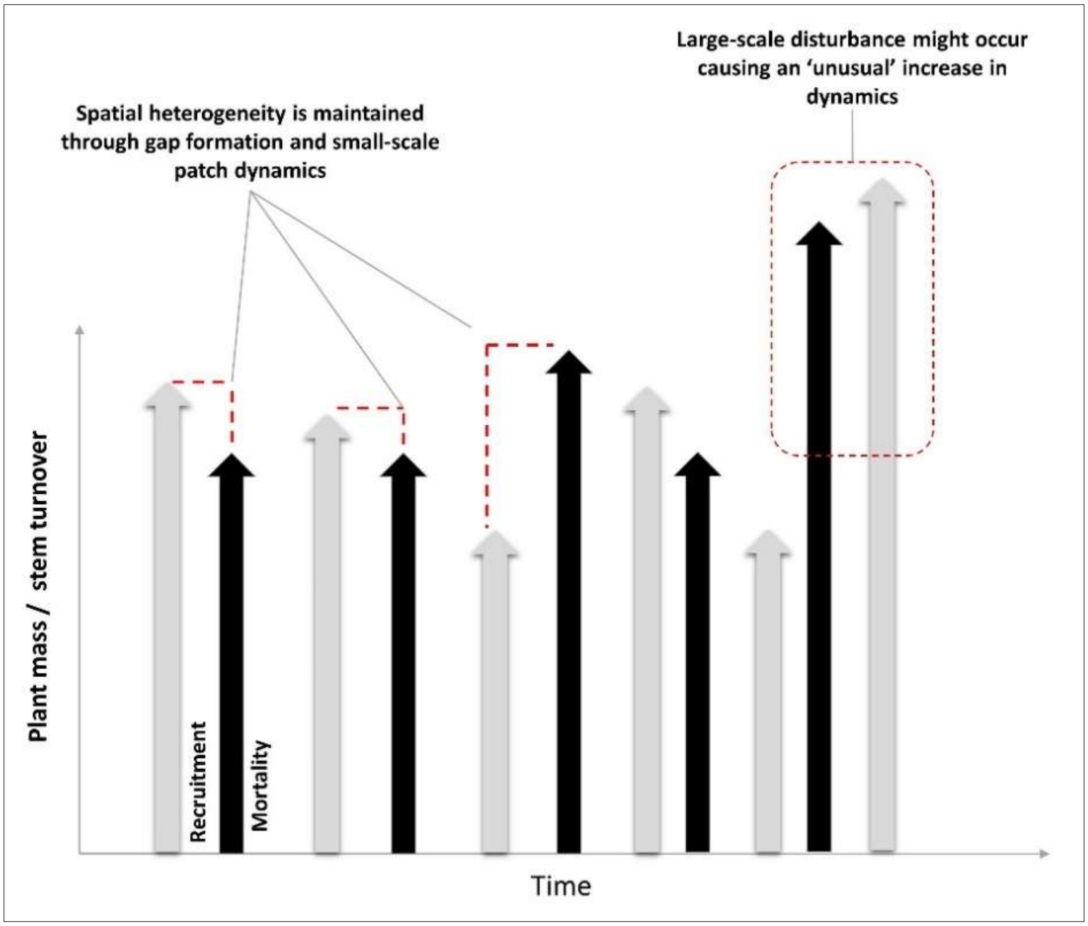

Figure 2. Conceptual model of temporal dynamics in tropical forests. Stand development process implies periods where mortality events may trigger high rates of recruitment. Under this hypothesis, only when conditions of severe disturbances occur, we could expect significant alterations in forest dynamics.

The study of recruitment and mortality (i.e. turnover) in forests in general, but particularly in the case of tropical forests, has also received a great deal of attention in ecological research in at least the last three decades after evidence was found in the early 1990's (cf. Phillips & Gentry, 1994) showing that mature tropical forests seem to have experienced alterations in their dynamics, including changes in stand structure, species composition, and species interactions with disturbance forces and the environment. For instance, increasing trends in mortality and recruitment rates in Amazonian forests have been reported (Phillips & Gentry, 1994; Phillips et al., 2004; Laurance et al., 2009), with tree growth exceeding losses from tree death, thus increasing productivity and the overall aboveground biomass both in the Amazon (Phillips et al., 1998; Baker et al., 2004) and African forests (Lewis et al., 2009a). In some cases, associated changes in species composition in Amazonia were also found with an increase in the abundance and dominance of early successional species and lianas (Laurance et al., 2004; Phillips et al., 2002). While similar changing patterns have not been found for other tropical sites in Costa Rica (Clark et al., 2003) or Asia (Feeley et al., 2007), the results of an apparent 'changing ecology' in mature tropical forests challenged the widely known assumption of a dynamic equilibrium in mature forests. The causes behind such alterations have been hotly debated in the scientific literature and these findings proved to be contentious including methodological aspects (e.g., site selection, field measurements) or underestimation of previous disturbances (Clark et al. 2003; Clark 2004; Fisher et al. 2008; Chambers et al. 2009; Lewis et al. 2009b; Lloyd et al. 2009).

Describing the patterns of tropical tree community structure, including the rates of temporal change and its potential drivers is complicated because of the large amount of spatial and temporal variation and heterogeneity that distinguish many tropical forests. Let's take the case of mortality rates for example. The analysis of tree mortality exemplifies how a particular ecological process shapes and alter forest complexity, but partitioning the causes or drivers is difficult. Tree mortality constitutes a fundamental process in forest development, influencing resource availability, tree regeneration, stand structure, and stand-level productivity (Franklin, Shugart, & Harmon, 1987). As an inherent process of forests dynamics, one can argue that tree death can be considered a natural consequence of the forest disturbance regime. Therefore, as many life-history traits in tree species, mortality might manifest in different ways and scales via localized events (i.e. stands), within forest communities, regionally, and/or globally and along broad-scale environmental gradients.

Because of recent reports of increasing tree mortality rates in many “old-growth” forests including the tropics (Lewis et al., 2004; Phillips et al., 2004), temperate western US (Smith et al., 2015; van Mantgem et al., 2009), and boreal ecosystems (Zhang et al., 2015), there is a growing interest for understanding the underlying causes of these patterns and the potential implications for biodiversity and nutrient cycling, especially the carbon balance in the context of climate change. Causes of tree mortality are related to at least three major categories including resource limitation, environmental stress or large-scale disturbances that often occurs at the same time (Reyer et al., 2015). The process of tree death can be seen as a gradual process of forest decline that typically involves a combination of pre-disposing factors including age, senescence, decline in tree vigor, poor site conditions, species vulnerability, and other stress-causing variables.

While some extensive tree mortality (i.e. ‘forest die-off’) events are relatively easy to address with regards to its causes (e.g. the 2012-2016 drought in the Sierra Nevada, California - Goulden & Bales, 2019), others are often more complex to understand, especially in tropical forests. Evidences of increasing rates of mortality in the Amazon between 1980 and 2010 for example have been argued to be a response of a combined effect from the accelerated dynamics observed in the early 1990’s and an increase in the intensity and frequency of severe droughts that limited growth and enhanced tree death in the last portion of the period (Brienen et al., 2015). Increasing resource availability (e.g. CO_2 and temperature) has often been cited as potential drivers of higher rates of both recruitment and mortality (Phillips & Lewis, 2014), but other forces such as recovery from past disturbances and competition (Muller-Landau, 2009; Muller-Landau et al., 2014) have also been proposed to explain the observed dynamics in some parts of the tropics. **In chapter three, I examine the temporal dynamics of turnover and productivity across a wide range of environmental conditions using long-term data from multiple plots in Venezuela. After describing the trends, I explore different causal mechanisms behind the dynamics of forest structure aiming at having a better understanding of how forest could respond to climate change.**

In the study of the structure, dynamics and function in tropical forests, the use of functional traits as a measure of the species identity has gained increasing importance in recent years. Functional characteristics of species may operate in contexts such as effects of dominant species, keystone species, ecological engineers, and interactions among species, including competition, facilitation, mutualism, disease, and predation (Hooper et al., 2005). In any case, an individual species, or a group of them can hold particular properties that can cause a relative larger impact on ecosystem functions such as productivity or carbon uptake. For example, most studies aimed at understanding carbon storage in tropical forests have improved since 'wood density' was incorporated in the allometric models used for estimating aboveground biomass in tropical trees (Baker et al., 2004; Chave et al., 2005; Chave et al., 2014). High variability in wood density implies that forests are heterogenous and diverse which we would expect to influence forest function through different ways. In a recent analysis for instance, Phillips et al., (2019) found that the impacts of species on forest biomass due to wood density occurs at all scales, from the individual tree up to the whole biome, thus variation in tree species composition may regulates how much carbon forests can store. For instance, low wood density is often an inherent trait linked to lower costs and thus faster growth rates, but with overall lower carbon storage capacity.

While the positive effects of an increasing number of species on productivity are still open to debate (e.g. Poorter et al., 2015; Sullivan et al., 2017), studies that have equally analyzed species richness (number of species), functional richness (number of functional groups), and functional composition (presence of certain functional groups or traits) indicates that the variance components of functional composition and functional richness tend to be larger than the variance component of species richness alone in influencing ecosystem processes (Díaz & Cabido, 2001). Grouping plant species into functional "clusters" can depend on many elements. In terms of the potential effects of functional traits in the diversity-productivity relationship, plants can be generally classified with respect to their structural, physiological, and/or life strategy characteristics (Korner, 1993). Yet, to some extent the use of one particular set of traits should be a reflection of the others. For instance, the well-known differential response of net photosynthesis of plants to changes in light intensity (see for example Shugart, 1997), can also be interpreted not only in terms of their physiology, but also in the context of structural (e.g. low wood density vs. high wood density species), life-history (e.g. short-lived vs. long-lived), and in terms of successional patterns of species and response to disturbances (Chazdon, 2014). **Using a selected group of traits in two contrasting sites in Western Venezuela, in chapter four I test the potential existence of a growth trade-off that can be explained using traits from the most**

important species in the community, while also testing the effects of these over rates of turnover, biomass and productivity.

THE SCALE OF THE PROJECT

The analysis of forest dynamics and changes in structure and function is closely linked to the spatial and temporal scale considered. The same forest can be viewed as changing rapidly or as remaining stable, depending on the spatial and temporal scales of observation (Chazdon, 2014). Even more important, whether the processes underlying change in a given ecological assemblage can be extrapolated across large spatial, temporal and taxonomic scales requires a good understanding of the explanatory power behind the data collected for any type of ecological research (Chave, 2013; Rapacciuolo & Blois, 2019), since it also affects the way we quantify the effects and dynamics of the myriad ecosystem services provided by forests (Raudsepp-Hearne & Peterson, 2016).

Across the numerous studies that have addressed similar questions to this research project, broadly focusing on the dynamics of tropical forests, we find that one of the fundamental and contentious points of discussion has always been the issue of scale. If tropical forests are changing due to ‘external’ forces involves weighing the advantages and limitations of permanent sample plots, one of the essential resources available when studying the patterns of tree turnover, and the dynamics of carbon and tree growth. Plot size, frequency of measurements, and how well represented the different and diverse forest communities are all scale-related issues (Brienen et al., 2015; Clark, 2004; Phillips et al., 1998).

Forests are characterized by patterns and processes distributed over a broad range of scales (Lertzmann & Fall, 1998). These spatial and temporal variations are driven by the occurrence of disturbances that can modify ecosystems in such a way that population structure, resource availability, and the physical environment may be affected. Variation includes differences not only in ecosystem scale but also in the type of disturbance and attributes such as frequency, distribution, intensity and severity (White & Picket, 1985). Some disturbances might be determined by complex interactions of bottom-up and top-down regulations that may influence potential successional trajectories and thus forest structure and species composition (Tepley et al. 2013). From these interactions one may understand that disturbance regime and its effects on vegetation vary depending on the different scales at which these mechanisms are being analyzed. For instance, fire may be viewed as extremely severe at the stand scale and therefore as a "catastrophic" event, but at larger scales might not be so severe. Similarly, increasing rates of tree turnover or changing patterns in forest carbon (e.g. Lewis et al., 2009; Phillips & Gentry, 1994; Phillips. et al., 2004) could be very well localized and with short-term effects. While this section is not intended to delve in the complexity of ecological scale (see for example McIntire & Fajardo, 2009 or Schneider, 2001 for additional discussion), understanding the implications of both temporal and spatial scales is an important step towards the critical evaluation of the results that are being reported in all of the three major research studies that are part of this dissertation (Figure 3).

A DESCRIPTION OF VENEZUELAN TROPICAL FORESTS

FOREST COVER, LAND USE CHANGE AND FOREST CARBON IN VENEZUELA

Venezuela has a total land area of about 916,445 km^2 with different studies often estimating in about 45-50% of this area to be covered by different types of forests (FAO, 2010, Pacheco et al. 2011). The variation in forest cover in Venezuela in the last three decades has followed a similar trend as in many tropical countries with a notorious peak in forest loss during the early 1990's and a slightly declining tendency towards the end of the twentieth century (Hansen et al., 2013). Over a longer time period, Pacheco et al. (2011) found that between 1920 and 2008 Venezuela had an average annual rate of forest loss of 0.30%, with a net decrease of 26.4% in the national forest cover, with the period beginning in the 1950s experiencing a sharp increase in deforestation especially in the Western Plains ecoregion, which remained as one of the national hotspots of deforestation for a long time (Pacheco et al. 2014). With the somewhat historical unbalanced distribution of Venezuelan population, largely concentrated to the northern portion of the country, from the 36% of forest cover that was estimated to exist in this region by the mid twentieth century, some estimates place this number to as low as 10% in recent decades (GFW, 2002; Torres-Lezama et al., 2008), leaving the vast region of the Guiana Shield to the south of the Orinoco river as the main forested area in the country. Western plains have been mostly cleared for agricultural lands with current forests being mostly in protected areas and other areas with limited access (Pacheco et al., 2011; Torres-Lezama et al., 2008).

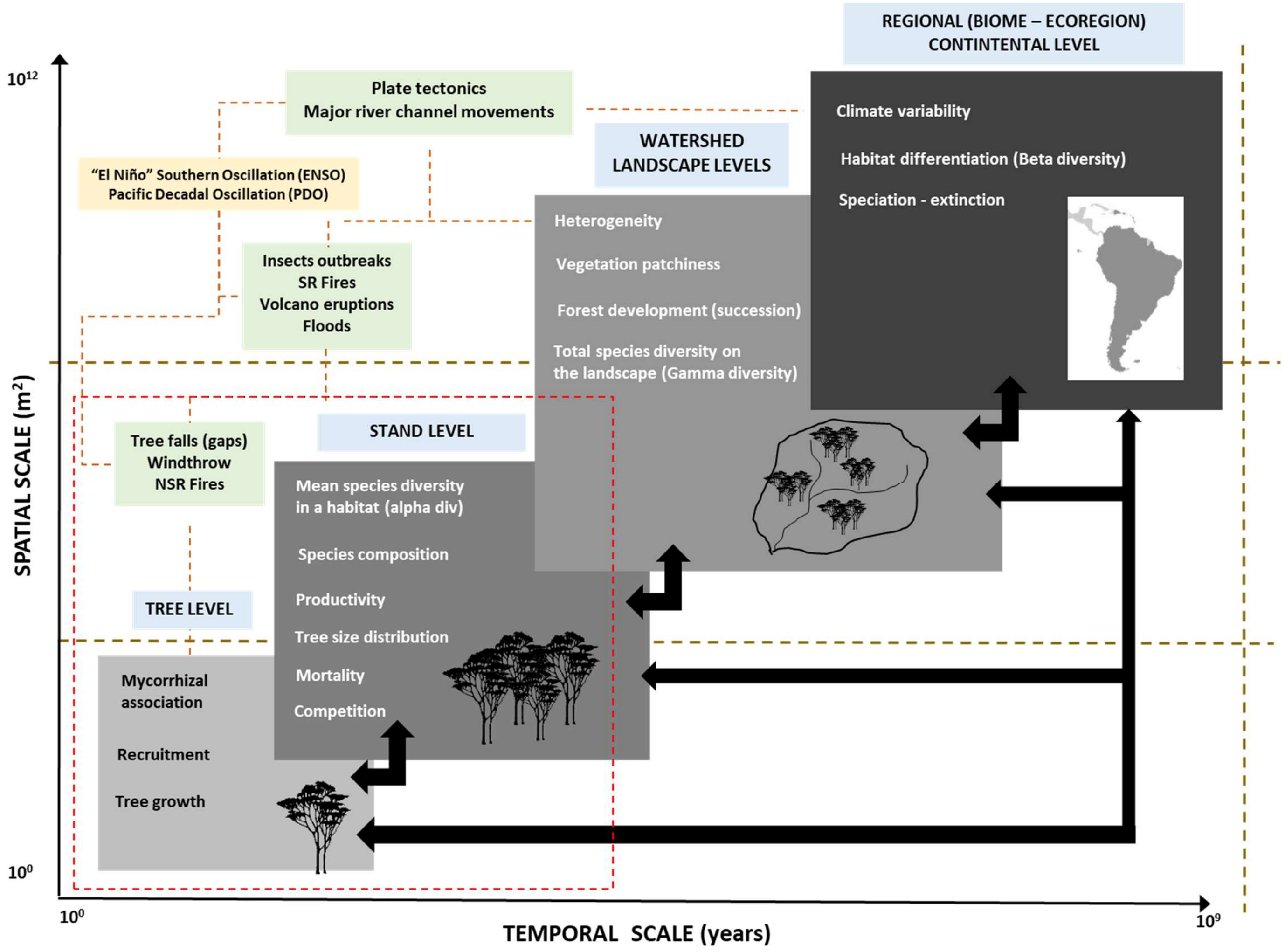

Figure 3. Conceptual diagram of forest disturbances at different spatial and temporal scales and its effects on vegetation structure with emphasis on forests. Each gray-colored box represents a different level from small (single tree) to large (regional – continental) scale. In red, I highlight the approximate scale assumed for this project. Within each level, the main ecological processes are listed, and major disturbances are indicated in green-colored boxes. The model accounts for certain proportion of overlapping among different levels highlighting the presence of complex interactions. Brown dashed lines highlight the major type of disturbances associated with each level at different temporal and spatial scales. For instance, at lower levels (tree to forest stand) and small scales, disturbances such as tree-fall gaps, frequent and low intensity windthrow events or frequent small non stand replacing (NSR) fires may follow a shifting mosaic steady state type (Sprugel, 1991). Conversely, large and catastrophic disturbances (e.g. infrequent stand replacement fires, flooding) can severely affect vegetation in such manner that large-scale ecological processes can be modified. Finally, black arrows connecting all levels are interpreted as top down and bottom up interactions operating over a range of spatial and temporal scales. Model derived from Delcourt et al. (1983); White & Picket (1985); Böhmer & Richter (1997); Lertzmann & Fall (1998).

According to recent FAO estimates (FAO, 2015), 287,500 ha were lost every year in Venezuela between 1990 and 2000 (−0.6 % year^{-1}), with a decrease during the 2000–2010 decade of about 164,600 ha per year (−0.3 % year^{-1}). Updated statistics from public available data in Global Forest Watch (www.globalforestwatch.org) that uses information from the study of Hansen et al., (2013) indicates that from 2001 to 2018, Venezuela lost 1.95 Million ha of forests[2] (Figures 4 and 5), while gained 191,000 ha of tree cover. In recent years, the spike in deforestation to the southern region in the Guiana Shield has been mostly driven by illegal gold mining (Bevilacqua et al., 2002; Torres-Lezama et al., 2008, Pacheco et al., 2017), while agriculture appeared to be the main driver of forest loss in the Andean region (Aide et al., 2019).

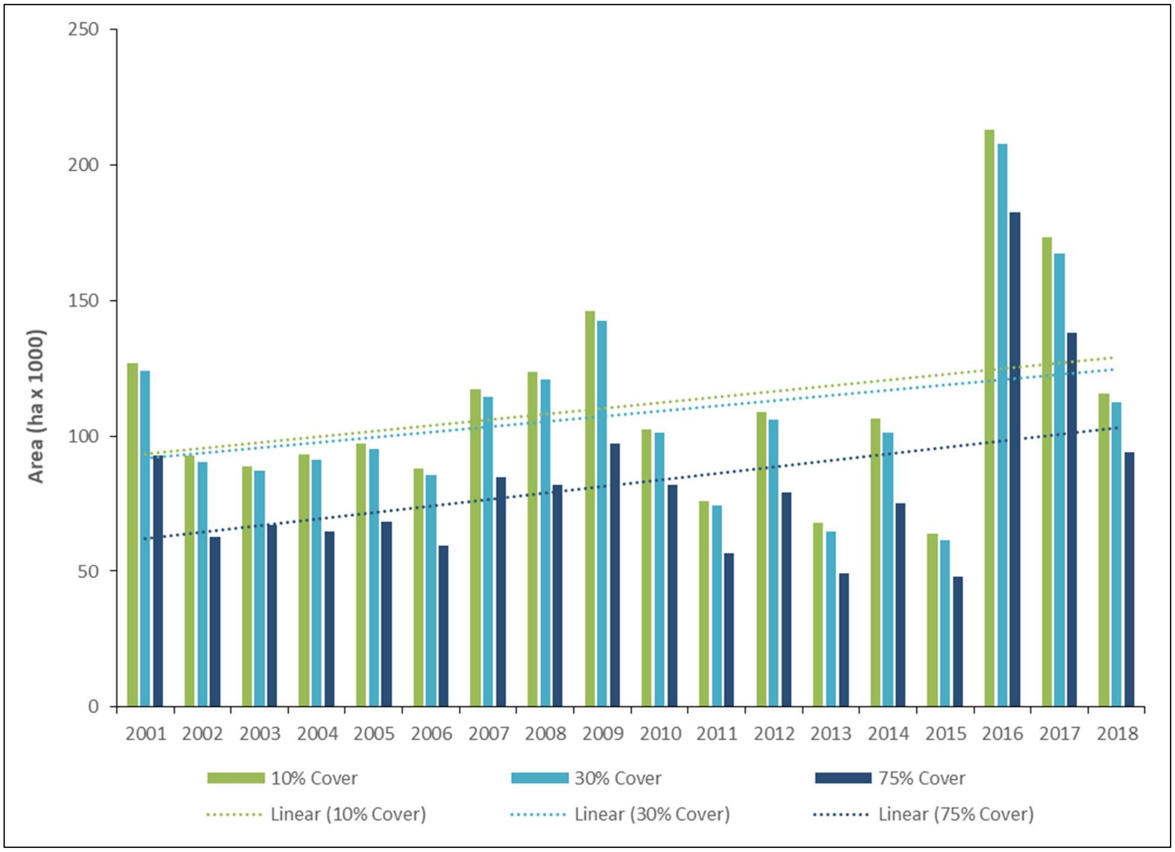

Figure 4. Total annual forest cover loss (in thousands of hectares per year) in Venezuela for the 2001-2018 period using different proportions of forest canopy cover. Each category includes a linear trend. The figure was built using public data available from the Global Forest Watch.

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[2] Defining forests as areas of at least 0.5 ha in minimum area, 30% canopy cover and at least > 5 m of total height.

Estimates of carbon loss from pantropical deforestation derived from carbon stock and forest area loss data have varied in recent years from 0.81 to 2.9 Pg annually (1 Pg = Gigaton (Gt), is equal to 10^{15} grams or one billion tones; Baccini et al., 2012; Pan et al., 2011) and with the greatest discrepancies found between studies that use earth observation satellite data and those that use forest inventory and other tabular reference data (Mitchard et al., 2014; Zarin et al., 2016). Roughly, these values have represented between 15 and 20% of global carbon emissions in the last decade (Asner et al., 2010; Curtis et al., 2018; Pan et al., 2013). Furthermore, combined effects of deforestation and climate change (i.e. drought-related mortality) in recent years seems to have created the conditions for these ecosystems to be functioning as a net carbon source (Baccini et al., 2017; Mitchard, 2018).

In Venezuela, the effects of deforestation and forest degradation in terms of carbon released have not been officially quantified. Lack of standardized methods for monitoring forest cover, undermining of institutional capacities, and a dramatic decline in professional training, among other factors helps explaining this situation. However, revising the literature in this topic we find few studies that have shown that carbon emissions due to deforestation and forest degradation in Venezuela can be significant. Most of these studies have been conducted at global or pantropical scale and includes a reference for Venezuela and its forests. For example, between 1980 and 1990, when national rates of deforestation peaked (FAO, 2010), Bonduki and Swisher (1995) reported that up to 44% of the national CO_2 emissions were caused by deforestation alone. Similarly, Harris et al. (2012) estimated that, between 2000 and 2005, about 9 Tg C $year^{-1}$ (units are 10^{12} grams of carbon per year) were lost due to deforestation in Venezuela, that according to some sources might have represented up to between 9% and 28% of national emissions during the last decade (Pacheco-Angulo et al., 2017), somewhat in agreement with the observed decline in deforestation rates. Additionally, Pearson et al., (2017) found for the 2005-2010 period that close to 10% of Venezuelan carbon emissions came from forest degradation, including selective logging, wood fuel harvest, fire, and grazing as the main factors. Combined, these findings are a strong reason for a more in-depth research about the national carbon budget and the implications of deforestation and forest degradation, for which this research project could be useful.

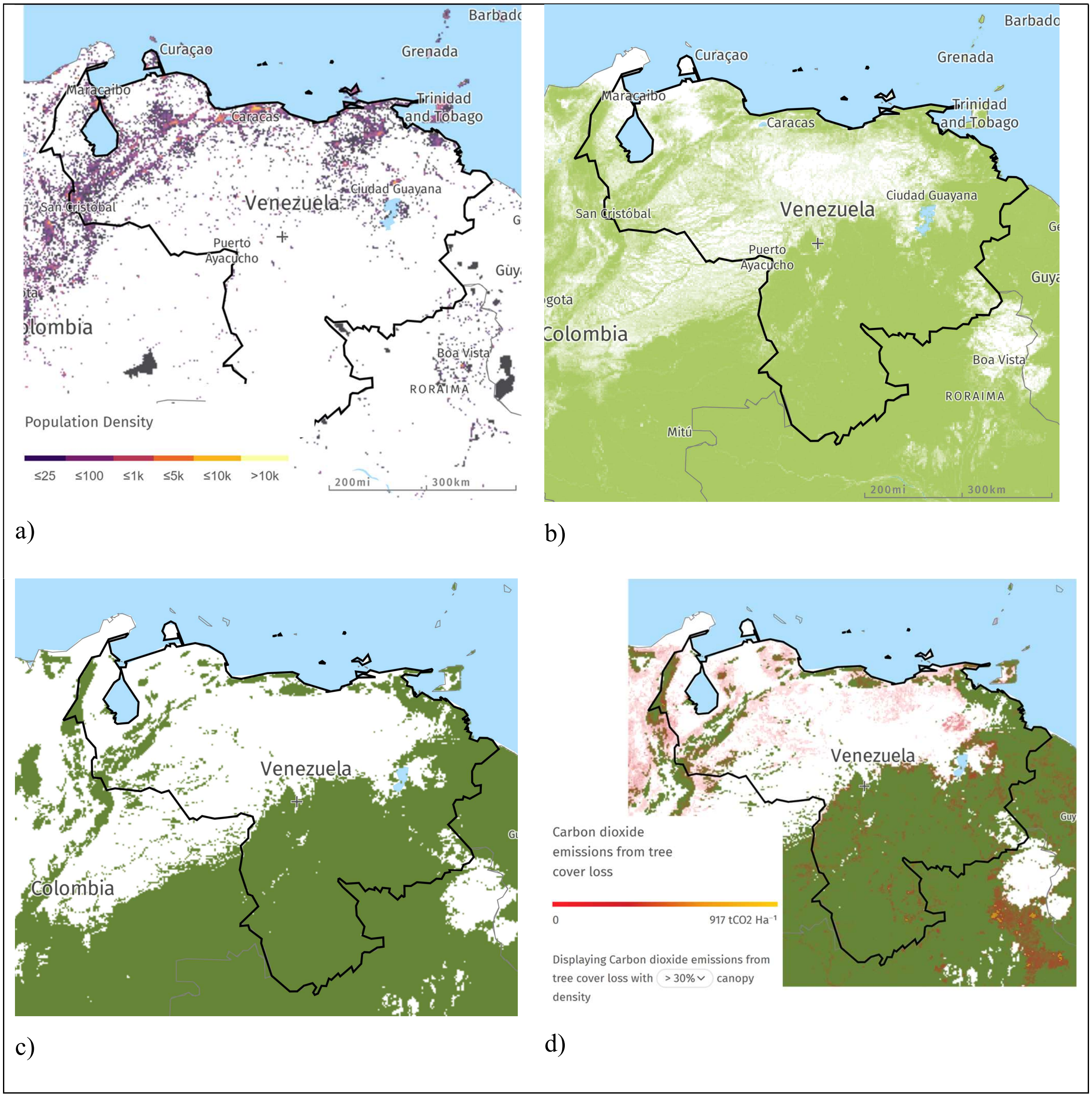

Figure 5. Different views of Venezuelan forests: a) human population density at national scale where the disparity in land occupation between the southern and northern portions of the country is clear; b) Total tree cover in 2010 using a 30% canopy density as reference. Tree cover is defined by Global Forest Watch as all vegetation taller than 5 meters in height, and is the biophysical presence of trees and may take the form of natural forests or plantations existing over a range of canopy densities (Hansen et al., 2013); c) Approximate extension of "primary forests" defined by De Sy et al. (2019) as mature natural tropical forest cover that has not been completely cleared and regrown in recent history; d) Carbon dioxide emissions from tree cover loss overlapping the map of primary forests in Venezuela between 2001 and 2018. All maps are publicly available from Global Forest Watch (GFW, 2014).

ENVIRONMENTAL SETTING AND FOREST-TYPES IN VENEZUELA

Located in the northern portion of South America, slightly above the equator, like much of the tropical region, Venezuela is largely subjected to the influence of the intertropical convergence zone (ITCZ), which affects rainfall patterns that results in the existence of wet and dry seasons in comparison to the cold and warm seasons of higher latitudes. ITCZ's position, structure, and migration influence ocean–atmosphere and land–atmosphere interactions on a local scale, the circulation of the tropical oceans on a basin scale, and a number of features of the Earth's climate on a global scale (Waliser & Jiang, 2015).

Globally, the mean annual precipitation of the tropical rainforest region is 2180 mm year^{-1}, the mean temperature is 25.4 °C (Malhi & Wright, 2004). Land form and relief, or the physiographical features in the land in Venezuela, largely expressed by the existence of three major mountain systems and different types of plains and savannas, are a major driver of the seasonal and geographical patterns in rainfall in Venezuela at local and regional scales (Huber & Oliveira-Miranda, 2010). It has been described that at least two major gradients in the distribution of precipitation exist in this part of the world: one from the Northeastern Atlantic to the Andes in the west, and a second one from the Caribbean Sea to the southern Amazonian flatlands (Andressen, 2007). Annual precipitation in Venezuela ranges from less than 400 mm per year in some of the driest portions of the country up to about 4500 mm year^{-1}, which along with its seasonal distribution influence the type and characteristics of the vegetation (Huber & Oliveira-Miranda, 2010) (Figures 6 and 7).

From the stand point of temperature, though much less variable than precipitation, there are important differences at regional scales, mostly as a response of elevation and latitude. With an elevational range from sea level up to close to 5,000 meters in the peaks of the Andean mountains, temperature varies accordingly (Arismendi, 2007). Consequently, a highly diverse set of vegetation types can be found across the country, where up to 18 different vegetation types have been identified in which lowland evergreen forests dominate the landscape (Huber & Oliveira-Miranda, 2010). Other formations include cloud forests restricted to a rather narrow elevational gradient in different parts of the country, palm-dominated and swamp forests in the Orinoco Delta, mangroves, riparian and semideciduous forests across much of the savanna and the plains, and different expressions of shrub-like vegetation, grasslands and savannas (Huber & Oliveira-Miranda, 2010). In fact, savannas might account for close to 25% of the country with major continuous savannas located in the central Orinoco Plains (*Llanos*) which are limited by the Andean and Coastal Mountains to the west and north, respectively, and with a second large savanna in the Guiana Plateau (*Gran Sabana*) in the southeast of the country (Baruch, 2005) (Figure 8).

THE DATA: A VENEZUELAN PERMANENT PLOT NETWORK

Beginning in the 1950s and extending into the 1970s, a consistent and systematic effort to monitor about 100 forest plots occurred in several areas of Venezuela with census periods extending for more than 50 years in some cases. The initial plot design aimed to provide information in support of timber management that was starting with the first timber-oriented concession in the Western Plains zone of Venezuela in 1970. A team of researchers lead by Jean Pierre Veillon (Veillon, 1985), and many others thereafter have supported the systematic monitoring of these forests. As of 1985, 62 plots with different areas and disturbance features were still being monitored. Other researchers from different institutions in Venezuela have been incorporating additional data from other areas over the last 15 years, and since 2004 most of these plots are part of the Amazon Forest Inventory Network (RAINFOR), a regional partnership of researchers involved in the study of tropical forests in the Amazon region (Malhi et al., 2002; www.rainfor.org). The entire national-level plot network includes today **99 sites with an area from 0.1 to 1 ha**, comprising a variety of environmental conditions and with distinctive ecological characteristics. Plots are not equally distributed across biogeographical regions, and thus some areas have been more extensively sampled than others. Nevertheless, they span a wide range of environmental conditions encompassing an important degree of variability in temperature, rainfall, altitude, and disturbance regime, forest structure and composition. Out of the total number of plots, 43 are square plots of 0.25 ha (50 x 50 m), 24 are of 1 ha (100 x 100 m), 31 plots are small transects of 0.1 ha (10 x 100 m), and one plot is 0.2 ha (20 x 100 m). Temporally, 53 plots have more than one measurement (hereafter census), with the rest being single-census plots (Figure 9).

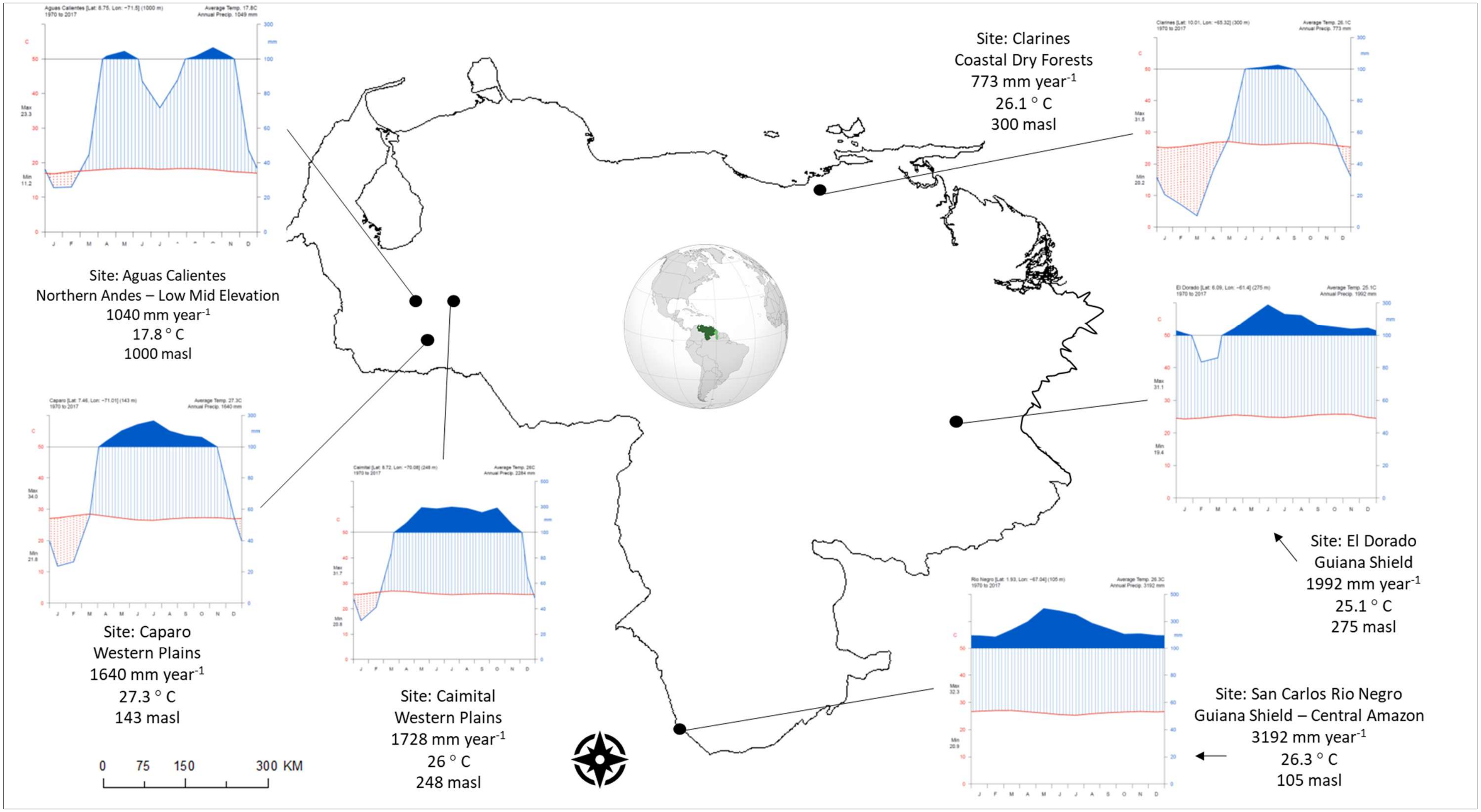

Figure 6. Distribution of annual temperature and precipitation for six different sites in Venezuela using the updated high-resolution grids (CRU TS3.10) of monthly climatic observations from the Climate Research Unit (CRU) at University of East Anglia (Harris et al., 2014). Data is the average for the period 1970-2017. Red lines depict mean temperature per month; blue polygons indicate months with precipitation greater than 100 mm. Western and northern sites are more seasonal compared to areas located to the south of the country.

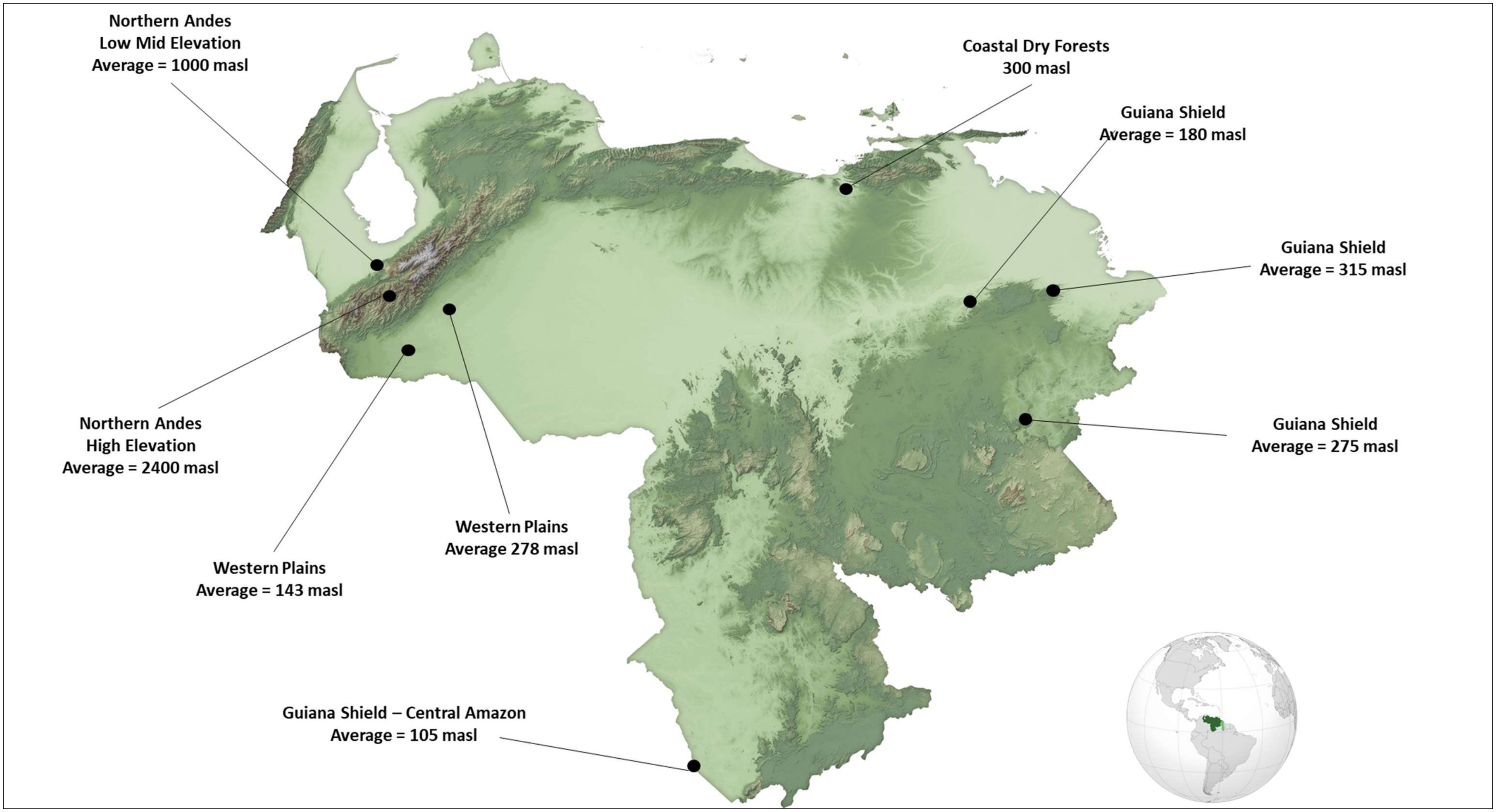

Figure 7. Digital shaded relief map of Venezuela with the location of major study sites. The map is a composite of 3-arc-second (approximately 90-meter) elevation data, captured during the Shuttle Radar Topography Mission (SRTM) and publicly available from Garrity et al., (2004) at https://pubs.er.usgs.gov/publication/ofr20041322

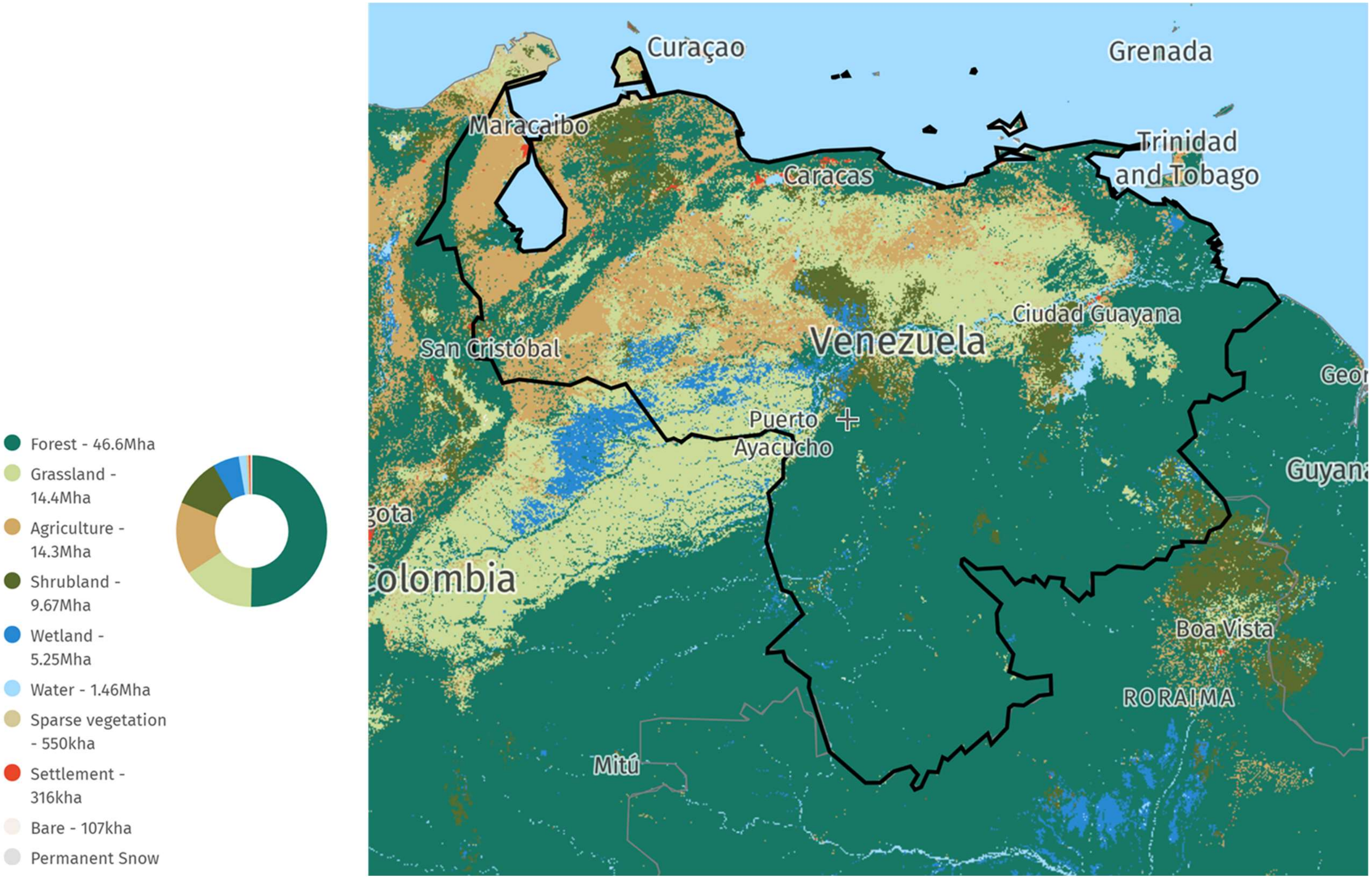

Figure 8. Land cover map of Venezuela showing major cover types for year 2015. Total land area is estimated at 92 Million hectares. Legend includes the approximate area of each land cover type. This data set was created by the European Space Agency (ESA) and is available from The Global Forest Watch (GFW, 2014).

The average number of censuses is 11.2 (Min = 4; Max = 41), with the longest period of monitoring spanning from 1961 up to 2016. In total, 26 plots are being continuously monitored up to 2015-2016 (Figures 10 and 11).

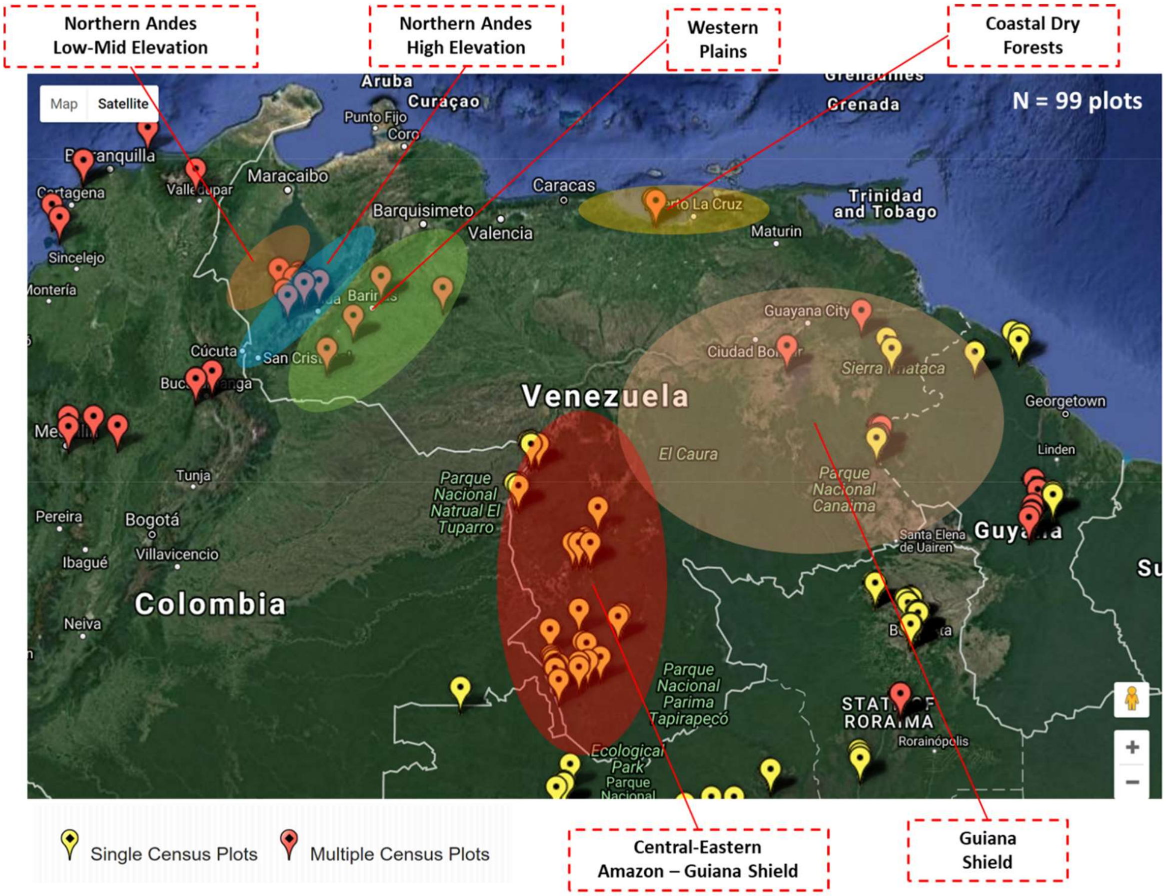

Figure 9. Geographical location of the permanent sample plot network in Venezuela, highlighting six major ecological regions. Yellow symbols depict single-census plots, while red symbols refer to plots with more than one census. Detailed information for the plots is found in the supplementary information of Chapters 2 and 3. Plot map available from RAINFOR website (www.rainfor.org). Base map from Google Earth.

For the most part, lacking accurate information on past disturbances for a high proportion of these, and given the structural and compositional features of majority of the plots, all sites have been assumed as having "old-growth" characteristics. However, in the case of Western Plains forests, some information exists showing that these areas were subjected to large-scale deforestation mostly for agriculture purposes between 1750 and 1810 (XIX century) during Venezuelan independence (Veillon, 1976). Furthermore, beginning in the 20th century selective logging operations have been documented for some areas characterized for high abundance of tropical cedar (*Cedrela odorata*) and Big-leaf Mahogany (*Swietenia macrophylla*) (Kammesheidt et al. 2001). Therefore, for the most part, the majority of the plots located in this region have been considered as late-successional or late second-growth forests.

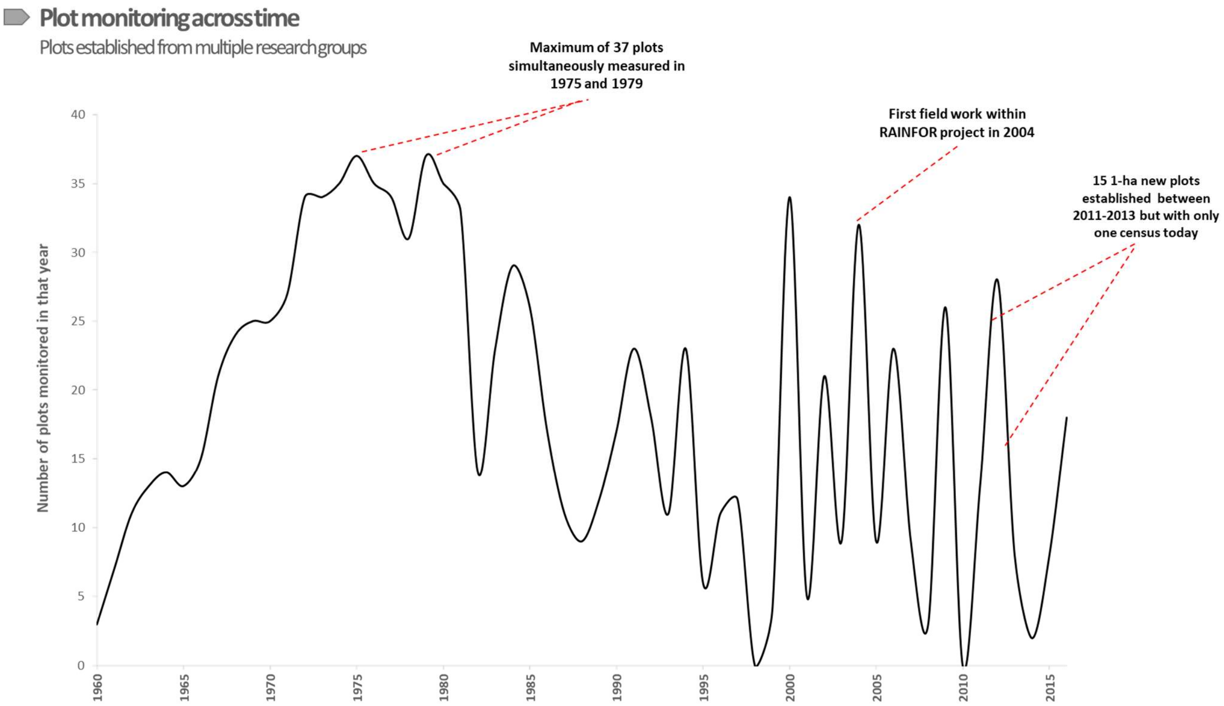

Figure 10. Number of forest plots measured per year between 1960 and 2016 within the sites included in the RAINFOR network and being managed by different research teams.

Using established plot protocols, forests have been sampled over multiple census intervals across all sites. Data collection typically involves the measurement of all live stems (trees, palms, and lianas) with diameter (D) ≥10 cm at 1.3 m height. For non-cylindrical stems owing to buttresses or other deformities, the point of measurement is raised above the point where it is more or less cylindrical, approximately 50 cm above the end of the buttress or deformity. The exact height of the point of measurement (POM) has been recorded and marked on the trees to ensure that future measurements would be taken at exactly the same point along the stem. For those trees where buttress growth threatened to reach the initial POM, the height of diameter measurement was raised to a new POM, located sufficiently high above the buttresses to avoid interference of buttresses with diameter measurements at next censuses. If a change in

POM was made, both the diameter at the original POM and the new POM were recorded, thus creating two disjoint series of diameters measured at different heights. These changes are reviewed later in the forestplot.net database to have standardized measurements of the diameter for every individual. In each census, we also account for all individuals that have died during the interval while adjusting for possible causes of death based on field protocols (Phillips et al. 2016; Supplementary Information).

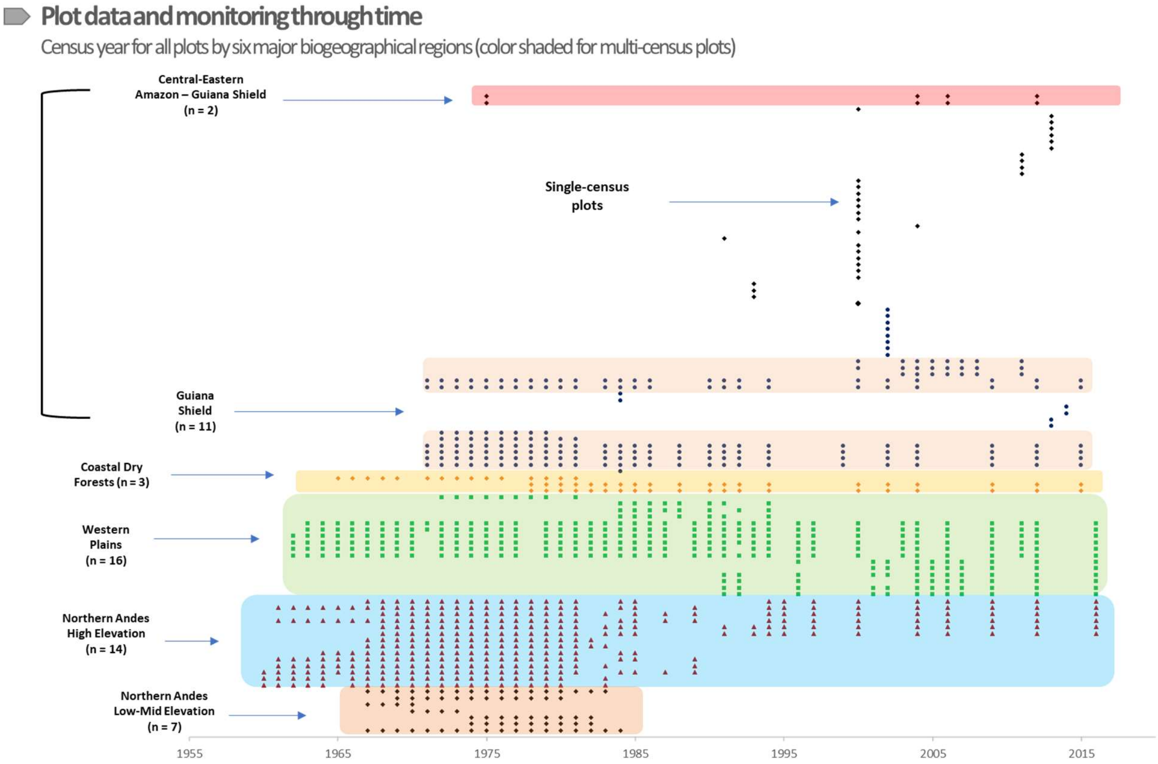

Figure 11. Details on the number of census per plot in Venezuelan plot-network. Different colors represent six different regions highlighting only those plots with more than one census. Each point indicates one census at a given time.

An effort to identify each individual at the species level has been made since the beginning of the field measurements. However, especially for plots that have not been monitored in the last decade, some degree of uncertainty remains with regards of botanical identification. For these cases, local names have been used and a verification procedure with botanists and other experts in this field was conducted. Since 2004, all data has been stored and curated in the ForestPlots.net web application and database (Lopez-Gonzalez et al., 2011; Peacock et al., 2007). The application allows for multiple queries regarding field measurements, taxonomical information, biomass and turnover estimations among several other options.

OUTLINE OF THE DISSERTATION AND RESEARCH QUESTIONS

This project consists of three main research components and the major characteristics and objectives have been outlined in this introductory chapter. Using the described data from permanent sample plots, a wide range of forest processes and patterns were analyzed with a major focus on tree turnover, growth, productivity, and carbon cycle. This dissertation broadly tried to answer the following questions:

- ✓ Q1: What are the patterns of tree turnover (i.e. recruitment and mortality) across different forest types?
- ✓ Q2: What are the factors controlling Wood NPP (AGWP) across a diverse environmental gradient?
- ✓ Q3: What is the relationship between turnover and productivity?
- ✓ Q4: What is the relationship between productivity and AGB?
- ✓ Q5: Have turnover rates and AGWP changed over the last three to four decades?
- ✓ Q6: What are the principal causal mechanisms behind the observed trends in turnover rates and AGWP?
- ✓ Q7: How predictable are these processes using species functional traits?

An individual tree of *Mora gonggrijpii* (Kleinhoonte) Sandwith (Leguminosae) in the Venezuelan Guiana Shield region. Photo: Emilio Vilanova

CHAPTER 2

ENVIRONMENTAL DRIVERS OF FOREST STRUCTURE AND STEM TURNOVER ACROSS VENEZUELAN TROPICAL FORESTS

CHAPTER 2.

ENVIRONMENTAL DRIVERS OF FOREST STRUCTURE AND STEM TURNOVER ACROSS VENEZUELAN TROPICAL FORESTS.

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ABSTRACT

Using data from 50 long-term permanent plots from across Venezuelan forests in northern South America, I explored large-scale patterns of stem turnover, aboveground biomass (AGB) and woody productivity (AGWP), and the relationships between them and with potential climatic drivers. I used principal component analysis coupled with generalized least squares models to analyze the relationship between climate, forest structure and stem dynamics. Two major axes associated with orthogonal temperature and moisture gradients effectively described more than 90% of the environmental variability in the dataset. Average turnover was 1.91 ± 0.10 % year^{-1} with mortality and recruitment being almost identical, and close to average rates for other mature tropical forests. Turnover rates were significantly different among regions ($p < 0.001$), with the lowland forests in Western alluvial plains being the most dynamic, and Guiana Shield forests showing the lowest turnover rates. I found a weak positive relationship between AGB and AGWP, with Guiana Shield forests having the highest values for both variables (204.8 ± 14.3 Mg C ha^{-1} and 3.27 ± 0.27 Mg C ha^{-1} year^{-1} respectively), but AGB was much more strongly and negatively related to stem turnover. The data suggest that moisture is a key driver of turnover, with longer dry seasons favoring greater rates of tree turnover and thus lower biomass, having important implications in the context of climate change, given the increase in drought frequency in many tropical forests. Regional variation in AGWP among Venezuelan forests strongly reflects the effects of climate, with greatest woody productivity where both precipitation and temperatures are high. Overall, forests in wet, low elevation sites and with slow turnover stored the greatest amounts of biomass. Although faster stand dynamics are closely associated with lower carbon storage, stem-level turnover rates and woody productivity did not show any correlation, indicating that stem dynamics and carbon dynamics are largely decoupled from one another.

INTRODUCTION

Tropical forests serve as habitats for more than 45,000 tree species (Slik et al., 2015), and store up to 262 Pg C or 66% of world's terrestrial biomass (Pan et al., 2013). In total, more than 1 billion people, most of them in the tropics, depend on goods and local and regional services provided by forests (Vira et al., 2012). Moreover, the whole world benefits from their global climate services, ultimately reflecting the enormous relevance of these ecosystems for species conservation, climate change mitigation and other ecosystem services.

Tropical deforestation remains a serious concern, with more than 2,000 km^2 year^{-1} lost between 2000-2012 (Hansen et al., 2013), despite a recent decline in deforestation rates in some countries (e.g., Nepstad et al.,, 2014)). Degradation and deforestation of tropical forests between 2005 and 2010 released between 0.56 and 1.69 Gt C year^{-1} respectively (Pearson et al., 2017), a number that may account for 10-20% of global carbon emissions (Houghton et al., 2012; Le Quéré et al., 2016). Yet, forests in the tropics have helped mitigate climate change by sequestering large amounts of carbon. For instance, between 1980 and 2010, net carbon sequestration in mature forests across countries in the Amazon region was estimated to be greater than carbon emissions from land-use change, and except for Venezuela, those from fossil fuels as well (Phillips & Brienen, 2017).

Understanding the factors driving carbon dynamics in tropical forests has become a fundamental task in ecology, management and conservation. The production of standing living biomass is primarily a function of the rate of fixation of CO_2 by photosynthesis in the forest canopy, and as such is the primary measure of carbon supply and metabolic activity at the individual tree scale (Malhi, 2012). At the stand scale, biomass is the cumulative outcome over time of how environmental factors (e.g., climate, soils) and functional traits (e.g., leaf area and wood density) impact forest structure and dynamics, including the rate at which wood is produced (growth) and lost (branch-fall and mortality) (Pan et al., 2013).

In highly diverse tropical forests, composed of hundreds or thousands of tree species, each with its own ecological properties, the importance of this diversity on biomass carbon storage is actively debated. Some studies have shown a positive effect of taxonomic diversity on forest carbon (e.g., Cavanaugh et al., 2014), but a recent analysis of more than 300 1-ha plots across the tropics found tree diversity and biomass to be largely uncorrelated in Amazonia, Africa, and tropical Asia (Sullivan et al., 2017). Also, while a recent review of empirical studies found that some biodiversity attributes (e.g., species richness) may affect carbon stocks, other vegetation attributes (e.g., community-mean of wood density or specific leaf area) and structural characteristics (e.g., tree density, basal area) appeared more influential (van der Sande et al., 2017). Thus, there is evidence that variables such as wood density (Baker et al., 2004; Malhi et al., 2004), tree density, and basal area all have some impact on the spatial variation in aboveground biomass of tropical forests (Baraloto et al., 2011; Malhi et al., 2006). Overall, these studies show that stands dominated by medium to high wood density species tend to have higher amounts of biomass, along with lower turnover rates, with water availability being a fundamental limiting factor (e.g., Álvarez-Dávila et al., 2017; Stegen et al., 2011). As a result, in the Amazon region, high biomass sites are often in the Central-Eastern and Guiana Shield systems (Malhi et al., 2006; Mitchard et al., 2014), including some sites in Southern Venezuela, while low biomass is associated with 'hyper-dynamic' forests of southern Amazonia (Marimon et al., 2014).

Other factors may be at play too, and potentially interacting in complex ways. For example, differences in forest biomass and structure across the Amazon Basin were found to be influenced by soil properties and climate (Quesada et al., 2012). Differences in woody productivity were correlated most strongly with total soil phosphorus, while stem turnover rates were most strongly correlated with a soil physical structure index which combines soil depth, texture, topography and anoxia (Quesada et al., 2012). An almost two-fold variation in turnover rates between the eastern and western portions of the basin, previously reported by Phillips et al. (2004), is associated with low fertility and well-developed soils in eastern, and central Amazonia, versus western Amazonian forests where higher fertility and less-structured substrates predominate. This implies that the processes of stem turnover (i.e., recruitment and mortality) and woody coarse productivity need to be considered to properly understand spatial variation in highly salient structural parameters such as biomass.

Rates of stem turnover have been shown to be well correlated with productivity patterns at global scales in at least two ways: a) through bottom-up relationships (e.g., higher soil fertility inducing faster growth) or b) top-down mechanisms (e.g., higher potential for secondary production) (Stephenson & van Mantgem, 2005). If high turnover does indeed drive higher productivity, or vice versa, we expect them to be correlated, as has been shown to a limited extent (e.g., Phillips et al., 2004). However, whether, and how, these translate into higher biomass is unclear. Most dynamic global vegetation models posit a clear link between the rate of carbon production and the rate of carbon storage, which can be traced back at least to the work of Whittaker and Likens (1973), revealing a positive relationship between productivity and biomass in forests of North America. Yet, spatial variation in tropical forest turnover rates is also associated with variations in floristic composition (Phillips et al., 2008; Swaine, Lieberman, & Putz, 1987), and so the relationship between productivity and biomass may not be straight forward. For instance, high turnover rates in high-productivity forests may limit biomass by promoting the dominance of species with a low wood density, and thus an increase in productivity does not necessarily favor increases in forest carbon storage (Keeling and Phillips, 2007). Furthermore, high productivity values have sometimes been documented at some lowland sites where turnover rates are usually low, including in the Guiana Shield region (Johnson et al., 2016).

Thus, while several empirical and simulation studies have contributed to understanding the process of biomass accumulation and its spatial variation in the tropics (Castanho et al., 2013; Malhi et al., 2006; Quesada et al., 2012; Rödig et al., 2017), it is important to explore how these interactions between environmental factors, turnover rates, productivity and biomass are operating at all scales. In this study, a comparative analysis of these processes was conducted in different forest types across six major bioregions in Venezuela, which has some of the world's greatest ecological variation of any country in the tropical zone or beyond (Huber & Oliveira-Miranda, 2010; Huber, 2001; Steyermark, 1961). I build the analytical approach upon previous studies which have analyzed these processes individually or simultaneously mostly at the pan-Amazon scale (Baraloto et al., 2011; Johnson et al., 2016; Quesada et al., 2012). A two-way interaction between stem dynamics and forest structure along with the influence of climatic factors are both key components of the proposed conceptual model (Figure 1). An important difference from previous studies is that this work expands the analysis beyond lowland forest sites to include middle to high elevation sites from the Andean biogeographical region, and dry forests sites near the Caribbean Sea in Eastern Venezuela.

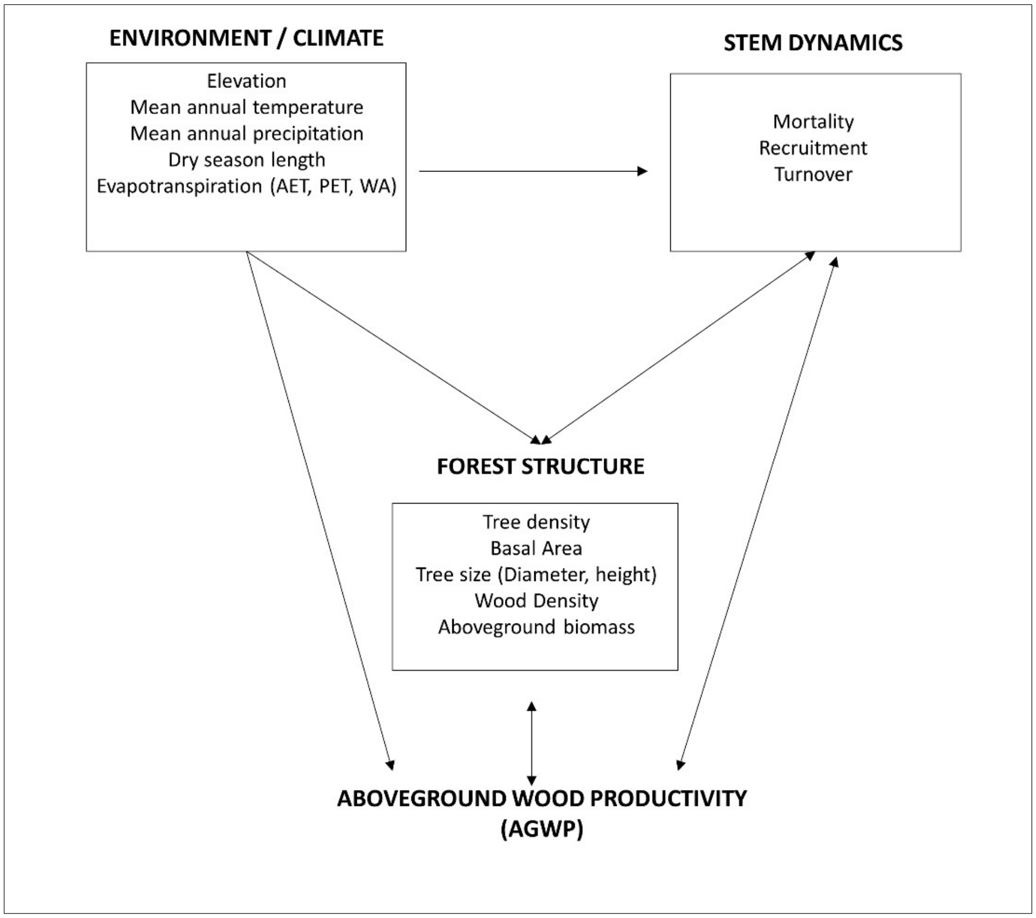


Figure 1. Conceptual model for the analysis of the relationships between turnover rates, aboveground woody productivity (AGWP), and biomass (AGB) including forest structure and environmental descriptors. Bidirectional arrows indicate potential two-way relationships.

Venezuela encompasses a highly diverse set of environmental conditions which are reflected in the diversity of biomes, regions and ecosystems where different forest-types cover about 50% of the land (Hansen et al., 2013), and with approximately 90% of forests located in the Guiana Shield region, south of the Orinoco river (Pacheco-Angulo et al., 2017), the last major forest frontier in Venezuela (Bevilacqua et al., 2002). In this study, I take advantage of continuous data from 50 permanent plots located in different parts of the country to address three main questions: 1) Are there differences in turnover, aboveground biomass (AGB) and wood productivity (AGWP) among contrasting ecological regions?; 2) To what extent does climate influence structure, stem dynamics and AGB?; and 3) What are the relationships between turnover rates, aboveground biomass and productivity? the general initial hypothesis that was tested was that turnover rates differ significantly between the regions and predict that lowland forests with shorter or no dry seasons potentially would have the lowest dynamic rates and would account for the highest values in AGB. A second hypothesis is that environmental conditions (i.e., high annual precipitation and high temperatures) are fundamental drivers of aboveground woody productivity (AGWP), and thus AGB, predicting a positive relationship between these two variables. Finally, I consider the results in relation to other studies that have simultaneously addressed turnover, AGB and AGWP, both from field data and/or using remote sensing techniques.

MATERIALS AND METHODS

PERMANENT SAMPLE PLOTS

A team of researchers initially led by Jean Pierre Veillon and others thereafter, established in the 1960s and late afterwards a systematic Venezuelan forests plot monitoring network, with some of these plots being the longest running sites in Latin America and the tropics (Hernández et al., 2012; Herrera et al., 1978; Veillon, 1985). Here, data from 50 mature forest plots ranging from 0.1 to 1 ha in area (mean plot size = 0.32 ha) and spanning a wide range of environmental conditions in temperature, rainfall, elevation, disturbance regime, soils, forest structure and species composition was used (Figure 2). Plots were not equally distributed across biogeographical regions, and thus some areas have been more extensively sampled than others. Temporally, the plots are characterized by a census period ranging from 8 to a maximum of 55 years. First censuses were conducted between 1960 and 2004 (mean year of first census = 1973.8 ± 12.2 Standard Deviation), and final plot censuses between 1972 and 2016 (mean year of last census = 2003.4 ± 15.6). On average, plots were resampled almost 20 times (min = 3 censuses; max = 41 censuses), with an average monitoring period of 29.7 ± 16.43 years (min = 2.0 years; max = 54.8 years) (Table S1).

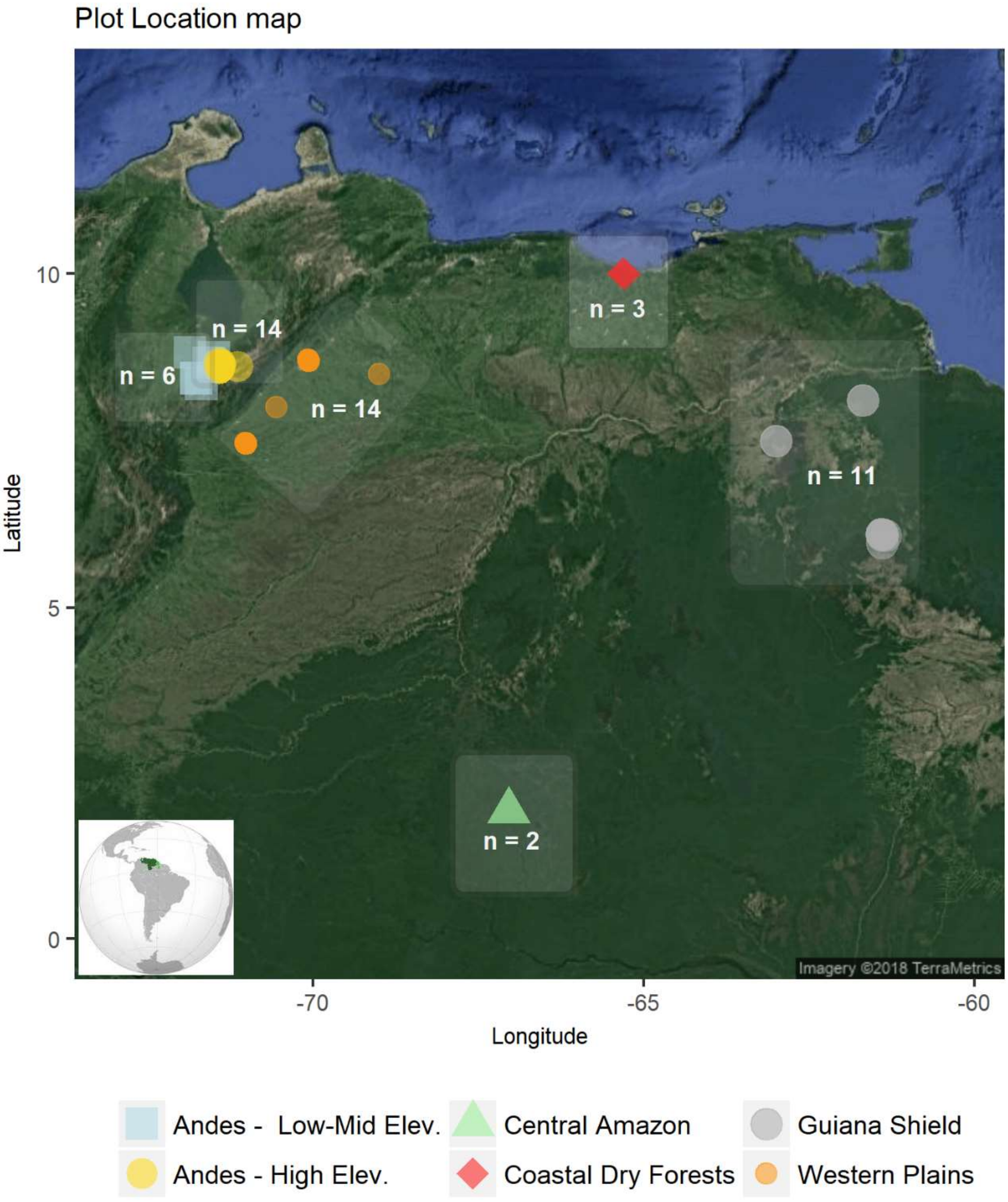


Figure 2. Geographical distribution of forest plots used in this study. Base map from Google Earth.

Plots were classified into six different regions defined by major climatic conditions, geographical location, and the nature and geological age of the soil substrate as: a) Central-Eastern Amazon (n = 2 plots); b) Andes Low-Mid Elevation (≤ 1.500 meters above sea level - masl) (n = 6); c) Andes High Elevation (> 1500 masl) (n = 14); d) Guiana Shield (n = 11); e) Coastal Dry Forests (n = 3); f) Western Plains (n = 14)

(Figure S1). Geomorphologically, there are clear differences with regards to soil genesis among all sites. Plots located in the Central-Eastern Amazon region correspond to the typical definition of a *´Terra Firme´* forest located on hills of Ferrasols covered by a sandy layer, and to a lesser extent by Acrisols and/or Alisols (Cuevas & Medina 1986). Soils are well-structured, and due to the presence of patches of macro-porosity and lower bulk density, roots can often penetrate to deeper horizons (Quesada et al., 2011). Montane forests located in the Andean region are established where soils are shallow and generally less developed (Cambisols) with increasing slope, and with a higher effective depth and development in flat or partially flat terrains, which are also typically enriched with clay (older Cambisols and/or Acrisols/Alisols) (Ramirez-Angulo, Torres-Lezama, & Serrano, 2002). Soils of the Guiana Shield fall into two major groups: Acrisols or Ferrasols (Hammond, 2005), typically with low fertility and high iron concentrations. For two of the plots in this region (ELD-3 and ELD-4) soils are mostly shallow with some trees growing directly on rocks that are highly resistant to weathering, with these being classified as Leptosols (Quesada et al., 2011). Poorly-developed soils are the main feature in the lower montane and dry forests of the eastern coast of Venezuela (plots CLA-03, CLA-04, SAR-03), characterized by clay-loamy textures (Delaney et al., 1998; Torres-Lezama, Bello, & Ramírez, 2002). Finally, the Western Plains region is formed as a Pleistocene-Holocene depositional area of Andean material mostly in the form of alluvial terraces, with microtopographic variations largely determining soil texture and structure (Kammesheidt et al., 2001; Schargel, 2015), and with water availability being a limiting factor for plants during dry season (Ramirez-Angulo et al., 2010).

Data collection involves the measurement of all live stems from all species with diameter (D) $\geq$ 10 cm at 1.3 m height when possible. Standardized protocols have been continuously employed for non-cylindrical stems owing to buttresses or other deformities. In these cases, the point of measurement is raised above the point where stems are more or less cylindrical, approximately 50 cm above the end of the buttress or deformity. The exact height of the point of measurement (POM) has been recorded and marked on the trees to ensure that subsequent measurements are taken at the same point along the stem. In each census, protocol included accounting for all individuals that had died or were recruited during the interval including possible causes of death (Phillips et al., 2016; Veillon, 1985). Since 2004, all plots are part of the Amazon Forest Inventory

Network (RAINFOR) (Malhi et al., 2002; Peacock et al., 2007) where data have been curated and shared via the ForestPlots.net database (Lopez-Gonzalez et al., 2011). Based on the information available for all censuses of each plot data was available for about 20,400 live stems from 571 identified species from 71 botanical families across all sites. Additional details about field protocols can be found in Brienen et al. (2015) and Phillips et al. (2016)

CLIMATIC VARIABLES

Climatic data (mean annual temperature and precipitation, and minimum monthly temperature) for each plot was obtained from local weather stations where available, and the WorldClim database at 2.5-min or 5-km spatial resolution (Fick and Hijmans, 2017) was used when local information was not available. Since water stress is important in predicting the shape of local allometric equations that are commonly used for estimating aboveground biomass, data on Maximum Climatic Water Deficit (CWD) as defined by Chave et al. (2014) was included. This metric accumulates on a monthly basis the differences between rainfall and evapotranspiration. Based on geographical location of each plot, CWD was extracted from a global raster file below 2.5 arc-minute resolution available from Chave et al. (2014) http://chave.upstlse.fr/pantropical_allometry.htm (see more in Table S1). Three additional variables related to water availability were also included: estimated actual evapotranspiration (AET; mm year^{-1}) and estimated potential evapotranspiration (PET; mm year^{-1}), both obtained from the Geospatial Database CGIAR Consortium for Spatial Information (Zomer et al., 2008), and available water (WA), estimated as the difference between mean annual precipitation (MAP) and PET.

Overall, mean annual precipitation is 1,676 ± 799.5 mm year^{-1} (standard deviation) and mean annual temperature 23.03 ± 4.88 ºC for all plots, with the highest temperature in the Central-Eastern Amazon region and precipitation in the '*Sierra de Lema'* zone (SDL plot cluster) of the Guiana Shield (Table S1, Figure S1). Plots covered a wide altitudinal range from 50 to 2,450 meters above sea level (mean = 894 masl). Most sites are characterized by one clear dry season (mean = 3.9 ± 2.1 dry months). Nine sites, mostly in the southern portion of the Guiana Shield and Central-Eastern Amazon were classified as non-seasonal. All climatic variables were included in a Principal

Component Analysis (PCA) as this method reduces multivariate data to a smaller number of variables by creating linear combinations of the original variables (Gotelli and Ellison, 2004). Following recommendations from McCune et al. (2002) all variables were normalized by range prior to the PCA analysis. These analyses were conducted using the `vegan` package version 2.4.4 (Oksanen et al., 2017) within the R software version 3.4.1 (R Development Core Team, 2016).

ESTIMATION OF TURNOVER RATES

Demographic rates (% year^{-1}) for each plot were estimated based on the instantaneous rates approach using the following equations reported in several studies (Báez et al., 2015; Johnson et al., 2016; Phillips et al., 2004; Swaine et al., 1987):

$$\text{Annual mortality } (m) = \frac{\ln(n_0) - \ln(n_0 - n_\mathrm{D})}{t} x\ 100$$

$$\text{Annual recruitment } (r) = \frac{\ln(n_0 - n_\mathrm{D} + n_\mathrm{r})/(n_0 - n_\mathrm{D})}{t} x\ 100$$

Where: n_0 is the number of individuals alive at the beginning of the census interval, n_D is the number of stems that died in the interval, n_r is the number of individuals recruited between censuses, and t corresponds to census interval length. Turnover rate was calculated as the average of recruitment and mortality (Phillips et al., 2004; Stephenson & van Mantgem, 2005). It has been shown that estimates of demographic rates for heterogeneous populations are influenced by the census interval (Phillips et al., 2004; Sheil, 1995). Therefore, estimates of all rates were standardized to comparable census intervals using the equation of Lewis et al. (2004): $\lambda_{\mathrm{corr}} = \lambda \text{ x } t^{0.0759}$, where λ_{corr} is the rate standardized to a 1-year census interval; λ is the uncorrected demographic rate; t is the length of census interval, and 0.0759 is a constant. I calculated corrected values of recruitment, mortality and turnover for each census interval and for each plot in the data set, and calculated average values per plot, weighted by the census interval length.

ABOVEGROUND BIOMASS AND WOODY PRODUCTIVITY

Aboveground biomass of each plot was calculated using the moist forest allometric equation from Chave et al. (2005):

$$\text{AGB} = 0.0509 \text{ x } \rho D^2 H$$

Where AGB is the biomass of each stem (kg), D is stem diameter (cm), ρ is stem wood density (g cm^{-3}) and H is stem height (m). The height of each tree was estimated from tree diameter using a height-diameter Weibull equation with different coefficients for each region (Feldpausch et al., 2012). Following Baker et al. (2004), the wood density of each tree was assigned on a taxonomic basis from the pan-tropical database of Zanne et al. (2009), first by species, and when this was not available data at the genus and family levels were used, while mean plot-level wood density values were used when taxonomic information was missing. Carbon was assumed to be 50% of total dry biomass, and as suggested by Malhi et al. (2006) and Johnson et al. (2016) I also added an additional 6.2% of carbon to each AGB-plot estimate to account for the unmeasured small trees (<10 cm in diameter).

For each census interval, above-ground wood productivity (AGWP) was estimated as the sum of AGB gains of surviving and recruiting trees, with AGB mortality as the summed AGB of trees dying over the interval. AGWP and AGB mortality were corrected to include two small unobserved components relating to trees that die within the census interval: (1) biomass gain and loss of the cohort of unobserved recruits that both enter and die between two successive censuses, and (2) unobserved biomass gain and loss of known trees that die between two successive censuses. To correct for this, the empirical procedure proposed by Talbot et al. (2014) was used:

$$\text{AGWP}_{\text{corr}} = \text{AGWP}_{\text{obs}} \text{ x } 0.0091 \text{ AGWP}_{\text{obs}} \text{ x } t$$

Where AGWP_{obs} is the uncorrected value of woody productivity, and t is the length of census interval. Since census intervals were frequent (mean number of censuses = 20, with an average of 29.6 years of total monitoring period), the effect of this adjustment is minor. Finally, to compute comparable estimates of AGWP, I calculated corrected values of every AGB component for each census interval and for each plot and calculated average values per plot weighted by census interval length.

STATISTICAL ANALYSIS

General statistics for all turnover rates, AGB and AGWP were calculated (i.e., mean, standard error) on a per plot basis and by region. All plots were allocated to three seasonality conditions: Aseasonal (0-1 months with less than 100 mm in precipitation); Moderately seasonal (2-3 dry months); Seasonal (> 3 dry months). Following Phillips et al. (2004), plots were allocated to two major soil fertility classes, broadly defined by published soil profiles from each region and data from a limited number of plots (Quesada et al., 2011) (Table S1). Estimates of recruitment and turnover rates were both normally distributed (Recruitment: $W = 0.975$, $p = 0.398$, Shapiro-Wilk normality tests; Turnover: $W = 0.965$, $p = 0.137$), while mortality rates were not ($W = 0.926$, $p = 0.004$). Thus, for recruitment and turnover I used an analysis of variance (ANOVA) to test for statistical differences among each region, seasonality condition and soil fertility, while a Kruskall-Wallis test was used for mortality. Similarly, a parametric post-hoc Tukey test was conducted for recruitment and turnover when differences were found, and a non-parametric Dunn-test in the case of mortality. Estimates of AGB and AGWP were normally distributed (AGB: $W = 0.987$, $p = 0.863$; AGWP: $W = 0.972$, $p = 0.282$), while biomass loss (AGB_{mort}) was not ($W = 0.905$, $p < 0.001$). To test for regional differences of AGB, AGWP and other AGB components in Venezuelan forest plots I followed the same approach as set out for turnover rates above.

To explore the question of potential drivers of turnover rates, biomass and productivity, I followed four analytical steps. First, individual simple correlations using Kendal's τ (tau) approach were used to examine overall trends between all variables as this method (i.e., tau correlation) does not rely on a particular distribution of the variables involved (Table S2). Second, the potential relationships between the three response variables (turnover, AGB and AGWP) with environmental descriptors were explored using the scores of the first two axes obtained from the Principal Component Analysis (PCA) explained earlier. Third, simple linear models were used to explore how turnover, AGB, and AGWP are affected by each one of the explanatory variables classified by group (i.e., climate, dynamics, and structure). To account for all potential correlations, I also included turnover rates as an explanatory variable of both AGB and AGWP. The effects of every AGB component on the total AGB including biomass and productivity were also included. Finally, generalized least squares (GLS) regression models were employed to further explore these relationships, where the potential spatial autocorrelation across the plot network was managed by specifying a Gaussian spatial correlation structure. GLS regressions were conducted using prior information from the linear modeling and literature (e.g., Álvarez-Dávila et al., 2017; Báez et al., 2015; Johnson et al., 2016; Phillips et al., 2004), and models were tested based on two groups of parameters (climate and structure). The explanatory variables were standardized by fitting a mean equal to 0 and variance to 1 to directly compare the effects of all variables. Model selection was based on the corrected version of the Akaike Information Criterion (AICc) to correct for small sample size (Johnson & Omland, 2004) combined with a k-fold cross-validation method (Picard and Cook, 1984). This approach allows the performance of models to be assessed randomly dividing the data into *k* groups (k = 10 in this study) and the model is adjusted k times, so in each run one of the *k* groups is used as a test set. Prediction error was calculated as the relative difference in the root mean squared error (RMSE) between the full version of the models and the training models. These analyses were conducted using the "`scale`" and "`gls`" functions from the *`nmle`* package (Pinheiro et al., 2017) and "`AICc`" function from the *`MuMIn`* package (Barton, 2018), all in the R software version 3.4.1 (R Development Core Team, 2016).

RESULTS

ENVIRONMENTAL VARIABILITY

Correlations between environmental factors were mixed. Not surprisingly, some of the highest values were found for actual evapotranspiration (AET) and annual precipitation (MAP) (Kendal's tau $\tau = 0.80$), and elevation and temperature ($\tau = - 0.78$) (Table S2, Figure S2). The Principal Component Analysis shows two major axes which explained more than 90 % of the environmental variability in the dataset (Figure 3). A first axis captured 57.6 % and was negatively correlated with latitude, elevation and length of dry season (DryM), and positively correlated with annual temperature (MAT), annual precipitation (MAP), actual and potential evapotranspiration (AET, PET), available water (WA) and Climatic Water Deficit (CWD). The second axis described 33.4 % of the variation with elevation, MAP, WA, and CWD negatively correlated, and positively correlated for Latitude, MAT, AET, PET, and length of dry season (Table 1).

Table 1. Loadings and variation explained by three major axes of variation using nine environmental variables recorded for 50 permanent plots in Venezuelan forests. In bold the variables with loadings above 0.3 for each PCA Axis. PCA axis 1 largely represents decreasing moisture supply, while axis 2 is mostly associated with increasing temperatures.

PCA variable	Comp.1	Comp.2	Comp.3
Latitude	**- 0.409**	0.016	0.220
Elevation	- 0.160	**- 0.526**	- 0.152
Mean Annual Temperature (MAT)	0.148	**0.535**	0.055
Mean Annual Precipitation (MAP)	**0.419**	- 0.052	**0.463**
Actual Evapotranspiration (AET)	**0.411**	0.029	-0.455
Potential Evapotranspiration (PET)	0.205	**0.495**	-0.218
Available Water (WA)	**0.388**	- 0.189	**0.549**
Number of Dry Months (DryM)	**- 0.389**	0.169	-0.012
Climatic Water Deficit (CWD)	**0.311**	**- 0.351**	-0.394
Standard Deviation	2.277	1.733	0.590
Proportion of Variance	0.576	0.334	0.037
Cumulative Proportion	0.576	0.910	0.948

TURNOVER RATES, BIOMASS AND PRODUCTIVITY

Average estimates of turnover rates were 1.91 ± 0.10 % year^{-1} (r = 1.91 ± 0.12; m = 1.89 ± 0.11 – Standard Error of the Mean) for all plots, and mortality rates and recruitment rates are positively correlated (Figure 4, Table S3). The maximum regional turnover is 2.74 ± 0.17 and the minimum of 1.36 ± 0.14 % y^{-1} for the Western Plains and Guiana Shield regions respectively. In most regions mortality and recruitment rates are balanced (i.e., close to the fitted line); however, some Western Plains sites showed mortality exceeding recruitment (Table S3).

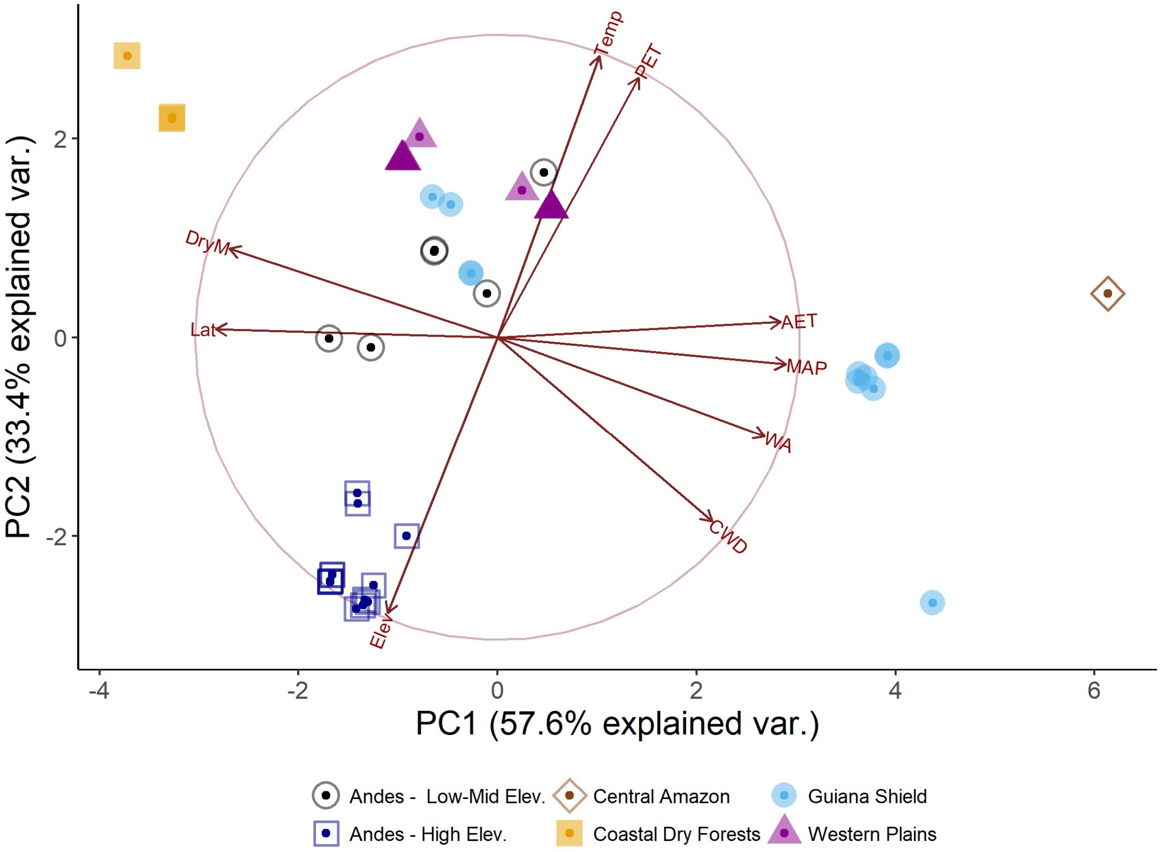


Figure 3. Principal Component Analysis (PCA) on nine environmental variables of all plots and bioregion. PCA axis 1 largely represents decreasing moisture supply, while axis 2 is mostly associated with increasing temperatures. See correlations between PCA variables in Table S2 and Figure S2.

The plots averaged 159.4 ± 7.3 Mg C ha^{-1} in AGB and varied regionally between 100.6 ± 26.5 Mg C ha^{-1} for Coastal Dry Forests, and 204.8 ± 14.3 Mg C ha^{-1} in the Guiana Shield. Similarly, Guiana Shield forests were the most productive with an average carbon uptake in the woody biomass (AGWP) of 3.26 ± 0.28 Mg C ha^{-1} y^{-1}, while AGWP was lowest in the drier areas of the eastern coast of Venezuela, with an average of 1.77 ± 0.48 Mg C ha^{-1} y^{-1} (Table 2).

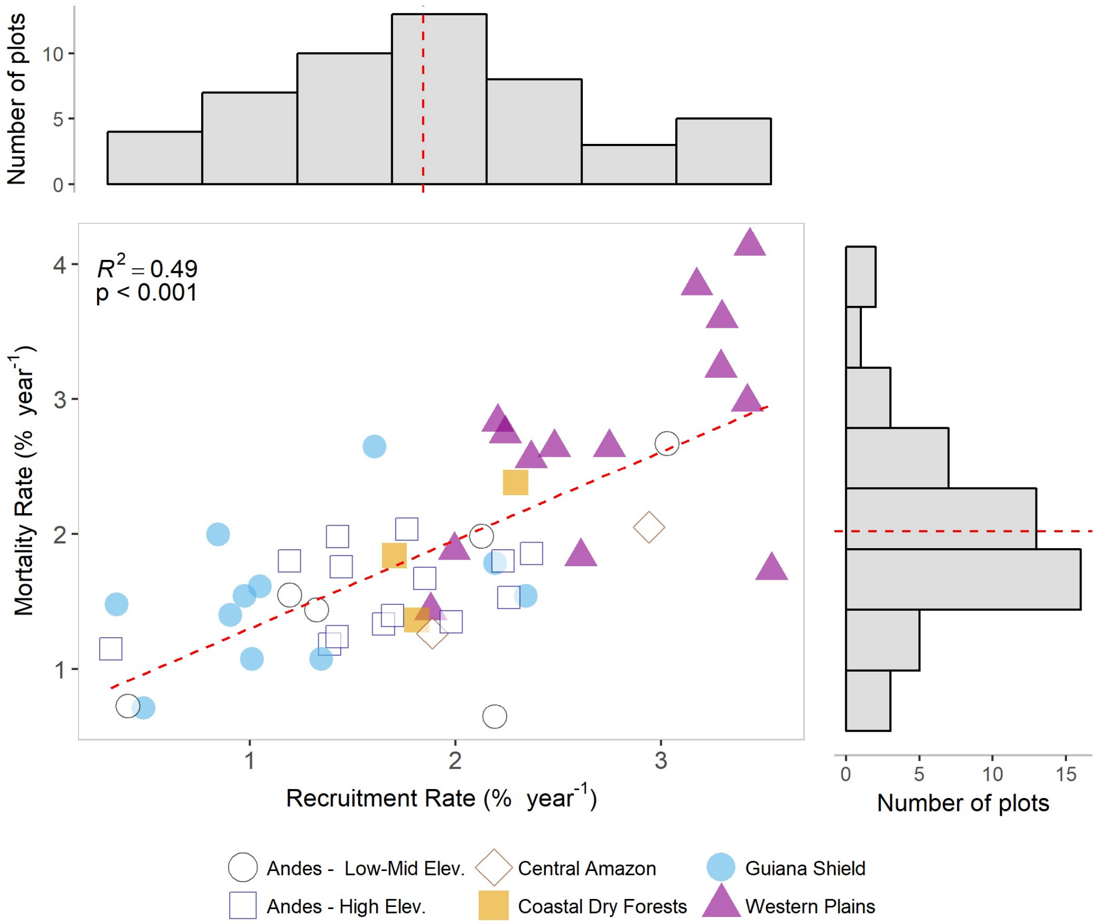


Figure 4. General distribution of mortality and recruitment rates classified by region. Red line in the histograms represent the average for both demographic rates. Red line in the scatter plot is a linear fit between mortality and recruitment.

ANOVA and Kruskal-Wallis tests showed significant differences for all three response variables (Turnover, AGB, AGWP) among the six regions (Table 2). Post-hoc tests were useful to compare the differences among regions. For instance, the Western Plains had significantly higher turnover than the other regions, while the Guiana Shield has significantly greater AGB and AGWP, while also being in the grouping of lowest turnover rates, with the Western Plains in the lowest group of AGB (Figure 5).

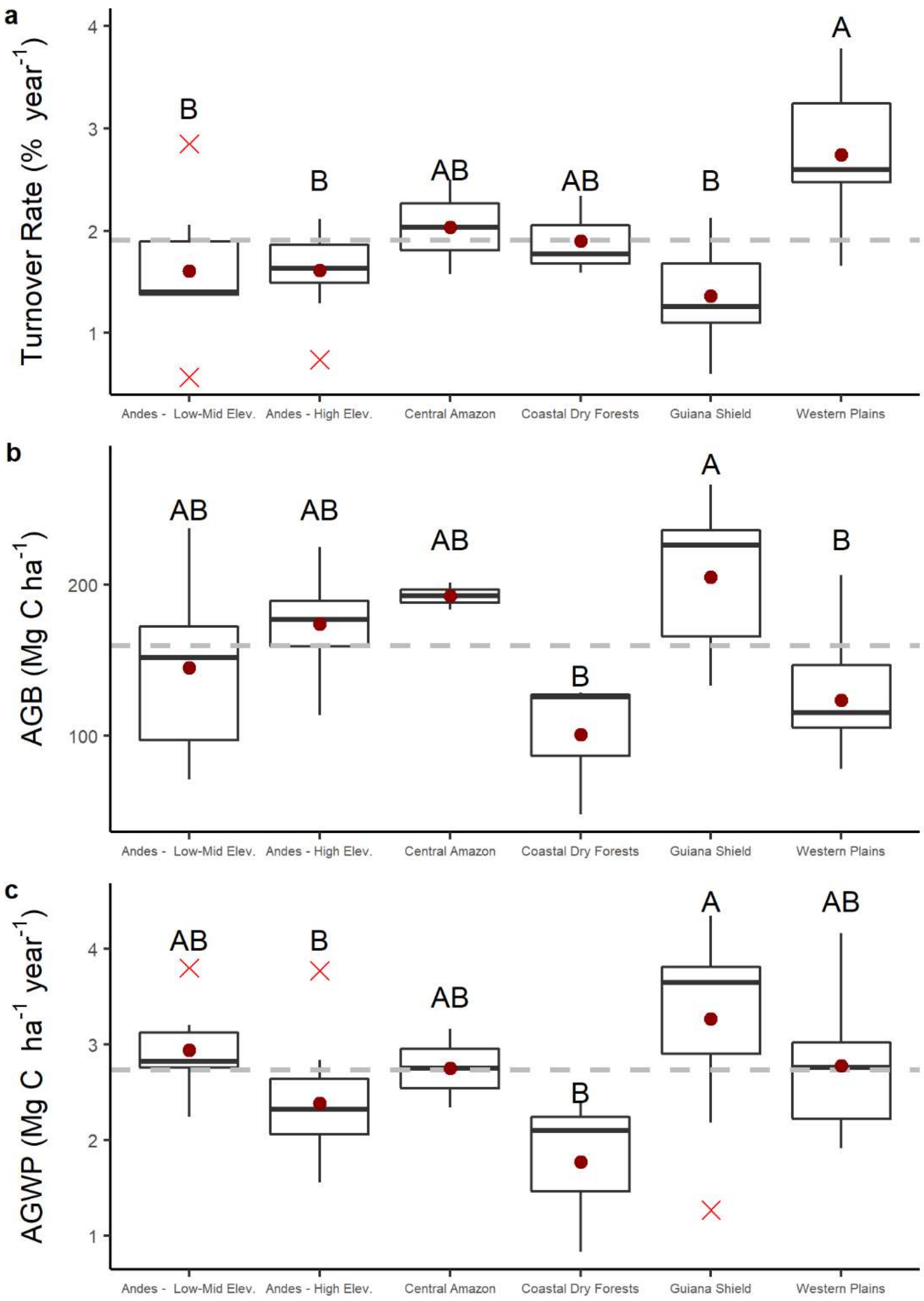


Figure 5. Boxplots of a) turnover rates; b) Aboveground biomass; and c) Wood productivity, including the results of pos-hoc grouping tests by region. Red dots indicate the average for each variable in each region. Gray dashed line is the overall mean for each variable. Statistically significant differences were found for turnover ($F_{44,5} = 10.39$; $p < 0.001$), AGB ($F_{44,5} = 7.008$; $p < 0.001$), and AGWP ($F_{44,5} = 3.284$; $p < 0.05$).

Table 2. Summary results of three groups of forest metrics for six major bioregions in Venezuelan forests. Values are means ± standard errors. Tests for differences among regions are provided. In bold the highest value for each variable.

Forest Property / Bioregion		**All regions (n = 50)**	**Andes Low-Mid Elevation (n = 6)**	**Andes - High Elevation (n = 14)**	**Central Eastern Amazon (n = 2) [a]**	**Coastal Dry Forests (n = 3)**	**Guiana Shield (n = 11)**	**Western Plains (n = 14)**	**Statistic [b]**	***p***
Forest structure	Basal Area (m^2 ha^{-1})	28.65 ± 1.09	26.87 ± 3.05	**36.17 ± 1.38**	28.68	19.38 ± 5.08	28.50 ± 2.06	23.99 ± 1.37	F = 7.614	< 0.001
	Stem Density (ha^{-1})	529.41 ± 34.53	428.25 ± 61.12	**731.5 ± 48.27**	656.75	482 ± 87.46	625.77 ± 79.44	286.92 ± 13.83	χ^2 = 32.021	< 0.001
	Plot Wood Density (g cm^{-3})	0.61 ± 0.01	0.59 ± 0.02	0.58 ± 0.01	0.68	**0.73 ± 0.01**	0.69 ± 0.02	0.57 ± 0.01	χ^2 = 26.69	< 0.001
Forest dynamics	Observed Recruitment Rate (% y^{-1})	1.913 ± 0.12	1.711 ± 0.38	1.642 ± 0.14	2.413	1.936 ± 0.18	1.191 ± 0.19	**2.763 ± 0.16**	F = 9.088	< 0.001
	Observed Mortality Rate (% y^{-1})	1.899 ± 0.11	1.503 ± 0.31	1.577 ± 0.08	1.657	1.861 ± 0.29	1.533 ±0.16	**2.721 ± 0.22**	χ^2 = 18.01	0.003
	Observed Turnover Rate (% y^{-1})	1.906 ± 0.10	1.607 ± 0.31	1.610 ± 0.09	2.035	1.898 ± 0.23	1.362 ± 0.14	**2.742 ± 0.17**	F = 10.39	< 0.001
Biomass components	Aboveground Biomass (Mg C ha^{-1})	159.39 ± 7.29	144.89 ± 25.37	173.98 ± 8.00	192.29	100.57 ± 26.47	**204.78 ± 14.28**	123.24 ± 9.00	F = 7.008	< 0.001
	Aboveground Biomass losses - AGB loss (Mg C ha^{-1} y^{-1})	2.20 ± 0.18	1.52 ± 0.36	2.20 ± 0.17	2.62	0.79 ± 0.13	**3.47 ± 0.53**	1.73 ± 0.21	χ^2 = 16.786	< 0.001
	Aboveground Woody Productivity (Mg C ha^{-1} y^{-1})	2.73 ± 0.11	2.94 ± 0.21	2.39 ± 0.14	2.75	1.76 ± 0.48	**3.26 ± 0.28**	2.77 ± 0.18	F = 3.284	0.0132

[a] Not possible to calculate standard error due to low sample size (n = 2).

[b] ANOVA for normally distributed data, and non-parametric Kruskall-Wallis χ^2 for other distributions.

Climate seasonality and soil fertility were associated with significant differences in turnover rates, AGB, and, to a lesser extent, AGWP. Turnover rates were different among the three categories of seasonality ($F = 4.669$, $p = 0.014$) with highly seasonal sites (> 3 dry months per year) being the most dynamic. These differences are mostly driven by recruitment. Although higher rates of mortality for these group of plots were found, a non-parametric test showed no differences in mortality with seasonality ($\chi^2 = 3.302$; $p = 0.19$). Both AGB and AGWP showed the same pattern with decreasing AGB and AGWP with increasing seasonality (aseasonal sites > moderately seasonal sites > highly seasonal sites). Turnover rates were higher for the high fertility plot group ($F = 13.19$, $p < 0.001$). Conversely, AGB was higher in the low fertility sites ($F = 8.933$, $p = 0.004$). AGWP was greater among the high soil fertility plots ($n = 22$, mostly in Western Plains and low-mid elevation forests in the Andes), but not significantly so when compared with the low fertility group ($n = 28$) ($F_{48,1} = 1.102$ $p= 0.299$) (Figure S3).

POTENTIAL DRIVERS OF TURNOVER RATES, BIOMASS AND ABOVEGROUND WOODY PRODUCTIVITY

TURNOVER RATES

Turnover rates were significantly positively correlated with the length of dry season, mean annual temperature, climatic water deficit, and potential evapotranspiration, but negatively with elevation. Turnover rates were uncorrelated with the scores of PCA1 axis, but positively correlated with the second PCA axis ($R^2 = 0.17$; $p = 0.002$). Aboveground biomass, basal area, stem density, and stand wood density were structural parameters negatively correlated with turnover (Table 3). Lower rates of turnover, including both recruitment and mortality, were found in sites characterized either by higher elevation and lower temperatures (i.e., Andean forests), or lowland forests with higher water availability from precipitation (i.e., Central Amazon and Guiana Shield) (Figure 6A-B).

13 different GLS models based on climatic parameters were tested, along with 10 additional models using forest structure as explanatory variables for turnover rates (Table S4). The 'best' climate-based model (i.e., lowest AICc) describing turnover

included the effects of mean annual temperature (MAT) with a regional interaction. Nevertheless, the difference in the log-likelihood and AICc among the first six models was relatively small with potential evapotranspiration (PET), length of dry season and climatic water deficit (CWD) following in relative importance as climatic drivers of turnover rates. Prediction errors in all models (i.e., the relative difference between the RMSE from the 10-fold validation and the RMSE from the selected model including all data) ranged between 0.2 and 16.5 %, with 11.7% in the case of the selected model (Pseudo r^2 = 0.55; AICc = 100.57). The average of plot basal area in combination with region were the two structure-based terms composing the 'best' model to explain turnover rates in the dataset. Prediction errors for this group of models ranged from 1.4 to 19.9 %. In both cases, the selected models showed a relatively good fit when comparing predicted vs. estimated values of turnover rates while also showing the estimated regional differences in turnover rates as well (Figure S4).

ABOVEGROUND BIOMASS (AGB)

AGB was negatively correlated with the length of dry season (R^2 = - 0.35, $p < 0.001$), and positively with available water and mean annual precipitation. The negative nature of CWD also implied a positive relationship with AGB with less negative values (e.g., Central Eastern Amazon) accounting for high biomass. There was also a positive correlation to PCA1 (increasing MAP, AET, WA and CWD) (R^2 = 0.14, $p = 0.005$), and a negative correlation with PCA2 (increasing MAT and PET and decreasing elevation). This negative relationship between the scores of PCA2 and AGB (R^2 = - 0.24, $p < 0.001$) suggests that sites with high turnover rates (e.g., Western Plains) have lower AGB and positive scores on the PCA2 axis (Figure 6D). Andean forests in general, along with Central Amazon and Guiana Shield comprised the sites with the highest aboveground biomass. All demographics rates were significantly negatively correlated with biomass. All forest structure explanatory variables (i.e., basal area, stem density, plot wood density, aboveground biomass losses from mortality, and woody productivity) were positively correlated with AGB (Table 3).

A combination of water availability (WA), CWD, potential evapotranspiration (PET), and region formed the 'best' climate model explaining AGB. The next 'best' single-parameter models showed the relative importance of CWD, PET, length of dry season and WA. Prediction error for all climatic models ranged between 1.8 and 13.9 %. Turnover rates, stem density, average wood density, biomass loss and woody productivity were all part of the ‘best’ structural-based model explaining AGB in the dataset. As in the case of turnover rates, the relationship between the predicted and estimated values was acceptable with a good coefficient of determination (0.51 for the best climate model and 0.63 for the structure-based model), while partially capturing the regional differences among the dataset (Table S4, Figure S4).

ABOVEGROUND WOODY PRODUCTIVITY (AGWP)

AGWP was negatively correlated with the number of dry months, increasing elevation and latitude, and positively correlated with AET, CWD, MAT, MAP, PET, and WA (Table 3). AGWP was significantly and positively correlated with the first PCA axis ($R^2 = 0.17$; $p = 0.002$) and uncorrelated with the second PCA axis (Figure 6E-F). Turnover rates were uncorrelated with AGWP; however, stem density was negatively correlated with AGWP. Most forest structure variables were not correlated with AGWP, but there was a positive correlation with AGB (Table 3, Figure 7).

Using climate variables as predictors, the ‘best-fit’ model describing AGWP included AET interacting with region, followed by length of dry season, and CWD. Average prediction errors for this group of models was 6.7% (min = 1.2; max = 11.6). GLS modeling confirmed the lack of relationship between most structure variables and AGWP, with only stem density slightly interacting with region as the terms of the best model describing woody productivity. However, the relationship between the predicted and estimated values was poor (Table S4, Figure S4).

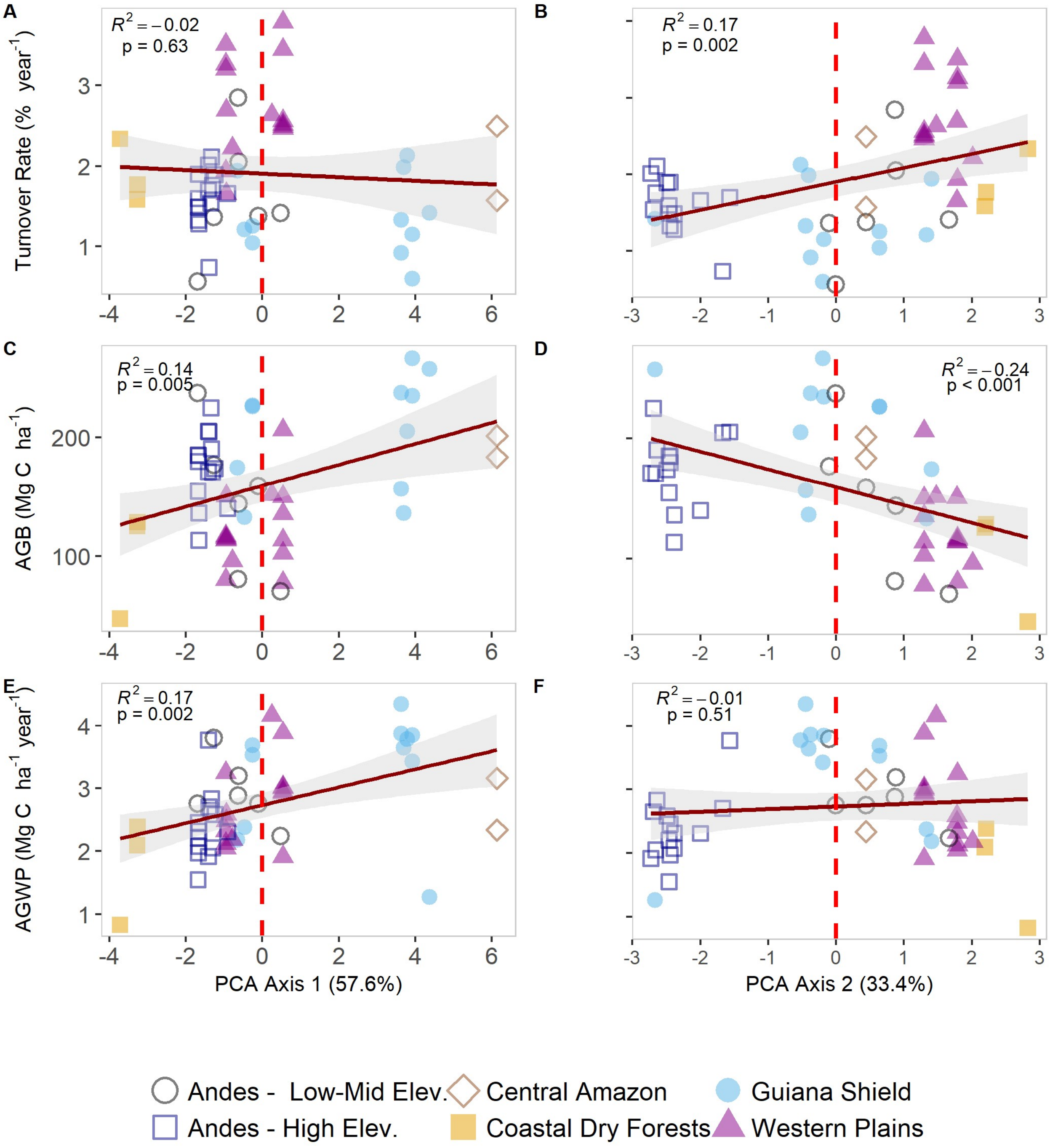


Figure 6. Relationships between turnover rates (A-B), aboveground biomass (C-D), and aboveground woody productivity (E-F) with two PCA axes by region. Red dashed line indicates the "zero" value for the scores in each axis. For details on direction of the vectors and loadings see Figure 3 and Table 1.

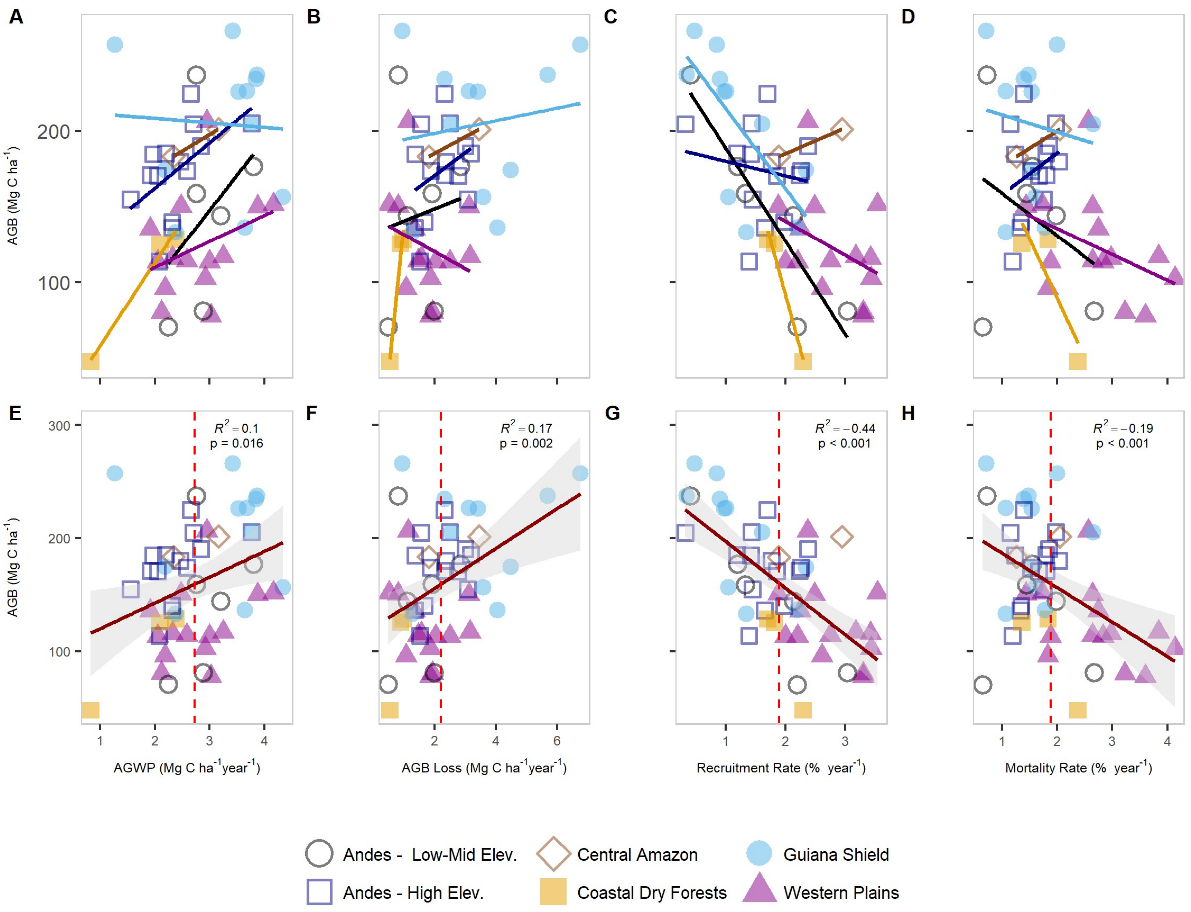


Figure 7. AGB relationships with AGWP (A & E), AGB loss (B & F), recruitment rate (C & G), and mortality rate (D & H). Upper panel depicts linear fits for every region. Bottom panels represents a linear fit for all data combined. Red dashed lines are the arithmetic mean for each explanatory variable**.**

Table 3. General correlations (R^2) between turnover rates, aboveground biomass and woody productivity and three groups of explanatory variables. Numbers in bold highlight the significant correlations, with numbers in parenthesis indicating the p-value.

Explanatory variables		**Response variables**		
		Turnover rate	**AGB**	**AGWP**
Environment	PCA 1	- 0.02 (0.64)	**0.14 (0.005)**	**0.17 (0.002)**
	PCA 2	**0.17 (0.002)**	**- 0.24 (<0.001)**	- 0.02 (0.51)
	Latitude (Lat)	- 0.02 (0.76)	**- 0.13 (0.007)**	**- 0.08 (0.03)**
	Elevation (Elev)	**- 0.10 (0.01)**	**0.06 (0.05)**	**- 0.05 (0.05)**
	Mean Annual Temperature (MAT)	**0.10 (0.01)**	**- 0.09 (0.02)**	**0.06 (0.05)**
	Mean Annual Precipitation (MAP)	- 0.01 (0.64)	**0.15 (0.003)**	**0.06 (0.04)**
	Number of Dry Months (DryM)	**0.11 (0.01)**	**- 0.35 (<0.001)**	**- 0.22 (<0.001)**
	Actual Evapotranspiration (AET)	- 0.02 (0.74)	**- 0.06 (0.05)**	**0.19 (0.001)**
	Potential Evapotranspiration (PET)	**0.09 (0.02)**	**- 0.05 (0.05)**	0.05 (0.06)
	Available Water (WA)	- 0.01 (0.27)	**0.24 (<0.001)**	0.04 (0.09)
	Climatic Water Deficit (CWD)	**0.09 (0.02)**	**0.30 (<0.001)**	**0.11 (0.01)**
Stem Dynamics	Turnover rate	----	**- 0.37 (<0.001)**	- 0.01 (0.79)
	Recruitment rate	**0.86 (<0.001)**	**- 0.44 (<0.001)**	- 0.02 (0.52)
	Mortality rate	**0.83 (<0.001)**	**- 0.19 (<0.001)**	- 0.02 (0.84)
Forest structure	Average Stem Density	**- 0.16 (0.002)**	**0.12 (0.007)**	**- 0.12 (0.008)**
	Average Basal Area	**- 0.19 (< 0.001)**	**0.57 (< 0.001)**	**- 0.01 (0.42)**
	Mean Plot Wood Density	**- 0.15 (0.003)**	**0.09 (0.019)**	0.01 (0.41)
	Aboveground biomass (AGB)	**- 0.36 (< 0.001)**	----	**0.10 (0.015)**
	AGB losses (AGB Mort)	- 0.01 (0.53)	**0.17 (0.002)**	0.01 (0.19)
	Woody productivity (AGWP)	- 0.01 (0.79)	**0.10 (0.015)**	----

DISCUSSION

Across Venezuelan forests and encompassing a wide environmental gradient, stem turnover rates, aboveground biomass (AGB) and woody productivity (AGWP) were estimated using state of the art approaches. The results reveal significant differences in stand and regional-level patterns of all variables for a broad range of forest habitat types in Venezuela (Figures 4 and 5).

First, PCA was useful in describing relevant environmental differences at the regional level and reflects the overall gradient captured by this dataset. Two orthogonal climatic axes describe two major gradients in moisture and temperature (Figure 3). Length of dry season and water availability differentiate the Central Amazon and Guiana Shield from other regions, with both characterized by the least negative values of CWD and thus highest water availability. At the other extreme of this gradient, as expected, the most negative values of CWD were found in the dry forests of the eastern coast of Venezuela. Lowland forests, both at the Guiana Shield and Western Plains were mostly defined by a warmer climate and medium to high levels of precipitation. As expected, lower temperatures at medium to high elevation characterize the position for most of the Andean sites along the ordination space (Figure 3, Table S1, Figure S2).

Secondly, in terms of stem dynamics, mean turnover rates (1.91 ± 0.10 % year^{-1}) closely matched previous studies that used a sub-sample of the plots used here and over a much shorter monitoring period (Carey et al., 1994; Phillips et al., 2004; Ramirez-Angulo et al., 2002). Turnover rates vary substantially between sites and regions (Figure 4), suggesting that larger samples for all regions may be needed to better distinguish large-scale patterns. However, despite the inherent noise in recruitment and mortality processes, taken together these results further reveal that tree turnover in mature seasonal forests located in the alluvial plains in western Venezuela (2.74 ± 0.17 % year^{-1}) is not only faster than other areas in Venezuela (mean of 1.82 ± 0.17 % year^{-1}), but also faster than for other forests of the northern central Andes of South America (e.g., 1.88 ± 0.11 % year^{-1} in Báez et al., 2015). For western forests in Venezuela, mean turnover rates are close to the range reported for other western Amazonia lowland forests (e.g., 2.49 ± 0.12 % year^{-1}, (Phillips et al., 2004)). Sites in the Guiana Shield region, however, had the overall lowest turnover rates (1.36 ± 0.14 % year^{-1}), with average mortality rates (1.53 ± 0.16 % year^{-1}) being close to other estimates from the region (e.g., 1.66 ± 0.16 % year^{-1} in Johnson et al., 2016) (Figures 4 and 5A).

These regional differences in stem dynamics might indicate a combined effect of prevailing climate, soil conditions and forest structure, hence revealing complex regional patterns in turnover, AGB and AWGP that were unveiled, at least partially, with this dataset. Although having low but significant correlations, the environmental conditions most strongly associated with turnover rates were mean annual temperature (MAT), length of dry season and, to a lesser extent, other moisture-related parameters such as potential evapotranspiration (PET) and climatic water deficit (CWD) (Table 3, Table S4). When these variables were grouped in the scores of the second PCA axis, a significant correlation with turnover rates was found (Figure 6B). Overall, sites with high dynamism tend to have a higher moisture deficit, which may shed light on the effects of water limitation not only on recruitment and mortality, but also on biomass and productivity.

Previous studies have shown that higher temperatures coupled with stronger water deficit, whether in the form of low precipitation or extended dry seasons or both, are well-known drivers of tree mortality (Meir et al., 2015; Phillips et al., 2010; Zhang et al., 2017). These results also corroborate other studies (e.g., Johnson et al., 2016; Pillet et al., 2017) and show that the highest rates of tree mortality were found in the two regions with the strongest water deficit, namely coastal dry forests in Eastern Venezuela and Western Plains (Table 2). The case of recruitment is less clear since sites with higher water availability (e.g., Central Amazon) also had high recruitment rates (mean of 2.41 % year^{-1}). For instance, in Phillips et al., (2004), and using data from 97 sites across the Amazon, a mean recruitment rate of 2.41 ± 0.15 % year^{-1} was found for plots classified as non-seasonal. In this study, significant differences for recruitment were found ($F = 5.271$, $p = 0.009$) but none for mortality ($\chi^2 = 3.85$, $p = 0.15$) when plots were classified according to seasonality, although highly seasonal sites had the highest mortality rates (2.05 ± 0.13 % year^{-1}) (Figure S3).

Estimates of AGB are well within the values reported in other regional studies (Johnson et al.,, 2016; Malhi et al., 2006; Mitchard et al., 2014) with the Guiana Shield region accounting for the most carbon-rich forests in Venezuela and the Amazon (204.78 ± 14.28 Mg C ha^{-1}), and dry forests in Eastern Venezuela having the lowest values in AGB (100.57 ± 26.47 Mg C ha^{-1}) (Figure 5B). Among the three response variables, AGB was the only one significantly correlated with both PC1 and PC2. Biomass increases with increasing water availability (WA) but decreases with an increase in temperature and PET, suggesting that while water deficit may promote higher turnover rates (Figure 6B), it may limit the amount of carbon stored in these forests (Figure 6D). Moreover, in this dataset, WA, CWD and PET were the best environmental predictors of AGB by means of linear and GLS modeling (Table 3, Table S4), with moderately and highly seasonal plots accounting for lower AGB values (162.84 ± 28.08 and 145.63 ± 7.43 Mg C ha^{-1} respectively) (Figure S3).

Two separate assessments conducted at the pan-Amazon scale (Baraloto et al., 2011; Quesada et al., 2012) similarly found strong effects of dry season length on the specific stand characteristics that explained the spatial variation in AGB across different forest types with an east to west gradient in turnover, AGB, and woody productivity (AGWP). These studies also indicated that wet and warm sites support higher biomass forests, which were predominantly composed of high wood density species (e.g., Guiana Shield). Contrastingly, seasonal sites sustained forests with lower tree density, basal area and therefore lower AGB (e.g., Western Plains). There was, however, an important combined effect of soil structure and fertility on turnover and AGB in Quesada et al., (2012) in which less weathered soils may promote higher dynamism through less effective-depth, and higher AGWP *via* higher phosphorous content. These areas are mostly in western Amazonia where AGB is frequently lower as has been shown previously (e.g., Johnson et al., 2016; Malhi et al., 2006)).

In this study, the lack of good quality standardized data limited the ability to fully test for the effects of soils in the response variables. However, using a simple approach, all 50 plots were allocated into two major soil fertility classes (Table S1), and turnover rates were indeed faster for the high fertility group (n = 22), while AGB was significantly higher for the low fertility group (n = 28). AGWP was also higher in the high fertility group but not significantly so (Figure S3). These results are consistent with studies showing that forests in tropical Amazonia growing on more fertile soils tend to have higher turnover rates than those with lower fertility, while also being more productive (Malhi et al., 2004; Phillips et al., 2004).

Both recruitment and mortality rates were strongly and negatively correlated with AGB (Table 3, Figure 7), showing that tropical forests characterized with a high stem mortality risk, mostly by environmental conditions that includes extremes of temperature or longer dry seasons, such as those represented by the plots in the Western plains and the dry coast of Venezuela, tend to support lower biomass (Stegen et al., 2011; Álvarez-Dávila et al., 2017). Although the relationship between mortality rate and AGB is somewhat weaker than that between recruitment and AGB, it is consistently negative across all sites, and within most of the regions with the strongest gradients in mortality (Figure 7). This supports recent findings showing that stem mortality rates determine spatial variation in AGB in the Amazon (Delbart et al., 2010; Johnson et al., 2016). However, contrary to the results from Johnson et al., (2016) where no correlation between AGB_{mort} and AGB was found, a positive relationship within the plots used here was found, matching the rather weak but significant relationship between AGB and woody productivity (Figure 7). Since the most productive plots (i.e., Guiana Shield) also had the highest estimates of both total AGB and AGB_{mort}, a larger sample size is needed to confirm whether the saturation effect in the AGB-AGWP relationship reported in Keeling and Phillips (2007) for high productivity sites also holds here.

The relationship between turnover and AGB is an example of how stem dynamics can drive biomass accumulation, thus different mechanisms of tree mortality may affect forest structure, which in turn may affect forest biomass. Observations on mode of mortality in the plots used here indicate that the high mortality rates of some plots (e.g., Western Plains) are driven by more dynamic death events (e.g., broken and/or uprooted trees, and often involving more than one individual). In less dense forests, trees with low to medium wood density are more exposed to strong wind disturbances and are more likely to die because of stem breakage or by being uprooted, likely associated with soil physical conditions as shown by Quesada et al. (2012). These particular modes of death are often associated with the creation of larger canopy gaps compared to those created by trees that die standing. In northern Amazonia, both growth rate and wood density were found to be good predictors of tree mortality and modes of death (Chao et al., 2008, 2009), with mortality probabilities depending both on physiological failure (e.g., drought) and mechanical failure (small size, slow growth and mode of breakage). However, in this dataset, the drier plots in eastern Venezuela, which had a high average plot wood density (Table S3), also had a high overall mortality rates with most trees dying standing. At least for this region, this pattern seems to be more consistent with climate-induced mortality being the leading cause of death (Greenwood et al., 2017; Álvarez-Dávila et al., 2017).

Only stem density coupled with a regional effect were part of the 'best' model describing AGWP while also having a considerable low predictive power (Table S4, Figure S4). In fact, although turnover was a good predictor of AGB, no major effect was found in the case of woody productivity (Figure S5). While at larger scales turnover and AGWP seem to be well correlated (e.g., Stephenson & van Mantgem, 2005), in this study carbon dynamics was largely uncoupled from stem dynamics (Table 3, Figure S5), and attempting to predict AGWP using forest structure variables in these plots resulted in overall poor correlations and high errors for most of the models tested (Table S4) .

In the relationship between tree mortality and productivity, at least four different mechanisms may be at play, with the dominant mechanisms depending on whether the underlying productivity gradients are caused by climate or soil fertility (Stephenson et al., 2011). In this study, the 'best' models describing AGWP, i.e., the ones with the lowest AICc, seem to confirm that, at least for the plot used here, woody productivity is largely driven by a combined effect from climate, mostly in the form of water availability (i.e., AET, dry season and CWD), and to a lesser extent by stem density (Table S4). For instance, in an analysis conducted at the pantropical scale, woody productivity was found to be largely driven by seasonal variation in precipitation and evapotranspiration respectively (Wagner et al., 2016), likely indicating the potential for an overall decrease in tropical forest productivity under a drier climate scenario. These results also show the inherent complexity underlying these patterns and how, for instance, some sites with high mortality rates also have high AGWP (e.g., Western Plains), while the highest productivity was found where turnover rates in general were among the lowest across all regions (e.g., Guiana Shield).

The effects of elevation on turnover, AGWP and AGB is less clear. Stands located at higher elevations can attain high AGB while having low rates of productivity and turnover. While the potential effect of using allometric equations to estimate biomass, which are based on lowland forests should be acknowledged, the patterns that were found for these sites still hold when basal area was included as a proxy variable for AGB. Moreover, AGB and other structural parameters (i.e., density and basal area) are aligned with other estimates made for mature tropical montane forests (Girardin et al., 2014), including previous studies where a reduced number of the plots included here (e.g., “Carbonera” cluster) were also used (Delaney et al., 1997). One potential explanation for these results is that, despite having a clear dry season, lower temperatures at higher elevations promotes lower evapotranspiration and a much higher carbon residence time (Mean of 74.7 years for Andes High elevation forests – Table). Furthermore, this region accounted for the highest stem density and basal area across all plots (Table 2), which may also explain the high AGB values. A similar trend in stem density but not for basal area was found in a tropical Andean gradient (Girardin et al., 2014), but high values in AGB for sites between 2000 and 3000 meters in altitude are common for tropical montane forests (Spracklen and Righelato, 2014).

With regards to AGWP, most studies have shown a decrease in net primary productivity with elevation, in most cases as a response of cooler temperatures, fog, reduced light incidence and higher relative humidity (Girardin et al., 2014). For instance, in an elevation gradient in Amazonia spanning sites from lowland forests up to 3,000 meters in elevation, Doughty et al. (2017) found that forests produce biomass less efficiently in stands with residence times > 40 years and in stands with lower soil fertility.

In this study, different empirical models that have been applied to other regions in South America were tested, while expanding the analysis to include other forest-types, such as the highly dynamic forests of the Western Plains region, the dry forests in the Caribbean coast, and the high elevation montane forests in the Venezuelan Andes, with the overall aim to contribute to the understanding how the structure of tropical forests influences forest function over a contrasting environmental gradient, and at a scale and region previously unexplored.

Adequately characterizing patterns of turnover, AGB and AGWP over a broad range of environmental conditions in tropical forests presents multiple challenges. For instance, having an adequate and balanced number of sites across all regions and monitoring these simultaneously are ideal, but constitutes an important limitation of this study. Future work should focus on expanding the number of sites and increasing the number of censuses in each region, particularly in the Central Amazon area, to further test the explanatory power of some of the conclusions. Moreover, the use of remote sensing techniques to increase the sample size and to better predict forest structure in many forest types across the tropics (e.g., Marvin et al., 2014; Da Conceiçao Bispo et al., 2016) would further connect the study of tropical forest structure and function at this scale and region.

CONCLUSIONS

Overall, the main findings if this study are 1) variation in turnover rates in Venezuelan forests are mostly explained by temperature and water availability, combined with stand-level parameters such as basal area and wood density, and that seasonal mature forests in the Western Plains are the most dynamic types; 2) turnover rates and climate are key drivers of forest biomass: where turnover rates are low, mostly as a result of shorter dry seasons (e.g., Central Amazon and Guiana Shield) or low temperatures at higher elevations (e.g., high elevation forests in the Andes), forests tend to have higher AGB with stands dominated by medium to high wood density species; 3) AGWP in Venezuelan forests is largely controlled by the amount of water available, while the effects of stem turnover or forest structural variables is less clear.

These findings strongly implicate that climate acts as a fundamental driver of neotropical forest turnover, AGB and AGWP. This study therefore has important implications in the context of climate change, given that recent increases in drought frequency have impacted the dynamics of tropical forests by inducing higher rates of tree mortality while diminishing their capacity to store biomass (e.g., Brienen et al.,, 2015; Feldpausch et al.,, 2016). If the trend to stronger dry seasons continue, some of the sites included here are likely to be increasingly challenged to continue providing the key ecosystem services of productivity, carbon storage and sequestration.

SUPPORTING INFORMATION

Table S1. General description of 50 Venezuelan permanent plots used in this study.

Plot location					Plot characteristics and General Inventory information							Elevation		Climate									Soil	
Plot Code	**State**	**Bioregion**	**Latitude Decimal**	**Longitude Decimal**	**Ground Area (ha)**	**Minimum Dimension (m)**	**Maximum Dimension (m)**	**Date Established**	**Last Census Date**	**Monitoring period (years)**	**No. of Censuses**	**Forest Elevation**	**Altitude (masl)**	**Mean Annual Temp. (ºC)**	**Avg. Min Temp (ºC)**	**Mean Annual Precipitation (mm year^{-1})**	**AET (mm year^{-1}) [a]**	**PET (mm year^{-1}) [a]**	**WA (mm year^{-1}) [a]**	**Climatic Water Deficit (CWD) [b]**	**No. Dry months**	**Seasonality [c]**	**Major Soil Type**	**Fertility [d]**
ACL-01	Merida	Andes - Low-Mid Elev.	8.75	-71.50	0.25	50	50	1967.20	1984.40	17.20	18	Premontane	1000	22.9	16.6	1200	794	1539	-339	-404.58	3	1	Old inceptisol	1
BAC-01	Barinas	Western Plains	7.46	-71.01	0.25	50	50	1991.28	2016.30	25.02	13	Lowland	141	26.8	20.5	1776	1298	1734	42	-427.66	4	2	Old inceptisol	1
BAC-02	Barinas	Western Plains	7.46	-71.01	0.25	50	50	1991.86	2016.30	24.44	12	Lowland	143	26.8	20.5	1776	1298	1734	42	-427.66	4	2	Old inceptisol	1
BAC-03	Barinas	Western Plains	7.46	-71.01	0.25	50	50	1991.28	2016.30	25.02	10	Lowland	144	26.8	20.5	1776	1298	1734	42	-427.66	4	2	Old inceptisol	1
BAC-04	Barinas	Western Plains	7.46	-71.01	0.25	50	50	1991.86	2016.31	24.45	12	Lowland	138	26.8	20.5	1776	1298	1734	42	-427.66	4	2	Old inceptisol	1
BAC-05	Barinas	Western Plains	7.47	-71.02	0.25	50	50	2001.26	2016.31	15.05	9	Lowland	142	26.8	20.5	1776	1298	1735	41	-423.66	4	2	Old inceptisol	1
BAC-06	Barinas	Western Plains	7.47	-71.02	0.25	50	50	1996.31	2016.31	20.00	10	Lowland	140	26.8	20.5	1776	1298	1735	41	-423.66	4	2	Old inceptisol	1
CAI-01	Barinas	Western Plains	8.70	-70.07	0.25	50	50	1975.07	2016.33	41.26	41	Lowland	173	27.1	20.8	1388	1156	1724	-336	-568.55	6	2	Old inceptisol	1
CAI-02	Barinas	Western Plains	8.70	-70.07	0.25	50	50	1962.95	2016.34	53.39	41	Lowland	176	27.1	20.8	1388	1156	1724	-336	-568.55	6	2	Old inceptisol	1
CAI-03	Barinas	Western Plains	8.70	-70.07	0.25	50	50	1962.95	2016.34	53.39	41	Lowland	165	27.1	20.8	1388	1156	1724	-336	-568.55	6	2	Old inceptisol	1
CAI-04	Barinas	Western Plains	8.70	-70.07	0.25	50	50	1962.95	2016.34	53.39	41	Lowland	171	27.1	20.8	1388	1156	1724	-336	-568.55	6	2	Old inceptisol	1
CAI-05	Barinas	Western Plains	8.72	-70.08	0.25	50	50	1963.13	2016.34	53.21	41	Lowland	168	27.2	20.9	1393	1161	1722	-329	-560.94	6	2	Old inceptisol	1
CAI-06	Barinas	Western Plains	8.72	-70.08	0.25	50	50	1963.13	2016.34	53.21	41	Lowland	169	27.2	20.9	1393	1161	1722	-329	-560.94	6	2	Old inceptisol	1
CAT-02	Merida	Andes - Low-Mid Elev.	8.44	-71.77	0.25	50	50	1974.31	1983.96	9.65	10	Lowland	380	24.9	18.4	1360	1106	1708	-348	-230.23	6	2	Old inceptisol	1
CAT-03	Merida	Andes - Low-Mid Elev.	8.44	-71.77	0.25	50	50	1974.31	1983.96	9.65	10	Lowland	350	24.9	18.4	1360	1106	1708	-348	-230.23	6	2	Old inceptisol	1
CBN-01	Merida	Andes - High Elev.	8.58	-71.42	0.25	50	50	1960.20	1983.28	23.08	22	Lower-Montane	2310	15.4	8.3	1191	1017	1277	-86	-263.65	5	2	Old inceptisol	0
CBN-02	Merida	Andes - High Elev.	8.58	-71.42	0.25	50	50	1960.21	1983.28	23.07	22	Lower-Montane	2320	15.4	8.3	1191	1017	1277	-86	-263.65	5	2	Old inceptisol	0
CBN-03	Merida	Andes - High Elev.	8.58	-71.42	0.25	50	50	1961.51	1989.87	28.36	25	Lower-Montane	2430	15.4	8.3	1191	1017	1277	-86	-263.65	5	2	Old inceptisol	0
CBN-04	Merida	Andes - High Elev.	8.58	-71.42	0.25	50	50	1961.51	1989.87	28.36	23	Lower-Montane	2430	15.4	8.3	1191	1017	1277	-86	-263.65	5	2	Old inceptisol	0
CBN-05	Merida	Andes - High Elev.	8.58	-71.42	0.25	50	50	1961.77	1989.88	28.11	24	Lower-Montane	2450	15.4	8.3	1191	1017	1277	-86	-263.65	5	2	Old inceptisol	0
CBN-06	Merida	Andes - High Elev.	8.58	-71.42	0.25	50	50	1961.52	1985.80	24.28	23	Lower-Montane	2450	15.4	8.3	1191	1017	1277	-86	-263.65	5	2	Old inceptisol	0
CLA-03	Anzoátegui	Coastal Dry Forests	10.01	-65.32	0.25	50	50	1978.43	2015.76	37.33	20	Lowland	316	25.7	19.3	793	715	1689	-896	-888.42	7	2	Entisol	0
CLA-04	Anzoátegui	Coastal Dry Forests	10.01	-65.32	0.25	50	50	1978.43	2015.76	37.33	20	Lowland	283	25.7	19.3	793	715	1689	-896	-888.42	7	2	Entisol	0
CRZ-01	Zulia	Andes - Low-Mid Elev.	8.83	-71.86	1	100	100	1970.69	1972.70	2.01	4	Lowland	60	28.8	22.1	1546	1280	1864	-318	-263.87	3	1	Young oxisol	1
ECM-06	Merida	Andes - High Elev.	8.67	-71.42	0.25	50	50	1967.53	1983.75	16.22	18	Lower-Montane	2060	18.8	12.3	1054	1099	1337	-283	-305.96	4	2	Old inceptisol	1
ELD-01	Bolivar	Guiana Shield	6.11	-61.41	0.25	50	50	1971.55	2015.75	44.20	26	Lowland	220	25.5	19.7	2974	1680	1733	1241	-31.53	0	0	Young oxisol	0

Plot location					Plot characteristics and General Inventory information							Elevation		Climate									Soil	
Plot Code	**State**	**Bioregion**	**Latitude Decimal**	**Longitude Decimal**	**Ground Area (ha)**	**Minimum Dimension (m)**	**Maximum Dimension (m)**	**Date Established**	**Last Census Date**	**Monitoring period (years)**	**No. of Censuses**	**Forest Elevation**	**Altitude (masl)**	**Mean Annual Temp. (ºC)**	**Avg. Min Temp (ºC)**	**Mean Annual Precipitation (mm year^{-1})**	**AET (mm year^{-1}) [a]**	**PET (mm year^{-1}) [a]**	**WA (mm year^{-1}) [a]**	**Climatic Water Deficit (CWD) [b]**	**No. Dry months**	**Seasonality [c]**	**Major Soil Type**	**Fertility [d]**
ELD-02	Bolivar	Guiana Shield	6.11	-61.41	0.25	50	50	1971.55	2015.75	44.20	26	Lowland	244	25.5	19.7	2974	1680	1733	1241	-31.53	0	0	Young oxisol	0
ELD-03	Bolivar	Guiana Shield	6.09	-61.40	0.25	50	50	1971.55	2015.75	44.20	26	Lowland	404	25.5	19.7	2974	1576	1681	1293	-49.71	0	1	Young oxisol	0
ELD-04	Bolivar	Guiana Shield	6.09	-61.35	0.25	50	50	1971.55	2015.75	44.20	26	Lowland	366	24.9	19.1	2974	1556	1672	1302	-69.45	0	1	Young oxisol	0
EMC-02	Barinas	Western Plains	8.01	-70.55	1	100	100	1984.26	1994.30	10.04	8	Lowland	140	27.6	21.4	1678	1275	1739	-61	-455.65	4	2	Old inceptisol	1
ESM-05	Merida	Andes - High Elev.	8.68	-71.43	0.25	50	50	1967.51	1982.53	15.02	17	Premontane	2040	18.8	12.3	1054	996	1380	-326	-350.04	3	1	Old inceptisol	1
GUR-05	Bolivar	Guiana Shield	7.50	-63.00	0.25	50	50	1972.13	1981.18	9.05	10	Lowland	180	26.0	20.3	1291	1091	1681	-390	-525.45	4	2	Young oxisol	0
GUR-06	Bolivar	Guiana Shield	7.50	-63.00	0.25	50	50	1972.13	1978.26	6.13	8	Lowland	180	26.0	20.3	1291	1091	1681	-390	-525.45	5	2	Young oxisol	0
HCU-01	Merida	Andes - Low-Mid Elev.	8.36	-71.69	0.25	50	50	1969.68	1980.72	11.05	12	Premontane	1150	20.6	14.3	894	800	1600	-706	-513.12	3	1	Old inceptisol	1
HSP-01	Portuguesa	Western Plains	8.50	-69.00	1	100	100	1972.27	1981.13	8.85	9	Lowland	100	27.7	21.3	1478	1126	1748	-270	-677.83	5	2	Old inceptisol	1
MOL-04	Merida	Andes - Low-Mid Elev.	8.67	-71.58	0.25	50	50	1967.48	1983.30	15.82	17	Premontane	1500	25.1	18.7	1252	1328	1819	-567	-267.76	3	1	Old inceptisol	1
RIO-01	Bolivar	Guiana Shield	8.11	-61.69	0.25	50	50	1971.57	2015.75	44.18	25	Lowland	312	25.4	20.0	1347	1143	1608	-261	-302.78	4	2	Young oxisol	0
RIO-02	Bolivar	Guiana Shield	8.11	-61.69	0.25	50	50	1971.57	2015.75	44.18	25	Lowland	318	25.4	20.0	1347	1143	1608	-261	-302.78	4	2	Young oxisol	0
SAR-02	Anzoátegui	Coastal Dry Forests	9.99	-65.28	0.25	50	50	1965.02	1981.16	16.15	17	Lowland	50	26.8	20.4	705	592	1746	-1041	-963.83	8	2	Entisol	0
SCR-04	Amazonas	Central Amazon	1.93	-67.04	1	100	100	1975.54	2012.13	36.59	3	Lowland	105	26.2	19.3	3423	1987	1987	1436	0.00	0	0	Older Oxisol	0
SCR-05	Amazonas	Central Amazon	1.93	-67.04	1	100	100	1975.62	2012.13	36.51	3	Lowland	105	26.2	19.3	3423	1987	1987	1436	0.00	0	0	Older Oxisol	0
SDL-01	Bolivar	Guiana Shield	6.10	-61.39	0.2	40	50	2004.50	2011.26	6.77	5	Lowland	220	25.5	19.7	2974	1525	1655	1319	-53.18	0	0	Young oxisol	0
SDL-04	Bolivar	Guiana Shield	6.10	-61.40	0.1	20	50	2000.18	2011.20	11.02	7	Lower-Montane	760	25.5	19.7	3000	1645	1714	1286	-45.84	0	0	Young oxisol	0
SDL-05	Bolivar	Guiana Shield	5.97	-61.40	0.1	20	50	2003.50	2011.21	7.71	6	Upper-Montane	1320	20.4	14.6	4500	1233	1426	3074	-49.51	0	0	Young oxisol	0
SEU-01	Merida	Andes - High Elev.	8.66	-71.40	0.25	50	50	1968.81	2016.25	47.44	28	Lower-Montane	2318	14.3	6.9	1326	1103	1323	3	-266.39	4	2	Old inceptisol	0
SEU-02	Merida	Andes - High Elev.	8.62	-71.14	0.25	50	50	1968.81	2016.25	47.44	28	Lower-Montane	2312	17.8	10.9	1414	1077	1423	-9	-184.62	4	2	Old inceptisol	0
SEU-03	Merida	Andes - High Elev.	8.64	-71.41	0.25	50	50	1961.51	2016.26	54.75	34	Lower-Montane	2421	14.3	6.9	1326	1039	1281	45	-251.86	4	2	Old inceptisol	0
SEU-04	Merida	Andes - High Elev.	8.64	-71.41	0.25	50	50	1968.60	2016.27	47.67	27	Lower-Montane	2321	14.3	6.9	1326	1039	1281	45	-251.86	4	2	Old inceptisol	0
SEU-05	Merida	Andes - High Elev.	8.64	-71.40	0.25	50	50	1961.78	2016.26	54.48	33	Premontane	2449	14.3	6.9	1326	1071	1297	29	-253.76	4	2	Old inceptisol	0
SEU-06	Merida	Andes - High Elev.	8.63	-71.40	0.25	50	50	1967.52	2016.26	48.74	26	Lower-Montane	2452	14.3	6.9	1326	1009	1270	56	-261.46	4	2	Old inceptisol	0

[a] Actual and potential evapotranspiration (AET and PET) data extracted from the were extracted from the Geospatial Database CGIAR Consortium for Spatial Information (Zommer et al., 2008) at http://www.cgiar-csi.org/data Water availability (WA) = Mean annual precipitation – PET.

[b] Climatic Water Deficit (CWD) as in Chave et al., 2014 was obtained from a global climate layer for the long-term average of CWD at 2.5 arc-minute resolution. See: http://chave.ups-tlse.fr/pantropical_allometry.htm. Climatic Water Deficit (CWD) as in Chave et al., 2014 was obtained from a global climate layer for the long-term average of CWD at 2.5 arc-minute resolution. See: http://chave.ups-tlse.fr/pantropical_allometry.htm. This factor is measured as the difference between rainfall and evapotranspiration during dry months only and is, by definition, negative. CWD=0 means not seasonally water-stressed; in contrast, sites with very negative CWD values are strongly seasonally water-stressed.

[c] Seasonality: 0 = Aseasonal (0-1 dry months); 1 = Moderately seasonal (2-3 dry months); 2 = Seasonal (> 3 dry months)

[d] Soil fertility: 0 = poor nutrient; 1 = richer

* Shaded cells indicate climatic data obtained directly from local weather stations, while WorldClim database was used for the rest.

Table S2. Pair-wise thau (τ) correlation between climate, dynamic and structure variables. Green colored cells highlight positive correlations > 0.5. Orange cells are negative correlations > -0.5. Gray cells are positive correlations between 0.2 and 0.5. Blue cells are negative correlations between -0.2 and -0.5.

	Latitude	**Elevation**	**MAT**	**T min**	**MAP**	**Dry M**	**AET**	**PET**	**WA**	**CWD**	**PCA 1**	**PCA 2**	**Rec. Rate**	**Mort. Rate**	**Turn. Rate**	**AGB**	**AGB Loss**	**AGB Gains**	**AGB Recruit**	**AGWP**	**Mean Stem Density**	**Mean Wood Density**	**Mean Basal Area**
Latitude	---																						
Elevation	0.098221	---																					
MAT	-0.03764	-0.78158	---																				
T min	-0.0222	-0.73646	0.916956	---																			
MAP	-0.52006	-0.34869	0.25216	0.236207	---																		
Dry M	0.505334	0.008209	0.110622	0.108559	-0.41667	---																	
AET	-0.47357	-0.38922	0.299806	0.283896	0.807538	-0.41053	---																
PET	-0.10628	-0.78228	0.671575	0.603884	0.393381	-0.09706	0.502535	---															
WA	-0.55963	0.035717	-0.14684	-0.16192	0.578515	-0.57169	0.434602	-0.03956	---														
CWD	-0.40624	0.256664	-0.35514	-0.36987	0.318183	-0.51997	0.286078	-0.15741	0.549201	---													
PCA 1	-0.55369	-0.36624	0.245892	0.230335	0.797232	-0.51563	0.794956	0.419305	0.428908	0.33931	---												
PCA 2	0.159621	-0.62843	0.720834	0.701094	0.005035	0.357118	0.047448	0.523924	-0.38577	-0.58487	0.01473	---											
Rec. Rate	0.092998	-0.3036	0.333061	0.293864	0.165956	0.298447	0.115564	0.324253	-0.03894	-0.23781	0.067021	0.289334	---										
Mort. Rate	-0.02989	-0.18903	0.233816	0.225016	0.18272	0.201998	0.118889	0.20981	0.040601	-0.15495	0.086637	0.184716	0.492245	---									
Turn. Rate	0.041517	-0.23977	0.29269	0.266996	0.181043	0.283889	0.110575	0.277812	-0.01077	-0.20301	0.078463	0.255006	0.782857	0.709388	---								
AGB	-0.25242	0.285598	-0.33306	-0.29722	0.028498	-0.44585	0.050715	-0.25293	0.28255	0.372038	0.091541	-0.39232	-0.46122	-0.27347	-0.41388	---							
AGB Loss	-0.2491	0.203765	-0.21195	-0.17968	0.162604	-0.27479	0.125541	-0.18825	0.300779	0.29415	0.178177	-0.28933	-0.12816	0.157551	-0.00898	0.242449	---						
AGB Gains	-0.20094	-0.07447	0.025232	0.080603	0.194454	-0.35486	0.28018	0.092051	0.082031	0.141689	0.304046	-0.03596	-0.13633	-0.05959	-0.1151	0.263673	0.133061	---					
AGB Recruit	0.028232	-0.0761	0.121113	0.08564	0.092198	0.158323	0.025773	0.103661	0.113517	-0.07872	-0.05558	0.055578	0.523265	0.257143	0.436735	-0.26857	-0.02041	-0.29959	---				
AGWP	-0.27069	-0.12848	0.075696	0.119225	0.271565	-0.36578	0.331726	0.160053	0.173176	0.169861	0.359624	-0.01635	-0.05469	0.031837	-0.01714	0.234286	0.198367	0.794286	-0.09388	---			
Mean Stem Density	-0.07479	0.439804	-0.52525	-0.53779	-0.05201	-0.26955	-0.08737	-0.37432	0.282781	0.443659	-0.03763	-0.52515	-0.32108	-0.26062	-0.29003	0.211601	0.206699	-0.11356	-0.02859	-0.13317	---		
Mean Wood Density	-0.08636	-0.05974	0.010093	0.011755	-0.00838	-0.20746	-0.03908	0.017415	0.040601	0.10026	0.040866	0.050674	-0.20327	-0.28	-0.24408	0.284898	0.033469	0.12	-0.16408	0.087347	0.090686	---	
Mean Basal Area	-0.03986	0.460722	-0.52651	-0.50545	-0.08717	-0.27661	-0.09062	-0.38064	0.267635	0.343866	-0.08173	-0.57213	-0.33714	-0.18204	-0.28653	0.601633	0.154286	0.057959	-0.14449	0.031837	0.348856	-0.02204	---

Table S3. Estimates of turnover rates, aboveground biomass and productivity for all plots.

Plot Code	Forest structure			Forest demography			Forest carbon					
	Avg Plot Basal Area (m^2 ha^{-1})	**Avg. Plot Stem density (stems ha^{-1})**	**Avg. Plot Wood Density (g cm^{-3})**	**Recruitment interval corrected [a] (% year^{-1})**	**Mortality interval corrected [a] (% year^{-1})**	**Turnover interval corrected [a] (% year^{-1})**	**AGB (Mg C ha^{-1}) [b]**	**AGB loss (Mg C ha^{-1} year^{-1})**	**AGB growth (Mg C ha^{-1} year^{-1})**	**AGB recruit (Mg C ha^{-1} year^{-1})**	**AGWP (Mg C ha^{-1} year^{-1}) [c]**	**Carbon Residence Time (years) [d]**
ACL-01	28.496	322	0.649	1.191	1.550	1.371	176.848	2.847	3.698	0.102	3.800	46.54
BAC-01	26.734	346	0.500	2.204	2.831	2.518	113.500	2.489	2.615	0.387	3.002	37.81
BAC-02	21.214	290	0.531	3.431	4.136	3.784	102.640	1.859	2.020	0.902	2.922	35.13
BAC-03	35.289	248	0.567	2.367	2.562	2.464	206.230	1.136	2.361	0.591	2.952	69.87
BAC-04	28.262	302	0.599	2.243	2.745	2.494	135.579	1.331	1.722	0.189	1.911	70.95
BAC-05	19.401	380	0.508	3.296	3.600	3.448	77.786	1.861	2.157	0.866	3.023	25.73
BAC-06	29.977	244	0.512	2.481	2.643	2.562	150.246	3.113	3.538	0.345	3.883	38.69
CAI-01	22.000	310	0.547	3.174	3.841	3.507	117.096	3.155	2.820	0.430	3.250	36.03
CAI-02	21.594	240	0.522	1.993	1.881	1.937	113.483	2.030	1.558	0.490	2.048	55.41
CAI-03	15.287	258	0.524	3.292	3.232	3.262	80.404	1.923	1.724	0.399	2.123	37.86
CAI-04	22.874	248	0.535	3.421	2.979	3.200	115.821	1.568	1.878	0.444	2.322	49.88
CAI-05	21.744	332	0.578	2.748	2.643	2.695	114.254	1.449	2.184	0.400	2.584	44.21
CAI-06	26.021	274	0.577	1.878	1.434	1.656	150.581	0.807	2.239	0.241	2.481	60.71
CAT-02	18.110	314	0.542	3.029	2.671	2.850	81.251	1.972	2.656	0.228	2.884	28.18
CAT-03	28.964	280	0.560	2.126	1.985	2.055	144.203	1.099	3.039	0.159	3.198	45.09
CBN-01	27.486	756	0.543	1.650	1.334	1.492	136.293	1.348	1.892	0.428	2.320	58.74
CBN-02	27.970	926	0.538	1.388	1.187	1.288	113.619	1.524	1.661	0.419	2.080	54.62
CBN-03	39.309	582	0.490	1.423	1.239	1.331	184.798	1.353	1.783	0.188	1.971	93.76
CBN-04	33.142	572	0.524	1.762	2.036	1.899	179.899	2.362	1.745	0.714	2.459	73.16
CBN-05	32.376	774	0.587	1.445	1.756	1.601	154.846	3.072	1.314	0.236	1.550	99.88
CBN-06	32.308	634	0.609	1.191	1.800	1.495	185.327	3.181	1.268	0.936	2.204	84.09
CLA-03	24.342	468	0.733	1.811	1.364	1.588	125.518	0.879	1.825	0.269	2.093	59.96
CLA-04	24.586	640	0.759	1.702	1.839	1.770	128.517	0.966	2.032	0.350	2.383	53.94
CRZ-01	17.662	547.5	0.576	2.191	0.648	1.419	70.749	0.469	1.932	0.309	2.240	31.58
ECM-06	44.421	502	0.523	0.323	1.150	0.737	204.674	1.555	2.678	0.026	2.704	75.69
ELD-01	28.109	430	0.738	0.903	1.399	1.151	234.506	2.323	3.724	0.121	3.845	60.99
ELD-02	31.171	494	0.742	0.483	0.712	0.597	266.224	0.935	3.353	0.073	3.426	77.70
ELD-03	21.118	546	0.674	2.192	1.783	1.987	136.338	4.044	3.271	0.372	3.643	37.43
ELD-04	27.842	672	0.645	1.048	1.612	1.330	156.565	3.592	4.145	0.201	4.346	36.03
EMC-02	26.058	197	0.621	3.538	1.730	2.634	151.633	0.503	2.481	1.683	4.165	36.41
ESM-05	42.872	532	0.589	1.427	1.980	1.703	205.316	2.494	3.558	0.210	3.768	54.48
GUR-05	16.843	328	0.775	1.346	1.074	1.210	133.051	1.273	2.119	0.260	2.379	55.94
GUR-06	21.306	410	0.764	2.343	1.543	1.943	174.418	4.488	1.904	0.278	2.182	79.95

Plot Code	Forest structure			Forest demography			Forest carbon					
	Avg Plot Basal Area (m^2 ha^{-1})	Avg. Plot Stem density (stems ha^{-1})	Avg. Plot Wood Density (g cm^{-3})	Recruitment interval corrected [a] (% $year^{-1}$)	Mortality interval corrected [a] (% $year^{-1}$)	Turnover interval corrected [a] (% $year^{-1}$)	AGB (Mg C ha^{-1}) [b]	AGB loss (Mg C ha^{-1} $year^{-1}$)	AGB growth (Mg C ha^{-1} $year^{-1}$)	AGB recruit (Mg C ha^{-1} $year^{-1}$)	AGWP (Mg C ha^{-1} $year^{-1}$) [c]	Carbon Residence Time (years) [d]
HCU-01	36.146	452	0.660	0.405	0.728	0.567	237.270	0.808	2.715	0.043	2.758	86.03
HSP-01	19.412	348	0.580	2.610	1.832	2.221	96.122	1.062	1.871	0.313	2.184	44.01
MOL-04	31.883	654	0.557	1.323	1.441	1.382	159.029	1.914	2.578	0.179	2.757	57.69
RIO-01	29.389	536	0.708	1.008	1.074	1.041	226.454	3.116	3.541	0.145	3.687	61.43
RIO-02	30.773	580	0.700	0.974	1.540	1.257	225.897	3.416	3.380	0.150	3.530	64.00
SAR-02	9.213	338	0.731	2.293	2.380	2.337	47.660	0.528	0.591	0.236	0.827	57.65
SCR-04	29.085	734	0.673	1.887	1.265	1.576	183.288	1.801	1.756	0.580	2.337	78.43
SCR-05	28.288	579.5	0.685	2.941	2.051	2.496	201.301	3.455	2.360	0.799	3.160	63.71
SDL-01	31.029	657.5	0.719	0.350	1.481	0.915	237.089	5.692	3.812	0.052	3.865	61.34
SDL-04	34.288	1065	0.628	1.605	2.650	2.127	204.805	2.532	3.498	0.279	3.777	54.23
SDL-05	41.634	1165	0.560	0.845	1.996	1.421	257.185	6.765	1.166	0.100	1.266	203.12
SEU-01	36.741	926	0.555	2.260	1.528	1.894	173.818	1.859	2.086	0.501	2.587	67.20
SEU-02	34.279	1135	0.591	1.978	1.348	1.663	140.132	1.652	1.700	0.612	2.312	60.61
SEU-03	41.203	638	0.645	1.694	1.395	1.544	224.870	2.315	2.373	0.281	2.654	84.73
SEU-04	38.923	652	0.614	2.370	1.856	2.113	190.334	2.998	2.431	0.405	2.836	67.11
SEU-05	37.852	866	0.654	1.851	1.671	1.761	170.767	2.770	1.586	0.466	2.052	83.24
SEU-06	37.599	746	0.650	2.231	1.801	2.016	171.071	2.331	1.495	0.420	1.915	89.32

[a] Rates are calculated and corrected for every census interval, and then weighted by census length. For details on the correction approach see methods section.

[b] Total aboveground biomass based on plot inventory data (trees > 10 cm) + 6.2% from small trees (< 10 cm D) as in Malhi et al., (2006).

[c] AGWP = AGB growth + AGB recruit.

[d] Carbon residence time = AGB / AGWP.

Table S4. Parameters of a series of Generalized Least Squares (GLS) models for turnover, aboveground biomass (AGB) and aboveground woody productivity (AGWP) among 50 forest plots in six different regions in Venezuela. Models were fitted upon prior information and region was added as an additional factor with interactions as appropriate (+ symbol). All models incorporated a Gaussian spatial correlation structure to account for spatial autocorrelation. Models are ranked by AICc values, and the final selected model is highlighted in bold.

Response variable 1: Turnover rate

Climate models

Model [A]	**Terms in the model**										**Model summary**								
	(Intercept)	**drym**	**REGION**	**drym:REGION**	**MAT**	**MAT:REGION**	**PET**	**PET:REGION**	**CWD**	**CWD:REGION**	**df**	**logLik**	**AICc**	**delta**	**weight**	**Pseudo r squared**	**RMSE**	**RMSE-Test**	**PE%** [B]
Turn.mod.gls2.2	1.38				0.61	+					9.00	-39.04	**100.57**	0.00	0.50	0.55	0.497	0.563	11.69
Turn.mod.gls3.2	1.39						0.34	+			9.00	-40.03	102.57	2.00	0.19	0.55	0.498	0.560	11.14
Turn.mod.gls3.1	1.55		+				0.12				9.00	-40.81	104.13	3.56	0.09	0.54	0.500	0.555	9.98
Turn.mod.gls2.1	1.61		+		0.00						9.00	-40.88	104.26	3.69	0.08	0.54	0.501	0.538	6.85
Turn.mod.gls4.1	1.59		+						0.16		9.00	-40.90	104.29	3.72	0.08	0.55	0.496	0.571	13.13
Turn.mod.gls1.1	1.60	0.13	+								9.00	-41.14	104.78	4.21	0.06	0.55	0.496	0.566	12.34
Turn.mod.clim	1.44	0.41	+		-0.41		0.41		0.44		12.00	-39.18	110.80	10.23	0.00	0.61	0.463	0.554	16.49
Turn.mod.gls4.2	1.70								1.15	+	9.00	-45.72	113.93	13.36	0.00	0.40	0.573	0.639	10.26
Turn.mod.gls1	1.90	0.29									4.00	-53.27	115.43	14.86	0.00	0.12	0.693	0.698	0.73
Turn.mod.gls2	1.91				0.27						4.00	-53.74	116.36	15.79	0.00	0.12	0.693	0.694	0.16
Turn.mod.gls4	1.90								-0.24		4.00	-54.19	117.27	16.70	0.00	0.10	0.699	0.705	0.78
Turn.mod.gls3	1.91						0.25				4.00	-54.20	117.28	16.71	0.00	0.11	0.700	0.710	1.38
Turn.mod.gls1.2	1.85	0.91		+							9.00	-47.99	118.48	17.91	0.00	0.34	0.600	0.659	8.96

Mean PE = 7.99 % | Min PE = 0.16% | Max PE = 16.49%

A*:* Model name refers to the script used during the analysis

B: Prediction Error = (1- RMSE/RMSE-Test) * 100

Table S4. Continuation….

Response variable 1: Turnover rate

Structure models

Model [A]	Terms in the model								Model summary								
	(Intercept)	AVGDen	REGION	AVGDen:REGION	AvgBA	AvgBA:REGION	AvgWD	AvgWD:REGION	df	logLik	AICc	delta	weight	Pseudo r squared	RMSE	RMSE-Test	PE% [B]
Turn.mod.gls6.1	1.55		+		-0.25				9.00	-38.86	**100.21**	0.00	0.72	0.60	0.468	0.502	6.70
Turn.mod.gls7.1	1.56		+				-0.15		9.00	-40.97	104.43	4.22	0.09	0.56	0.493	0.541	8.95
Turn.mod.gls6.2	1.74				-0.50	+			9.00	-41.10	104.70	4.49	0.08	0.38	0.581	0.669	13.20
Turn.mod.gls5.1	1.63	0.04	+						9.00	-41.66	105.82	5.60	0.04	0.54	0.500	0.553	9.53
Turn.mod.gls7.2	1.74						-0.65	+	9.00	-41.77	106.04	5.83	0.04	0.54	0.504	0.582	13.45
Turn.mod.gls6	1.91				-0.38				4.00	-49.42	107.73	7.52	0.02	0.22	0.656	0.665	1.39
Turn.mod.gls5.2	1.51	-0.48		+					9.00	-43.23	108.96	8.74	0.01	0.47	0.534	0.666	19.87
Turn.mod.str	1.53	0.07	+		-0.28		-0.15		11.00	-40.10	109.15	8.94	0.01	0.62	0.455	0.522	12.79
Turn.mod.gls5	1.90	-0.31							4.00	-52.91	114.72	14.50	0.00	0.18	0.670	0.682	1.69
Turn.mod.gls7	1.91						-0.28		4.00	-53.59	116.06	15.85	0.00	0.17	0.676	0.703	3.81

Mean PE = 9.14 % | Min PE = 1.39% | Max PE = 19.87%

Response variable 2: Aboveground biomass (AGB)

Climate models

Model [A]	Terms in the model										Model summary								
	(Intercept)	drym	REGION	drym:REGION	WA	REGION:WA	CWD	CWD:REGION	PET	PET:REGION	df	logLik	AICc	delta	weight	Pseudo r squared	RMSE	RMSE-Test	PE% [B]
AGB.mod.gls5	167.44		+		-10.05		26.37		-61.65		11	-216.40	**461.74**	0.00	0.88	0.52	35.2	39.50	10.89
AGB.mod.gls3.2	172.84						-110.89	+			9	-222.09	466.67	4.93	0.07	0.56	33.7	37.84	10.94
AGB.mod.gls4.2	202.67								-88.76	+	9	-222.84	468.18	6.44	0.04	0.53	35.1	38.61	9.10
AGB.mod.gls4.1	169.32		+						-46.48		9	-224.34	471.18	9.44	0.01	0.51	35.7	40.57	12.01
AGB.mod.gls1.1	146.26	-20.77	+								9	-225.51	473.51	11.77	0.00	0.50	36.1	39.42	8.42
AGB.mod.gls2.1	152.35		+		11.07						9	-227.14	476.77	15.03	0.00	0.46	37.4	40.94	8.65
AGB.mod.gls3.1	143.76		+				8.50				9	-227.36	477.22	15.47	0.00	0.45	37.9	44.05	13.95
AGB.mod.gls2.2	161.96				5.78	+					9	-227.90	478.30	16.55	0.00	0.40	39.6	43.30	8.54
AGB.mod.gls1.2	165.52	-36.55		+							9	-229.02	480.53	18.79	0.00	0.41	39.3	41.85	6.08
AGB.mod.gls1	159.41	-31.09									4	-250.96	510.81	49.07	0.00	0.36	40.8	42.18	3.27
AGB.mod.gls3	159.43						28.62				4	-252.60	514.08	52.34	0.00	0.31	42.3	43.20	2.09
AGB.mod.gls2	159.48				25.68						4	-254.56	518.01	56.27	0.00	0.25	44.1	45.38	2.83
AGB.mod.gls4	159.41								-17.29		4	-258.25	525.38	63.64	0.00	0.08	49.2	50.12	1.83

Mean PE = 7.58 % | Min PE = 1.83% | Max PE = 13.95%

A*:* Model name refers to the script used during the analysis | B: Prediction Error = (1- RMSE/RMSE-Test) * 100

Table S4. Continuation….

Response variable 2: Aboveground biomass (AGB)

Structure models

Model [A]	**Terms in the model**												**Model summary**								
	(Intercept)	**Turn**	**REGION**	**REGION:Turn**	**AVGDen**	**AVGDen:REGION**	**AvgWD**	**AvgWD:REGION**	**AGBMortPlot**	**AGBMortPlot:REGION**	**AGWPPlot**	**AGWPPlot:REGION**	**df**	**logLik**	**AICc**	**delta**	**weight**	**Pseudo r squared**	**RMSE**	**RMSE-Test**	**PE% [B]**
AGB.mod.gls11	142.00	-35.31	+		-1.29		6.71		14.13		18.53		13.00	-204.41	**444.94**	0.00	1.00	0.64	30.9	36.03	14.25
AGB.mod.gls6.1	138.70	-29.47	+										9.00	-222.25	467.00	22.06	0.00	0.56	34.1	38.74	11.98
AGB.mod.gls6.2	153.52	-35.57		+									9.00	-224.76	472.03	27.09	0.00	0.45	37.8	44.19	14.46
AGB.mod.gls8.2	176.22						80.55	+					9.00	-226.54	475.58	30.65	0.00	0.47	37	40.63	8.93
AGB.mod.gls10.1	141.65		+								12.11		9.00	-226.57	475.65	30.71	0.00	0.48	36.7	37.27	1.54
AGB.mod.gls8.1	148.60		+				12.25						9.00	-227.01	476.53	31.59	0.00	0.46	37.3	42.32	11.86
AGB.mod.gls9.1	147.46		+						4.81				9.00	-227.90	478.29	33.36	0.00	0.45	37.9	42.01	9.78
AGB.mod.gls7.1	144.25		+		-1.56								9.00	-227.93	478.36	33.42	0.00	0.44	38.1	43.23	11.86
AGB.mod.gls7.2	175.11				18.49	+							9.00	-230.01	482.52	37.58	0.00	0.30	42.8	50.40	15.09
AGB.mod.gls9.2	163.20								18.81	+			9.00	-233.80	490.11	45.17	0.00	0.22	45	50.61	11.08
AGB.mod.gls10.2	162.76										35.04	+	9.00	-233.97	490.45	45.51	0.00	0.16	47	52.66	10.74
AGB.mod.gls6	159.52	-33.69											4.00	-248.07	505.02	60.08	0.00	0.38	40.2	40.31	0.26
AGB.mod.gls9	159.42								20.85				4.00	-256.60	522.10	77.16	0.00	0.19	46.0	46.59	1.26
AGB.mod.gls10	159.50										18.97		4.00	-257.37	523.64	78.70	0.00	0.12	48	49.43	2.89
AGB.mod.gls7	159.49				18.14								4.00	-257.87	524.63	79.69	0.00	0.14	47.4	48.21	1.68
AGB.mod.gls8	159.42						15.58						4.00	-258.71	526.30	81.36	0.00	0.11	48.2	49.36	2.35

Mean PE = 8.13 % | Min PE = 0.26% | Max PE = 15.09%

A*:* Model name refers to the script used during the analysis

B: Prediction Error = (1- RMSE/RMSE-Test) * 100

Table S4. Continuation….

Response variable 3: Aboveground woody productivity (AGWP)

Climate models

Model [A]	Terms in the model								Model summary								
	(Intercept)	drym	REGION	drym:REGION	AET	AET:REGION	CWD	CWD:REGION	df	logLik	AICc	delta	weight	Pseudo r squared	RMSE	RMSE-Test	PE% [B]
AGWP.mod.gls2.2	2.61				-0.55	+			9.00	-41.96	**106.42**	0.00	0.57	0.43	0.577	0.645	10.52
AGWP.mod.gls1	2.74	-0.36							4.00	-49.81	108.52	2.09	0.20	0.24	0.665	0.683	2.64
AGWP.mod.gls2	2.74				0.33				4.00	-50.24	109.36	2.94	0.13	0.20	0.681	0.690	1.23
AGWP.mod.gls3	2.74						0.30		4.00	-50.78	110.45	4.03	0.08	0.14	0.709	0.744	4.69
AGWP.mod.gls3.2	3.04						-0.48	+	9.00	-45.58	113.66	7.24	0.02	0.40	0.592	0.654	9.43
AGWP.mod.gls1.2	2.94	0.07		+					9.00	-45.79	114.08	7.65	0.01	0.40	0.592	0.645	8.21
AGWP.mod.gls2.1	3.05		+		0.39				9.00	-47.98	118.45	12.03	0.00	0.32	0.631	0.678	6.99
AGWP.mod.gls1.1	2.90	-0.32	+						9.00	-48.52	119.54	13.11	0.00	0.35	0.618	0.651	5.02
AGWP.mod.gls3.1	2.88		+				0.28		9.00	-48.99	120.48	14.06	0.00	0.31	0.637	0.685	6.99
AGWP.mod.gls4	3.15	-0.24	+		0.53		-0.47		11.00	-47.82	124.59	18.17	0.00	0.32	0.632	0.715	11.62

Mean PE = 6.73 % | Min PE = 1.23% | Max PE = 11.62%

Structure models

Model [A]	Terms in the model								Model summary								
	(Intercept)	Turn	REGION	REGION:Turn	AVGDen	AVGDen:REGION	AvgWD	AvgWD:REGION	df	logLik	AICc	delta	weight	Pseudo r squared	RMSE	RMSE-Test	PE% [B]
AGWP.mod.gls6.2	2.87				-0.53	+			9.00	-47.63	**117.77**	0.00	0.30	0.16	0.697	0.847	17.75
AGWP.mod.gls7	2.74						0.05		4.00	-54.75	118.38	0.61	0.22	0.01	0.758	0.780	2.83
AGWP.mod.gls5	2.74	-0.02							4.00	-55.04	118.97	1.20	0.16	0.00	0.762	0.764	0.30
AGWP.mod.gls6	2.89		+		-0.25				9.00	-48.69	119.88	2.11	0.10	0.04	0.651	0.734	11.26
AGWP.mod.gls6.1	2.89		+		-0.25				9.00	-48.69	119.88	2.11	0.10	0.27	0.651	0.749	13.10
AGWP.mod.gls7.1	2.98		+				0.14		9.00	-49.56	121.62	3.85	0.04	0.23	0.669	0.737	9.28
AGWP.mod.gls7.2	2.72						0.29	+	9.00	-49.72	121.95	4.18	0.04	0.18	0.69	0.803	14.06
AGWP.mod.gls5.1	2.98	0.07	+						9.00	-50.10	122.69	4.92	0.03	0.24	0.667	0.741	10.00
AGWP.mod.gls5.2	2.70	-0.14		+					9.00	-51.47	125.43	7.66	0.01	0.13	0.711	0.839	15.25
AGWP.mod.gls8	2.94	0.08	+		-0.23		0.07		11.00	-50.47	129.89	12.12	0.00	0.27	0.652	0.742	12.18

Mean PE = 10.6 % | Min PE = 0.30% | Max PE = 17.75%

A*:* Model name refers to the script used during the analysis | B: Prediction Error = (1- RMSE/RMSE-Test) * 100

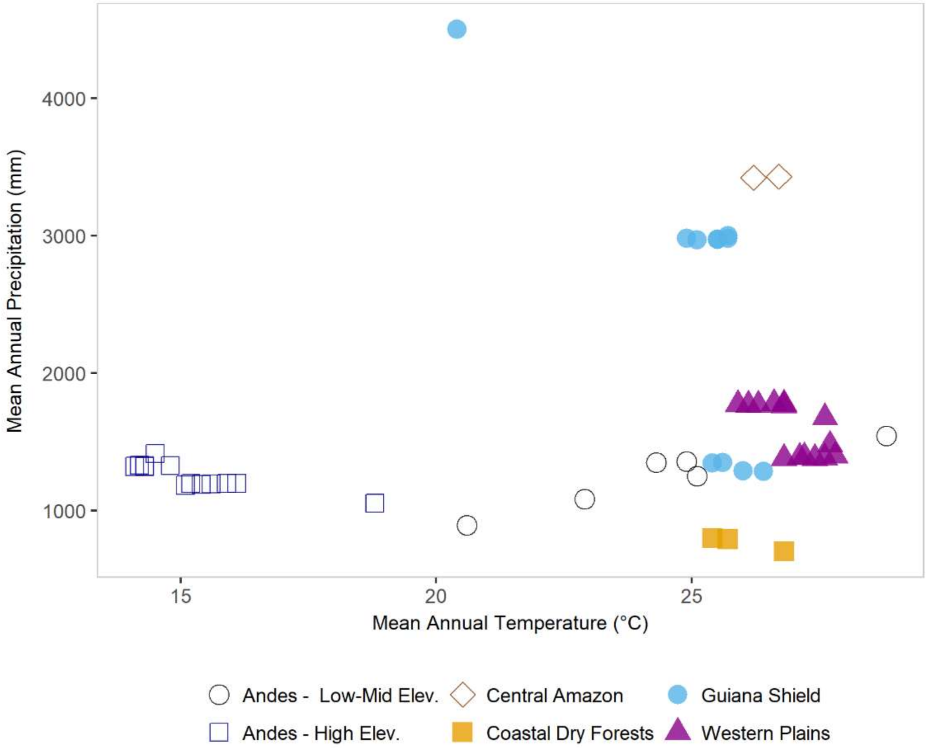
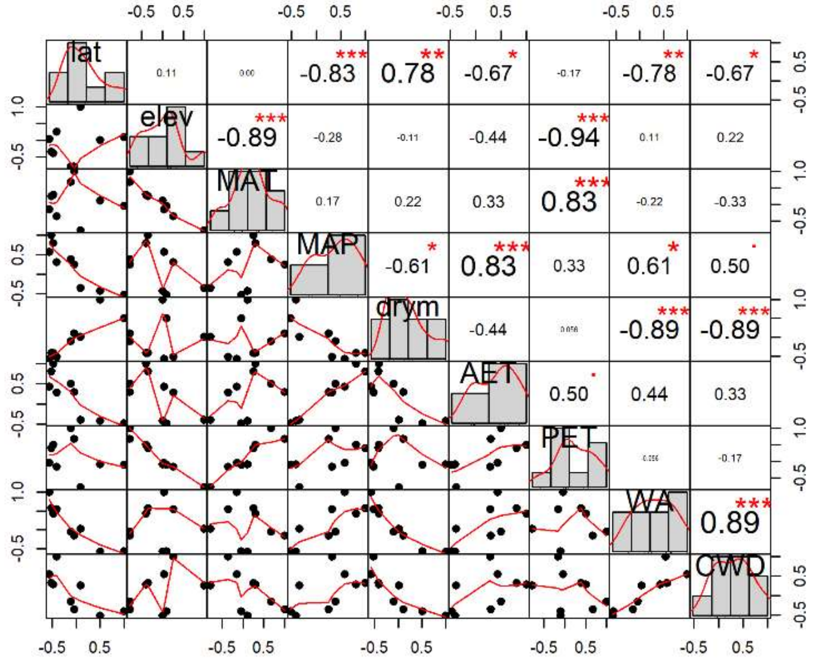


Figure S1. Bioclimatic description of 50 plots in Venezuelan forests.

A)



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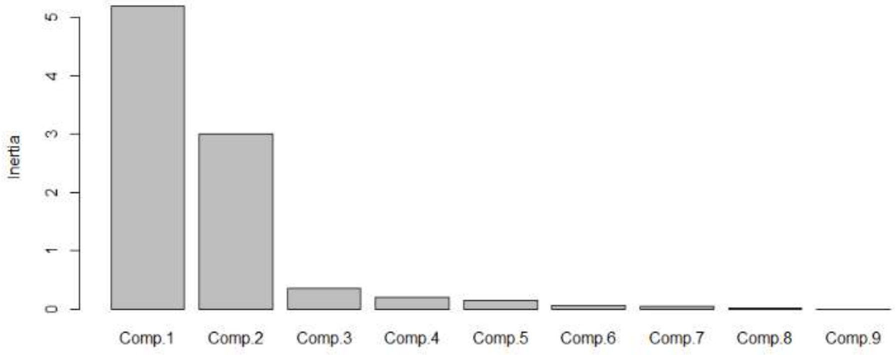


C)

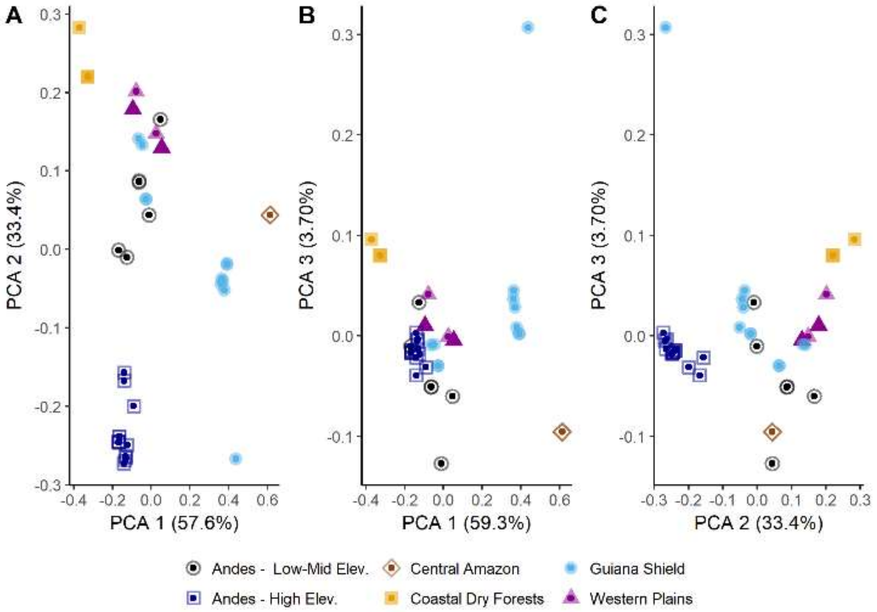


Figure S2. A) Kendall's tau correlation matrix for 10 environmental variables used in the Principal Component Analysis; B) Inertia plot of PCA; C) Relationships between three major axes of variation by region.

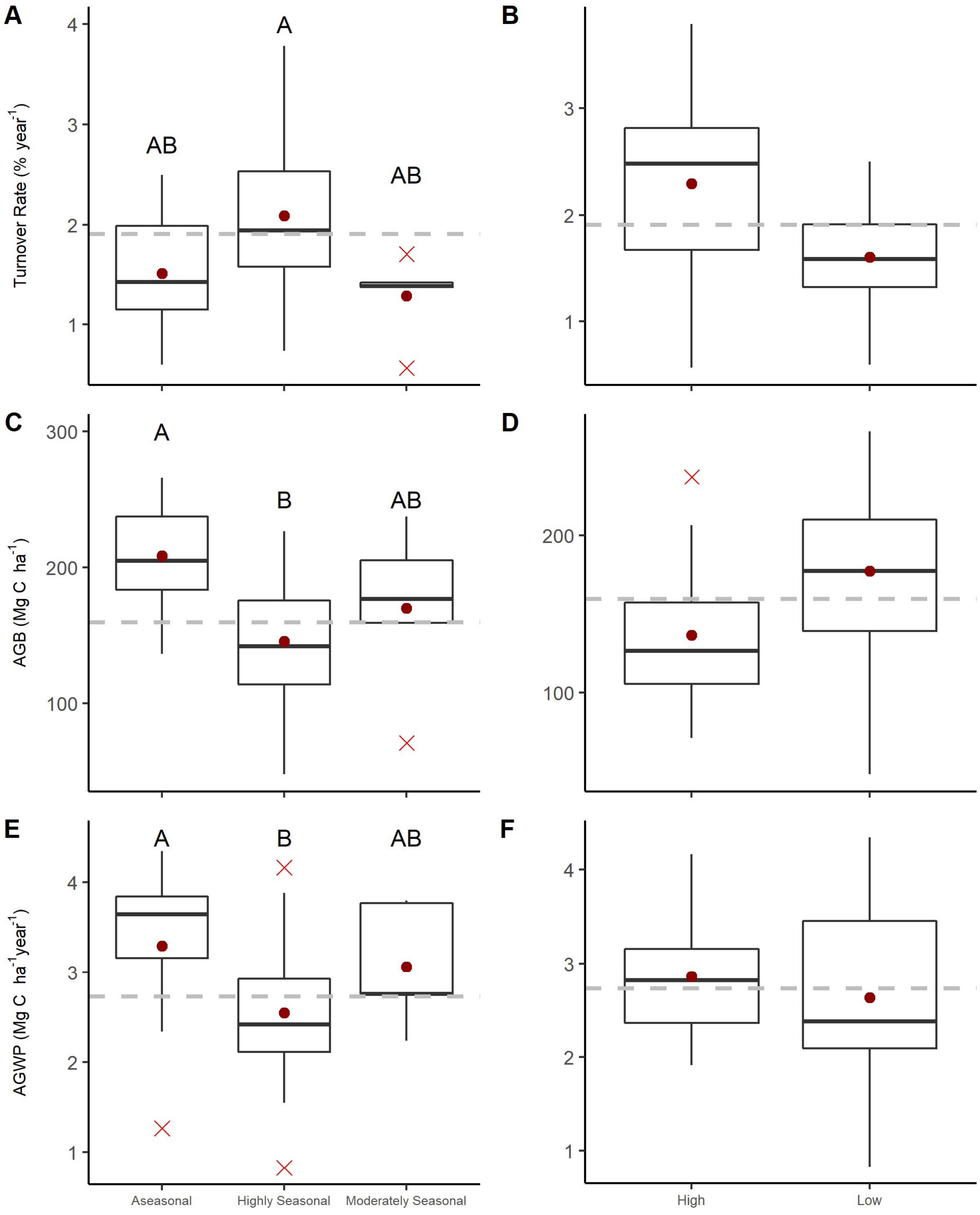


Figure S3. Boxplots of turnover rates (A-B), AGB (C-D), and AGWP (E-F) by three seasonality conditions, and two major soil fertility groups. Letters indicate results from pos-hoc tests when significant differences were found: Turnover and seasonality: F = 4.669, p = 0.014*; Turnover and fertility: F = 13.19, p = 0.000682 ***; AGB and seasonality: F = 6.774, p = 0.003**; AGB and fertility: F = 8.933, p = 0.004**; AGWP and seasonality: F = 4.488, p = 0.0165*; AGWP and fertility: F = 1.102, p = 0.299 ns.

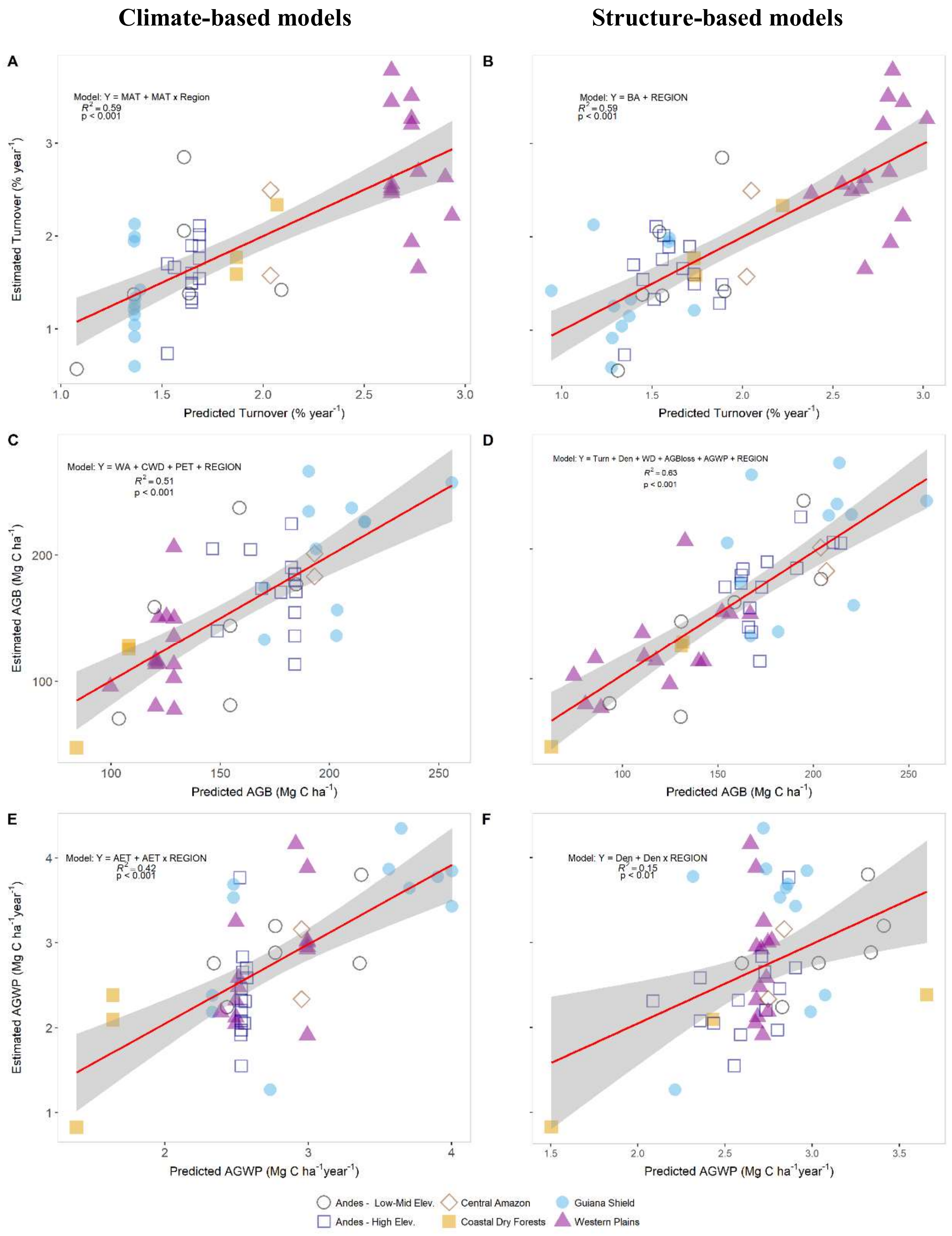


Figure S4. Relationships between the predicted and estimated values of turnover rates (A-B), AGB (C-D), and AGWP (E-F) based on the "best" regression models selected. Left panel refers to climatic models, while the right panel shows structure-based models for each response variable. Correlation values here are based on simple linear models between predicted and estimated values. For additional information for all the models tested see Table S4.

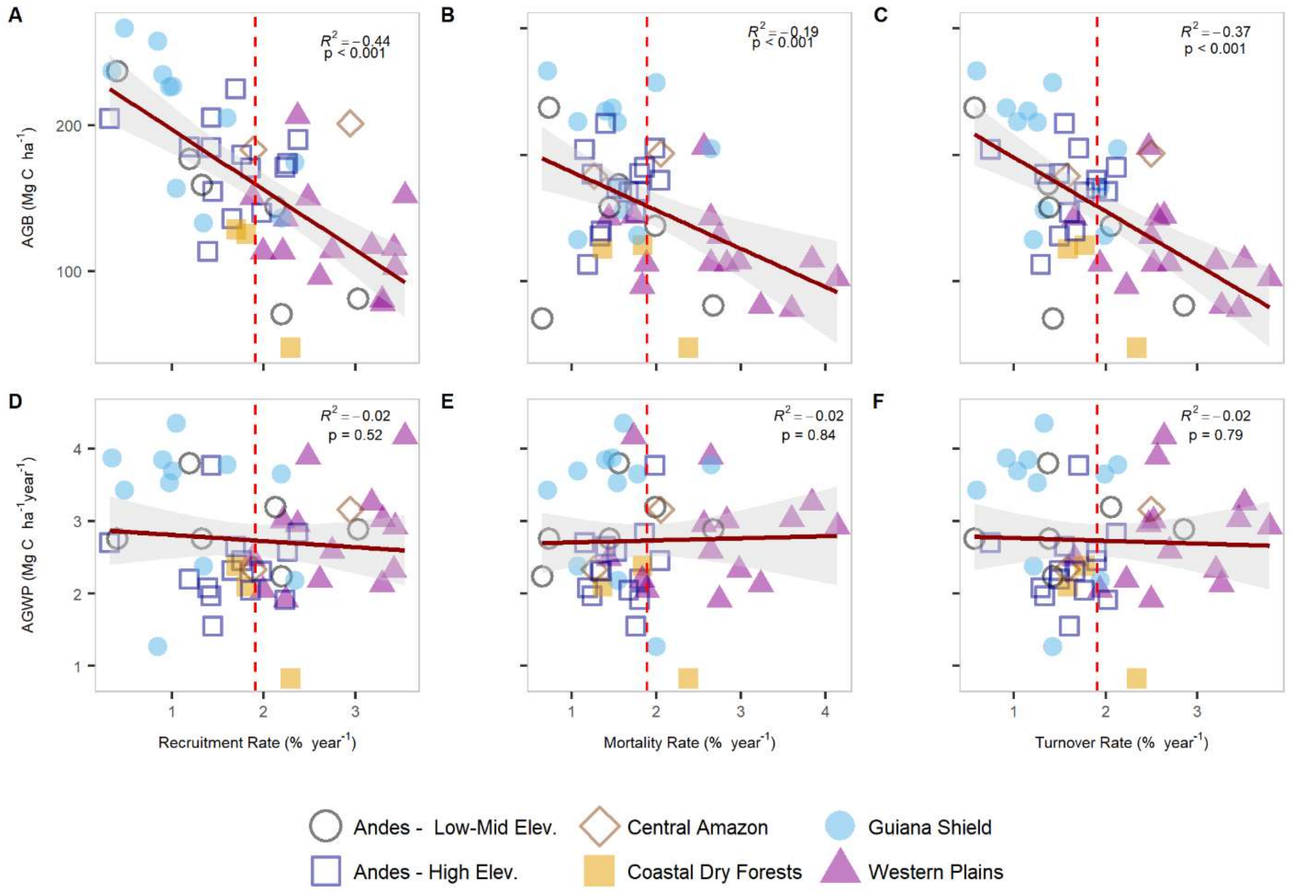
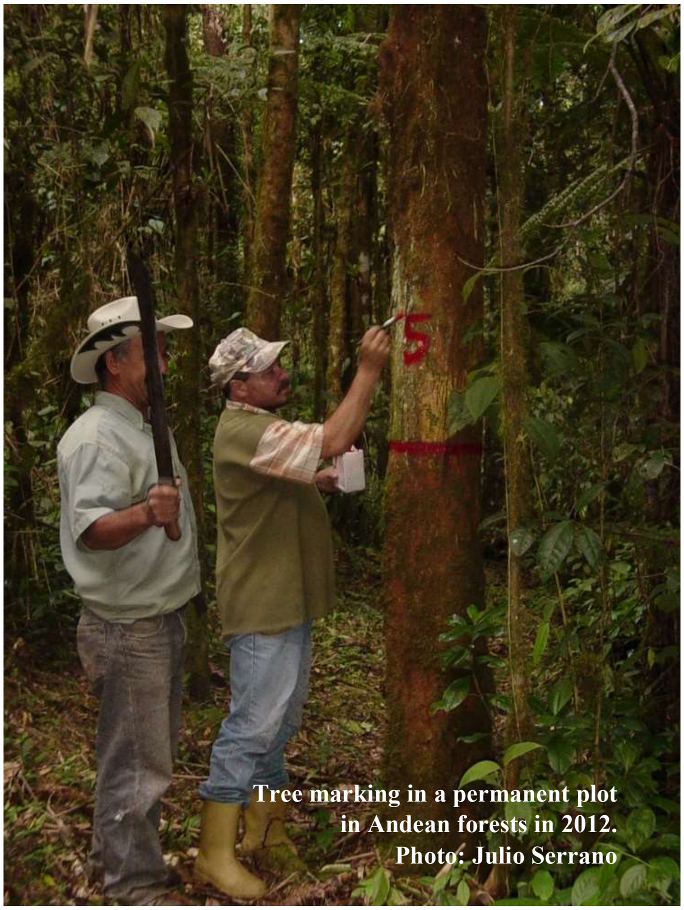


Figure S5. Relationships between turnover rates and aboveground biomass (A-C), and aboveground woody productivity (D-F). Red line indicates the mean of each turnover rate. Shaded line is the confidence interval of the linear fit between pairs of variables.

A permanent sample plot in French Guiana – Photo: Emilio Vilanova

Measuring a permanent plot in Venezuelan Western Plains in 2016. Photo: Luis Gamez.



Tree marking in a permanent plot in Andean forests in 2012. Photo: Julio Serrano

CHAPTER 3

A MULTIDECADAL ANALYSIS OF FOREST STRUCTURE AND STEM TURNOVER IN VENEZUELAN TROPICAL FORESTS: TRENDS AND POTENTIAL DRIVERS

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A MULTIDECADAL ANALYSIS OF FOREST STRUCTURE AND STEM TURNOVER IN VENEZUELAN TROPICAL FORESTS: TRENDS AND POTENTIAL DRIVERS

ABSTRACT

Have recruitment, mortality, stand dynamics, biomass and productivity of tropical forests in northern South America changed over recent decades? If so, are changes primarily driven by changes in climate and or stand-level development factors? To answer these questions, multi-census tree data from 44 permanent sample plots distributed across Venezuela were used to analyze temporal trends and associated changes in recruitment (*r*) and mortality (*m*) rates, aboveground woody productivity (AGWP) and net biomass change (Net_{AGB}). Generalized mixed models were used to differentiate between competition and climate or their interactions as potential drivers of forest dynamics. Venezuelan forests show increasing trends in AGB, AGWP, mortality and recruitment over the last 30 years. Thirty-two plots showed a positive slope in *m* over time (average slope 0.02 % year^{-1}, $p < 0.001$), and regardless of region, elevation, soil fertility or climate seasonality classes, the increase in tree mortality was highly significant ($p < 0.001$) in all cases. Recruitment also increased through time, where 21 plots had a positive slope in *r* (average slope 0.02 % year^{-1}, $p < 0.001$), and mostly occurred towards Andean forests while *r* declined for most lowland forest plots. A significant increase in the amount of biomass from dead trees (average AGB_{loss} slope = 0.02 Mg C ha^{-1} year^{-2}, $p < 0.001$) was also found combined with a modest but steady increase in AGWP (average AGWP slope = 0.02 Mg C ha^{-1} year^{-2}, $p < 0.001$). Although a decline in AGB change was found, the magnitude was not sufficient to significantly affect the forest carbon sink (average slope for net AGB change = - 0.003 Mg C ha^{-1} year^{-2}, $p < 0.117$). Increases in AGB through time were partially and positively associated with gap-level stand dynamics (Gap Phase Index - GPI) a measure of increasing size complexity. AGWP was also positively associated with gap dynamics and negatively associated with metrics of high stand density. Mean annual temperature (MAT) was the single best predictor of the increase in mortality rates, while changes in stand dynamics (high Stand Density Index or advancing structural complexity [GPI]) were also important in some regions. In contrast, recruitment rates were more

responsive to stand dynamics overall, but often interacting with climate. Increases in recruitment, AGB, and AGWP are more complicated, and are often driven by changes in stand-level forest dynamics. Advancing stand development through time is an important component explaining the observed trends and changes in biomass, productivity, and recruitment rates. While the effects of increasing temperatures on tree mortality is aligned with regional and global trends of massive tree die-off events in tropical and extra tropical regions, the results also suggest that natural stand dynamics in some of these long-term permanent plots is at least as important as changes in climate especially in explaining observed trends in recruitment, biomass, and productivity.

INTRODUCTION

Tropical forests worldwide are hotspots of biological diversity, store large amounts of atmospheric carbon and are pivotal resources in support of local and regional economies. Thus, biome-wide changes in these functions could have profound consequences for biogeochemical cycles and conservation of biodiversity, with potential societal repercussions at multiple scales (Lewis et al., 2015; Barlow et al., 2016).

Several studies over the last three decades show mature tropical forests have experienced changes in stand structure, species composition, and species interactions with disturbance forces and the environment. For instance, increasing trends in mortality and recruitment rates in Amazonian forests have been reported (Phillips & Gentry, 1994; Phillips et al., 2004; Laurance et al., 2009), with tree growth exceeding losses from tree death, thus increasing productivity and the overall aboveground biomass both in the Amazon (Phillips et al., 1998; Baker et al., 2004) and African forests (Lewis et al., 2009a). In some cases, associated changes in species composition in Amazonia were also found with an increase in the abundance and dominance of early successional species and lianas (Laurance et al., 2004; Phillips et al., 2002).

While similar changing patterns have not been found for other tropical sites in Costa Rica (Clark et al., 2017), Panama (Rutishauer et al., 2019) or Asia (Feeley et al., 2007a), the results of an apparent ‘changing ecology’ in mature tropical forests (*sensu* Lewis et al., 2009b) challenged the widely held assumption that in the absence of significant disturbances or major environmental changes, old-growth forests experience little or no long-term changes in their dynamics. Under these circumstances, most mature forest types would be characterized by highly predictable turnover rates with only large-scale disturbances being capable of modifying such dynamics, and with tree mortality somewhat balanced with the gains of new individuals (i.e. recruitment) in an apparent state of 'dynamic equilibrium' (Oliver & Larson, 1996; Swaine et al., 1987). Thus, the causes behind the observed alterations in stand dynamics have been hotly debated in the scientific literature and these findings proved to be contentious (Clark et al., 2003; Clark 2004; Fisher et al., 2008; Chambers et al., 2009; Lewis et al., 2009b; Lloyd et al., 2009; Rutishauser et al., 2019).

Analyzing the temporal trends in the dynamics of mature or old-growth forests is an intricate task and the interpretation of the potential causes behind the fluctuations that characterize long-term demographic processes in forest ecosystems has been diverse. Increased resource availability (i.e., increase in CO_2 levels and higher temperatures) has been argued as a possibility for increasing levels of dynamism (Lewis et al., 2009b; Phillips & Lewis, 2014). Yet, some forests might be responding to past natural or anthropogenic disturbances (Wright, 2005; Muller-Landau, 2009; McMichael et al., 2017), thus stand development and maturation processes (i.e. competition followed by gap-replacement dynamics) could also be driving these changes. In addition, methodological issues have been discussed as a potential driver of the observed patterns, which includes problems with field protocols, the possibility of advanced secondary forests being part of the analysis (Clark, 2002), or analytical artifacts used when quantifying turnover rates (Sheil, 1995; Kohyama et al., 2018).

While it is certainly possible that old-growth tropical forests can exhibit complex large-scale structures as a response to disturbance and recovery cycles, potentially driving these changing patterns in some areas (e.g. Chambers et al., 2013), simulations conducted for growth and mortality rates in the Amazon indicates that even when all carbon losses from intermediate and large-scale disturbances are considered, these are outweighed by the net biomass accumulation by tree growth, supporting the inference of an Amazon carbon sink in recent decades (Espírito-Santo et al., 2014; Brienen et al., 2015), Thus, from the perspective of natural disturbances, that is, events caused by normal environmental fluctuations or destructive events, tree-fall gaps are by far the most documented and frequent form of natural disturbance in tropical forests (Denslow

1987; Chazdon 2014) but with an apparent limited capacity to influence the large-scale changes observed (Espírito-Santo et al., 2014). In fact, stand-replacing disturbances are rare in tropical forests with return intervals than can range between 850 to more than 1000 years (Pugh et al., 2019). Similarly, ancient populations might have altered the structure and composition in some areas in tropical forests via the cultivation and/or domestication of a group of important species, so that the current structure or the abundance of certain species in some areas could be a reflection of this (e.g. Levis et al., 2017; Palace et al., 2017). Yet, other studies suggest that prehistoric human modification of Amazonian forests and creation of species hyperdominance (*sensu* ter Steege et al., 2013) might be localized and less influential in shaping today's tropical forests structure and dynamics (Bush et al., 2015; Piperno et al., 2019).

The potential effects of sampling biases during field work in many of these sites were addressed early in the debate (see for example Phillips et al., 2002). In this regard, standardized protocols have been applied and significant improvements have been made in the overall process of data collection and curation in the last decade when analyzing permanent plot data, the main source for this type of research (Peacock et al., 2007; Lopez-Gonzalez et al., 2011). Furthermore, after improvements were made to the allometric models being used to estimate the aboveground biomass in tropical forests (e.g. Chave et al., 2005; Chave et al., 2014), and correction methods have been developed and applied when estimating turnover rates (Lewis et al., 2004a) and productivity (Talbot et al., 2014), recent analyses suggest that these trends are unlikely to be caused by artefactual explanations of forests recovering from disturbances or selection of mature forest patches, and mature Amazonian forests have been functioning as a net carbon sink over the last three decades (Brienen et al., 2015).

Outside the tropics, other studies have been reporting similar findings. For instance, after accounting for stand age, disturbance history and natural stand dynamics, Mcmahon et al. (2010) and more recently Hember et al. (2019) reported an accelerated growth for multiple-censused plots in boreal forests, arguing for a clear climatic effect that might have also influenced an increase in the aboveground biomass change and mortality rates in this biome (e.g. Luo & Chen 2015; Searle & Chen 2018; Luo et al., 2019). The rise in temperature and extended growing seasons seemed to have contributed to an acceleration of tree growth since 1870 in forests of Central Europe

(Pretzsch et al., 2014), and significant increasing rates of tree mortality of old-growth forests in western US were also found by van Mantgem et al. (2009), likely due to a decline in long-term water availability and/or induced droughts.

Because of the stochastic nature of forest dynamics, discriminating between competition and gap-phase regeneration and subsequent stand development and climate – and their interactions - as drivers of forest demography and structure over long periods of time and environmental gradients is a complex task which has become a subject of research both inside and outside the tropics (e.g. Brienen et al., 2015; Pillet et al., 2017; Price et al., 2015; Zhang et al., 2015; McDowell et al., 2018; Rutishauer et al., 2019). Warming trends in the last three to four decades, particularly in the Amazon region (Malhi & Wright 2004; Marengo et al., 2018), with an associated increased frequency in major drought events (Feldpausch et al., 2016), seemed to have weakened the carbon sink due to the increase in the biomass from mortality (Brienen et al., 2015), and these trends have been accompanied by a slow shift to more dry-affiliated tree species, with changes in compositional dynamics (i.e. recruits and mortality) consistent with climate-change drivers (Esquivel-Muelbert et al., 2019). Between 1991 and 2011, using multi-census tree data in the Guiana Shield, Aubry-Kientz et al., (2015) found that while drought decreased annual growth and mortality rates, high precipitation increased mortality rates and high temperature decreased growth. However, models that simultaneously combined competition and climate factors to distinguish drivers of tree mortality in lowland forests of the Guiana Shield were much more informative than those that were based on each factor individually (Pillet et al., 2017), suggesting the need for a better understanding of climate and stand development interactions. For example, in boreal forests of Western Canada, competition was shown to be a much more important factor compared to climate in causing decadal changes in forest dynamics with higher rates of tree mortality but declining recruitment rates between 1959 and 2009 (Zhang et al., 2015). However, the interpretation of these results has been contentious with some arguments favoring climate change as the primary force driving the increasingly levels of competition (Price et al., 2015, but see He et al., 2015).

The main objective of this study was to describe the temporal trends in stem turnover rates, aboveground woody productivity and net biomass change over several decades for a group of 44 permanent forest plots located in different forest-types in Venezuela in northern South America. While a selected group of the lowland plots that was part of the study of Brienen et al., (2015) was used, other equally important forest-types, particularly the montane forests of the Andes were included here. These areas have been monitored for at least five decades (Vilanova et al., 2018; Supporting Information) and have received much less attention than their lowland counterparts. The goal was to produce an updated and synthetized picture of the temporal trends and potential drivers of the dynamics of Venezuelan forests in northern South America over the last four decades. Specifically, the following questions were asked in this study:

- What are the temporal trends in climate (i.e. mean annual temperature, precipitation, evapotranspiration, climatic water deficit) across different forest-types in Venezuela over the last 100 years?
- Is there a significant change in turnover rates (i.e. recruitment and mortality) for different forest-types in Venezuela in the last four decades?
- Are the trends in woody productivity and net biomass change for different forest-types in Venezuela consistent with the evidence of a recent weakening in the carbon sink of lowland forests in Amazonia (c.f. Brienen et al., 2015)?
- What are the potential drivers of forest dynamics between competition, gap-phase dynamics, and climate factors?

METHODS

STUDY SITES

Long-term data from 44 plots in five distinct regions from a country-wide network of permanent sample plots distributed across Venezuela was used (Figure S1). The history and characteristics of these plots are extensively described in previous work (Veillon 1985; Vilanova et al., 2018; Chapters 1 and 2 of this dissertation). Data on approximately 20,000 continuously monitored individuals larger than 10 cm in diameter from 570 identified species were selected from the forestplot.net database (Lopez-Gonzalez et al., 2011) where information has been curated and stored for analysis since 2009. Average plot size is 0.35 ha (Min = 0.25 ha; Max = 1 ha), with a census period ranging from 2 to a maximum of 55 years. First censuses were conducted between 1960 and 2001 (mean year of first census = 1972.5 ± 10.3 Standard Deviation), and final plot censuses between 1972 and 2016 (mean year of last census = 2001.9 ± 16.1). On average, plots were resampled almost 20 times (min = 3 censuses; max = 41 censuses), with an average monitoring period of 29.5 years (min = 2.0 years; max = 54.8 years). Plots were classified into five different regions defined by geographical location, major environmental conditions, and the nature and geological age of the soil substrate as: a) Andes Low-Mid Elevation (≤ 1.500 meters above sea level - masl) (n = 6 plots); c) Andes High Elevation (> 1500 masl) (n = 14); d) Guiana Shield (n = 10); e) Coastal Dry Forests (n = 3); f) Western Plains (n = 11). Also, to explore the observed trends in all response variables, and as in Vilanova et al., (2018) and Chapter 2, I classified the dataset in different subgroups of plots based on: a) total number of months with precipitation lower than 100 mm as: Aseasonal (0-1 dry months); Moderately seasonal (2-3); Highly seasonal (> 3 dry months); b) Soil fertility: from general soil profile descriptions two major soil fertility groups were formed (i.e. Low; High); c) Elevation: using a cut-off of 1500 meters two groups were formed (Low elevation plots < 1500 masl; high elevation plots > 1500 masl). Additional details of the plots and their environmental characteristics are included in the supplementary information.

CLIMATE DATA

Based on the geographical location of each site, plot-based climate data was extracted from the updated high-resolution grids (CRU TS3.10) of monthly climatic observations from the Climate Research Unit (CRU) at University of East Anglia (Harris et al., 2014). In order to assess how climate has changed in the past, trends in climate for these plots and regions were analyzed in which information on mean annual temperature (MAT), precipitation (MAP) and potential evapotranspiration (PET) was converted to annual estimates for the entire period covered by the CRU dataset (1901-2017). The approach detailed in Esquivel-Muelbert et al., (2019) for the calculation of the plot-based temporal trends in the maximum cumulative water deficit (MCWD - Aragão et al., 2007) was used as a measure of the change in moisture stress that represents the most negative value of cumulative water deficit (wd), i.e., the difference between precipitation (P) and evapotranspiration (E) within each year (Esquivel-Muelbert et al., 2019). Once trends were analyzed, climate data was superimposed with the specific periods where plots were measured to adequately assess the potential link between climate and forest dynamics.

TREE INVENTORY DATA

Since the establishment of each plot, data collection involved the measurement of all live individuals from all species with diameter (D) $\geq$ 10 cm at 1.3 m height when possible. Standardized protocols have been continuously employed for non-cylindrical stems in which case the point of measurement has been raised above the point where stems were more or less cylindrical, approximately 50 cm above the end of the buttress or deformity. The exact height of the point of measurement (POM) has been recorded and marked on each individual to ensure that subsequent measurements are taken at the same point along the stem. In each census, protocols included accounting for all individuals that were recruited and died during the interval including an assessment of possible causes of death. Additional details about data collection and field protocols can be found elsewhere (Brienen et al., 2015; Phillips et al., 2016; Vilanova et al., 2018 and Chapters 1 and 2).

ESTIMATION OF TURNOVER RATES, ABOVEGROUND BIOMASS AND PRODUCTIVITY

Demographic rates of recruitment and mortality were calculated for each plot based on the instantaneous rates approach (% year^{-1}) using the equations reported in several studies (Phillips et al., 2004; Báez et al., 2015; Johnson et al., 2016; Vilanova et al., 2018) and detailed in Chapter 2 of this dissertation and in Appendix S2 of this chapter. Since demographic rates for heterogeneous populations are likely to be influenced by the length of census interval (Sheil 1995; Phillips et al., 2004; Kohyama et al., 2018), these estimates were standardized to equivalent census intervals using the equation of Lewis et al., (2004a): $\lambda_{corr} = \lambda \text{ x } t^{0.0759}$, where λ_{corr} is the rate standardized to a 1-year census interval; λ is the uncorrected demographic rate; t is the length of census interval, and 0.0759 is a constant. Corrected values of recruitment and mortality for each census interval and for each plot in the data set were later calculated weighted by the census interval length in all cases.

Diameter measurements from each individual were transformed into aboveground biomass (AGB) estimates using the widely known moist tropical-based allometric equation from Chave et al., (2005) that includes data on wood density (WD) and tree height. WD information was extracted from the Global Wood Density Database described in Zanne et al., (2009). Specifically, 34.64 % of the WD data was at the species level, 40.01% at the genus level, and 12.49 % at the family level. When this information was unknown, the average value from the plot (12.85 % of the cases) was used in the equation. Total height was estimated from pantropical diameter-height relationships described in Feldpausch et al., (2012). Assuming carbon to be 50% of total dry biomass, the final purpose was to obtain plot-level estimates of aboveground carbon (i.e. Mg C ha^{-1}) for every interval where each plot was measured. Additional details are offered in Appendix S2 and in Vilanova et al., (2018).

For each census interval, rates of above-ground wood productivity (AGWP) (Mg C ha^{-1} year^{-1}) were estimated as the sum of AGB gains of surviving and recruiting trees. Mortality rates were also expressed in terms of carbon estimates as the summed AGB of trees dying over each interval (AGB$_{\text{loss}}$). AGWP and AGB$_{\text{loss}}$ were corrected for variations in census intervals using the empirical procedure proposed in Talbot et al., (2014) also developed for multiple-census plots in tropical forests:

$$\mathrm{AGWP}_{\mathrm{corr}} = \mathrm{AGWP}_{\mathrm{obs}} \text{ x } 0.0091 \ \mathrm{AGWP}_{\mathrm{obs}} \text{ x } t$$

Where AGWP$_{\text{obs}}$ is the uncorrected value of woody productivity, and *t* is the length of census interval. Finally, to compute comparable estimates of AGWP, corrected values of every AGB component (AGB$_{\text{gains}}$, AGB$_{\text{rec}}$, AGB$_{\text{mort}}$) were calculated for each census interval per plot weighted by census interval length.

STATISTICAL ANALYSIS AND HYPOTHESES

TEMPORAL TRENDS IN CLIMATE

Given the current and projected warming trends in the Amazon region (e.g. Marengo et al., 2018) and in most parts of the tropical Andes (Urrutia & Vuille 2009), including an intensification of changes in climate and climate variability in the tropics (Duffy et al., 2015) with more frequent and severe drought events in the last few decades (Phillips et al., 2009; Feldpauschet al., 2016), a widespread increase in annual temperatures in all regions was expected, with associated declines in precipitation. Hence, an increase in the water deficit expressed both in higher evapotranspiration and *via* more negative values of the MCWD were also expected. Since seasonal dry forests are already limited by water, in some cases close to climatic thresholds, these regions are likely to be more sensitive to drought events (Allen et al., 2017). Thus, seasonal forests in the Western Plains were predicted to be more sensitive showing a stronger signal of changes in climate, followed by the Coastal Dry Forests region in Eastern Venezuela and the Andean forests. The analysis of the plot and region-based trends in temperature (MAT), precipitation (MAP), evapotranspiration (PET) and maximum climatic water deficit (MCWD) was conducted for the 1901-2017 period using simple linear models to test for significant changes in the slope through time.

TEMPORAL TRENDS IN TURNOVER RATES AND BIOMASS COMPONENTS

Based on previous evidences, a widespread increase in turnover rates (i.e. recruitment and mortality) in all regions was originally expected, with a potential decline in aboveground woody productivity (AGWP), an increase in the biomass from mortality (AGB_{mort}), thus a negative trend in the net biomass change (Net_{AGB}). From a previous analysis of these variables (c.f. Chapter 2; Vilanova et al., 2018) we know now that significant differences between regions exist with seasonal forests in the Western Plains having faster turnover (i.e. higher recruitment and mortality), while higher levels of AGWP were found in the Guiana Shield. Thus, with the associated changes in climate predicted for the Western Plains, I also expected that increasing trends in turnover should be more evident in plots located in these conditions. An additional prediction is that Andean forests may have experienced a similar process of change in turnover rates affecting the carbon absorption as in the lowland forests in other parts of the Amazon (Brienen et al., 2015), potentially with declining rates of net biomass change.

All estimated rates (i.e. recruitment, mortality, AGWP, Net_{AGB}) were regressed against the midpoint year of each census interval with 95% confidence intervals calculated for each point. Aiming at standardizing our estimations, short intervals (< 1 year) were collapsed together where possible to analyze the temporal trends of each variable over periods between 3 to 5 years. The combination of multiple sites with different census intervals may cause a calendar year signal confounding within-site change with among-site changes, so aggregated results could be influenced by biases that could arise through unequal sampling of forest types across time (‘site-switching’ effect) (Phillips et al., 2004; Brienen et al., 2015). Thus, the classification of plots by regions, seasonality, soil fertility, and elevation described earlier was used here to evaluate the consistency of the temporal trends for all variables. Moreover, since most plots within regions were surveyed almost simultaneously (Figure S3), I believe this to be an accurate approach to deal with the potential effect of site-switching, but temporal trends for each individual plot were also considered.

Two statistical approaches were used to analyze the observed temporal trends of recruitment, mortality, AGWP, AGB_{mort}, and Net_{AGB}. First, using every plot-interval, and then classified by region and other subgroups of plots (i.e. seasonality, elevation, soil fertility), a simple *Response vs. time* regression was applied using general additive mixed models (GAMM) from the version 1.16 of the 'gam' R package (Hastie & Tibshirani 1986; Hastie 2018), with plots as a random effect, with the goal of testing for a significant slope trend in the models. A second method involved using linear models to test for a significant slope change in the temporal trends for each individual plot and for each response variable and quantify the distribution of these values.

POTENTIAL DRIVERS OF FOREST DYNAMICS

To address the question of discriminating between endogenous (i.e. competition and stand development dynamics) and exogenous (i.e. climate) drivers of turnover rates and biomass change in our plots, I followed two main approaches. First, the relative change (% $year^{-1}$) in the aboveground biomass (AGB) for each plot, that is, the difference between the estimated AGB of the last minus the first census divided by the total monitoring period of each plot, was regressed against the relative change of a modified version of the Gap Phase Index (GPI) proposed by Feeley et al., (2007b). The objective was to explicitly account for the contribution of gap phase processes when quantifying rates of change in AGB. The GPI is calculated as the logged ratio of basal area from large versus small stems and provides a measure of stem size complexity. As mentioned earlier, no information from trees < 10 cm in diameter as in the original GPI formula was available, thus the GPI was calculated as follows:

$$GPI = \ln (BA_{>400} + 1) - \ln (BA_{100\text{-}200} + 1)$$

where $BA_{>400}$ is the total basal area of all trees with diameter ≥ 400 millimeters (mm; 40 cm); $BA_{100\text{-}200}$ is the total basal area of all stems with diameter ≥ 100 mm and < 200 mm (10-20 cm). The size cut-off was chosen to make a clear distinction between canopy and understory stems but the index has been shown to be robust to choices of size categories (Feeley et al., 2007b). To facilitate comparisons between plots while accounting for the inherent differences in the forest structure between plots and regions, GPI was standardized based on the maximum value of the entire dataset, such that it is on a scale of 0–1, with 1 representing the greatest structural variation or most mature conditions. To analyze if the changes in biomass were independent of gap-phase dynamics, a reduced major axis regression method (RMA, type II) was used between the changes in AGB and the changes in GPI with confidence intervals estimated through bootstrapping (5000 resamples). This type of model accounts for the uncertainty in both explanatory and response variables by minimizing the errors in both directions (Smith 2009). The hypothesis being tested is that if biomass is changing independently from changes in GPI, then the intercept of the relationship is predicted to differ significantly from zero (Feeley et al., 2007b), thus additional factors would be driving the changes in AGB. Here, the 1.7.3 version of the 'lmodel2' package in R was used (Legendre 2018).

Next to further examine the potential drivers of the temporal trends in turnover rates and AGWP, predictors were classified in two major categories. First, to test for endogenous drivers (i.e. competition and stand development), in addition to using the temporal trends in the Gap Phase Index (GPI) explained above, two additional variables widely used for the analysis of stand-level competition and development were used: Quadratic Mean diameter (QMD) and the Stand Density Index (SDI) (Oliver & Larson 1996). QMD is the diameter of a tree of average basal area that compared to the arithmetic mean assigns greater weight to larger trees and has the practical advantage of being directly related to basal area, and thus to biomass (Brown et al., 1989; Curtis & Marshall 2000). The SDI, originally proposed for even-aged stands (Reineke 1933), though rarely applied in tropical forest ecology, has been increasingly used for mixed-species and uneven-aged stands (e.g. Ducey & Knapp 2010; Zhang et al., 2015) is based on the relationship between the number of trees per unit area and the QMD, and provides information on the degree of crowding and likelihood of self-thinning processes when trees compete for increasingly scarce water, nutrient and light resources during stand maturation (Ducey & Knapp 2010; Zhang et al., 2015). Combined, these variables were expected to be reasonably good predictors of the degree of competition-driven dynamics through time among all the plots. Equations used for QMD and SDI are included in Appendix S2. On the other hand, a climate-based group of drivers was based on the CRU data described earlier and included temporal trends in MAT, MAP, PET and MCWD. For both competition and climate factors, the data was aligned as close as possible across all years within each census interval for a given plot.

Once the temporal dataset was assembled, the statistical approach employed consisted on using generalized mixed models (GLMMs) that allows for fitting different statistical distributions to the data without the need of applying a specific transformation (Zuur et al., 2009). The temporal data for all response variables followed a non-normal distribution, so the '*descdist*' function from the 'fitdistrplus' package (Delignette-Muller et al., 2019) was used to find the most accurate distribution in each case (Appendix S3). The '*glmer*' function in the 1.1-21 version of the 'lme4' R package (Bates et al., 2019) was used for this analysis.

To better select the appropriate number of predictors and minimize multicollinearity, pair-wised Pearson correlations among all variables were analyzed (Appendix S4). There was a high degree of correlation among some of the selected climate variables (e.g. PET and MAT; PET and MWCD). Thus, some variables were not included in the final models. Five modeling approaches were tested for each response variable, first including a full additive model with all predictors included, followed by a complete climate vs. competition interaction model, to later test for competition and climate factors separately. A final model that included only those predictors that had significant values ($p < 0.05$) from the four previous approaches was also tested. The models tested were of the form:

A) Full additive model:

$$Y \sim \beta_0 + \beta_1 t_j + \beta_2 GPI_j + \beta_3 SDI_j + \beta_4 QMD_j + \beta_5 MAT_j + \beta_6 MAP_j + \beta_7 MCWD_j + \gamma_i$$

B) Full Interaction model:

$$Y \sim \beta_0 + \beta_1 t_j + \beta_2 GPI_j + \beta_3 SDI_j + \beta_4 QMD_j + \beta_5 MAT_j + \beta_6 MAP_j + \beta_7 MCWD_j + \\ \beta_8 GPI_j * \beta_9 MAT_j + \beta_{10} GPI_j * \beta_{11} MAP_j + \beta_{12} GPI_j * \beta_{13} MCWD_j + \\ \beta_{14} SDI_j * \beta_{15} MAT_j + \beta_{16} SDI_j * \beta_{17} MAP_j + \beta_{18} SDI_j * \beta_{19} MCWD_j + \\ \beta_{20} QMD_j * \beta_{21} MAT_j + \beta_{22} QMD_j * \beta_{23} MAP_j + \beta_{24} QMD_j * \beta_{25} MCWD_j + \gamma_i$$

C) Climate model:

$$Y \sim \beta_0 + \beta_1 t_j + \beta_5 MAT_j + \beta_6 MAP_j + \beta_7 MCWD_j + \gamma_i$$

D) Competition model:

$$Y \sim \beta_0 + \beta_1 t_j + \beta_2 GPI_j + \beta_3 SDI_j + \beta_4 QMD_j + \gamma_i$$

Where:
Y: Response variables (recruitment, mortality, AGWP);
β_n: standardized coefficients of the predictors;
t_j: mid-year of the *j*th census interval for each plot;
GPI_j: Plot-level Gap Phase Index estimated at the *j*th census interval;
SDI_j: Plot-level Stand Density Index estimated at the *j*th census interval;
QMD_j: Plot-level Quadratic Mean Diameter estimated at the *j*th census interval;
MAT_j: Plot-level Mean annual temperature during the *j*th census interval;
MAP_j: Plot-level Mean annual precipitation during the *j*th census interval;
$MCWD_j$: Plot-level Maximum Climatic Water Deficit estimated at the *j*th census interval;
γ_i: Random effect for plots.

The standardized (β) coefficients in each model were calculated to test for significant effects that predictors could have on each response variable. From the complete list of competing models, the 'best' model was selected based on the ranking of the values from the corrected version of the Akaike information criterion (AICc) (Johnson & Omland 2004). Considering the contrasting environmental conditions that explain structure and dynamics in these forests (c.f. Vilanova et al., 2018), different regional dynamics and responses were expected. Thus, these modeling approaches were not only tested initially for all plots and intervals combined but the models were also tested for each of the five regions separately (Supporting information). Finally, among all the models tested, both with all plots combined and by region, the percentage of cases in which each of the variables and their interactions was positively significant, negatively significant, or nonsignificant related to the responses was calculated.

RESULTS

TEMPORAL TRENDS IN CLIMATE

During the 1901-2017 period covered by the CRU dataset, increasing trends in mean annual temperature (MAT) and potential evapotranspiration (PET) were ubiquitous with positive and significant slopes for all plots. Plot-level slopes for Mean Annual Precipitation (MAP) shows a slight decline overall, however for three plots (CRZ-01 in the low-mid elevation region of the Andes; SCR-04 and SCR-05 in the southern portion of the Guiana Shield region) MAP appeared to have increased (Figure 1). Trends in maximum climatic water deficit (MCWD) were almost evenly distributed among the dataset, 26 plots had negative slopes, and 18 plots had positive slopes. Negative slopes in this case signal a strengthening of the dry season (Figure 1). When plots were grouped by region, the increase in MAT was highly significant in all cases. MAP declined in every region except for the Guiana Shield, and the slope was only significant in the case of the seasonal forests of the Western Plains. PET increased in all regions but not significantly for both Andean subregions. The observed increase in the negative values of the MCWD was found for all regions but was significant ($p<0.05$) only in the Guiana Shield (Appendix S4).

TRENDS IN TURNOVER RATES AND BIOMASS COMPONENTS

The overall recruitment (r) and mortality (m) rates both showed significantly increasing trends and averaged similar slopes through time (Figure 2). When results were plotted for individual sites, turnover rates vary substantially from site-to-site and interval-to interval (Appendix S5, Figure S5). An examination of the distribution of recruitment and mortality rates (bin counts of sites with rates) shows that these are skewed slightly positively, especially for mortality. Thirty-two of forty-four plots showed a positive slope of m over time (average slope 0.02 % year^{-1}, $p < 0.001$), and 21 of 44 plots also had a positive slope in r (average slope 0.02 % year^{-1}, $p < 0.001$) while in 32 plots recruitment appeared to have declined (Figure 2). In this analysis CRZ-01 plot was excluded due to lack of more than one census interval.

Regionally, recruitment and mortality slopes were higher in the western portion of the country which includes the Andean and Western Plains plots reflecting the overall differences in their average values (West plots: $r = 1.63 \pm 0.28$ % year^{-1} – 95% CI; $m = 1.58 \pm 0.27$ % year^{-1}; East plots: $r = 1.36 \pm 0.31$ % year^{-1}; $m = 1.32 \pm 0.29$ % year^{-1}) (Appendix S5). Recruitment rates significantly increased in both Andean sub-regions and Western Plains, while declined in the rest. Positive and significant slopes in mortality and recruitment were also found for the group of high elevation plots (> 1500 meters). At lower elevations, however, recruitment declined significantly through time, and within the seasonality subgroups, only in the non-seasonal plots (i.e. 0-1 dry months) recruitment declined through time. When plots were classified into two soil fertility groups, recruitment increased in both high and low fertility but with the latter having a non-significant slope ($p > 0.05$) (Appendix S5, Table S2).

Regardless of region, elevation or soil fertility, mortality rates have increased substantially and significantly ($p < 0.001$) across all sites. While similar results were found when plots were filtered by seasonality, only the small group of non-seasonal forests showed a positive, yet non-significant trend in mortality rates. An important finding is that the increase in mortality rates seems to be more evident in the second half of the temporal timeframe in most plots (Appendix S5, Figure S5).

Analyzed together, all plots showed a modest but steady increase in AGWP (average AGWP slope = 0.02 Mg C ha^{-1} year^{-2}, $p < 0.001$), and a small but significant increase in the amount of biomass from dead trees (average AGB_{loss} slope = 0.02 Mg C ha^{-1} year^{-2}, $p < 0.001$), which seems to affect, although not significantly, the net biomass change (average slope for Net_{AGB} = - 0.003 Mg C ha^{-1} year^{-2}, $p = 0.117$) (Figure 3). When analyzed regionally, AGB loss from mortality significantly increased across all regions with an associated decline in the net AGB change in all cases. This decline occurs simultaneously with a strong long-term increase in mortality rates and associated AGB_{loss} that occurred despite a long-term increase in productivity in two of the regions. AGWP declined in the Low-Mid elevation region of the Andes, the Guiana Shield and in the Coastal dry forests as well, while remained relatively stable or increased for the high elevation forests in the Andes and the Western Plains respectively (Appendix S6, Figure S6). AGB loss increased in both high and low elevation groups with a mean slope in both cases of 0.02 Mg C ha^{-1} year^{-2} ($p < 0.001$). Net AGB change significantly declined for both elevational groups (mean slope = - 0.02 Mg C ha^{-1} year^{-2}, $p < 0.001$). AGWP declined at lower elevations (mean slope = - 0.002 Mg C ha^{-1} year^{-2}, $p < 0.05$) while increased, tough not significantly, at higher elevations (mean slope = 0.002 Mg C ha^{-1} year^{-2}, $p = 0.11$).

Analyzed for forest seasonality, non-seasonal plots showed AGB$_{\text{loss}}$ significantly increased (mean slope = 0.03 Mg C ha^{-1} year^{-2}, $p < 0.001$), with an associated decline in net AGB change (mean slope = - 0.05 Mg C ha^{-1} year^{-2}, $p < 0.001$) and AGWP (- 0.02 Mg C ha^{-1} year^{-2}, $p < 0.001$). Moderately seasonal plots experienced similar trends in all variables (AGB$_{\text{loss}}$ mean slope = 0.06 Mg C ha^{-1} year^{-2}, $p < 0.001$; AGWP = 0.001 Mg C ha^{-1} year^{-2}, $p = 0.62$; Net AGB change = - 0.06 Mg C ha^{-1} year^{-2}, $p < 0.001$). While AGB$_{\text{loss}}$ increased (0.02 Mg C ha^{-1} year^{-2}, $p < 0.001$) and the net change in AGB declined (-0.01 Mg C ha^{-1} year^{-2}, $p < 0.001$) in highly seasonal plots, for AGWP the trend was a significant and positive one (0.01 Mg C ha^{-1} year^{-2}, $p < 0.001$).

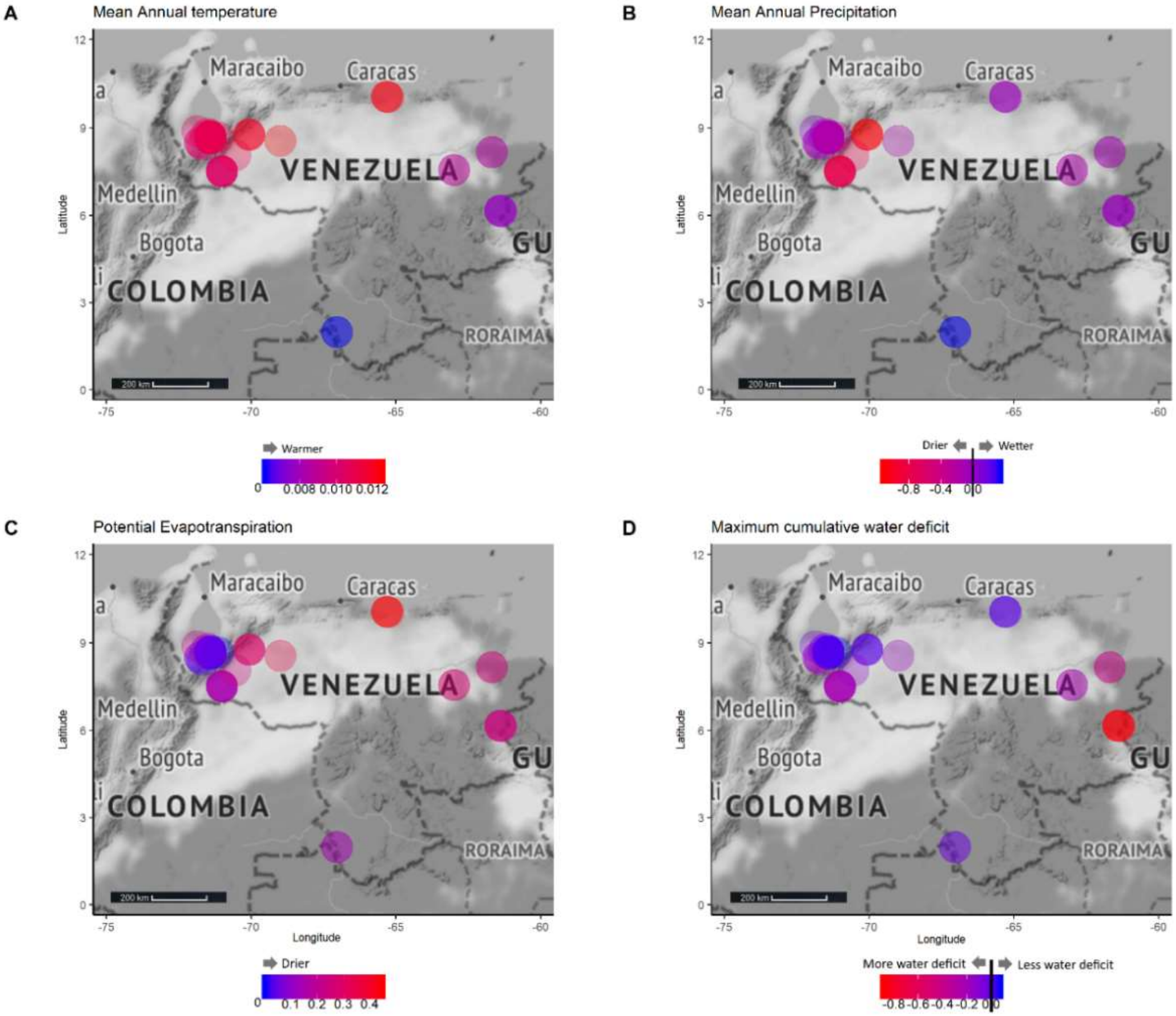


Figure 1. Trends in A) mean annual temperature (MAT) expressed in °C year^{-1}, B) Mean annual precipitation (MAP; mm year^{-1}), C) Potential evapotranspiration (PET; mm year^{-1}), and D) maximum cumulative water deficit (MCWD) across 44 forest plots in Venezuela between 1901 and 2017. The values indicate the slopes obtained from linear models for each variable. Values for MAT and PET are all positive indicating an increase for these parameters through time with the slopes being all significant on a plot-level ($p < 0.05$). Values in MAP includes some sites towards the positive side indicating an increase in precipitation through time. Warmer (i.e., positive slopes in MAP), and drier (i.e., positive slope in PET) trends are reflected in the negative slopes found for MCWD, signaling a strengthening of the water deficit for the 1901-2017 period. Temporal trends for each region are shown in Appendix S4.

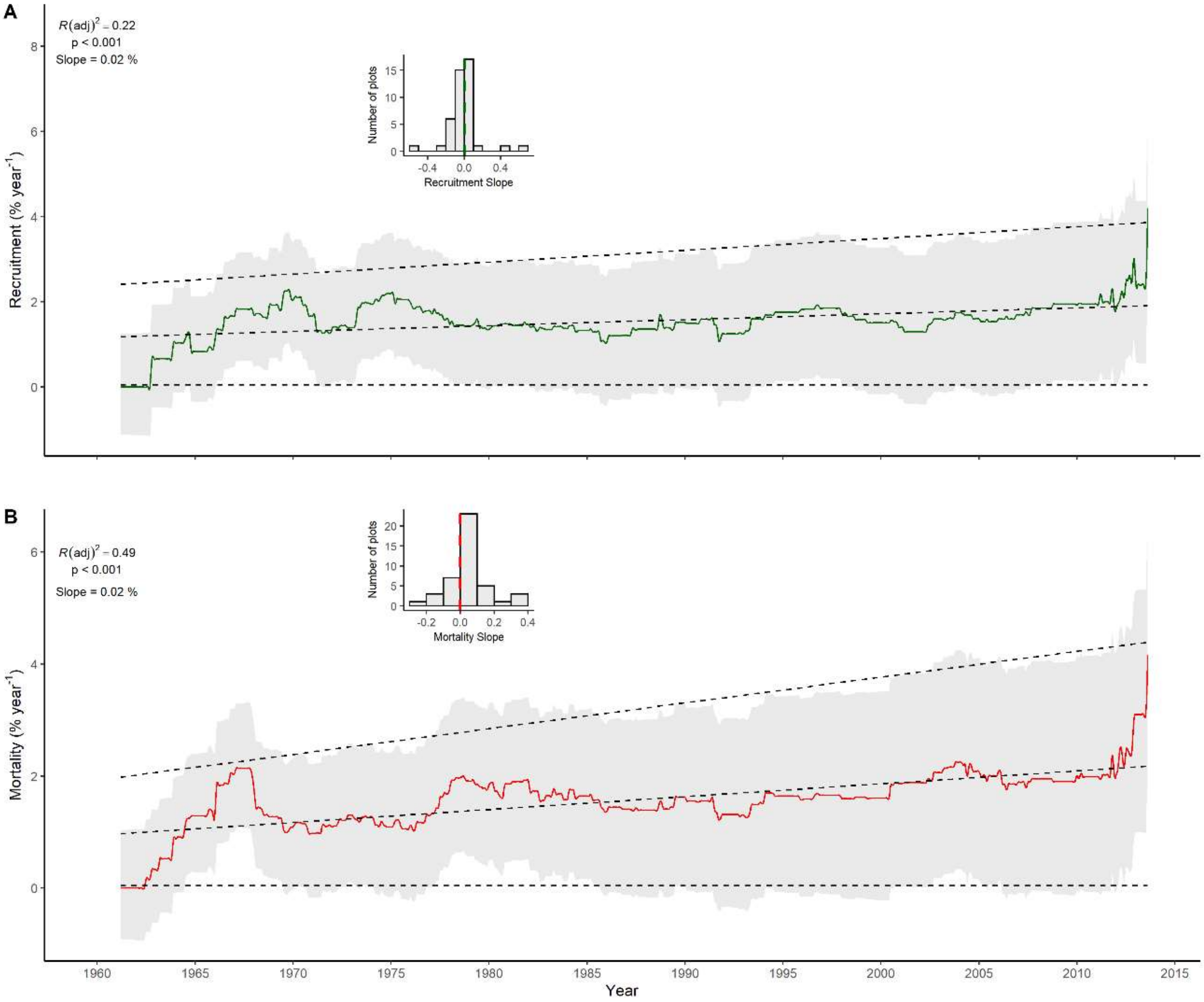


Figure 2. Temporal trends in a) recruitment and b) mortality rates for 44 forest plots in Venezuela. Solid lines represent the observed rates while the gray shaded area indicates the 95% confidence intervals (CI). Dashed lines are the trends from general additive models (GAMs) for the observed values and both the lower and upper 95% CI limits. Insets in each panel show the frequency distribution of the slopes, with the mean slope and *p*-value for a t-test of difference from no slope change. Trends for each individual plot are shown in Appendix S5 (Figure S5).

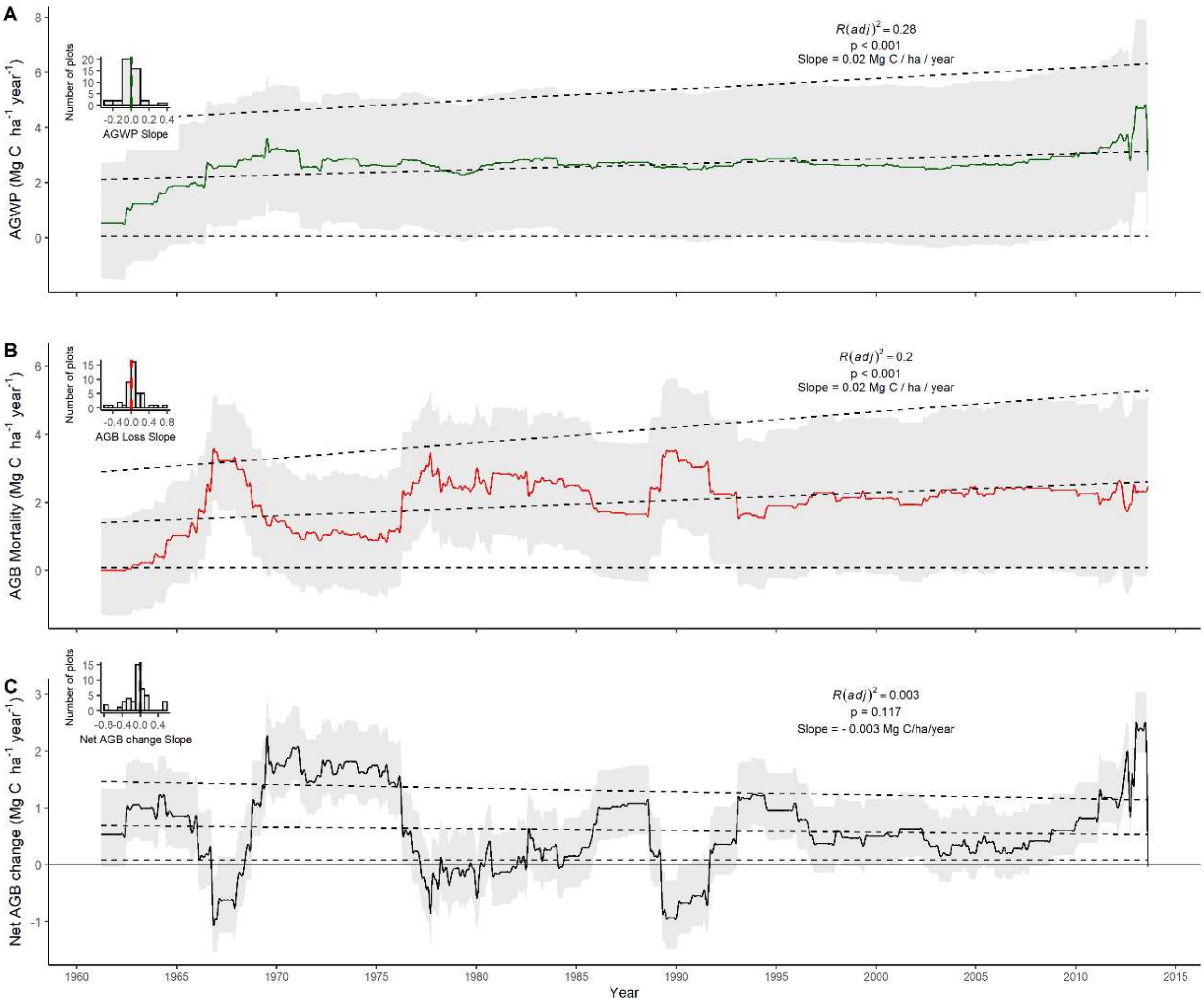


Figure 3. Temporal trends in a) AGWP, b) AGB loss from mortality, and c) Net AGB change for 44 forest plots in Venezuela. Solid lines represent the observed rates while the gray shaded area indicates the 95% confidence intervals. Dashed lines are the trends from general additive models (GAMs) for the observed values and both the lower and upper 95% limits. Insets in each panel show the frequency distribution of the slopes, with the mean slope and *p*-value for a t-test of difference from no slope change. Trends for each individual plot are shown in Appendix S6 (Figure S7).

POTENTIAL DRIVERS OF FOREST DYNAMICS

RELATIVE CHANGES IN ABOVEGROUND BIOMASS (AGB) AND GAP PHASE INDEX (GPI)

On average, Venezuelan forest plots had a positive net change in AGB of 0.71 ± 0.24 Mg C ha^{-1} y^{-1}, with 80% of the plots gaining biomass through time (mean relative change in AGB = 0.39 % year^{-1}). For only two of the eight plots where AGB declined from the first to last census, a negative change greater than -1% per year was found. For the group of plots where total AGB changed negatively, five plots are in the high elevation forests in the Andes and three in the Guiana Shield (Figure 4). Sixty-three percent (63%) of all plots increased in their 'matureness' or size complexity (i.e., increasing GPI) with positive values in the relative change of the Gap Phase Index (mean relative change in GPI = 0.29 % year^{-1}). GPI and the quadratic mean diameter (QMD) significantly increased in all the regions except for the high elevation forests in the Andes that had a sharp declining slope in both variables (Appendix S8). Overall, in all the plots where AGB declined through time, GPI also declined. In addition, a second group of plots, all from the Andean region, experienced a decline in GPI but gained biomass from the first to the last census. The stand density index (SDI) significantly increased for all regions except in the high elevation sites in the Andes where it remained relatively stable through time, while at lower elevations in the Andes SDI declined significantly (Appendix S7).

The intercept of the RMA regression between the change in GPI and AGB was significantly positive (intercept = 0.28, $p < 0.001$), indicating that there was an increase in biomass beyond what could be attributed to changes in GPI (Figure 4). Indeed, while the relative change in AGB was overall positive, no relationship with changes in the mean plot levels of number of individuals, wood density, AGB_{growth}, and recruitment rates was found. Mortality rates increased for most plots (average relative change in m = 4.85 % year^{-1}), while a great proportion of the plots simultaneously gained biomass with an associated increase in the average tree size (average relative change in QMD = 5.03 % year^{-1}) (Appendix S8).

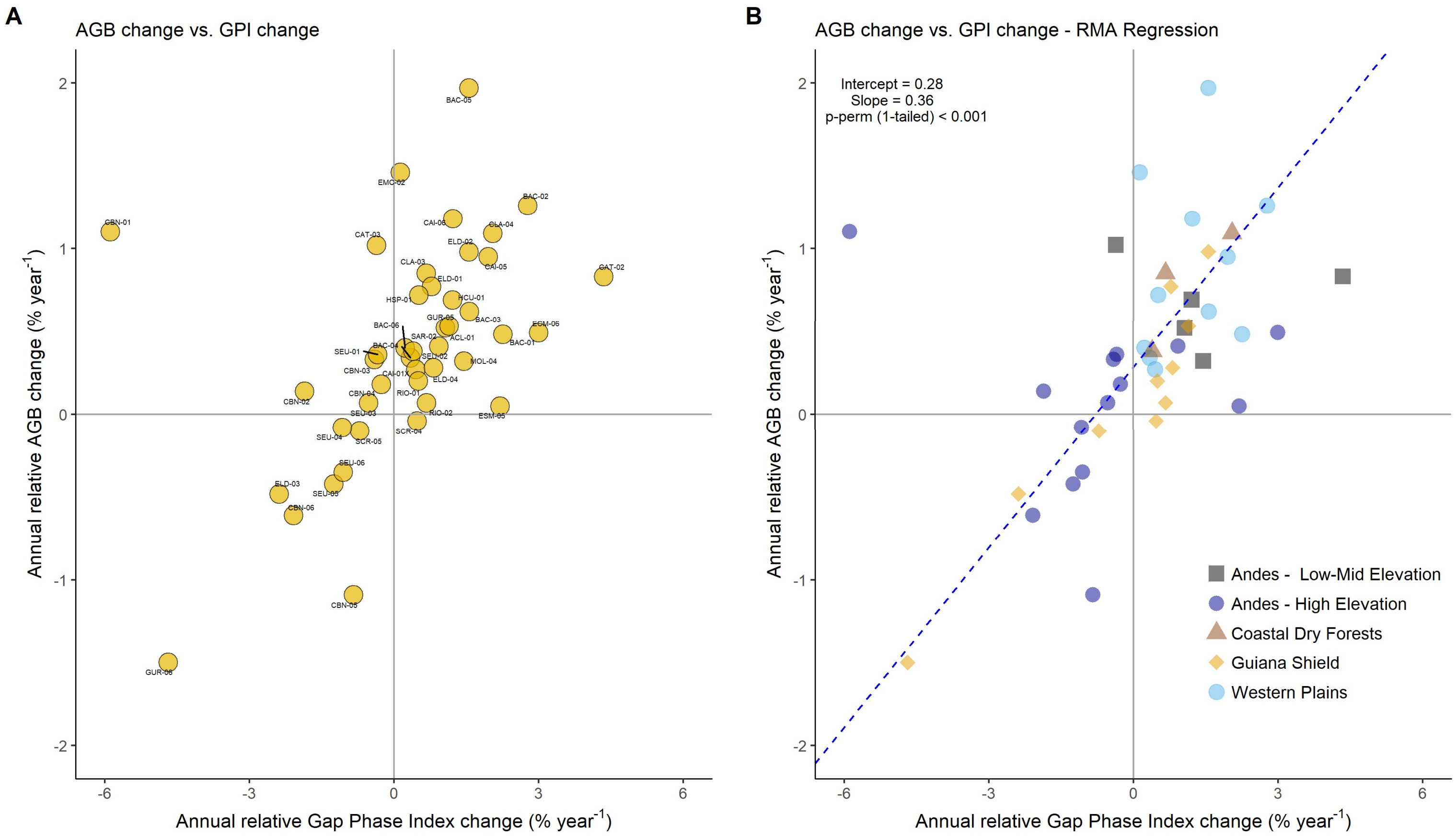


Figure 4. A) Relative change in above-ground forest biomass (AGB) accounting for gap phase dynamics in Venezuelan forest plots. Plot codes are included for reference in connection with the supporting information; B) Relative change in AGB vs change in Gap Phase Index by plot and region including the result of the RMA regression where the intercept differs significantly from zero.

GENERALIZED MIXED MODELS TO ANALYZE FOREST DYNAMICS

Data from all four response variables (i.e. recruitment (*r*) and mortality (*m*) rates, AGWP and AGB_{loss}) were not normally distributed, so all models were fitted using a *log-normal* distribution term based on the comparison of different distributions and their AIC values (Appendix S3). The results of the GLMM modeling approach included below are focused exclusively on the analysis of all plots simultaneously but results from the regional-based GLMMs are included in the supplementary information and are discussed accordingly in the next section.

RECRUITMENT RATES (*r*)

The ‘best’ - AICc-based - model to explain the observed trends in recruitment rates included a negative and significant effect from competition *via* SDI (β coefficient = -0.16; $p < 0.001$), and a positive and significant effect from the interaction between SDI and mean annual precipitation (SDI x MAP) (β coefficient = 0.06; $p < 0.01$). Overall, models showed an almost even proportion of positive and negative effects with regards to the relationships between recruitment rates and the predictors (49.4% had a positive and 50.6% of models showed a negative effect on *r*), representing the plot by plot differences, the regional variation as well as the differences in modeling approaches (Figure 5).

From the stand point of competition-only models (i.e., models including GPI, SDI, and QMD), about 70% of the cases showed these predictors having a negative effect on *r*, with 35% of these being significant effects ($p < 0.05$). Stand density index (SDI) was found to be consistently and negatively affecting recruitment. A very low proportion of cases (< 1%) where the competition factors appeared to positively affect recruitment had significant effects (Figure 5).

Climate-based models (i.e., models including MAT, MAP, and MWCD) showed that most predictors were positively related with *r*. Yet, in only 18% of the cases the effects were significant, but with mean annual temperature (MAT) having the strongest effect (Figure 5). In the group of models with negative coefficients, less than 1% had statistically significant effects. Surprisingly, the maximum climatic water deficit

(MCWD) was completely absent as a significant predictor of recruitment in all tested models. Finally, in the instances where competition and climate interactions were tested, an almost equal number of cases had positive (48.6%) and negative (51.3%) effects on recruitment. Only in 17% of these interaction models, predictors had significantly and positive effects on *r* with SDI x MAP and GPI x MAT being the most prominent interaction terms (Figure 5).

Among the five regions, the 'best' statistical model (AICc-based) varied with different factors affecting recruitment potentially reflecting the different regional dynamics. Overall, competition or maturation factors such as the SDI or the Gap Phase Index (GPI), alone or interacting with climate factors, consistently explained trends in recruitment in each region. For instance, SDI alone was negatively and significantly associated with recruitment in 3 of the 5 regions (Guiana Shield and both Andean subregions), while positively, yet not-significantly associated in the Coastal Dry Forests and was absent as a predictor in the selected model for *r* in the Western Plains (Appendix S9). In this region, the degree of 'matureness', measured by the GPI, negatively affected recruitment and positively so when interacting with MAT. The Coastal Dry Forests had the most factors in the best-fit model, with QMD negatively and GPI positively affecting recruitment along with other interaction terms (Appendix S9, Figure S12).

MORTALITY RATES (*m*)

The best-fit model shows mean annual temperature (MAT) as the single-best predictor positively associated with mortality rates (β coefficient = 0.13; $p < 0.05$). In fact, regardless of the modeling approach, MAT showed significant and positive effects on *m* where it was included (Figure 6). When testing competition-based models, SDI was found to be negatively associated with mortality rates, with a low proportion of these models showing significant effects. Similarly, looking at the proportion of competition-based predictors and their effects on *m*, the Gap Phase Index (GPI) was found to be negatively associated with mortality, while the effects of the quadratic mean diameter (QMD) were mostly positive, although their effects on mortality were predominantly non-significant ($p > 0.05$) (Figure 6).

Climate-based models showed that most predictors (76.6%) were positively related with *m*, with the previously mentioned effects of MAT contributing with the highest proportion (Figure 6). The effects of mean annual precipitation (MAP) on mortality, although mostly positive, were not significant in majority of cases. The case of the maximum climatic water deficit (MCWD) indicates an even proportion between negative and positive effects on mortality but lacked statistical significance overall. The interaction between the gap phase index (GPI) with MAT had consistently positive effects on mortality rates with almost half of the cases being statistically significant. The interaction of SDI with the MAT also showed positive effects on mortality rates (Figure 6).

Regional-based models of mortality rates showed large differences in the response of the Andes versus all other regions. The Andes high nor the Andes low-mid elevation regions showed any significant factors predicting mortality, but SDI alone, and its interaction with MAT had the highest and positive β-coefficient values in both subregions. In terms of competition factors, the Gap Phase Index (GPI) for the Western Plains, and the SDI for the Guiana Shield and the Coastal Dry Forests, had both significant and negative correlation with mortality rates in these regions. MAT predicted mortality rates for the lowland plots in the Western Plains and Guiana Shield, but was not important in the Coastal Dry Forests (Appendix S9; Figure S13).

ABOVEGROUND WOODY PRODUCTIVITY (AGWP)

All plots analyzed together showed the 'best' (AIC-based) model explaining trends in aboveground woody productivity (AGWP) included all stand development factors (SDI, QMD with negative estimators, and GPI with positive), along with MAP positively correlated with AGWP, and a significant and negative estimator from the interaction term GPI x MAP (Figure 7). SDI and QMD were negatively associated with trends in AGWP, demonstrating that as stands become overstocked (i.e. high QMD and/or high SDI) AGWP declines. On the contrary, the GPI was strongly positively associated with a change in AGWP suggesting production increases with stand maturation (Figure 7).

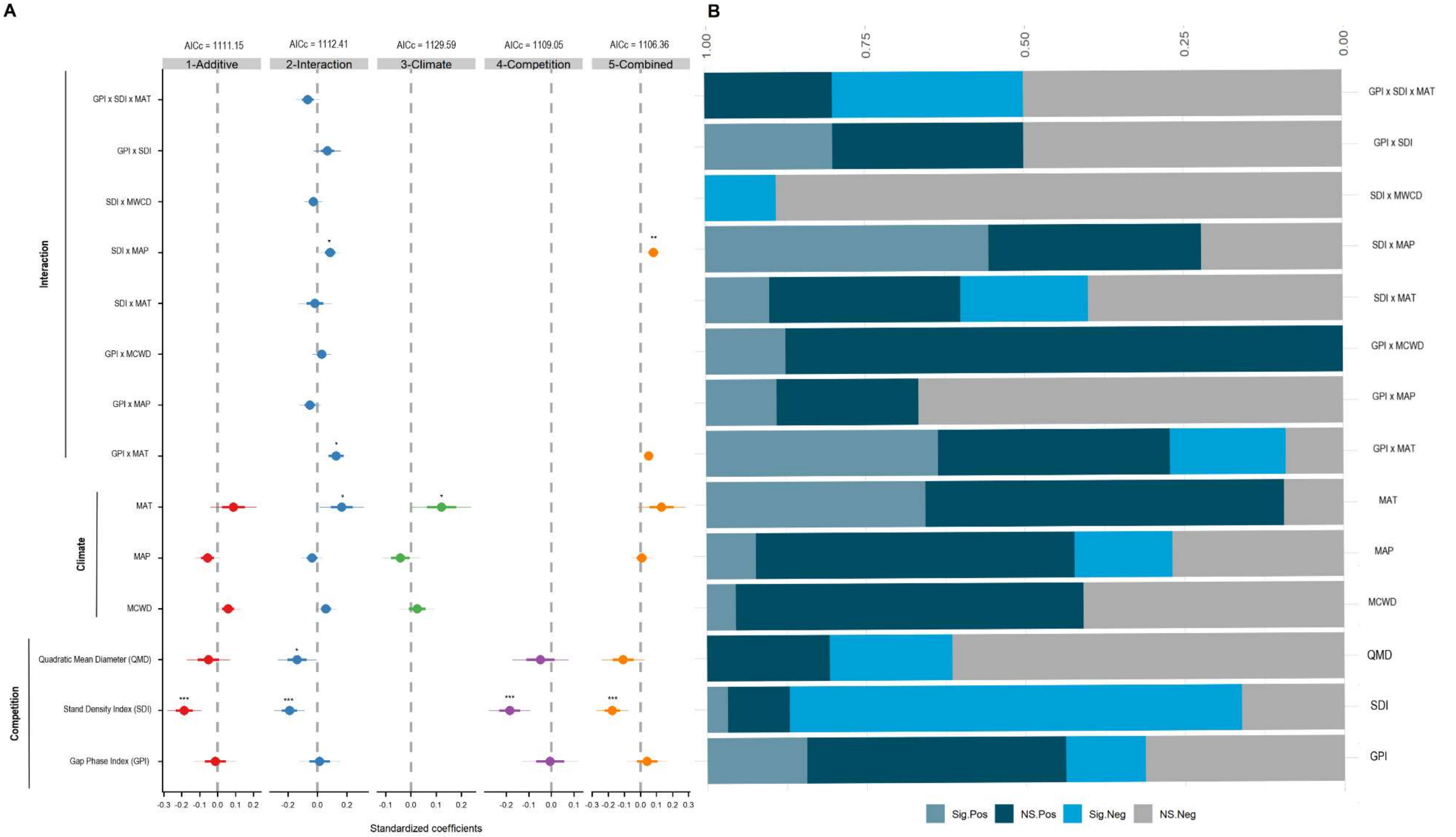


Figure 5. A) Five modeling approaches to explain the observed trends in recruitment rates in Venezuelan forest plots. Models were tested in order, starting with a full additive approach with all predictors included, followed by a complete climate vs. competition interaction model, to later test for competition and climate factors separately. The final approach (namely here as ‘combined’) included only those predictors that had significant values ($p < 0.05$) from the four previous approaches. The colors indicated different models. Each factor is labelled according to their category (i.e. climate, competition, or interaction) showing the standardized coefficients with 95% confidence intervals. Significant values, negative or positive, are labelled with asterisks (*$p<0.05$; ** $p<0.01$; *** $p<0.001$). The AICc values are shown for each model with the lowest indicating the potential ‘best’ model. B) Predictor’s relative proportion of positive or negative, and significant and non-significant effects on recruitment rates. The ‘best’ models for each region are shown in Appendix S9.

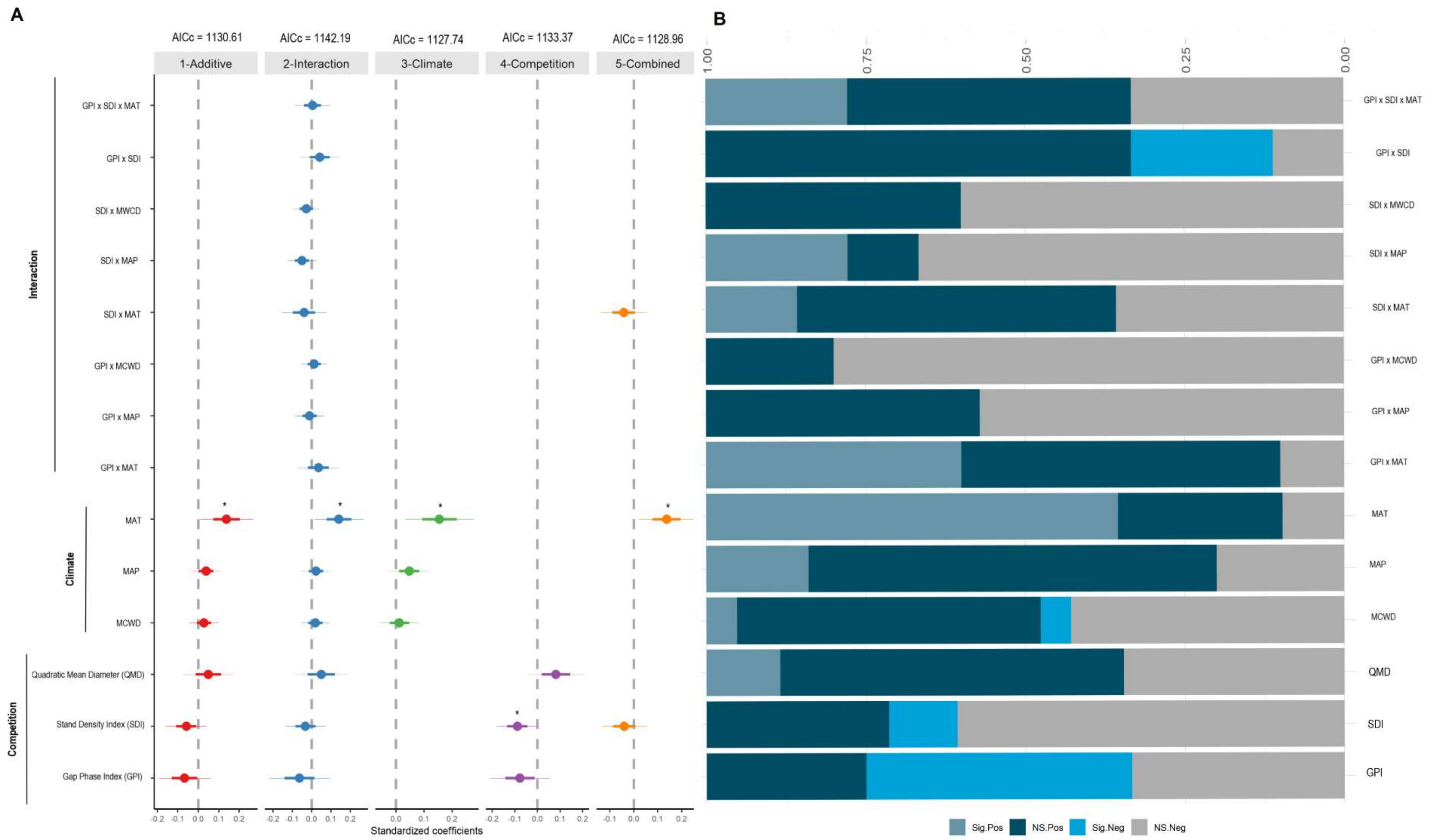


Figure 6. A) Five modeling approaches to explain the observed trends in mortality rates in Venezuelan forest plots. Models were tested in order, starting with a full additive approach with all predictors included, followed by a complete climate vs. competition interaction model, to later test for competition and climate factors separately. The final approach (namely here as ‘combined’) included only those predictors that had significant values ($p < 0.05$) from the four previous approaches. The colors indicated different models. Each factor is labelled according to their category (i.e. climate, competition, or interaction) showing the standardized coefficients with 95% confidence intervals. Significant values, negative or positive, are labelled with asterisks (*p<0.05; ** p<0.01; *** p<0.001). The AICc values are shown for each model with the lowest indicating the potential ‘best’ model. B) Predictor’s relative proportion of positive or negative, and significant and non-significant effects on mortality rates. The ‘best’ models for each region are shown in Appendix S9.

Despite the negative, yet not-significant trends observed in MAP (Figure S4), climate-based models show that the trends in AGWP were positively associated with MAP. Indeed, when AGWP trends were modelled by regions, MAP mostly showed positive and significant effects (Appendix S9; Figure S14). The positive correlation between GPI and productivity shifted to a negative effect in the GPI x MAP interaction term, which was significant ($p < 0.05$) for the case of the Guiana Shield where in fact water stress significantly increased (Appendix S4; Figure S14). When significant estimates were found for the AGWP~MAT relationship, these were more likely negative showing that the observed trends in MAT could be negatively affecting AGWP, possibly in connection to the reported positive relationship between MAT and mortality rates described earlier. However, the GPI x MAT interaction showed a positive interactive effect most of the times when the term was included as a predictor.

Two interaction terms were the most important when attempting to explain the trends in AGWP for all plots combined. First, the interaction between two stand development factors, being these the degree of ‘matureness’ (GPI) and ‘crowding’ (SDI) negatively affected AGWP trends, and significantly so in the case of the Guiana Shield region (Figure S14). In addition, when these two factors also interacted with MAT there was an almost even proportion between positive and negative effects (Figure 7).

The ‘best’ regional statistical models explaining trends in AGWP varied in the relative importance of factors. For instance, a climate-only model best described trends in AGWP in the Western Plains and the Andes Low-Mid elevation regions, while a combined model with competition and climate factors together seems more important in the rest of the regions. Surprisingly, for both the Andes low-middle elevation region and the Western Plains, AGWP showed a significant positive association with MCWD. The low elevation Andes sites also showed a positive association with MAP and negative with MAT, while the Western Plains showed the opposite response (MAT positive and MAP negative), perhaps in connection with the significant decline observed in MAP for this region (Figure S4). The Andes high elevation sites had the most complex model with stand development factors GPI (+), QMD & SDI (-), and MAT &MAP (+) associated with AGWP, and then 4 related interaction terms. The selected models and their effects on AGWP for each region are shown in Appendix S9.

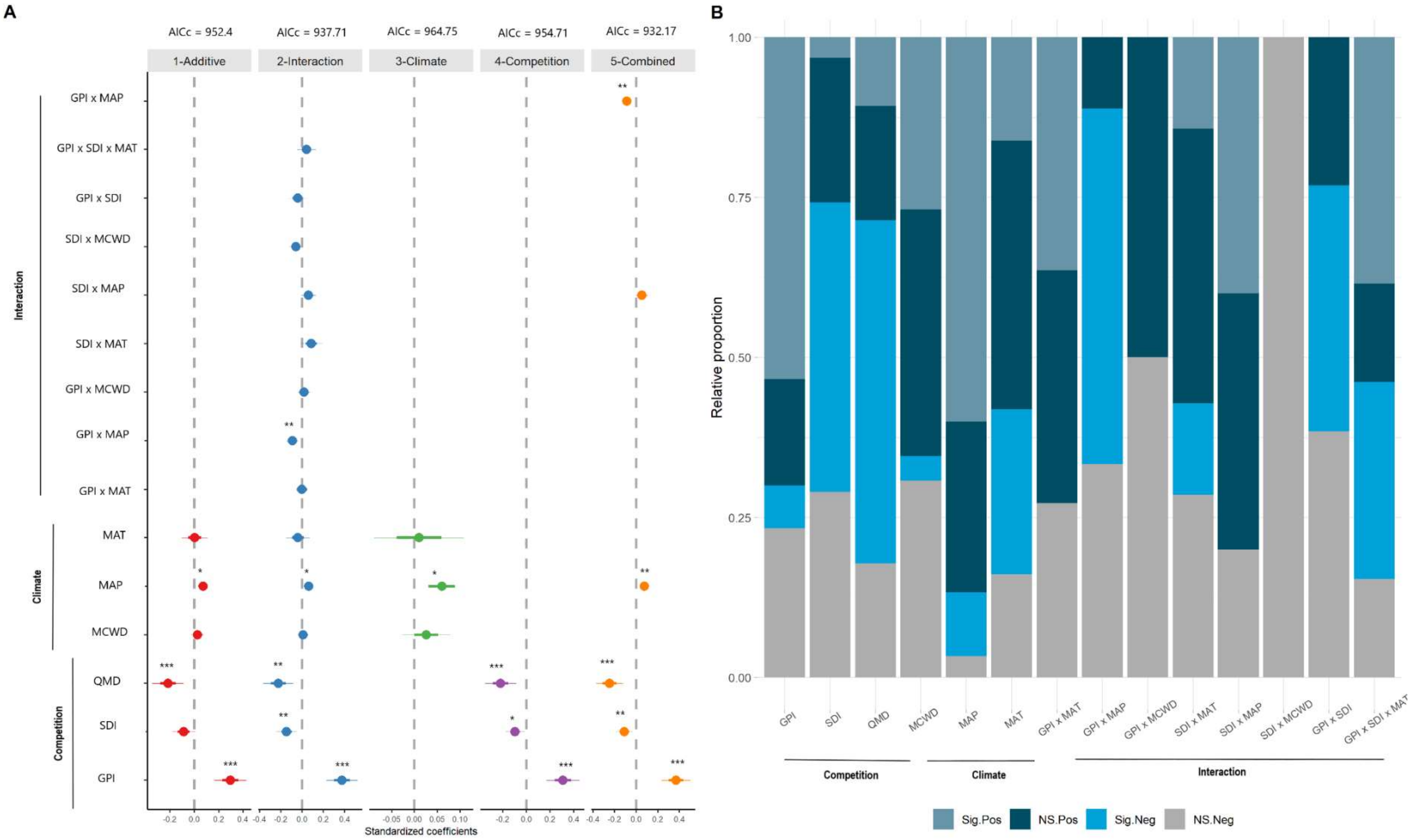


Figure 7. A) Five modeling approaches to explain the observed trends in aboveground woody productivity (AGWP) in Venezuelan forest plots. Models were tested in order, starting with a full additive approach with all predictors included, followed by a complete climate vs. competition interaction model, to later test for competition and climate factors separately. The final approach (namely here as 'combined') included only those predictors that had significant values ($p < 0.05$) from the four previous approaches. Each factor is labelled according to their category (i.e. climate, competition, or interaction) showing the standardized coefficients with 95% confidence intervals. Significant values, negative or positive, are labelled with asterisks (*p<0.05; ** p<0.01; *** p<0.001). The AICc values are shown for each model with the lowest indicating the potential 'best' model. B) Predictor's relative proportion of positive or negative, and significant and non-significant effects on AGWP. The 'best' models for each region are shown in Appendix S9.

DISCUSSION

Have recruitment, mortality, stand dynamics, biomass and productivity of different tropical forest-types in northern South America changed over recent decades?

We found increases in aboveground biomass (AGB), aboveground woody productivity (AGWP), recruitment (*r*) and mortality (*m*) overall across five different mature tropical forest-types in northern south America. First, these results reflect turnover rates and productivity varying systematically with environmental and/or regional factors. For instance, Western Plains are the most dynamic forests with higher turnover rates, while Guiana Shield are the most productive. Turnover rates are highest on richer soils, and in partly seasonal sites (Vilanova et al., 2018) (Appendix S5).

Unequivocal evidence was found for a significant multidecadal change in turnover patterns, with potential long-term effects on carbon dynamics. An overall increase in recruitment and mortality rates was found, similar to patterns observed for Amazonian forests during the last part of the 20th century (Phillips & Gentry 1994; Phillips 1996; Phillips et al., 2004; Laurance et al., 2009) highlighted by changes over recent decades (Brienen et al., 2015). The average slope for both recruitment and mortality was similar to Phillips et al., (2004) estimates for Amazonian forests (+ 0.02 % y^{-1}), and the frequency distribution for individual sites indicates the observed increasing trends were more pronounced for mortality than for recruitment (Figure 2).

The overall increase in recruitment is indicative of increasing stand turnover rates, however this trend is driven by the positive slopes found in the Andean subgroup of plots, since recruitment in lowland regions appears to have mostly declined over time (Appendix S5). Yet, several plots within these regions also showed increasing trends in recruitment. Even for similar timeframes, these positive trends in *r* have not been found in other tropical sites. For instance, recruitment rates estimated in two independent studies in lowland Amazon forests did not show a significant trend, neither a decline nor increase in the recruitment of new individuals between 1983 and 2012 (de Avila et al., 2017) or between 1990 and 2014 (Amaral et al., 2019). Similarly, patterns of stem recruitment for an old-growth forest landscape in Central America did not show a long-term directional trend between 1998 and 2014 (Clark et al., 2017). Thus, patterns of recruitment in neotropical forests may be unpredictable or more restricted or localized in response to local environmental conditions, species composition, and stand development (Norden et al., 2015; Rutishauser et al., 2019).

Mortality rates have increased across most of this dataset, and the trends are robust regardless of region, elevation, soil or seasonality, and the result is apparent even with the noise shown in the plot-by-plot results, all censuses results (Figure 2, Appendix S5), or in the form of annual change (% y^{-1}; Appendix S7). Furthermore, the trends were also robust regardless of the monitoring period and census intervals of each plot. Individual sites with several remeasurements and long full intervals as close to 50 years that combined could potentially lead to declining trends in demographic rates (Sheil & May 1996; Phillips et al., 2002; Lewis et al., 2004; Phillips et al., 2004; Kohyama et al., 2018) also had increasing trends in mortality. Observed increasing trends in mortality is aligned with widespread evidence of recent mortality events reported for many forest-types across the globe (van Mantgem et al., 2009; Allen et al., 2010; Anderegg et al., 2013; Zhang et al., 2015; Greenwood et al., 2017; Hartmann et al., 2018; Senf et al., 2018), including the tropics (Phillips et al., 2009; Phillips et al., 2010; McDowell et al., 2018).

Increasing mortality rates in Amazonian forests have also been tied to biomass loss from mortality with dead biomass increasing at a rate close to 0.05 Mg C ha^{-1} y^{-2} between 1980 and 2010 (Brienen et al., 2015). In this study, a slightly, yet still significant and positive slope of 0.02 Mg C ha^{-1} y^{-2} in AGB_{loss} was also found (Figure 3). However, the significant decline in the carbon sink found in the Brienen et al. (2015) study (mean slope = – 0.034 Mg C ha^{-1} y^{-2}, $p = 0.034$) was not found here. The trends found here in Net_{AGB}, although negative, were not significant (mean slope = –0.003 Mg C ha^{-1} y^{-1}, $p = 0.18$) and the 'sink' effect seems prevalent for most parts of the period considered here (Figure 3, Appendix S6). Some of the plots used in this study were also part of the Brienen et al. (2015) study. However, the analysis was expanded beyond lowland forests alone by adding several plots that were not part of the 2015 study including 12 plots in Andean forests, some of which were established in the early 1960s of the 20th century. In fact, in this region, results show a significant decline in the net biomass change (Andes Low-mid Elevation mean slope = – 0.35 Mg C ha^{-1} y^{-2}, $p < 0.001$; Andes High Elevation mean slope = – 0.02 Mg C ha^{-1} y^{-2}, $p < 0.001$) while

AGB_{loss} simultaneously increased in both regions (Appendix S6). These findings thus confirm that the changing patterns previously observed for lowland forests within Amazonia occurred, and in some cases are still happening, in other biomes and environmental contexts like the tropical Andes.

A positive and significant slope overall for AGWP was found when all plots were analyzed together (Figure 2), but on a regional level an apparent flattening or significant declines of the aboveground woody productivity over time was also detected in some cases. These results first agree with positive changes in tree growth from mature stands found recently not only in tropical forests of Amazonia and Africa (Lewis et al., 2004; Lewis et al., 2009a; Lewis et al., 2009b; Phillips et al., 2013; Brienen et al., 2015; Brienen et al., 2017), but also in temperate and boreal forests as well (McMahon et al., 2010; Pretzsch et al., 2014; Searle & Chen 2018) in an apparent response to global drivers. However, when considered regionally, the decline in AGWP found here is directly connected with the observed significant increase in AGB_{loss} (Appendix S6) that could be related to climatic factors. For example, different periods show decreases in AGWP for the Guiana Shield and Coastal Dry forests, both in the Eastern part of Venezuela, along with the low-mid elevation forests in the Andes.

This apparent overall increase in growth rates, potentially connected to climate warming and positively associated with MAT could be weakening due to several climate-related factors such as more frequent and severe droughts (e.g. Phillips et al., 2009; Brienen et al., 2015; Feldpausch et al., 2016). For example, a decrease in growth rates along the elevational tree line of the southern Andes have been associated with warmer and drier summer conditions in the region (Fajardo et al., 2019). Warm summers as well as high seasonal variability in precipitation increased the likelihood of tree death in temperate forests of Europe (Neumann et al., 2017), and rising temperatures have amplified moisture stress and increase the climatic water deficit and competition in forests of Western US with the associated increase in mortality rates (van Mantgem et al., 2009; Young et al., 2017).

Is it possible to partition the potential drivers of forest dynamics between competition and climate for Venezuelan tropical forests?

Most sites/regions have experienced a concerted increase in mean annual temperatures and potential evapotranspiration, accompanied by a slight decline in mean annual precipitation, that combined may have triggered an increase in the maximum climatic water deficit (Figure 1, Appendix S4). Together, these elements led me to initially expect a change in forest structure and functioning, either through periodic enhancement of tree growth, or declining levels of productivity and increasing levels of dynamism (i.e., higher rates of mortality and recruitment). Most plots continued gaining biomass despite a significant increase in stem mortality, and that no significant correlation with the rate of change in stem density or with changes in the plot-level wood density (WD) was found (Appendix S8). Although some sites showed a decline in WD likely associated with a shift in species composition following disturbance (Poorter et al., 2019), these changes were not correlated with gains in AGB nor basal area for most plots. Furthermore, higher levels of stand 'matureness' *via* the Gap Phase Index were only partially correlated with changes in AGB (Figure 4, Appendix S7). Except for the high elevation forests in the Andes, all regions have also experienced an increase in the average size of trees (i.e. Quadratic Mean Diameter), which combined could suggest that while competition factors related to stand maturation might be important drivers of the changes in AGB other factors should be considered as well.

Models showed trends in recruitment rates could be mostly explained as a negative association with competition alone (i.e. Stand Density Index, SDI) or through the interaction of SDI with mean annual precipitation (MAP), and to a lesser extent with the positive influence from mean annual temperature (MAT) (Figure 5). In this regard, SDI was found to increase through time in four of the five regions (Appendix S7), so it is possible that competition-induced suppression (e.g., shading and root competition) has been a fundamental limiting factor of recruitment following models of stand development (Oliver & Larson 1996; Zhang et al., 2015). For instance, SDI imputed alone in the models appeared to be a significant limiting factor for recruitment especially in the denser forests of the Guiana Shield and the Andes (Appendix S9). However, I argue that this apparent intensification in competition levels limiting recruitment could be primarily driven by the increasing size in trees and basal area growth rather than driven by the increase in stem density that was absent for many of these plots (Appendix S8), which would be expected if changes were driven by gap-phase disturbance events (Swaine et al., 1987; Oliver & Larson 1996). Nevertheless, a major challenge in describing the causes of changing trends in tropical forest dynamics, particularly in recruitment and mortality is the difficulty in documenting and describing historic stand development in the absence of known ages and reliable stand reconstruction techniques (i.e., lack of reliable annual tree-rings) (Baker et al., 2005).

The positive trends in MAT observed for all plots/regions (Figure 1, Appendix S4) could be accelerating competition by enhancing tree death as shown by the positive and significant relationship found between MAT and mortality rates in these plots (Figure 6). Thus, finding MAT alone as an important variable positively correlated with the trends in recruitment (Figure 5) appears to be in coordination with how turnover processes work, since pulses of mortality would often imply pulses of stem recruitment as competition for limiting resources declines making possible for new trees to establish (Oliver & Larson 1996).

High temperatures can have multiple effects on forest dynamics, both at the individual or stand levels. For instance, elevated temperatures could potentially trigger an increase in vapor pressure deficit and atmospheric drought, with the associated increasing risk of hydraulic failure and death (Wang et al., 2014; Aubry-Kientz et al., 2015). Increasing respiration rates can also lead to carbon starvation, consistent with higher tree mortality with increasing temperatures affecting the physiology of tropical trees (McDowell et al., 2018; Aleixo et al., 2019). The combination of high temperatures and reduced precipitation can cause periodic drought periods, which may further contribute to reducing productivity and carbon uptake, including increasing the risk of tree mortality events (Phillips et al., 2009; Allen et al., 2010; Phillips et al., 2010; Luo & Chen 2013; Anderegg et al., 2015). However, despite finding a trend towards more negative values over time in the maximum climatic water deficit (MCWD), especially in the Guiana Shield and Western Plains regions (Appendix S4), no clear signal of drought effects was found as originally expected. Nevertheless, effects of MCWD were mostly positive for both recruitment and mortality, and accelerated dynamics could have been triggered during some of the dry and warm periods (Aleixo et al., 2019).

Contrary to the initial expectation, there were no significant effects of competition variables on the observed trends in tree mortality, except for the QMD, which had a positive yet not significant effects on *m* (Figure 6). When the analysis was conducted on a regional level, SDI alone was found to be negatively and significantly correlated to tree mortality rates for the Western Plains region and was only positive, although not significantly, for the much denser plots in the high elevation forests of the Andes (Appendix S9). The lack of evidence for effects of competition on mortality could be partly because only trees ≥ 10 cm dbh were included in this study. In mature tropical forests, mortality rates are generally highest for seedlings and saplings (trees < 10 cm dbh; Clark & Clark 1992; Condit et al., 1995) compared to large individuals because of the low-light conditions that are typical in the understory. However, using long-term data from a large plot in the Guiana Shield, Pillet et al., (2017) found that sometimes lower mortality odds were also associated with higher values for a competition index, which might be caused by gap-phase dynamics.

In this study, competition measured via SDI had significant and positive effects on mortality only when interacting with MAT in the 'best-fit' model for the Western Plain regions (Figure S13). In this region, SDI significantly increased (Figure S8) while most plots showed a decline in the number of individuals (Figure S11). Combined, this could indicate that the growth from large trees might be driving the positive trends observed in AGWP (Figure S6), overall suggesting that in a future warming climate, large trees in this region might be at a higher risk of mortality as has been reported in other tropical settings (Phillips et al., 2009; Nepstad et al., 2007). Thus, it appears that the overall dominant causes of stem mortality in Venezuelan forests could be more closely associated to hydraulic failures (e.g. Rowland et al., 2015) and more stochastic wind-disturbances (Espírito-Santo et al., 2014; Aleixo et al., 2019) not captured in this analysis, rather than competition *per se*, while the accelerated growth trends observed in some cases might increase the mortality risk by ensuring tress reach larger sizes more quickly (e.g. Brienen et al., 2015; McDowell et al., 2018). Nevertheless, these results also suggest the need to further explore the process of mortality including a more detailed analysis by size classes, functional groups including and, when possible, a spatial analysis of the process of mortality could help improving our understanding of the nature of resource-competition among individuals in these systems.

With regards to growth and productivity, in a recent modeling study conducted for Guiana Shield forests, Aubry-Kientz et al., (2019) identified temperature as the strongest climate driver of reduced levels of stand dynamics also highlighting a possible temperature-driven drop of 40% in average forest growth in the Guiana Shield in the future. Thus, the decline in AGWP observed in this study for the Guiana Shield and the Low-Mid elevation forests in the Andes (Appendix S6) could be driven by the increase observed in MAT. In the case of the Guiana Shield, although the effects of MAT over AGWP were not significant, these were negative, and for the Low-mid elevation forest in the Andes this effect was significantly negative (Figure S14). Indeed, based on the available climate data, in these two regions MAT appeared to have increased between 0.89 °C and 1.21 °C respectively for the 1901-2017 period (between ~ 0.007 and 0.01 °C year^{-1}; Appendix S4), closer to other estimates of warming trends found for example in the lowland Amazon of 0.6-0.7 °C between 1949 and 2019 (~ 0.01 °C year^{-1}; Marengo et al., 2018).

Endogenous (i.e. competition, stand development) or exogenous (i.e. climate) factors rarely act alone when driving the demographic processes and carbon dynamics of forests, thus partitioning the effects of individual factors or for particular interactions remains elusive often due to the stochastic nature of stand dynamics and the need for large datasets. Nevertheless, we attempted an exploration of the drivers of the observed trends in three of our studies variables (i.e. recruitment, mortality, aboveground woody productivity) and the models used helped to unveil interesting patterns that, although we consider to be preliminary, can help in understanding the mechanisms behind the dynamics of Venezuelan forests in the last three to four decades.

CONCLUSION

In this study, I provide a general overview of the temporal dynamics of turnover and carbon for different tropical forests in Venezuela. Significant changes in these processes were detected with an acceleration of recruitment and mortality especially in the last decade, along with a slow decline in the carbon storage capacity associated with increasing levels of tree mortality. Overall, competition seems to be more closely related to the observed trends in recruitment while climate, via higher temperatures, was the main factor driving the trends in mortality. The observed trends in AGWP were explained by a complex combination of both groups of variables, with competition having a preponderant negative effect on productivity and climate acting both as a limiting factor for growth via higher MAT or enhancing it via precipitation.

The dataset used here includes inventory data from monitoring periods as long as 50 years in some cases while covering different environmental conditions that allows for a comparative analysis on forest dynamics over time. While this could be quite useful to test for temporal trends in these forests, it might be a small sample to fully uncover large-scale patterns of forest dynamics over time and its associated drivers. Yet, the evidences are partially aligned with other larger studies showing that tropical forests are experiencing concerted changes in dynamics, structure and function. Furthermore, assessing the role of specific drivers also requires of additional sites in many of the regions covered in the study including large-sized plots. Nevertheless, both as a confirmation study from previous analyses (cf. Brienen et al., 2015), and as an independent and preliminary analysis of drivers of forest dynamics, I believe this study could be useful in opening new ways to think about the study of tropical forests, particularly for Venezuela, one of the regions with higher ecosystem diversity across the tropics that could be severely impacted by future climate change.

SUPPORTING INFORMATION

Appendix S1. Additional information on the characteristics of the data used in this study.

Table S1. Detailed description of 44 permanent plots in different forest-types of Venezuela.

Plot location					Plot characteristics and General Inventory information							Elevation		Climate[a]							Soil	
Plot Code	State	Bioregion	Latitude Decimal	Longitude Decimal	Ground Area (ha)	Minimum Dimension (m)	Maximum Dimension (m)	Date Established**	Last Census Date	Monitoring period (years)	No. of Censuses	Forest Elevation	Altitude (masl)	Mean Annual Temp. (ºC)	Mean Annual Precipitation (mm year^{-1})	PET (mm year^{-1})	WA (mm year^{-1}) [b]	Maximum Climatic Water Deficit (CWD) [b]	No. Dry months	Seasonality Class [c]	Major Soil Type	Fertility Class [d]
ACL-01	Merida	Andes - Low-Mid Elev.	8.75	-71.50	0.25	50	50	1967.20	1984.40	17.20	18	Premontane	1000	22.7	1377	1231	147	-207.96	3	1	Old inceptisol	1
BAC-01	Barinas	Western Plains	7.46	-71.01	0.25	50	50	1991.28	2016.30	25.02	13	Lowland	141	26.9	1629	1206	423	-327.97	4	2	Old inceptisol	1
BAC-02	Barinas	Western Plains	7.46	-71.01	0.25	50	50	1991.86	2016.30	24.44	12	Lowland	143	26.9	1629	1206	423	-327.97	4	2	Old inceptisol	1
BAC-03	Barinas	Western Plains	7.46	-71.01	0.25	50	50	1991.28	2016.30	25.02	10	Lowland	144	26.9	1629	1206	423	-327.97	4	2	Old inceptisol	1
BAC-04	Barinas	Western Plains	7.46	-71.01	0.25	50	50	1991.86	2016.31	24.45	12	Lowland	138	26.9	1629	1206	423	-327.97	4	2	Old inceptisol	1
BAC-05	Barinas	Western Plains	7.47	-71.02	0.25	50	50	2001.26	2016.31	15.05	9	Lowland	142	26.9	1625	1207	418	-326.48	4	2	Old inceptisol	1
BAC-06	Barinas	Western Plains	7.47	-71.02	0.25	50	50	1996.31	2016.31	20.00	10	Lowland	140	26.9	1625	1207	418	-326.48	4	2	Old inceptisol	1
CAI-X	Barinas	Western Plains	8.70	-70.07	1.00	50	200	1975.07	2016.33	41.26	41	Lowland	173	26.3	2098	1309	789	-350.51	6	2	Old inceptisol	1
CAI-05	Barinas	Western Plains	8.72	-70.08	0.25	50	50	1963.13	2016.34	53.21	41	Lowland	168	26.3	2098	1309	789	-350.51	6	2	Old inceptisol	1
CAI-06	Barinas	Western Plains	8.72	-70.08	0.25	50	50	1963.13	2016.34	53.21	41	Lowland	169	26.4	2068	1315	753	-358.76	6	2	Old inceptisol	1
CAT-02	Merida	Andes - Low-Mid Elev.	8.44	-71.77	0.25	50	50	1974.31	1983.96	9.65	10	Lowland	380	22.5	1188	1222	-35	-253.85	6	2	Old inceptisol	1
CAT-03	Merida	Andes - Low-Mid Elev.	8.44	-71.77	0.25	50	50	1974.31	1983.96	9.65	10	Lowland	350	22.5	1188	1222	-35	-253.85	6	2	Old inceptisol	1
CBN-01	Merida	Andes - High Elev.	8.58	-71.42	0.25	50	50	1960.20	1983.28	23.08	22	Lower-Montane	2310	20.0	1189	1136	53	-231.71	5	2	Old inceptisol	0
CBN-02	Merida	Andes - High Elev.	8.58	-71.42	0.25	50	50	1960.21	1983.28	23.07	22	Lower-Montane	2320	20.0	1189	1136	53	-231.71	5	2	Old inceptisol	0
CBN-03	Merida	Andes - High Elev.	8.58	-71.42	0.25	50	50	1961.51	1989.87	28.36	25	Lower-Montane	2430	20.0	1189	1136	53	-231.71	5	2	Old inceptisol	0
CBN-04	Merida	Andes - High Elev.	8.58	-71.42	0.25	50	50	1961.51	1989.87	28.36	23	Lower-Montane	2430	20.0	1189	1136	53	-231.71	5	2	Old inceptisol	0
CBN-05	Merida	Andes - High Elev.	8.58	-71.42	0.25	50	50	1961.77	1989.88	28.11	24	Lower-Montane	2450	20.0	1189	1136	53	-231.71	5	2	Old inceptisol	0
CBN-06	Merida	Andes - High Elev.	8.58	-71.42	0.25	50	50	1961.52	1985.80	24.28	23	Lower-Montane	2450	20.0	1189	1136	53	-231.71	5	2	Old inceptisol	0
CLA-03	Anzoátegui	Coastal Dry Forests	10.01	-65.32	0.25	50	50	1978.43	2015.76	37.33	20	Lowland	316	26.1	907	1417	-509	-646.98	7	2	Entisol	0
CLA-04	Anzoátegui	Coastal Dry Forests	10.01	-65.32	0.25	50	50	1978.43	2015.76	37.33	20	Lowland	283	26.1	907	1417	-509	-646.98	7	2	Entisol	0
CRZ-01	Zulia	Andes - Low-Mid Elev.	8.83	-71.86	1.00	100	100	1970.69	1972.70	2.01	4	Lowland	60	28.0	1747	1446	302	-205.49	3	1	Young oxisol	1
ECM-06	Merida	Andes - High Elev.	8.67	-71.42	0.25	50	50	1967.53	1983.75	16.22	18	Lower-Montane	2060	20.6	1233	1155	78	-224.70	4	2	Old inceptisol	1
ELD-01	Bolivar	Guiana Shield	6.11	-61.41	0.25	50	50	1971.55	2015.75	44.20	26	Lowland	220	23.5	2091	1262	829	-126.47	0	0	Young oxisol	0
ELD-02	Bolivar	Guiana Shield	6.11	-61.41	0.25	50	50	1971.55	2015.75	44.20	26	Lowland	244	23.5	2091	1262	829	-126.47	0	0	Young oxisol	0
ELD-03	Bolivar	Guiana Shield	6.09	-61.40	0.25	50	50	1971.55	2015.75	44.20	26	Lowland	404	23.3	2110	1254	856	-122.44	0	1	Young oxisol	0
ELD-04	Bolivar	Guiana Shield	6.09	-61.35	0.25	50	50	1971.55	2015.75	44.20	26	Lowland	366	23.4	2110	1254	856	-116.95	0	1	Young oxisol	0
EMC-02	Barinas	Western Plains	8.01	-70.55	1.00	100	100	1984.26	1994.30	10.04	8	Lowland	140	26.9	1675	1286	389	-369.20	4	2	Old inceptisol	1
ESM-05	Merida	Andes - High Elev.	8.68	-71.43	0.25	50	50	1967.51	1982.53	15.02	17	Premontane	2040	20.8	1249	1164	85	-222.80	3	1	Old inceptisol	1
GUR-05	Bolivar	Guiana Shield	7.50	-63.00	0.25	50	50	1972.13	1981.18	9.05	10	Lowland	180	25.6	1335	1437	-102	-476.30	4	2	Young oxisol	0
GUR-06	Bolivar	Guiana Shield	7.50	-63.00	0.25	50	50	1972.13	1978.26	6.13	8	Lowland	180	25.6	1335	1437	-102	-476.30	5	2	Young oxisol	0
HCU-01	Merida	Andes - Low-Mid Elev.	8.36	-71.69	0.25	50	50	1969.68	1980.72	11.05	12	Premontane	1150	20.5	1012	1150	-137	-287.66	3	1	Old inceptisol	1
HSP-01	Portuguesa	Western Plains	8.50	-69.00	1.00	100	100	1972.27	1981.13	8.85	9	Lowland	100	27.6	1691	1465	225	-597.07	5	2	Old inceptisol	1
MOL-04	Merida	Andes - Low-Mid Elev.	8.67	-71.58	0.25	50	50	1967.48	1983.30	15.82	17	Premontane	1500	23.4	1391	1255	136	-210.60	3	1	Old inceptisol	1

Plot location					Plot characteristics and General Inventory information							Elevation		Climate^a							Soil	
Plot Code	**State**	**Bioregion**	**Latitude Decimal**	**Longitude Decimal**	**Ground Area (ha)**	**Minimum Dimension (m)**	**Maximum Dimension (m)**	**Date Established****	**Last Census Date**	**Monitoring period (years)**	**No. of Censuses**	**Forest Elevation**	**Altitude (masl)**	**Mean Annual Temp. (ºC)**	**Mean Annual Precipitation (mm year^{-1})**	**PET (mm year^{-1})**	**WA (mm year^{-1}) ^{b}**	**Maximum Climatic Water Deficit (CWD) ^{b}**	**No. Dry months**	**Seasonality Class ^{c}**	**Major Soil Type**	**Fertility Class ^{d}**
RIO-01	Bolivar	Guiana Shield	8.11	-61.69	0.25	50	50	1971.57	2015.75	44.18	25	Lowland	312	25.0	1235	1304	-69	-327.24	4	2	Young oxisol	0
RIO-02	Bolivar	Guiana Shield	8.11	-61.69	0.25	50	50	1971.57	2015.75	44.18	25	Lowland	318	25.0	1235	1304	-69	-327.24	4	2	Young oxisol	0
SAR-02	Anzoátegui	Coastal Dry Forests	9.99	-65.28	0.25	50	50	1965.02	1981.16	16.15	17	Lowland	50	26.1	878	1421	-544	-675.66	8	2	Entisol	0
SCR-04	Amazonas	Guiana Shield	1.93	-67.04	1.00	100	100	1975.54	2012.13	36.59	3	Lowland	105	26.2	3154	1162	1992	-0.81	0	0	Older Oxisol	0
SCR-05	Amazonas	Guiana Shield	1.93	-67.04	1.00	100	100	1975.62	2012.13	36.51	3	Lowland	105	26.2	3154	1162	1992	-0.81	0	0	Older Oxisol	0
SEU-01	Merida	Andes - High Elev.	8.66	-71.40	0.25	50	50	1968.81	2016.25	47.44	28	Lower-Montane	2318	20.1	1209	1141	68	-227.84	4	2	Old inceptisol	0
SEU-02	Merida	Andes - High Elev.	8.62	-71.40	0.25	50	50	1968.81	2016.25	47.44	28	Lower-Montane	2312	20.1	1078	1058	20	-265.17	4	2	Old inceptisol	0
SEU-03	Merida	Andes - High Elev.	8.64	-71.41	0.25	50	50	1961.51	2016.26	54.75	34	Lower-Montane	2421	20.2	1210	1143	67	-227.96	4	2	Old inceptisol	0
SEU-04	Merida	Andes - High Elev.	8.64	-71.41	0.25	50	50	1968.60	2016.27	47.67	27	Lower-Montane	2321	20.2	1210	1143	67	-227.96	4	2	Old inceptisol	0
SEU-05	Merida	Andes - High Elev.	8.64	-71.40	0.25	50	50	1961.78	2016.26	54.48	33	Lower-Montane	2449	20.0	1201	1137	64	-229.17	4	2	Old inceptisol	0
SEU-06	Merida	Andes - High Elev.	8.63	-71.40	0.25	50	50	1967.52	2016.26	48.74	26	Lower-Montane	2452	20.0	1197	1135	62	-229.86	4	2	Old inceptisol	0

[a] All climate data comes from the updated high-resolution grids of monthly climatic observations – the CRU TS3.10 Dataset for the 1901-2017 period. Data extracted from the Climate Research Unit (CRU) at University of East Anglia (Harris et al., 2014) at http://www.cru.uea.ac.uk/data. Water availability (WA) = Mean annual precipitation – PET.

[b] Maximum Climatic Water Deficit (CWD) as in Aragão et al., (2007) and Esquivel-Muelbert et al., (2019)). MCWD represents the most negative value of water deficit (wd), that is, the difference between precipitation (P) and evapotranspiration (E) within each year. Values in table are the annual average for the 1901-2017 period based on the CRU data.

[c] Seasonality class: 0 = Aseasonal (0-1 dry months); 1 = Slightly seasonal (2-3 dry months); 2 = Seasonal (> 3 dry months).

[d] Soil fertility class: 0 = poor nutrient; 1 = richer.

** Dates are in decimal format.

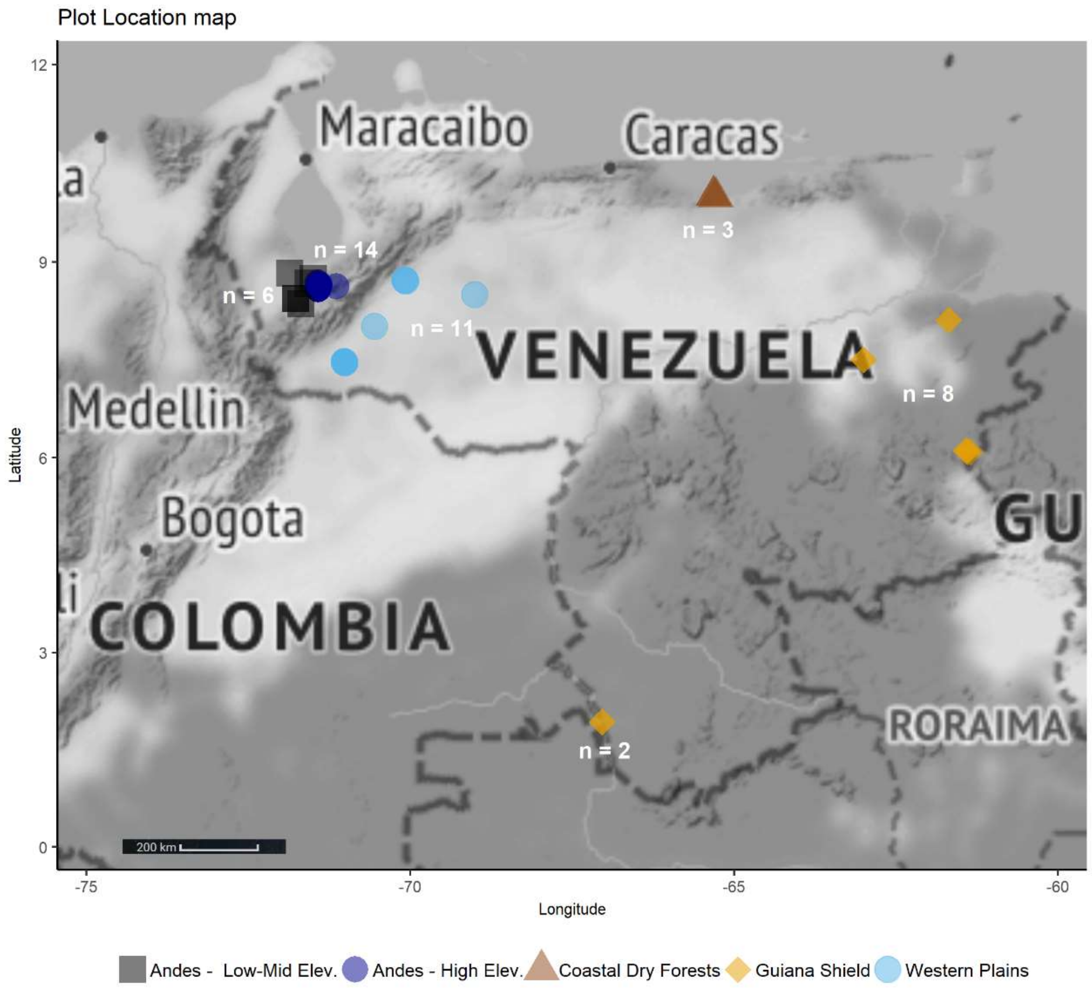


Figure S1. Geographical location of the permanent plots used in this study.

<u>Additional description of the plots</u>

Overall, mean annual precipitation is 1,512.7 ± 511.3 mm year^{-1} (standard deviation) and mean annual temperature 23.7 ± 2.9 ºC for all plots (Min = 19.9; Max = 28.02). Plots covered a wide altitudinal range from 50 to 2,450 meters above sea level (mean = 951.9 masl). Most sites are characterized by one clear dry season with on average 3.9 ± 1.9 dry months (precipitation less than 100 mm). All climatic variables were included in a Principal Component Analysis (PCA) to further characterize the environment of each region. Following recommendations from McCune et al., (2002) all variables were normalized by range prior to the PCA analysis. The PCA was conducted using the NIPALS function with a maximum of 500 iterations in the 1.7-13 version of the '`ade4`' R package (Dray et al., 2017) to better infer the associations between plots and the environmental conditions. PCA visualization was done using the 1.41 version of the '`FactoMineR`' package (Husson et al., 2017), all within the R software version 3.6.0 (R Development Core Team 2019) (Fig. S2).

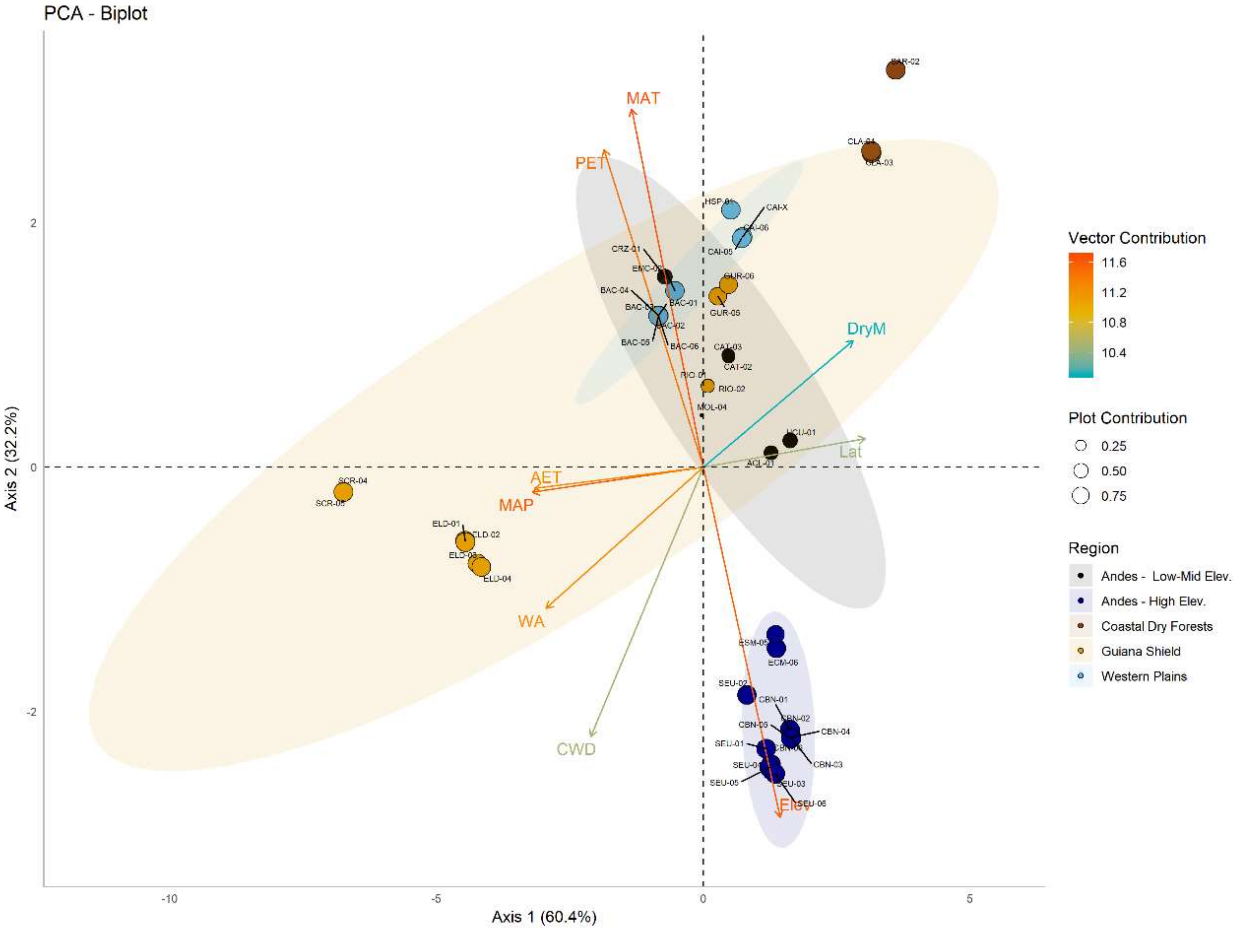


Figure S2. Principal component analysis on the environmental data for 44 Venezuelan forest plots using the information from the Climate Research Unit (Harris et al., 2014). Colors in trait vectors represent the contribution (%) to the variance in the first two axes, with MAT and elevation being the most prominent factors. Circle size indicates the contribution of each plot to the variation in the first two axes of the PCA. Elev = Elevation; CWD = Maximum climatic water deficit. MAP = Mean Annual precipitation; MAT = Mean Annual Temperature; PET = Potential evapotranspiration; AET = Actual evapotranspiration; DryM = Number of months with precipitation < 100 mm; WA = Water available (MAP – PET).

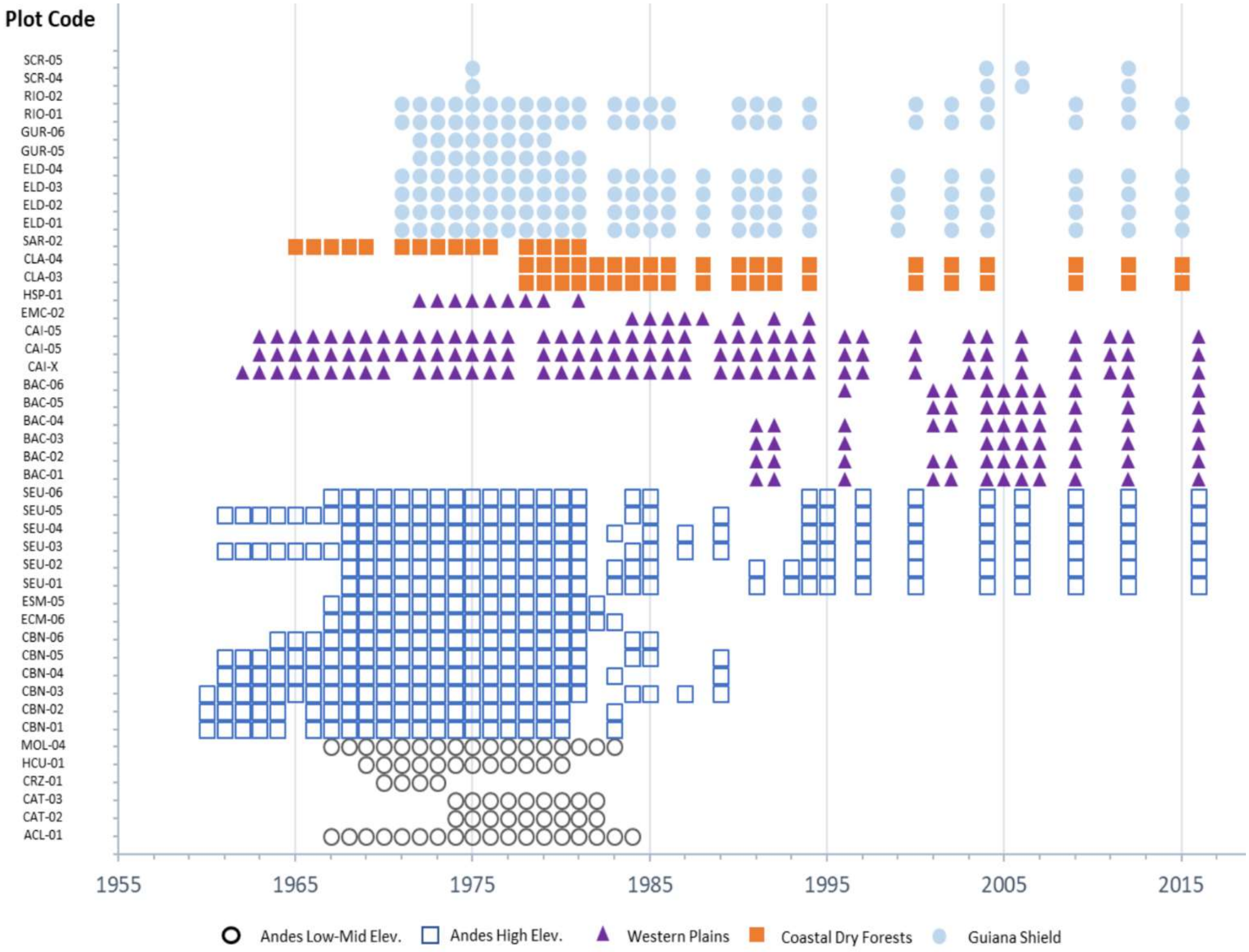


Figure S3. Number of censuses in each plot and region. For details on individual plots see Table S1.

Soil description

Geomorphologically, there are clear differences with regards to soil genesis among all sites. Soils of the Guiana Shield fall into two major groups: Acrisols or Ferrasols (Hammond 2005), typically with low fertility and high iron concentrations. For two of the plots in this region (ELD-3 and ELD-4) soils are mostly shallow with some trees growing directly on rocks that are highly resistant to weathering, with these being classified as Leptosols (Quesada et al., 2011). Plots located in the southern portion of the Guiana Shield region (SCR-04, SCR-05) correspond to the typical definition of a *´Terra Firme´* forest located on hills of Ferrasols covered by a sandy layer, and to a lesser extent by Acrisols and/or Alisols (Cuevas & Medina 1986). Soils are well-structured, and due to the presence of patches of macro-porosity and lower bulk density, roots can often penetrate to deeper horizons (Quesada et al., 2011). Montane forests located in the Andean region are established where soils are shallow and generally less developed (Cambisols) with increasing slope, and with a higher effective depth and development in flat or partially flat terrains, which are also typically enriched with clay (older Cambisols and/or Acrisols/Alisols) (Ramirez-Angulo et al., 2002). Poorly-developed soils are the main feature in the lower montane and dry forests of the eastern coast of Venezuela (plots CLA-03, CLA-04, SAR-03), characterized by clay-loamy textures (Delaney et al., 1998; Torres-Lezama et al., 2002). Finally, the Western Plains region is formed as a Pleistocene-Holocene depositional area of Andean material mostly in the form of alluvial terraces, with microtopographic variations largely determining soil texture and structure (Kammesheidt et al., 2001; Schargel 2015), and with water availability being a limiting factor for plants during dry season (Ramirez Angulo et al., 2010).

Appendix S2. Additional explanation on the methods used in this study.

Estimation of turnover rates, aboveground biomass and woody productivity

We estimated demographic rates (% year^{-1}) for each plot based on the instantaneous rates approach using the following equations reported in several studies (Swaine et al., 1987; Phillips et al., 2004; Báez et al., 2015; Johnson et al., 2016):

$$\text{Annual mortality } (m) = \frac{\ln(n_0) - \ln(n_0 - n_\mathrm{D})}{t} x\ 100$$

$$\text{Annual recruitment } (r) = \frac{\ln(n_0 - n_\mathrm{D} + n_\mathrm{r})/(n_0 - n_\mathrm{D})}{t} x\ 100$$

Where: n_0 is the number of individuals alive at the beginning of the census interval, n_D is the number of stems that died in the interval, n_r is the number of individuals recruited between censuses, and t corresponds to census interval length. For an analysis of the differences in turnover rates between regions we refer the reader to a previous study (Vilanova et al., 2018).

Aboveground biomass of each plot was calculated using the moist forest allometric equation from Chave et al., (2005):

$$\mathrm{AGB} = 0.0509 \text{ x } \rho D^2 H$$

Where AGB is the biomass of each stem (kg), D is stem diameter (cm), ρ is stem wood density (g cm^{-3}) and H is stem height (m). The height of each tree was estimated from tree diameter using a height-diameter Weibull equation with different coefficients for each region (Feldpausch, Lloyd, Lewis, Brienen, Phillips, et al., 2012). The wood density of each tree was assigned on a taxonomic basis from the pan-tropical database of Zanne et al., (2009), first by species, and when this was not available we used data at the genus and family levels, while mean plot-level wood density values were used when taxonomic information was missing. We assumed carbon to be 50% of total dry biomass, and as suggested by Malhi et al., (2006) and Johnson et al., (2016) we added an additional 6.2% of carbon to each AGB-plot estimate to account for the unmeasured small trees (<10 cm in diameter).

Estimation of quadratic mean diameter (QMD) and Stand Density Index (SDI).

$$QMD = \sqrt{\frac{\left(BA/N\right)}{0.00007854}}$$

Where:

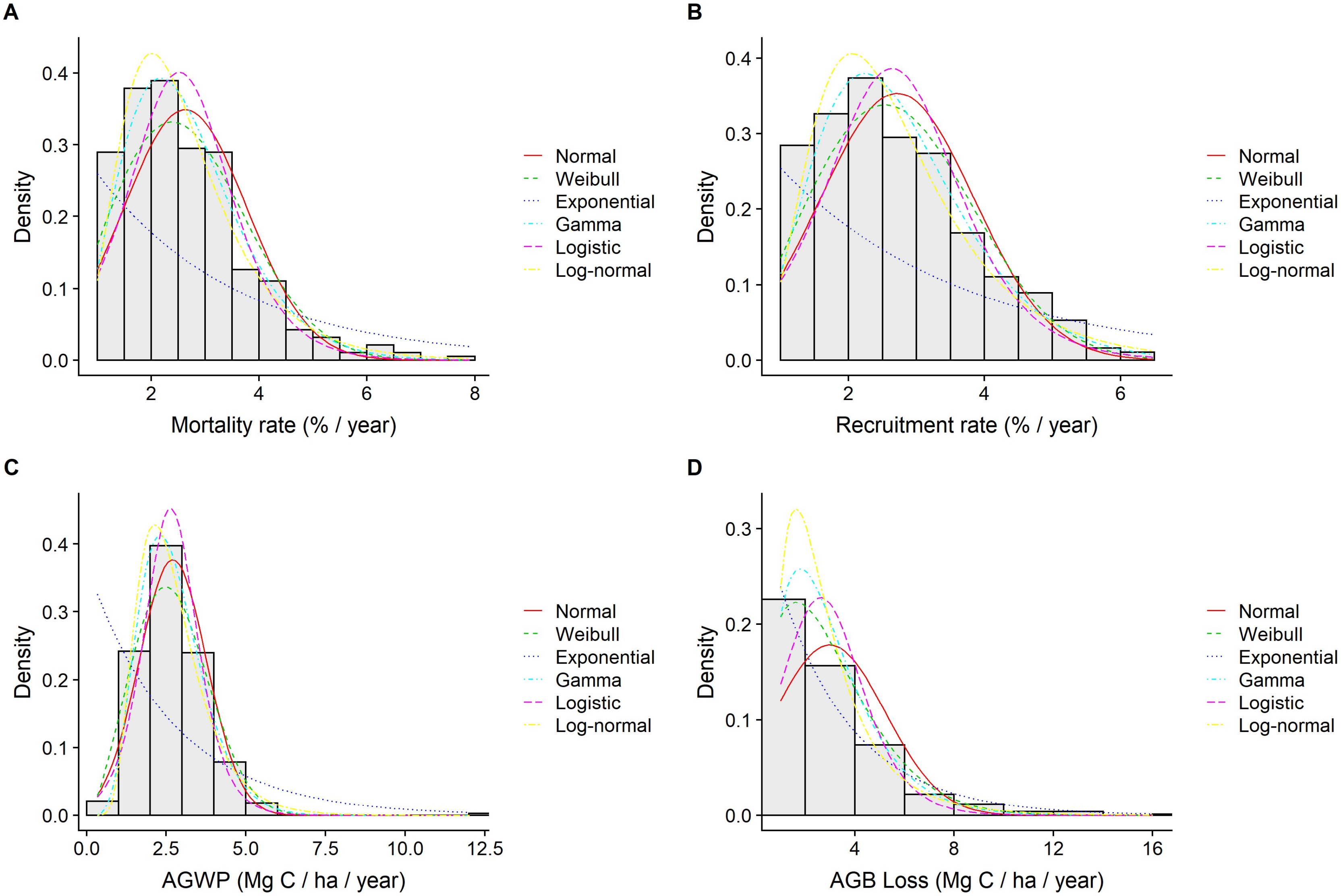
QMD = Quadratic Mean Diameter or quadratic stand diameter for any given census in cm;
BA = plot-based basal area at any given census in m^2 ha^{-1};
N = Stand density in stems ha^{-1};
0.0007854 is a constant

$$SDI = N \times \left(\frac{QMD}{25.4}\right)^{1.605}$$

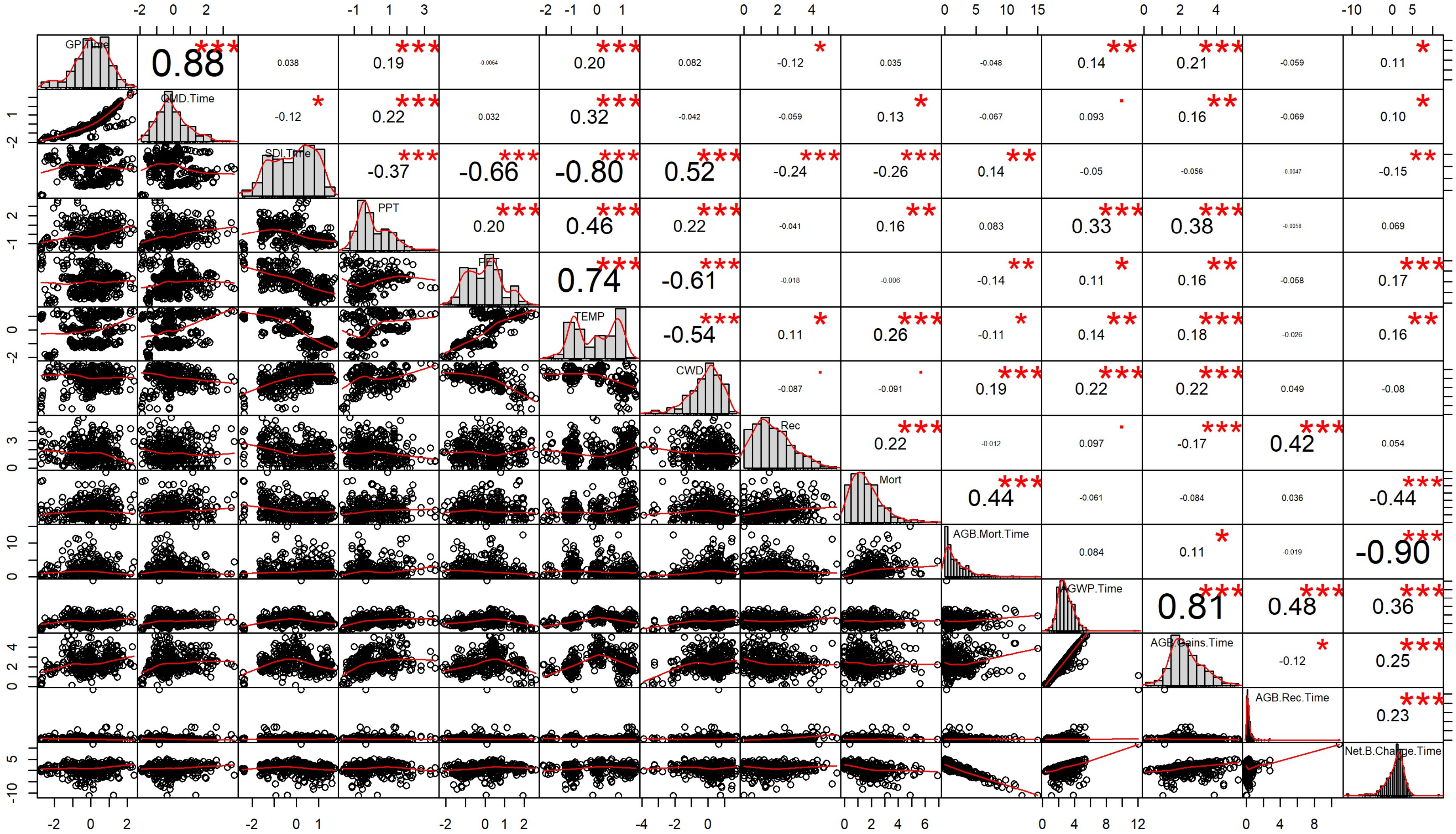
Where:

SDI = Stand Density Index for any given census interval;
QMD = Quadratic Mean Diameter or quadratic stand diameter for any given census in cm;
N = Stand density in stems ha^{-1};
1.605 is a constant

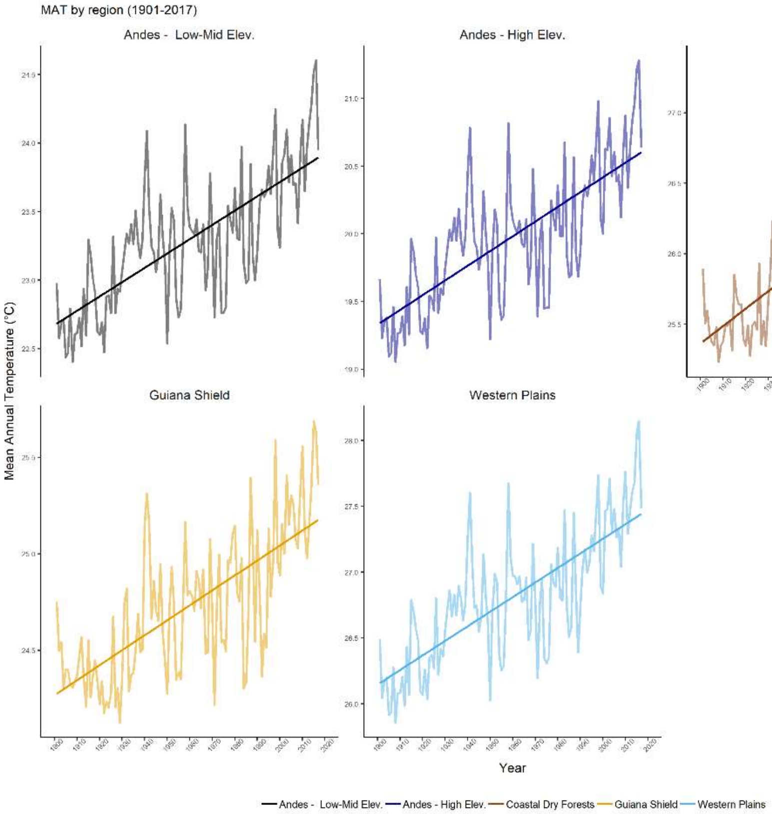
Appendix S3. Graphics of different statistical distribution approaches of A) mortality rates; B) recruitment rates; C) Aboveground woody productivity – AGWP), and D) AGB loss from mortality. In our analyses, all models were fitted using the *log-normal* distribution based on the lowest value of the AIC in response variable.

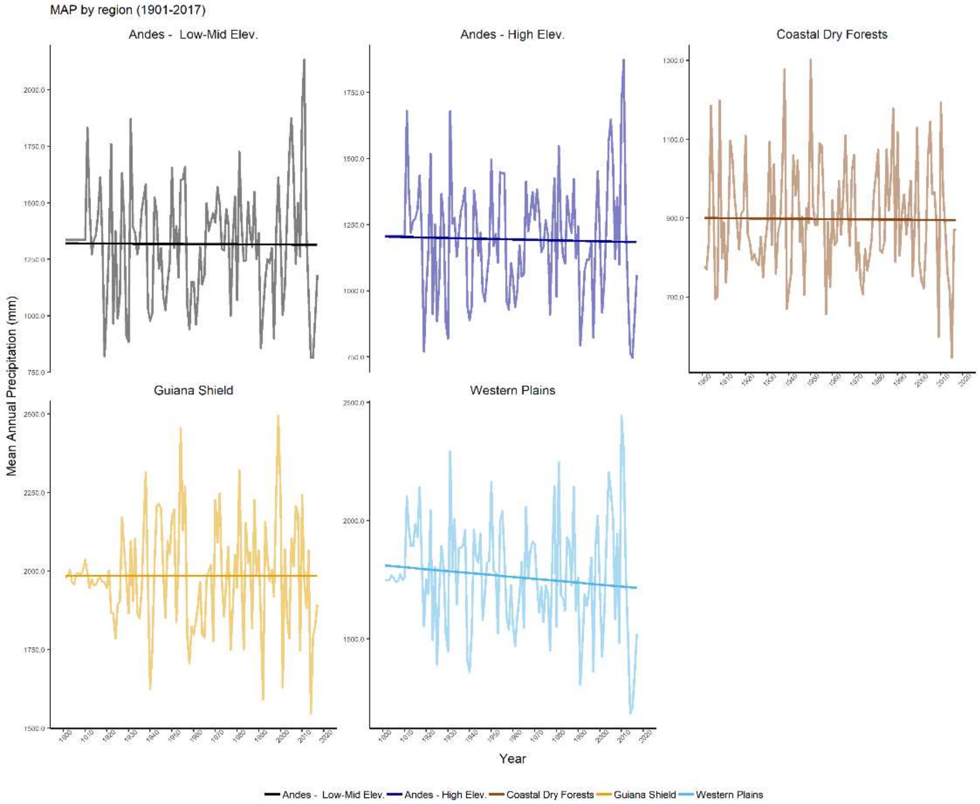


Appendix S4. Pair-wise Pearson correlations between all explanatory and response variables in this study.



Appendix S4. Climate trends by region.





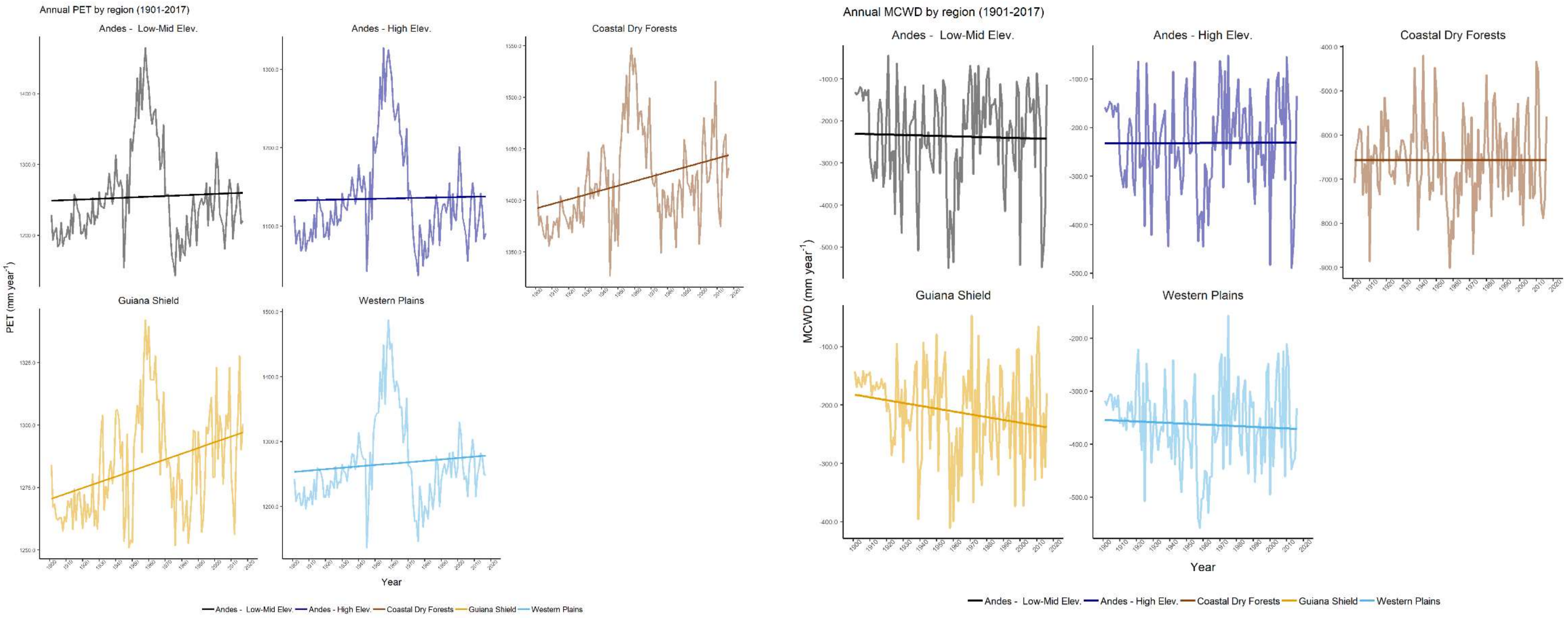


Figure S4. Linear trends in mean annual temperature (MAT), mean annual precipitation (MAP), potential evapotranspiration (PET) and maximum climatic water deficit (MCWD) for five regions in Venezuela based on the Climate Research Unit (CRU) (Harris et al., 2014). MAT increased significantly in all regions. MAP declined in all regions but the Guiana Shield, and the slope was significant only in the case of the Western Plains. PET increased in all regions but not significantly for both Andean subregions. The observed increase in the negative values of the MCWD was found for all regions but was significant ($p<0.05$) only in the Guiana Shield.

Appendix S5. Additional information on turnover rates.

Table S2. Trends in turnover rates (i.e. recruitment and mortality) for regions, elevation, seasonality and soil fertility classes. In brackets the number of plots (n) per group and in bold all significant values ($p < 0.05$). Mortality significantly increased in all but one among the categories in which the plots were classified, where the slope was still positive.

Grouping variable	**Recruitment rates**		**Mortality rates**	
	Slope (% year^{-1})	**p-value**	**Slope (% year^{-1})**	**p-value**
All plots combined (n=44)	0.02	**< 0.001**	0.02	**< 0.001**
Region				
Andes Low-Mid elevation (n = 6)	0.05	**< 0.001**	0.18	**< 0.001**
Andes High elevation (n = 14)	0.02	**< 0.001**	0.01	**< 0.001**
Coastal Dry Forests (n = 3)	-0.01	**< 0.001**	0.01	**< 0.001**
Guiana Shield (n = 10)	-0.01	**< 0.001**	0.01	**< 0.001**
Western Plains (n = 11)	0.01	**< 0.001**	0.02	**< 0.001**
Elevation				
High (> 1500 meters; n = 14)	0.02	**< 0.001**	0.01	**< 0.001**
Low (< 1500 meters; n = 30)	-0.01	**< 0.001**	0.02	**< 0.001**
Seasonality				
Aseasonal (0-1 dry months; n = 4)	-0.01	**< 0.001**	0.002	0.15
Moderately seasonal (1-3 dry months; n = 7)	0.01	**< 0.001**	0.02	**< 0.001**
Highly seasonal (> 3 dry months; n = 33)	0.01	**< 0.001**	0.02	**< 0.001**
Soil fertility				
High (n = 19)	0.01	**< 0.001**	0.03	**< 0.001**
Low (n = 25)	0.0002	0.73	0.01	**< 0.001**

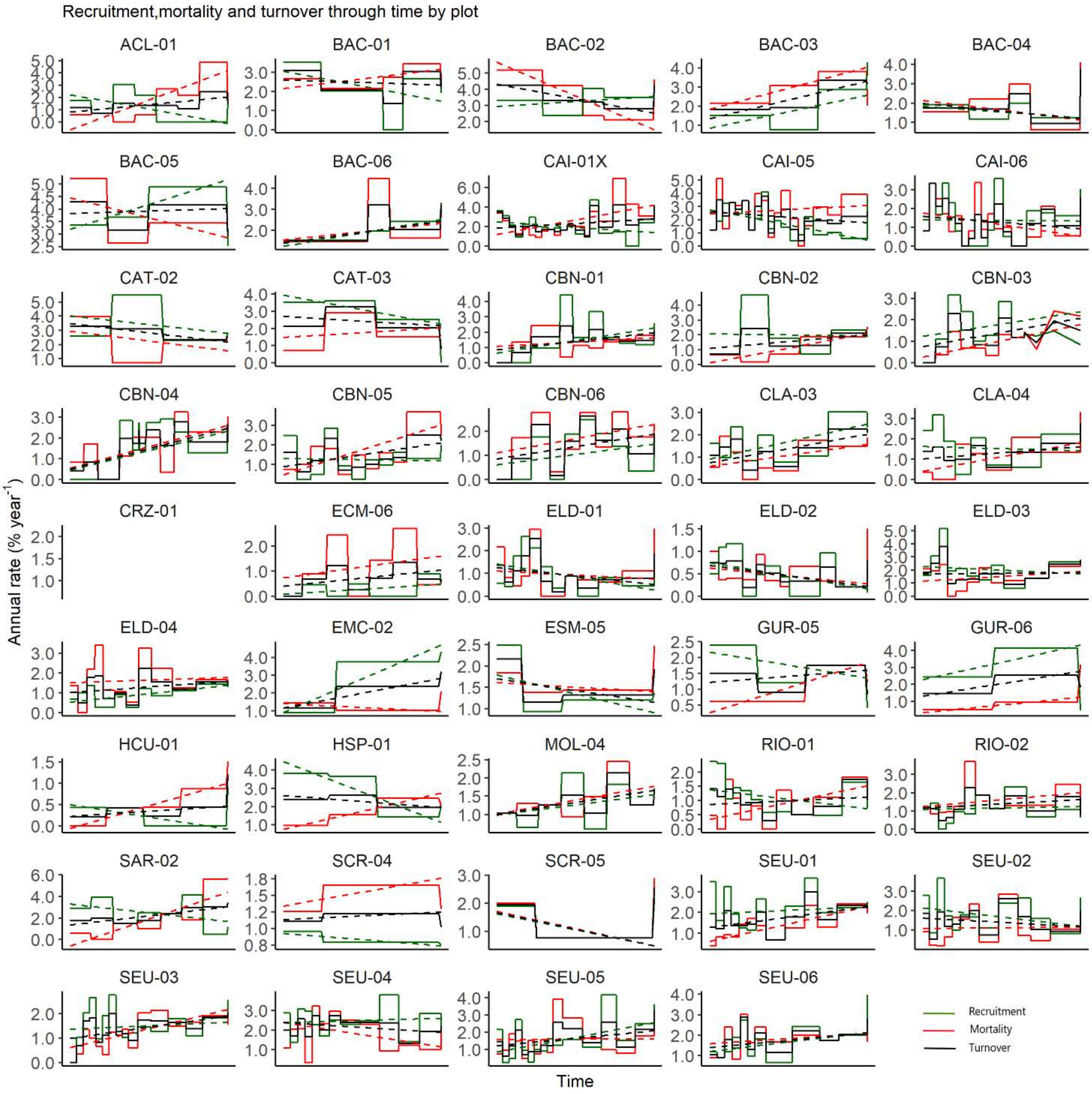
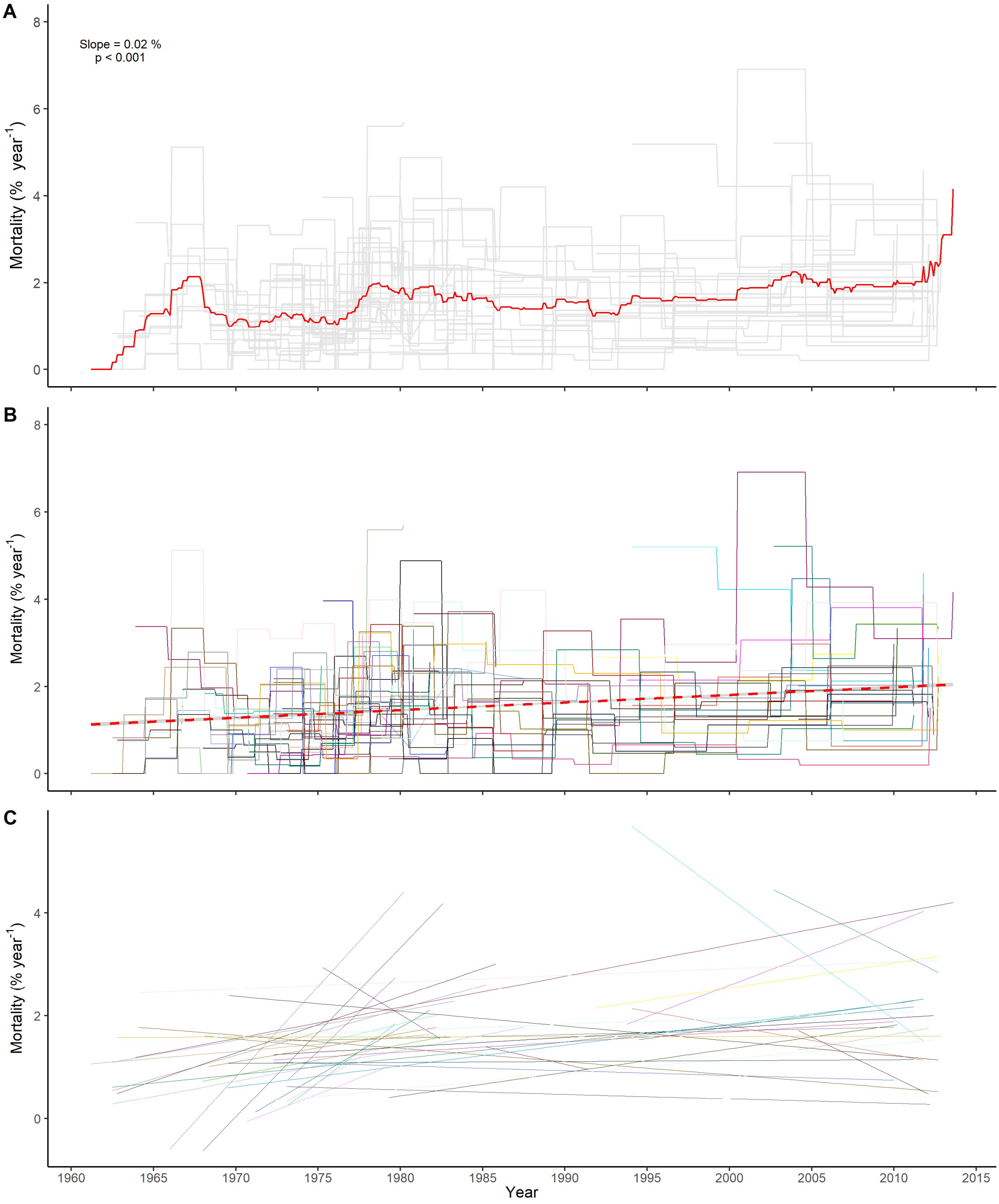
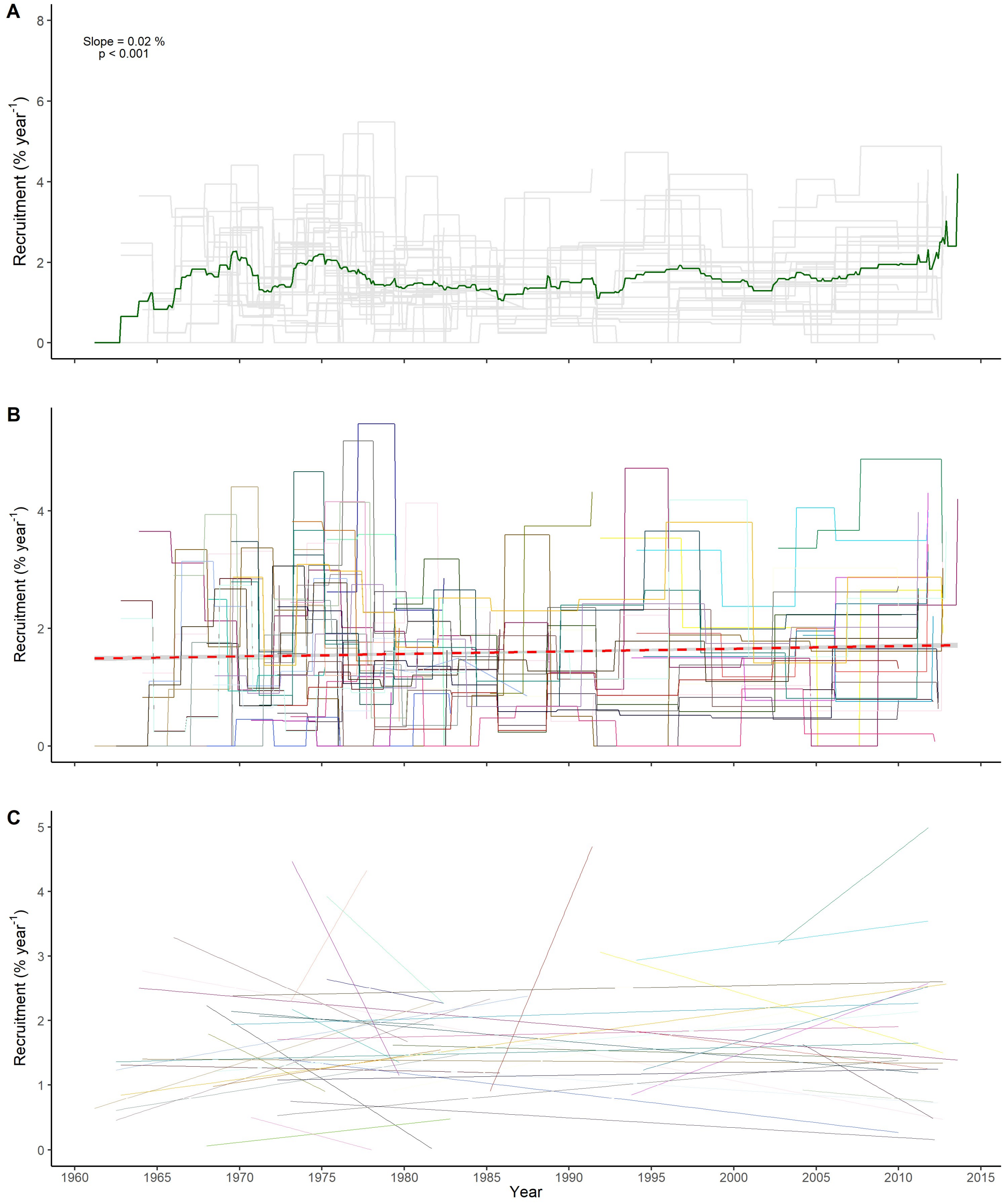


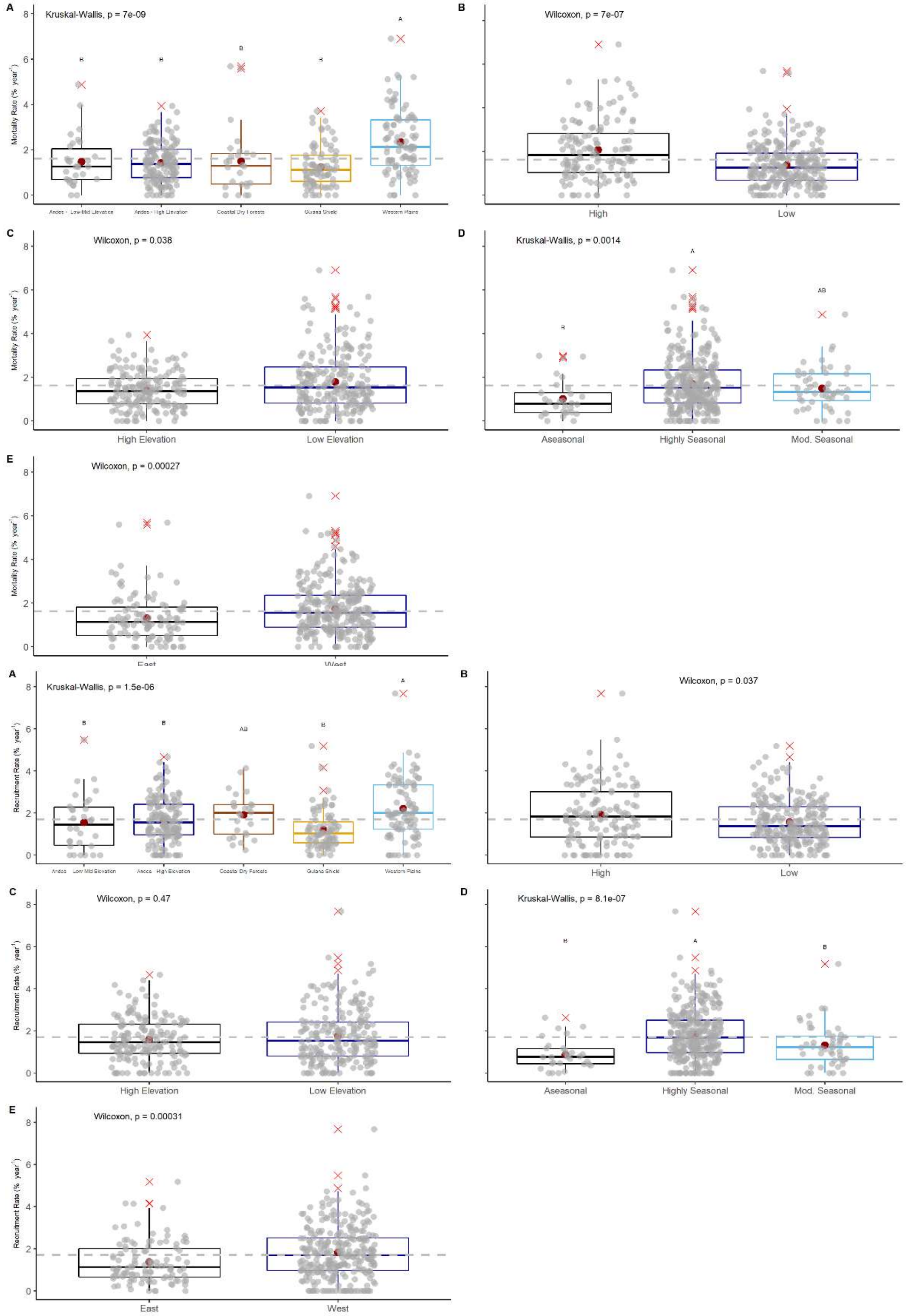
Figure S5. Temporal trends in recruitment (green), mortality (red) and its average (turnover - black) for 43 permanent forest plots in Venezuela. With one interval in CRZ-01 trends for this plot were not included. A histogram of slopes is included in Figure 2 in the main text. Dashed lines are linear trends for each variable.



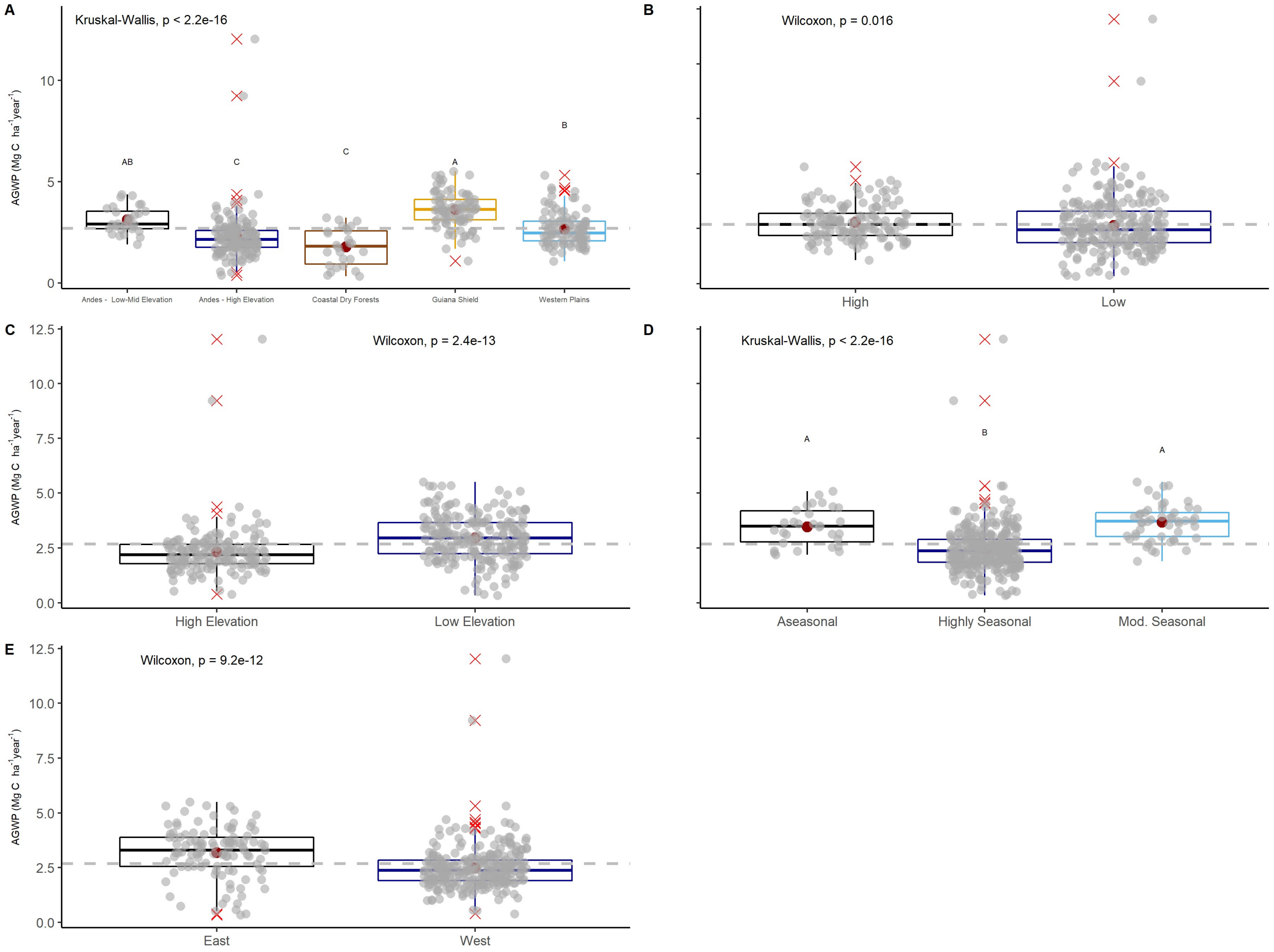
Extra Figure Appendix S5. Temporal trends in mortality rates for 44 permanent forest plots in Venezuela. A) Mean annual rate of mortality (red line) along with the individual trends per plot; B) Temporal trends for individual plots; C) Slope trends in mortality rates for each plot. A histogram of slopes is included in Figure 2 in the main text.



Extra Figure Appendix S5. Temporal trends in recruitment rates for 43 permanent forest plots in Venezuela. A) Mean annual rate of recruitment (green line) along with the individual trends per plot; B) Temporal trends for individual plots; C) Slope trends in recruitment rates for each plot. A histogram of slopes is included in Figure 2 in the main text.



Extra figure Appendix S5. General differences in turnover rates (Mortality upper panel; Recruitment lower panel) between regions, soil fertility, elevation, seasonality and location in Venezuelan forests.



Extra Figure Appendix S5. General differences in aboveground woody productivity between regions, soil fertility, elevation, seasonality and location in Venezuelan forests.

Appendix S6. Additional information on AGB components.

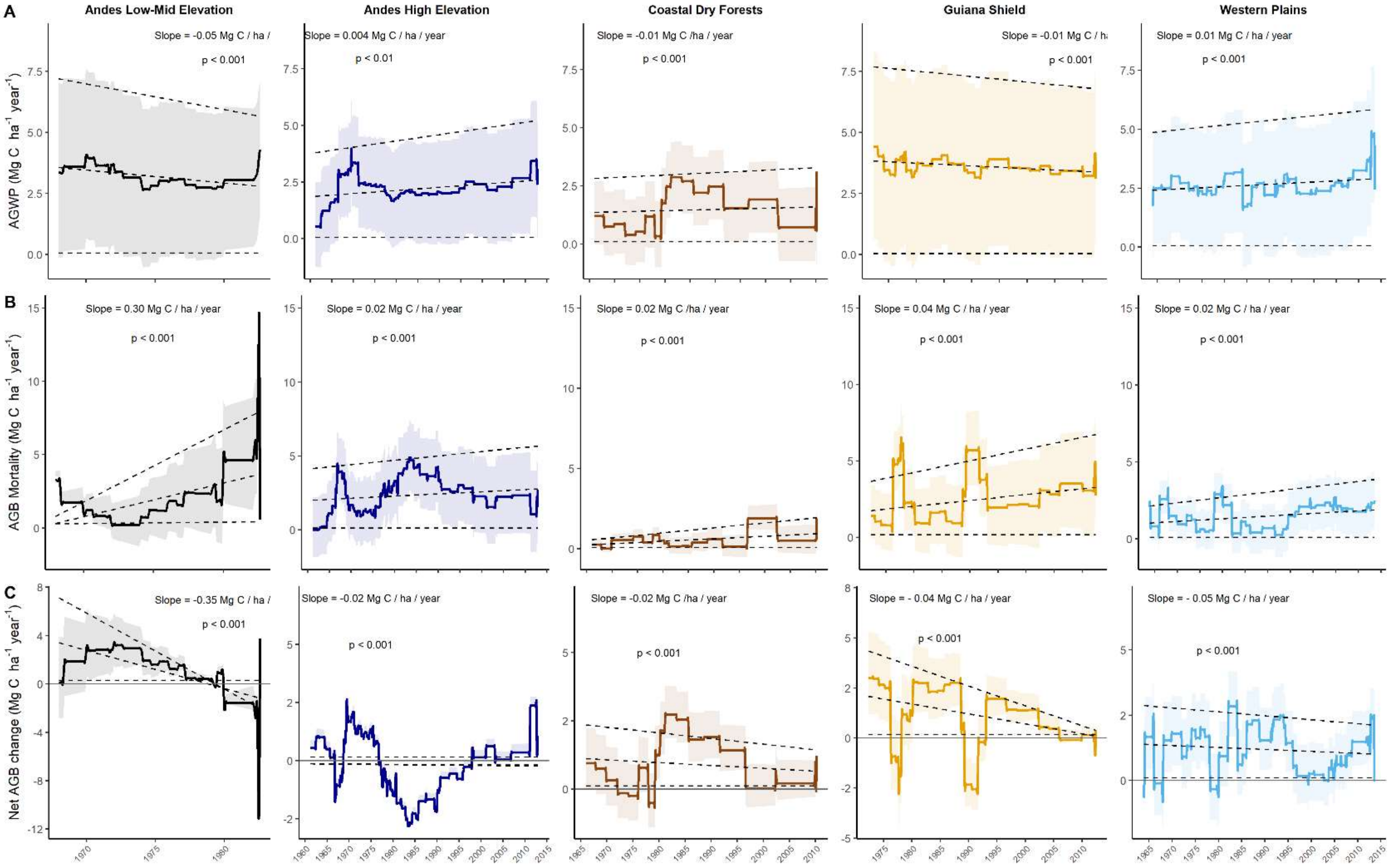


Figure S6. Temporal trends in A) AGWP, B) AGB Loss and C) Net biomass change for five different regions in Venezuelan forests, including 95% confidence intervals (CI). Dashed lines represent the trends from general additive models (GAMs) for the observed values and both the lower and upper limits of the 95% CI intervals. Mean slope and p-values are included.

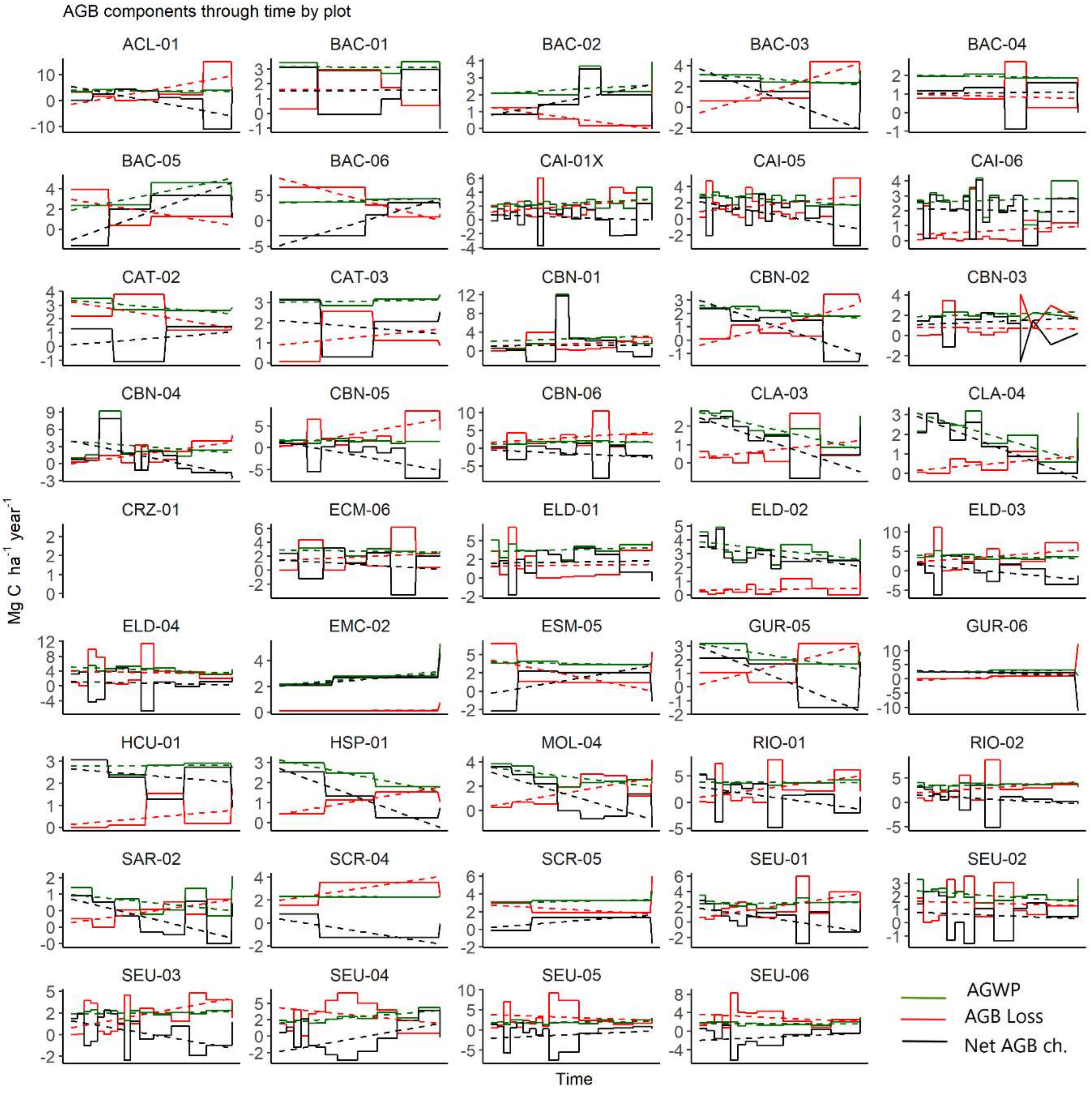


Figure S7. Temporal trends in AGWP (green), AGB loss from mortality (red) and Net AGB change (black) for 43 permanent forest plots in Venezuela. With one interval in CRZ-01 trends for this plot were not included. A histogram of slopes for each variable is included in Figure 3 in the main text. Dashed lines are linear trends for each variable.

Appendix S7. Temporal trends in Quadratic Mean Diameter, Stand Density Index, and Gap Phase Index for five regions in Venezuela.

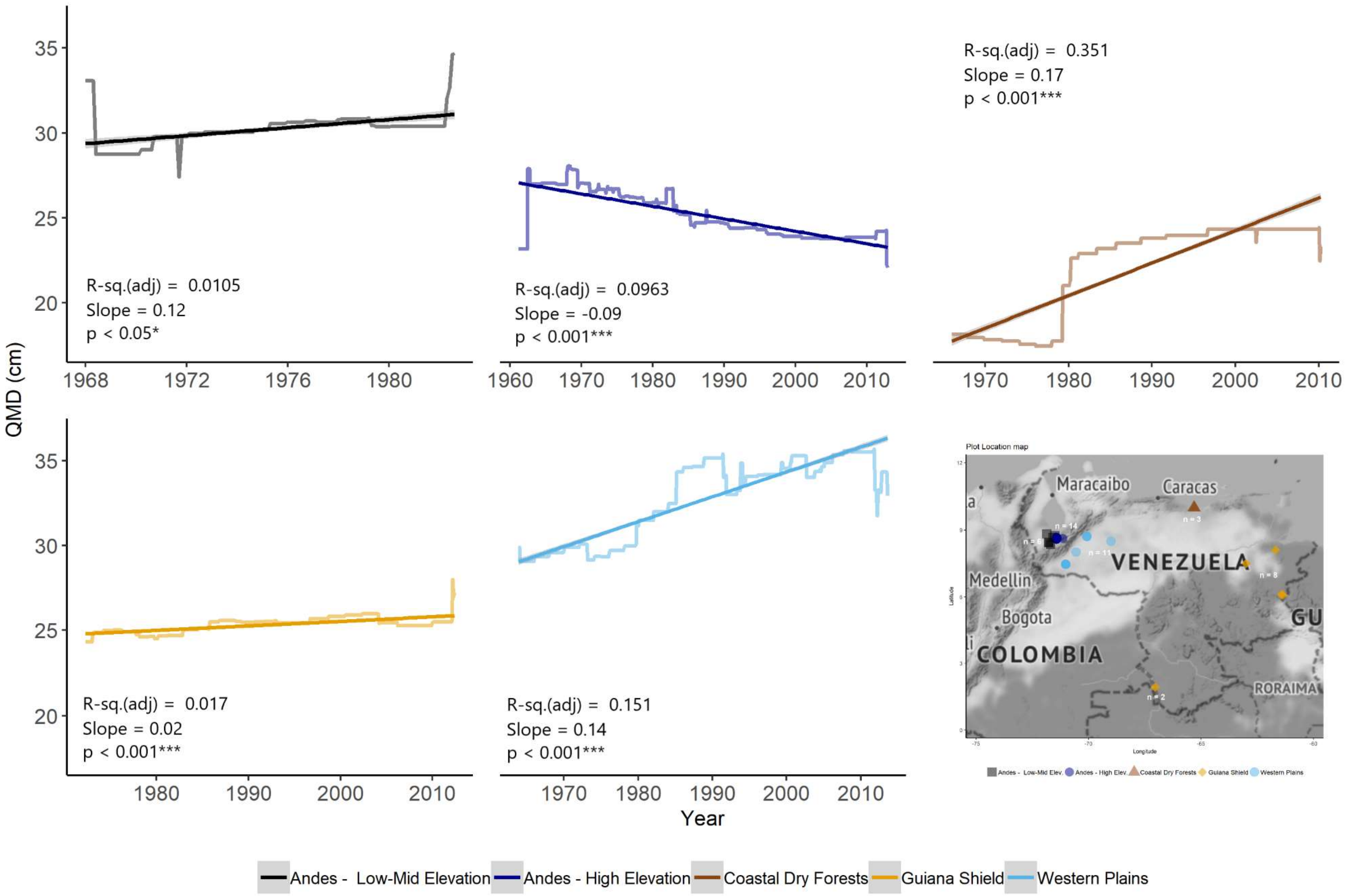


Figure S8. Regional-based temporal trends in the Quadratic Mean Diameter (QMD). The adjusted R^2, slope and *p*-values are derived from a simple *Response vs Time* generalized additive model (GAM).

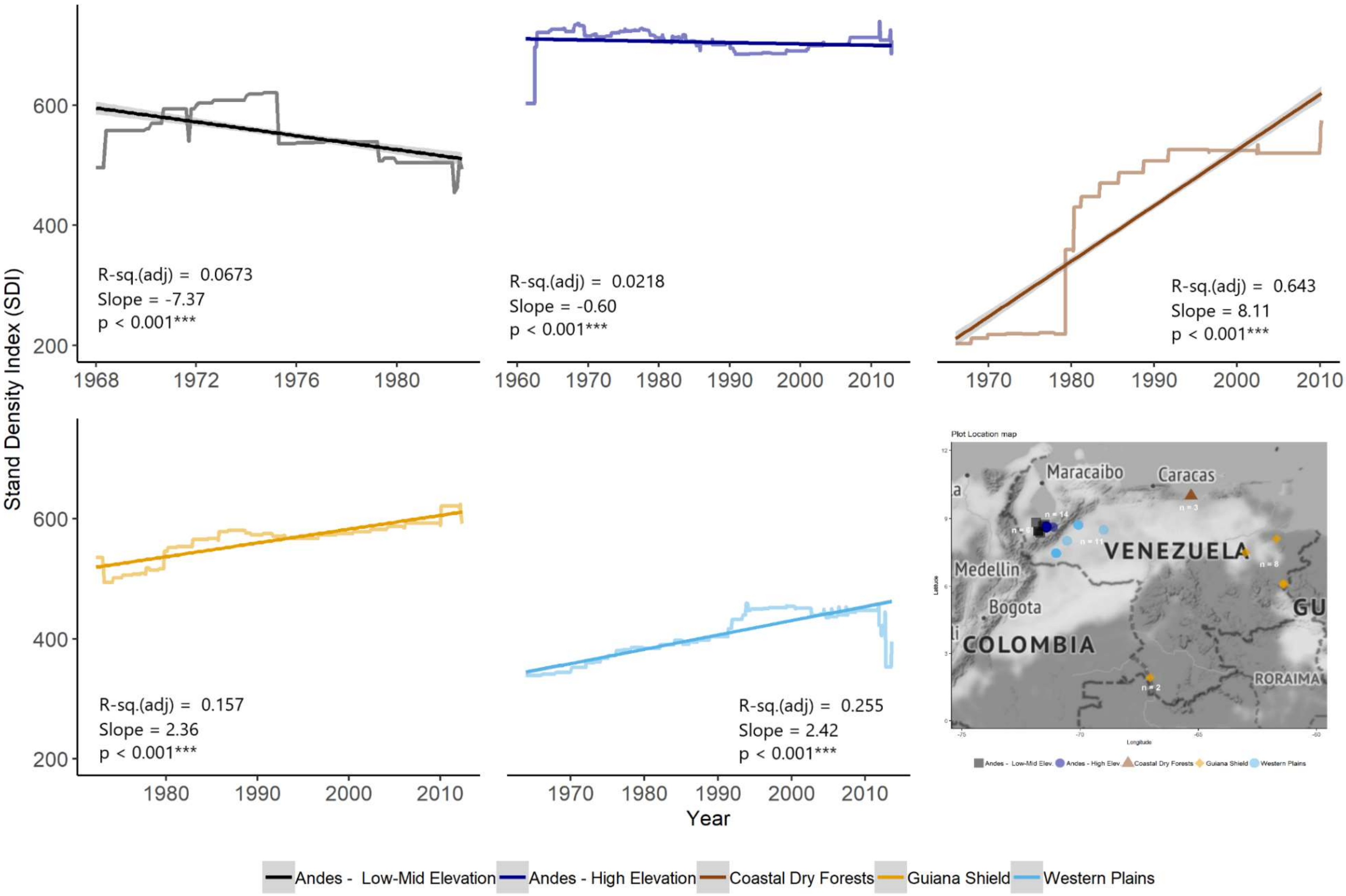


Figure S9. Regional-based temporal trends in the Stand Density Index (SDI). The adjusted R^2, slope and *p*-values are derived from a simple *Response vs Time* generalized additive model (GAM).

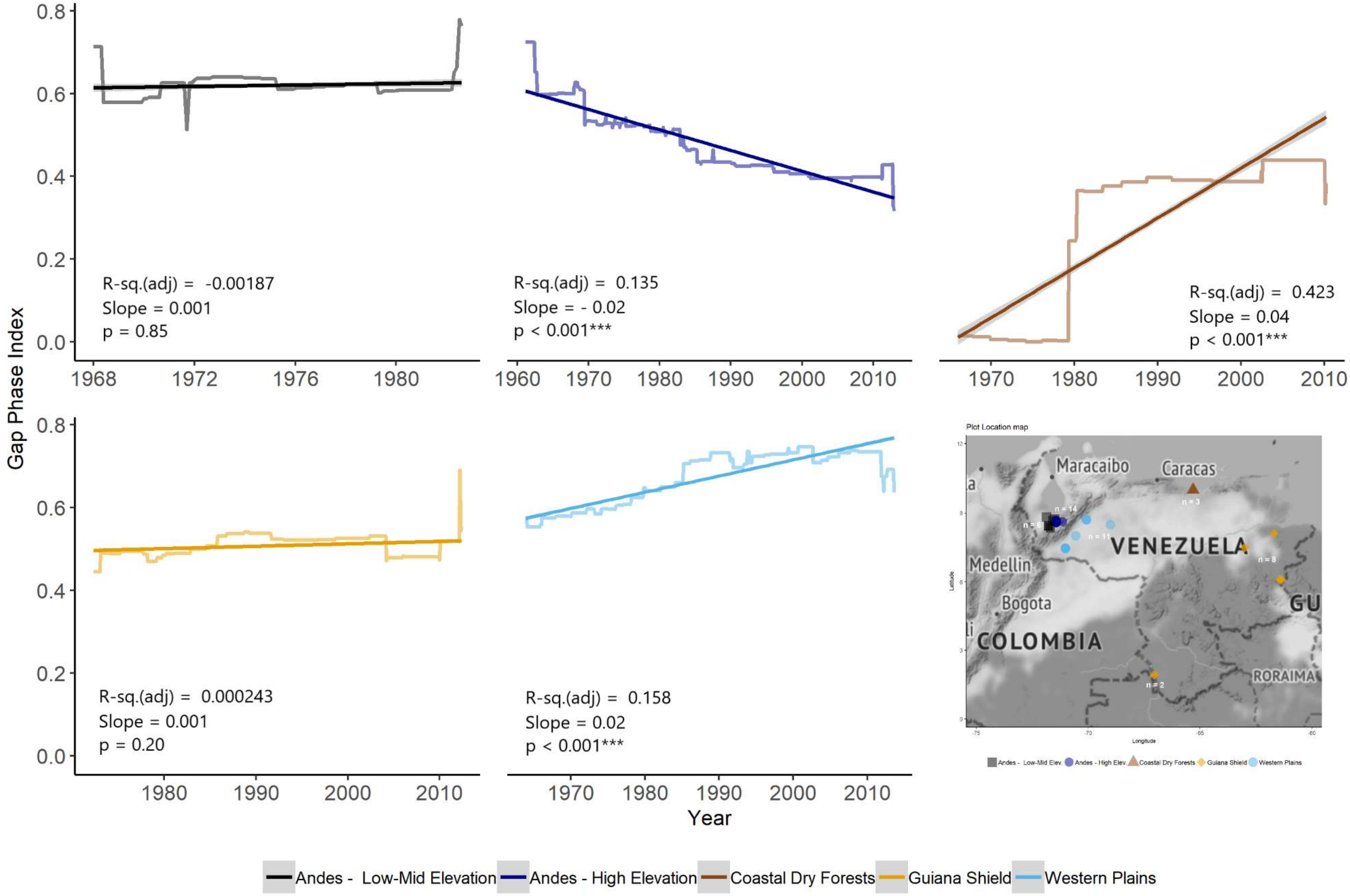


Figure S10. Regional-based temporal trends in the Gap Phase Index (GPI). The adjusted R^2, slope and *p*-values are derived from a simple *Response vs Time* generalized additive model (GAM).

Appendix S8. Analysis of relative change in aboveground biomass (AGB).

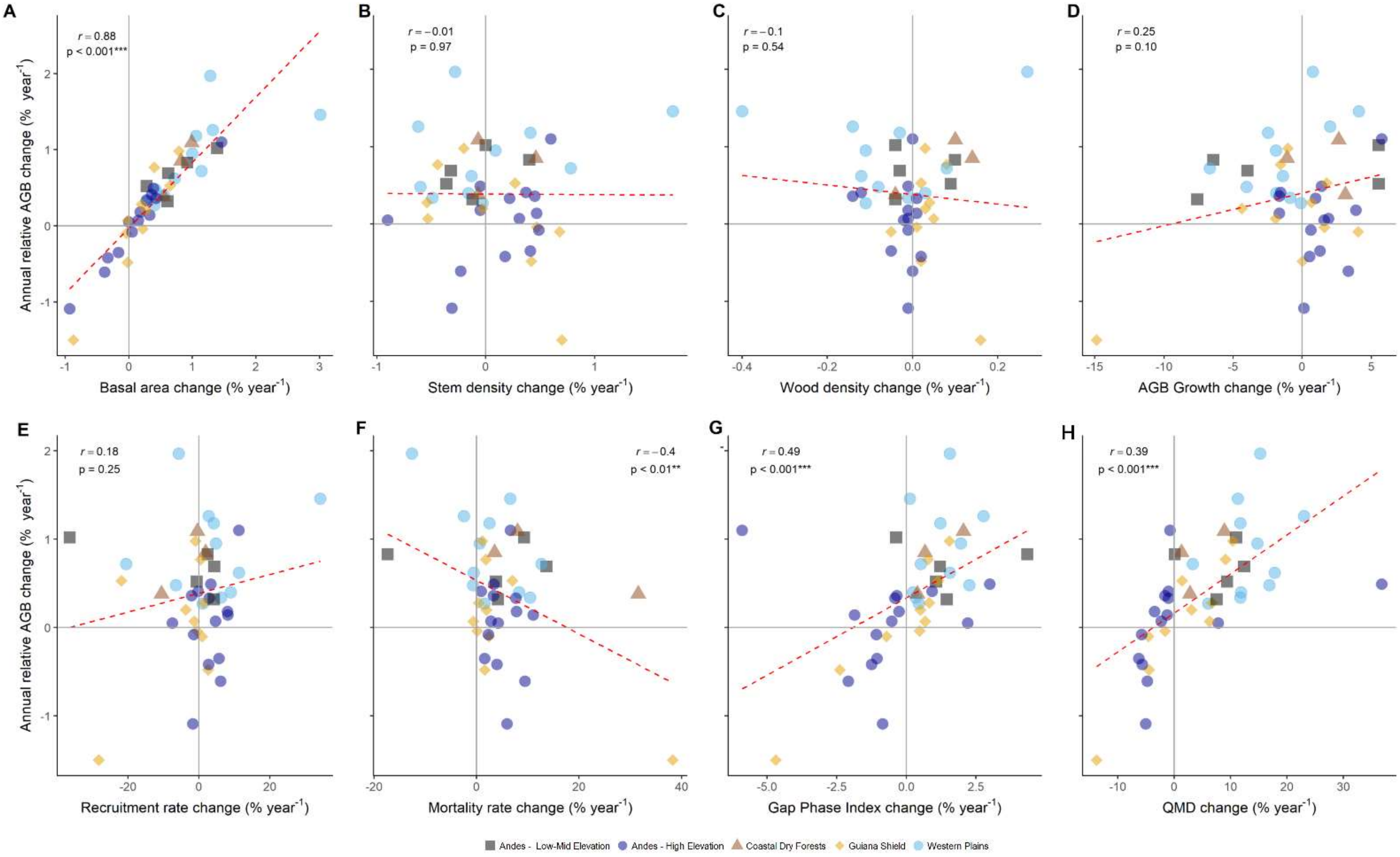


Figure S11. Plot and regional-based relationships between the relative change in AGB (% $year^{-1}$) and the relative change of a selected group of predictors including a) Basal area, b) number of stems, c) plot-level wood density, d) biomass from growth (AGB_{growth}), e) recruitment rates, f) mortality rates, G) Gap phase index (GPI), and h) quadratic mean diameter (QMD). Red dashed lines represent the trend from a linear model. The correlation coefficient (*r*) and p-values are included in each case.

Appendix S9. Additional information on the generalized mixed models used to explore drivers of stand dynamics and structure.

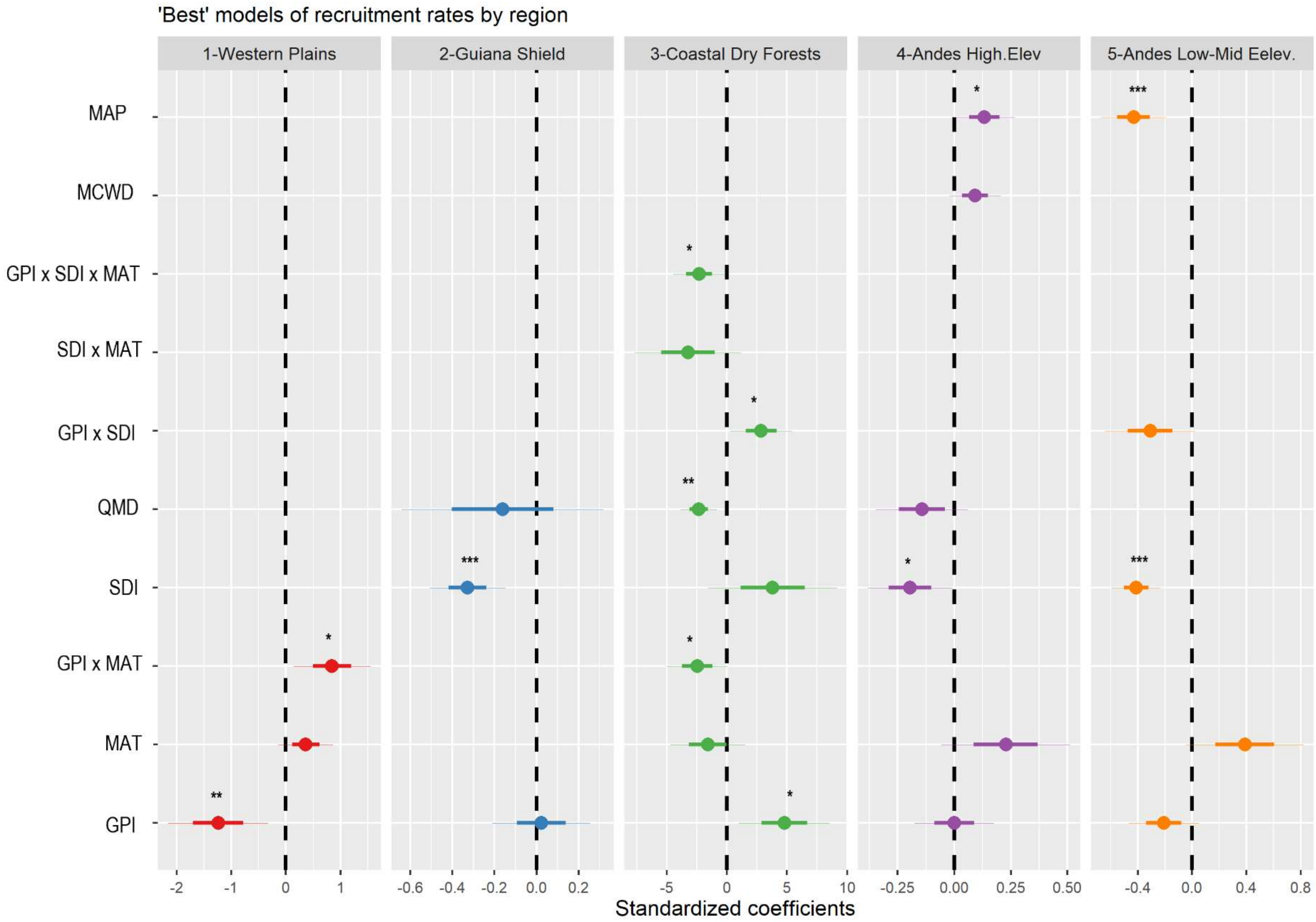


Figure S12. 'Best' selected statistical models to explain trends in recruitment rates in five different regions in Venezuela. The standardized coefficients with 95% confidence intervals from each model are shown. Significant values, negative or positive, are labelled with asterisks (*p<0.05; ** p<0.01; *** p<0.001).

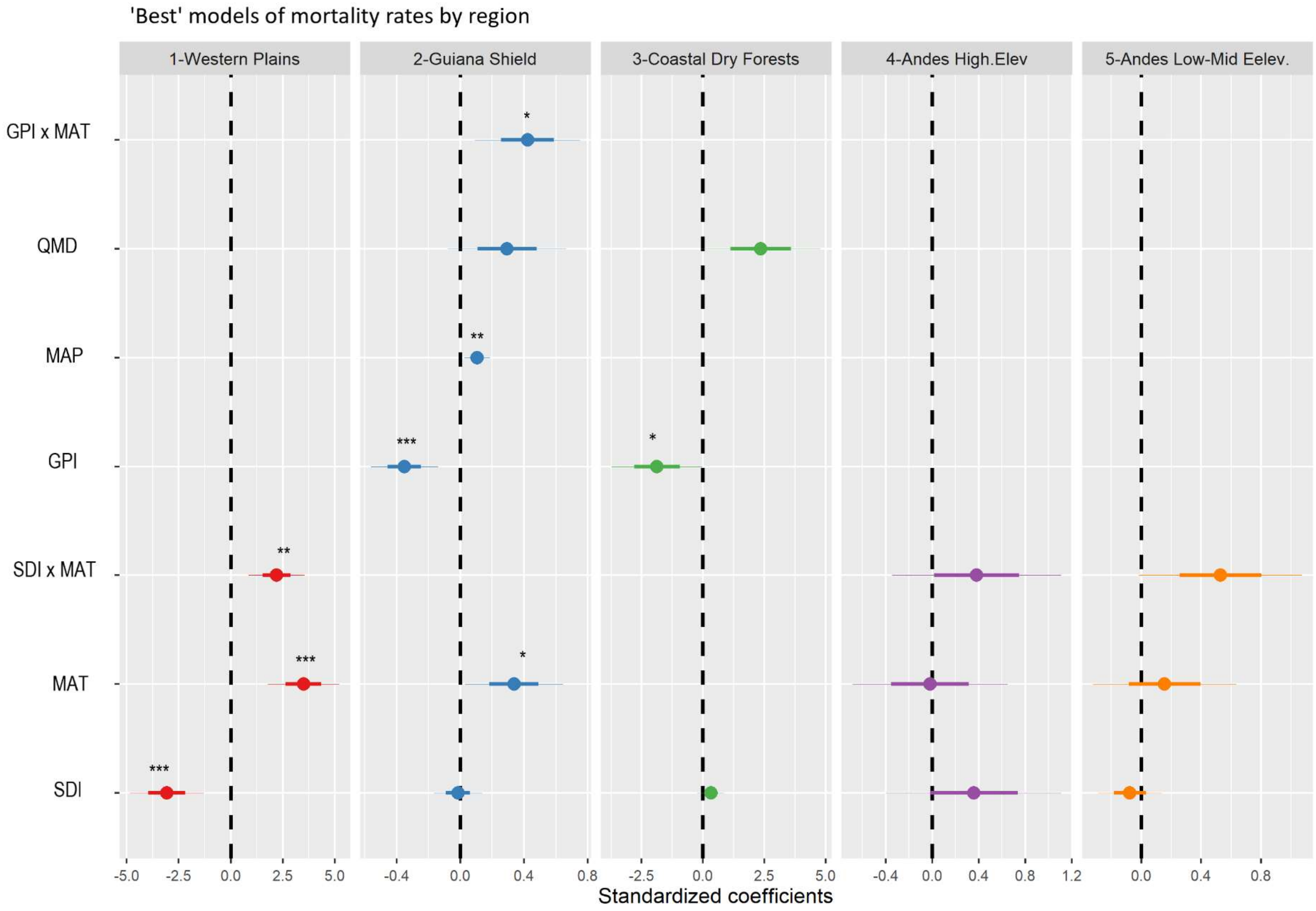


Figure S13. 'Best' selected statistical models to explain trends in mortality rates in five different regions in Venezuela. The standardized coefficients with 95% confidence intervals from each model are shown. Significant values, negative or positive, are labelled with asterisks (*p<0.05; ** p<0.01; *** p<0.001).

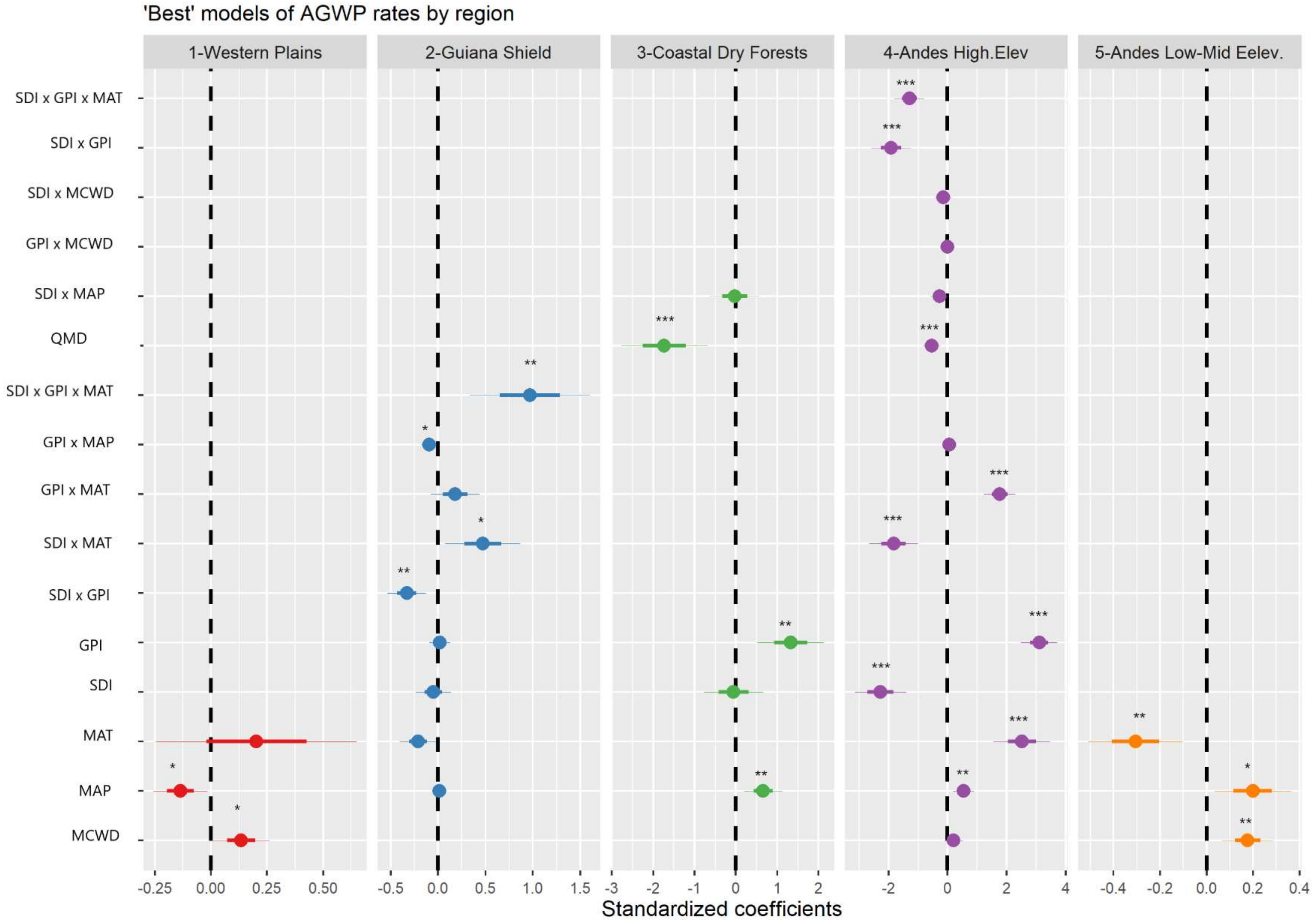


Figure S14. 'Best' selected statistical models to explain trends in aboveground woody productivity in five different regions in Venezuela. The standardized coefficients with 95% confidence intervals from each model are shown. Significant values, negative or positive, are labelled with asterisks (*p<0.05; ** p<0.01; *** p<0.001).

Functional trait data collection in montane forests in the Andes

Photo: Luis Gámez

CHAPTER 4

A FUNCTIONAL TRAIT-BASED APPROACH TO STUDY THE STRUCTURE AND STEM TURNOVER OF TROPICAL FORESTS: AN ANALYSIS FROM TWO CONTRASTING SITES IN NORTHERN SOUTH AMERICA

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A FUNCTIONAL TRAIT-BASED APPROACH TO STUDY THE STRUCTURE AND STEM TURNOVER OF TROPICAL FORESTS: AN ANALYSIS FROM TWO CONTRASTING SITES IN NORTHERN SOUTH AMERICA

ABSTRACT

Previous work has suggested the existence of a slow–fast continuum in lowland tropical forests where resource-rich Amazon forests have higher woody productivity (AGWP), faster stem recruitment and mortality (*r*, *m*), but often lower biomass (AGB) than resource-poor forests, and with these stand-level metrics being closely associated to the traits of their constituent tree species. Here, using data from long-term sample plots from western Venezuela, I extend this approach to examine whether such considerations also apply to the montane-lowland forest contrast. Specifically, I expect lowland forests to be dominated by acquisitive traits (e.g. high Specific Leaf Area – SLA), influencing faster stem dynamics and AGWP, while conservative traits (e.g. high leaf mass per area - LMA) would govern stand dynamics in high-elevation forests with slower turnover, reduced AGWP but higher AGB. I employed a principal component analysis combined with linear mixed models, using data from 10 functional leaf and stem-level traits to describe the functional trait space in two contrasting tropical environmental settings, and analyze the differences in stand-level turnover rates (i.e. recruitment – *r* and mortality – *m*), aboveground biomass (AGB) and productivity (AGWP), using traits, soil nutrient content and chemistry, and stem density as potential predictors. Results show that both sites are noticeably different ($p < 0.001$) with regards to their structure, dynamics and function, with lowland forests having higher annual recruitment (2.67 ± 0.55 % year^{-1} – Mean ± Standard deviation), mortality (3.09 ± 0.63 % year^{-1}), and AGWP (2.95 ± 0.63 Mg C ha^{-1} year^{-1}), but overall lower AGB (130.99 ± 44.71 Mg C ha^{-1}) when compared to montane forests ($r = 2.06 \pm 0.26$ % year^{-1}; $m = 1.59 \pm 0.21$ % year^{-1}; AGWP = 2.39 ± 0.36 Mg C ha^{-1} year^{-1}; AGB = 178.49 ± 27.95 Mg C ha^{-1}). Species' traits in high elevation forests were mostly associated with adaptation to high soil moisture, greater shade tolerance and thus lower growth rates, whereas for lowland species, traits were more associated with higher resource availability. I found that different CWMs of traits have effects over different responses with CWM of leaf nitrogen simultaneously involved in all of the studied response variables. Yet,

functional traits were more important when predicting AGB and AGWP compared to stem turnover highlighting the importance of other factors such as soil fertility and environmental conditions when studying stem dynamics.

INTRODUCTION

In mature tropical forests, dynamic processes such as stem turnover (i.e. recruitment and mortality), biomass and net primary production are related to environmental factors (Vilanova et al., 2018 - Chapter 2). In lowland Amazonian forests, the environmental controls on stand structure and dynamics include at least two major components. One is evident in edaphic factors, with soil phosphorus and cations positively influencing productivity but with poorly structured soils associated to richer soil chemistry also promoting faster turnover rates (Quesada et al., 2012). The other is climatic, with a combination of higher temperatures and precipitation having been shown to be positively correlated with the total aboveground biomass (AGB) and with woody productivity (AGWP) (Malhi et al., 2004; Johnson et al., 2016; Vilanova et al., 2018).

In parallel with these large-scale geographic differences, differences within and between forests may also be modulated by species-level differences, with tropical trees experiencing a trade-off between growth and survival largely maintained by trait differences among the species (Wright et al., 2010). A large, wider body of research has also shown that some species adopt a conservative (or slow maturation) growth approach, while others precociously prioritize light acquisition and seed production - implying the existence of different ‘ecological strategies’ (e.g. Grime 1977; Westoby et al., 2002) that ultimately define community assembly processes and ecosystem functioning (Swaine & Whitmore 1988; Reich 2014). Since this slow-fast continuum of resource acquisition (c.f. Reich et al., 1997; Garnier et al., 2016) is to some extent reflected in species’ functional traits this suggests the existence of a few main axes of trait variation in plant ecology (Westoby & Wright 2006; Díaz et al., 2016).

Functional traits can be defined as any morpho-physio-phenological attribute which impact fitness via their effects on the three components of individual performance: growth, reproduction and survival (Violle et al., 2007). In plant ecology, collecting data on traits has been a fundamental tool to assist in the classification of individuals and species with respect to their structural, physiological, and/or life strategy characteristics (Korner 1993; Poorter et al., 2019). For instance, the well-known differential response of plant growth to changes in light intensity (Shugart 1997; Ameztegui et al., 2017), can be interpreted in terms of their physiology, and also in the context of structural (e.g. low wood density vs. high wood density species) (Chave et al., 2009; Swenson and Enquist 2007), life-history (e.g. short-lived vs. long-lived), and successional patterns of tree species (Swaine & Whitmore 1988; Lasky et al., 2014). Thus, functional traits can provide insight into a variety of ecological questions within a wide range of scales, from individuals to species, extending to communities and landscapes.

At regional and global scales more dynamic forests are often expected to also be more productive (Stephenson and van Mantgem, 2005), and in lowland tropical forests high productivity may support higher species richness via increased stem turnover (Phillips et al., 1994). Yet, woody productivity and stem turnover can be decoupled in some cases. For example, some ‘slow forests’ in the Guiana Shield region, with low recruitment and mortality rates, also show high rates of woody productivity (Johnson et al., 2016; Vilanova et al., 2018 - Chapter 2), while some of the fastest stem dynamics forests in southern Amazonia are associated with rather low productivity (Marimon et al., 2014). And, while several studies suggest that more species enhance productivity and carbon storage in forest ecosystems (e.g. Liang et al., 2016; Huang et al., 2018) this is not always the case (e.g. Sullivan et al., 2017; Dormann et al., 2019), presumably because species composition and functional diversity may be more important than diversity *per se* in affecting productivity and other stand-level processes. Indeed, studies that have simultaneously analyzed species richness (number of species), functional richness (number of functional groups) and functional composition (presence of certain functional groups or traits) indicate that the functional variance components tend to be more important than the variance component of species richness alone in influencing ecosystem processes (Díaz & Cabido 2001).

Several examples exist in the literature showing the importance of specific traits in some community processes in tropical forests. For instance, for large trees of 240 tree species from five Neotropical forests, Poorter et al., (2008) found that both growth and mortality rates declined with an increase in wood density, while also declining as seed volume increased. Using a functional trait approach for several tree species of dipterocarp-dominated forests in Asia, Philipson et al., (2014) report that only WD was important in explaining the growth mortality trade-off and thus appears to be independent of species crossovers performing in different light environments. While WD is indeed an important plant trait (Swenson & Enquist 2007; Phillips et al., 2019) and is a key variable when estimating total aboveground carbon in tropical forests (Chave et al., 2009; Flores & Coomes 2011), the relationship between functional traits and demographic processes in general (i.e. recruitment and mortality rates) is not a direct one and might be conditional to spatial, taxonomical and temporal variations that need to be considered (Kraft et al., 2010; Yang and Swenson 2018).

Studies on functional ecology in tropical forests have shown that a combination of physiological and life-history traits can yield useful information (e.g. Prado-Junior et al.,, 2016; van der Sande et al.,, 2016), and we expect these to be relatively easy to measure and eventually can be supplemented with values from databases or secondary sources (Baraloto et al., 2010; Kattge et al., 2011; Perez-Harguindeguy et al., 2013). A recent study (Díaz et al., 2016) concluded that most of the trait variation in plants can be captured in a two-dimensional global spectrum of plant form and function reflecting the size of whole plants and their parts, while also representing the 'leaf economics spectrum' (Wright et al., 2004), which balances leaf construction costs against growth potential. This means that while the range of potential traits to consider in a trait-based approach is wide, a few specific traits such as wood density (Swenson & Enquist 2007; Wright 2010; Francis et al., 2017; Phillips et al., 2019), leaf mass per area - LMA (Duursma & Falster 2016), specific leaf area - SLA (Wilson et al., 1999), and maximum height (Díaz et al., 2016; Kunstler et al., 2016) can be informative when studying the relationship of species traits and ecosystem functions in many environmental conditions and vegetation types.

Several functional diversity measures at the community-level have also been created to summarize distinct facets of the extent of trait differences among coexisting species, and are expected to express different mechanisms of community assembly, thus could serve as better descriptors when analyzing species diversity and its effects on community processes (Mason et al., 2005; Ricotta et al., 2014; Finegan et al., 2015; Prado-Junior et al., 2016). The most common ones are functional richness (F_{Ric}), evenness (F_{Eve}), divergence (F_{Div}), and dispersion (F_{Dis}). F_{Ric} is the amount of multivariate-trait space filled by the community, and F_{eve} indicates how species' basal area is spread over the multivariate-trait space (Mason et al., 2005; Prado-Junior et al., 2016). Functional divergence (F_{Div}) is the degree of separation from the center that most dominant species occupy in the multivariate-trait space (Mason et al., 2005). F_{Dis} is the mean distance in multidimensional trait space of individual species to the centroid of all species (Legendre & Laliberté, 2010).

Most of the literature regarding the use of functional trait data to explain ecosystem function in the tropics has focused almost entirely on lowland forests, while other forest-types such as those in mid to high elevations (i.e. montane or cloud forests) have received less attention. These ecosystems are also critical in providing hydrological services and are habitat hotspots for biodiversity (Hostettler, 2002; Bruijnzeel et al., 2011), while storing an important amount of global carbon despite covering a relatively small area compared to other forest-types (Spracklen & Righelato, 2014; Cuni-Sanchez et al., 2017). In Venezuela, typical cloud forests are found along the orographic condensation zone in the mountainous areas in the western Andes, and to the north along some of the coastal mountains covering an approximate area of 700,000 ha (Oliveira-Miranda et al., 2010). Yet, compared to forests in the Andean mountain range in South America, forests in Venezuelan Andes have suffered one of the highest deforestation rates in the last two decades (Aide et al., 2019).

This study aims at analyzing the trade-off between rapid acquisition (i.e. fast growth) and conservation of resources (i.e. slow growth) using functional traits in the context of two neotropical forests. I assessed the extent to which community functional trait differences are associated with differences in turnover rates (i.e. recruitment and mortality) and function (i.e. aboveground biomass – AGB, and aboveground woody productivity - AGWP) in two contrasting forest sites in western Venezuela. The sites selected are environmentally and floristically different which combined make an interesting case study for applying a functional trait-approach, comparing a lowland seasonal forest site characterized by alluvial soils with high fertility, and a high elevation montane forest characterized by low temperatures and relative low fertility soils (Figure 1). With a higher availability of resources (i.e. soil nutrients, solar radiation and temperature), I hypothesized that higher F_{Ric} at the lowland forest plots would have a positive influence on growth and AGWP. Assuming resource availability is even throughout the niche space, lower F_{Eve} indicates that some parts of niche space, while occupied, are under-utilized which will tend to decrease productivity (Mason et al., 2005). Thus, since montane forests are characterized by a more regular size distribution compared to lowland sites (Vilanova et al., 2018), I expected F_{eve} to be lower for this site compared to lowland forests while negatively affecting growth and productivity. Specifically, the trait-based approach used here includes:

1) Describing the functional trait variation within and between two distinct forest communities. I expect montane and lowland forests to differ in a wide range of traits given the contrasting adaptation and environmental conditions. Moreover, if traits are good predictors of plant performance, I hypothesize that plant growth should increase with resource availability (light, soil nutrients) in combination with traits which enhance resource acquisition (e.g. high specific leaf area – SLA, low wood density – WD), thus lowland forests should reflect these conditions;

2) Determining if functional traits predict growth rates at the species level in both sites. I hypothesize traits to accurately predict plant performance and that plant growth should increase with resource availability (light, soil nutrients) in combination with traits which enhance resource acquisition (e.g. high specific leaf area – SLA, low wood density – WD), all of which are expected conditions of the lowland forest sites;

3) Analyzing the potential drivers of turnover rates, AGB, and AGWP on a community (plot-level) scale to compare the relative importance of edaphic factors and functional diversity under three different hypotheses: a) the *biomass-ratio hypothesis*, which stipulates that ecosystem processes are driven by the (traits of the) most abundant species in the community (Grime 1998). This would mean that sites dominated by species with traits that predominately enhance resource acquisition (e.g. high specific leaf area, low wood density) should have faster turnover rates (higher recruitment and mortality rates) and higher productivity as AGWP should be closely related to the community-weighted means (CWMs) of traits; b) as shown by Finegan et al., (2015) and Prado-Junior et al., (2016) I also tested the *niche complementarity hypothesis* which predicts

that sites with a higher diversity of species or functional traits (i.e. lowland forests in this study) would use available resources more efficiently because of higher niche differentiation and interspecific facilitation, thus increasing biomass productivity of the community; and c) the *soil fertility hypothesis* predicts that higher nutrient availability should have a positive effect on productivity (Wright et al., 2011; Quesada et al., 2012). Thus, high elevation forests would have a lower productivity compared to the forests located in alluvial terraces of the Western Plains.

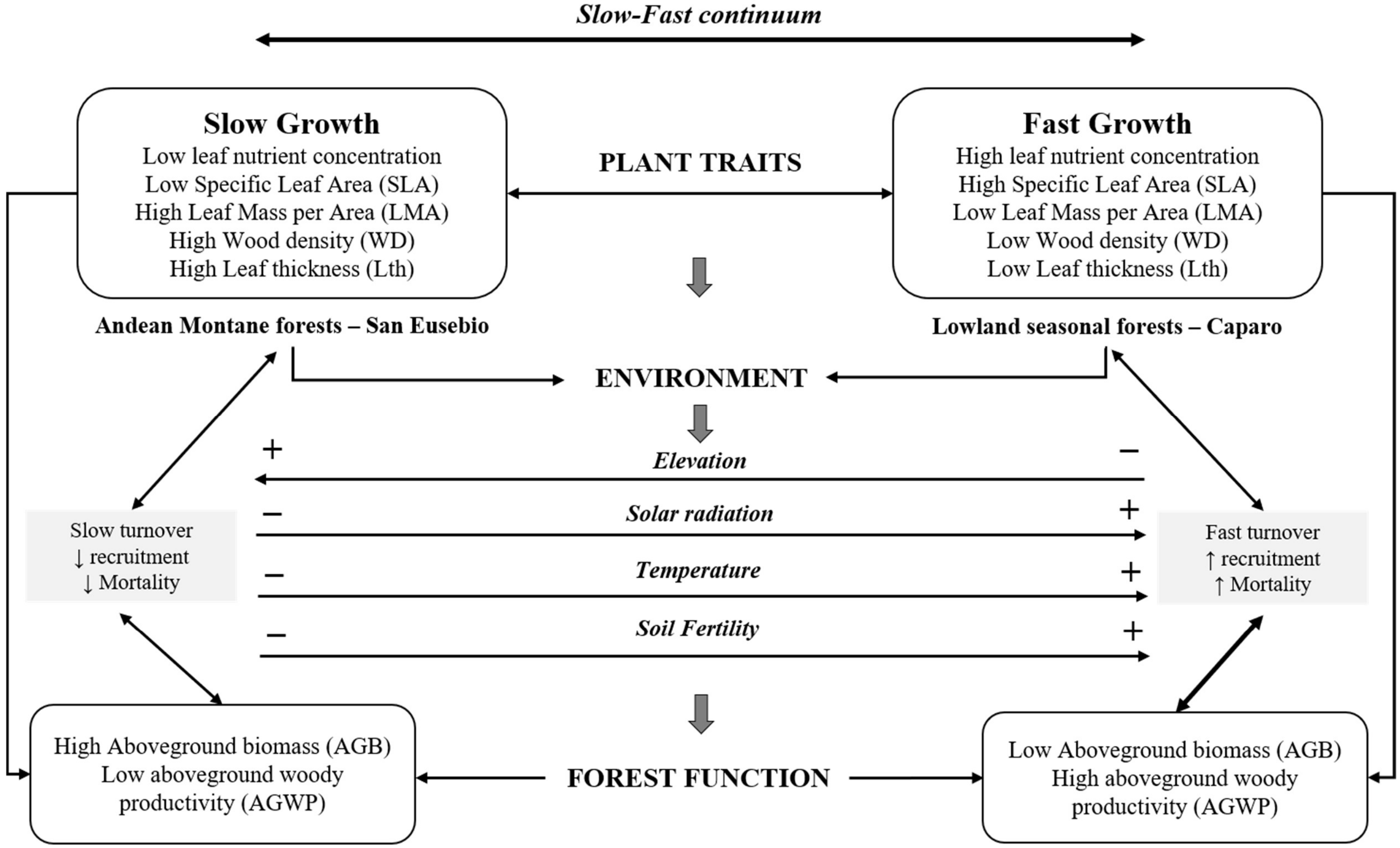


Figure 1. Conceptual model showing three major components (traits, environment, and function) of the slow-fast growth trade-off between lowland seasonal forests and high elevation forests in Western Venezuela. Plant traits interact with different environmental factors to potentially drive turnover rates and function. Faster turnover rates and thus higher tree growth and stand productivity are associated with a dominance of traits that facilitate resource acquisition, having its expression in the lowland seasonal forests, whereas slow turnover rates (i.e. lower recruitment and mortality rates), as well as low productivity are associated with temperature and soil-limited ecosystem in the Andes. Figure modified from the model proposed by Garnier et al. (2016).

MATERIALS AND METHODS

STUDY SITES

The large network of long-term sample plots established in different forest-types in Venezuela is one of the oldest in the tropics, dating from the 1960's, and extensively described by Veillon (1985) and Vilanova et al. (2018) (Chapter 2). In this study I used 12 of these units located in two contrasting sites to the west of the country (Figure S1). Specifically, I used information from long-term monitoring of six (6) plots from the Western Plains bioregion (*Caparo*) and six (6) plots from the high elevation montane forests in the Andes (*San Eusebio*). Lowland plots are located in a ~7,000 has continuous fragment in which different ecosystem types from mature and secondary forests to savannas occur. The montane plots were established in a well-preserved continuous forest patch of ~ 370 has. All plots are similar in size (0.25 ha) and shape (a 50 x 50 meters square) and were randomly located within the extent of mature, old-growth forests without evidence of human disturbance. Data collection involved the measurement of all live stems from all species with diameter (D) ≥ 10 cm at 1.3 m height when possible, else above any stem deformation. In all cases, the initial monitoring was conducted on an annual basis, and then more recently in intervals between four to five years. On average, the plots located in the lowland forests have been monitored for over 22 years (Min = 15 y; Max = 25 y) and revisited, on average, 11 times (Min = 9; Max = 13). The plots from montane cloud forests have been monitored for ~ 50 years (Min = 47 y; Max = 55 y) and resampled 29 times (Min = 26; Max = 34). For further details about the plots see Table S1. Since 2004, these plots have been part of the Amazon Forest Inventory Network (RAINFOR) (Malhi et al., 2002). Based on the information available for all censuses I have monitoring data for ~1,900 live stems from 139 identified species across both sites. Additional details about field protocols and data management can be found in Phillips et al. (2016) and Vilanova et al. (2018) (Chapter 2).

SOIL SAMPLING

In each plot, soils were sampled at 0.3 m depth in five different locations (four corners and center of the plot) for an analysis on texture (particle size), pH, % Nitrogen, %

Phosphorus, % organic carbon in top soil, and exchangeable cations (Al, Ca, K, Mg, Na). Details on the methods used to analyze these samples are provided in Quesada et al. (2011) (Table S2).

FUNCTIONAL TRAITS

The traits selected have been shown to be important when studying plant growth and turnover, and hence for above-ground biomass and woody productivity (Poorter et al., 2008; Wright et al., 2010; Finegan et al., 2015). They include: leaf thickness (L_{th}), leaf chlorophyll content (Chlor), leaf area (LA), specific leaf area (SLA), leaf mass per area (LMA), leaf dry mater content (LDMC), leaf nitrogen content ($Leaf_N$), leaf phosphorous content (L_P), Nitrogen and Phosphorous ratio in leaves ($Leaf_{N:P}$), and wood density (WD). While all the information for the leaf traits comes directly from sampling in the field, the primary source for WD is the species-level values in the Global Wood density database (Chave et al., 2009; Zanne et al., 2009). For additional information on traits see Table 1, and the protocols for measuring or estimating these was as follows:

Leaf thickness (L_{th}): this trait was measured once the sampled was collected in the field. Five measurements per leaf lamina were taken at five different positions using a digital micrometer: one in the base, one at the top, one at an intermediate position between the border and the midrib, and one at each side of the leaf, always avoiding important secondary veins. These numbers were averaged for each leaf sample. For species with compound leaves, a similar procedure was performed for each of five leaflets randomly chosen from every leaf sampled.

Leaf chlorophyll content (Chlor): Using a SPAD meter (SPAD 502 Chlorophyll Meter, Spectrum Technologies Inc., Plainfield, IL, USA), a proxy chlorophyll measurement of all sampled leaves was obtained. SPAD readings for fresh leaves were obtained in the field to avoid water loss, shrinkage and other undesirable modifications in leaf tissue. As for the case of L_{th} I took five readings in different positions in the leaf. SPAD values were later transformed to direct chlorophyll readings using the equation from Coste et al. (2010): $Chlor = 117.1 * X / (148.84 - X)$, where X is the SPAD value, and the final results are expressed as the chlorophyll content per unit of leaf area ($\mu g\ cm^{-2}$).

Leaf Area (LA) and *Specific Leaf Area (SLA)*: I took photos to each leaf sample and LA was estimated using the open access software ImageJ (Rueden et al., 2017) (https://imagej.nih.gov/ij/). SLA is the one-sided area (LA) in cm^2 of a fresh leaf, divided by its oven-dry mass in grams (g), and was based on the whole leaf (including rachis for compound leaves).

Leaf Mass per area (LMA): Leaf mass per area is calculated as the inverse of SLA (1/SLA), expressed either as g cm^{-2} or g m^{-2}.

Leaf Dry Matter Content (LDMC): LDMC is the oven-dry mass (g) of a leaf, divided by its water-saturated fresh mass (g), hence expressed in g g^{-1}. After collected, leaf samples were weighted, and then dried up in a laboratory oven for up to three days at 70 °C until reaching constant weight.

Leaf nitrogen and phosphorous content ($Leaf_N$*,* $Leaf_P$*,* $Leaf_{N:P}$*)*: Nitrogen and Phosphorous concentration in leaves is the total amounts of N and P per unit of dry leaf mass (% of dry-leaf mass here). Once leaves were dried and weighted to estimate LDMC, samples were merged for each sampled tree, so enough material was available for laboratory analysis. A micro-Kjeldahl (acidic) digestion, followed by a colorimetric (flow-injection) analysis was used, and the ratio of $Leaf_N$ and $Leaf_P$ was also calculated.

Wood density (WD): Wood-specific density is the oven-dry mass of a section of the main stem of a plant divided by the volume of the same section, when still fresh. The primary source for this trait comes from the species-level values in the Global Wood density database (Chave et al., 2009; Zanne et al., 2009).

SAMPLING STRATEGY

A dominance-based strategy was used to collect data on functional traits, based on the dominant species that make up a large proportion of the estimated basal area (BA) in each individual plot. This ensured that all species representing between 70 and 80% of the total plot BA were sampled. This was estimated after analyzing species composition in 5-year intervals throughout the entire monitoring period for each plot, and ordering species based on the percentage of total basal area they represented. Following this approach, a total of 25 species in the lowland forests, and 30 in the montane forest plots were sampled.

For all leaf-related traits, one to three individuals per species were sampled, with the lowest sample size usually occurring in the case of lowland plots in which the largest individual in the plot was selected for sampling. I did not quantify intraspecific variation as this is relatively small in comparison to trait variation found between species in tropical forests (Rozendaal et al., 2006; Asner et al., 2014). Due to leaf dehydration problems in the field, and after a preliminary analysis on the trait data, I removed five (5) species from the final analysis. In the lowland forests two long-leaved palm species *Attalea butyracea* and *Syagrus sancona* (Arecaceae), and *Fissicalyx fendleri* (Fabaceae) were excluded. Two species in the montane site (*Wettinia praemorsa* – Arecaceae; *Cyathea* spp. – Cyatheaceae) were also excluded. Consequently, these species were also removed from the plot-level analysis when estimating turnover rates, aboveground biomass (AGB) and aboveground woody productivity (AGWP). Based on the recommendations of Pérez-Harguindeguy et al., (2013), five (5) young, fully expanded canopy leaves without epiphylls and signs of herbivore damage, or other obvious symptoms of pathogens, were sampled from each individual. Ultimately, I assembled a trait-growth database for 125 individuals, 43 from the lowland forests (n = 22 species) and 82 in the montane forest plots of San Eusebio (n = 28 species) (Table S3).

Table 1. Summary of functional traits and correspondent units of measurement. A column for the hypothesis of differences between sites (Lowland forests; Montane forests) is included, along with a second column for the hypothesized correlations (+: positive; −: negative) with four response variables: plot-level recruitment (*r*) and mortality (*m*) rates; aboveground biomass (AGB), and aboveground woody productivity (AGWP).

Trait Abbreviation	Description	Units	Indicator of	Expected differences between sites: Lowland or Montane higher?	Correlation with response variables	References
LA	Leaf Area	cm^2	Light interception efficiency	Lowland	$r + \mid m + \mid$ $AGB - \mid AGWP +$	Wilson et al. (1999); van der Sande et al. (2016); Medeiros et al. (2018)
SLA	Specific Leaf Area	cm^2 g^{-1}	Expected return on previously captured resources. Light interception efficiency	Lowland	$r + \mid m + \mid$ $AGB - \mid AGWP +$	Wilson et al. (1999); Prado-Junior et al. (2016); van der Sande et al. (2016)
LMA	Leaf Mass per area	g cm^{-2}	Leaf-level costs of light interception. Photosynthetic and respiratory rates, chemical composition, resistance to herbivory.	Montane	$\mid r - \mid m - \mid$ $AGB + \mid AGWP -$	Poorter et al. (2009); Prado-Junior et al. (2016); van der Sande et al. (2016)
L_{th}	Leaf thickness	mm	Component of SLA. Resistance to herbivory, photosynthetic capacity and sensitive indicator of plant water status	Montane	$r - \mid m - \mid$ $AGB + \mid AGWP -$	McBurney (1992); Perez-Harguindeguy et al. (2013); van der Sande et al. (2016)

Leaf$_{N}$	Leaf Nitrogen concentration	% of dry mass	Photosynthetic capacity	Lowland	$r+\mid m+\mid$ $AGB-\mid AGWP+$	Perez-Harguindeguy et al. (2013); van der Sande et al. (2016)
Leaf$_{P}$	Leaf Phosphorous concentration	% of dry mass	Growth and photosynthetic capacity	Lowland	$r+\mid m+\mid$ $AGB-\mid AGWP+$	Perez-Harguindeguy et al. (2013); van der Sande et al. (2016); Muscarella et al. (2017)
Leaf $_{N:P}$	Leaf Nitrogen: Phosphorous ratio	% of dry mass	Relative nutrient limitation	Montane	$r-\mid m-\mid$ $AGB+\mid AGWP-$	Perez-Harguindeguy et al. (2013); van der Sande et al. (2016)
Chlor	Leaf chlorophyll content	µg cm^{-2}	Light-harvesting and photosynthetic capacity	Lowland	$r+\mid m+\mid$ $AGB-\mid AGWP+$	Perez-Harguindeguy et al. (2013); van der Sande et al. (2016); Li et al. (2018)
LDMC	Leaf Dry Matter Content	g g^{-1}	Leaf defense	Montane	$r-\mid m-\mid$ $AGB+\mid AGWP-$	Poorter et al. (2009); Perez-Harguindeguy et al. (2013); van der Sande et al. (2016); Medeiros et al. (2018)
WD	Wood Density	g cm^{-3}	Life history, volume growth, stem defense, drought tolerance	Montane	$r-\mid m-\mid$ $AGB+\mid AGWP-$	Baker et al. (2004); Swenson and Enquist (2007); Wright et al. (2010); Prado-Junior et al. (2016); Medeiros et al. (2018)

FUNCTIONAL DIVERSITY (FD) INDEXES

Four complementary indices of functional diversity were calculated for each plot: functional richness (F_{Ric}), evenness (F_{Eve}), divergence (F_{Div}), and dispersion (F_{Dis}). An overall description of the origins and characteristics of the equations used are included in Mouchet et al. (2010), Schleuter et al. (2010) and Laliberté and Legendre (2010). Those used in this study are indicated below, and were calculated using the 'FD' package in R (Laliberté et al., 2015).

- Functional richness (F_{Ric}) (from Schleuter et al., 2010):

$$\mathrm{F_{Ric}} = \frac{\int max_{s \in Sc}[1_{st}(x)]dx}{\int max_{s \in \cup Sc}[1_{st}(x)]dx}$$

Where:

1_{st} (x) is 1 if x is between in and max, else it is 0 for categorical variables, L_{tc}/L_t
s = species
S_c = set of species in the community c
L_{tc} = number of levels of categorical trait t covered by community c
L_t = total number of levels of trait t

- Functional evenness (F_{Eve}) (from Mouchet et al., 2010):

$$F_{\mathrm{Eve}} = \frac{\sum_{i=1}^{S-1} min\left(\mathrm{PEW}_i \frac{1}{S-1}\right) - \frac{1}{S-1}}{1 - \frac{1}{S-1}}$$

Where:

S = total species richness
PEW = partial weighted evenness

- Functional divergence (F_{Div}) (from Mouchet et al., 2010):

$$\mathrm{F_{Div}} = \frac{\Delta d + \overline{dG}}{\Delta|d| + dG}$$

Where:

dG = mean distance to the centre of gravity
Δd = sum of abundance-weighted deviances
$\Delta|d|$ = absolute abundance-weighted deviances from the centre of gravity

- Functional dispersion (F_{Dis}) (from Laliberté and Legendre 2010):

$$F_{Dis} = \frac{\sum a_j z_j}{\sum a_j}$$

Where:

a_j = abundance of species *j*

z_j = distance of species *j* to the weighted centroid **c**

COMMUNITY WEIGHTED MEAN OF TRAITS (CWMS)

The per-plot Community Weighted Means (CWMs) and a measure of community weighted dispersion (Standard Deviation) for each trait were calculated using species basal area as percentage of total biomass for weighting. Again, all CWMs were calculated using the 'FD' package in R (Laliberté et al., 2015). I used species basal area as a weighting-factor which is a better indicator of plant performance than abundance (Prado-Junior et al., 2016). The calculation follows the approach proposed by Violle et al., (2007):

$$\mathrm{CWM}_{TP} = \sum_{i=1}^{N} w_i \times \mathrm{T}_i / \sum_{i=1}^{N} w_i$$

Where:

CWM_{TP} = Community weighted mean of a given functional trait *T* at each plot *P*;

N = total number of species sampled in the community or plot *P*;

T = Functional trait of each species *i* (e.g. SLA, WD);

W_i = weighting factor (i.e. Basal Area of species *i* in each plot *P*).

ESTIMATION OF RESPONSE VARIABLES

RELATIVE GROWTH RATES (RGRS)

Using stem diameter data, relative growth rate (RGR) of each individual from all species sampled that survived the entire census interval in each plot was calculated as $RGR = (DBH_2 - DBH_1) * (t_2 - t_1)^{-1}$, where *t* is the last (t_2) or first (t_1) census for each individual.

TURNOVER RATES, ABOVEGROUND BIOMASS (AGB), AND ABOVEGROUND WOODY PRODUCTIVITY (AGWP)

Demographic rates (% year^{-1}) of recruitment (*r*) and mortality (*m*) for each plot were estimated based on the instantaneous rates approach using the equations and correction methods reported in several studies (c.f. Swaine et al., 1987; Phillips et al., 2004; Báez et al., 2015; Johnson et al., 2016), and that were used in all previous chapters of this dissertation. Aboveground biomass of each plot was calculated using the moist forest allometric equation from Chave et al., (2005) that includes information of stem diameter, total height and wood density. Woody productivity was estimated as the sum of AGB gains of surviving and recruiting trees, with AGB mortality as the summed AGB of trees dying over the interval. Details of procedures are in Vilanova et al. (2018) and in the supplementary information of this chapter.

STATISTICAL ANALYSIS

TURNOVER RATES, AGB AND AGWP

Stem turnover (i.e. recruitment and mortality), AGB and AGWP were calculated (i.e., mean, standard error) for each plot. Census-based recruitment rates were normally distributed ($W = 0.979$, $p = 0.08$; Shapiro-Wilk normality tests), while mortality rates were not ($W = 0.973$, $p < 0.001$). Thus, I used an analysis of variance (ANOVA) to test for statistical differences among plots for *r* and a Kruskall-Wallis test was used for *m*. Similarly, a parametric post-hoc Tukey test was conducted for *r* when differences were found, and a non-parametric Dunn-test in the case of *m*. AGB and AGWP were both not normally distributed (AGB: $W = 0.968$, $p < 0.05$; AGWP: $W = 0.947$, $p < 0.01$), so to test for differences between plots and sites for these variables I followed the same procedure as for mortality rates.

DISTRIBUTION AND VARIATION IN FUNCTIONAL TRAITS

Shapiro-Wilk normality tests revealed that all traits were not normally distributed, so the differences in trait values between plots and sites were analyzed using both the arithmetic-unweighted and basal-area weighted mean of all traits and a Chi-Squared

Kruskall-Wallis test. To analyze the species distributions in the trait space I applied a Principal Component Analysis (PCA) using the NIPALS function with a maximum of 500 iterations in the 1.7-13 version of the ‘`ade4`’ R package (Dray et al., 2017) to better infer species associations to the traits used (Aguirre-Gutiérrez et al., 2019). Trait values were normalized by range prior to the PCA analysis, and PCA visualization was done using the 1.41 version of the ‘`FactoMineR`’ package (Husson et al., 2017).

SPECIES TRAITS AND RELATIVE GROWTH RELATIONSHIPS

Individual bivariate correlations between the arithmetic means of each trait and the relative growth rates (RGRs) of each sampled species were initially applied using Kendal’s τ (tau) approach as it does not rely on a particular distribution of the variables involved. Secondly, I tested the association between RGRs with functional traits by correlating RGRs with the scores of the first two axes from the Principal Component Analysis (PCA) explained earlier.

RELATIONSHIPS BETWEEN THE RESPONSE VARIABLES WITH CWMS OF TRAITS AND SOILS

On a plot scale, and with plots as a random effect, linear mixed effects models were used to test how turnover rates, AGB and AGWP are potentially driven by different predictors. Thus, models were built for every response variable to test its relationship with several soil descriptors (% Nitrogen, % Carbon, Phosphorous, Aluminum, pH and Cation Exchange Capacity - CEC), the community-weighted means of all traits, and four functional diversity (FD) indices. Plot-level rates of recruitment were not normally distributed ($W = 0.856$, $p = 0.04$) and were log-transformed, while all explanatory variables were standardized by fitting a mean equal to 0 and variance to 1 prior to model testing. Using prior information, a total of 33 different models were tested for the four main response variables (5 for recruitment, 6 for mortality, 12 for AGB, and 10 for AGWP), plus 21 additional models for other AGB components (7 in each case for $AGB_{recruits}$, AGB_{mort}, AGB_{growth}; results not shown). Models were built using the “`lme`” function from the ‘`nmle`’ package (Pinheiro et al., 2017).

Model selection was based on the corrected version of the Akaike Information Criterion (AICc) to correct for small sample sizes (Johnson & Omland, 2004). The influence between random and fixed effects was analyzed by calculating the conditional (c) and marginal (m) R^2 for all models. R^2_c is indicative of the variance explained by both fixed and random effects, whereas R^2_m indicates the variance explained by fixed effects only (Prado-Junior et al., 2016). When the R^2_m value is close to R^2_c, most of the variation explained in the biomass components is caused by the predictors (fixed effects), rather than by plot differences (random effect). This analysis was conducted using the '`MuMIn`' package (Barton, 2019). Finally, and for each response variable, I evaluated the relative importance of each explanatory variable by comparing the standardized regression coefficients (ß) of predictors retained in the 'best' models previously selected. All analyses were done using the 3.5.3 version of the R software (R Development Core Team, 2019).

RESULTS

DIFFERENCES IN TURNOVER RATES, AGB AND AGWP

Parametric and non-parametric tests revealed that all response variables were significantly different between plots and sites as expected. First, lowland forests had faster stem turnover, with mean recruitment ($r = 2.67 \pm 0.44$, 95% CI) and mortality rates ($m = 3.09 \pm 0.51$) being greater than those of montane forests ($r = 2.06 \pm 0.21$; $m = 1.59 \pm 0.17$). Recruitment was significantly correlated with mortality rates ($\tau = 0.55$; $p < 0.001$). Second, aboveground biomass (AGB) was considerably higher in the montane (178.49 ± 22.34 Mg C ha^{-1}) compared to lowland plots (130.99 ± 35.77 Mg C ha^{-1}). Finally, woody productivity (AGWP) followed a similar trend as turnover rates with the lowland forests having, on average, higher woody productivity (mean AGWP = 2.94 ± 0.50 Mg C ha^{-1} $year^{-1}$) than montane plots (2.39 ± 0.28 Mg C ha^{-1} $year^{-1}$ (Figure S2; Table S4). AGB and AGWP were not correlated among each other. Turnover rates and AGB were negatively correlated, but with mortality especially being tightly linked to biomass ($\tau = -0.24$, $p = 0.012$ for r and AGB; $\tau = -0.52$, $p = 0.007$ for m and AGB). Neither of the turnover parameters had a significant relation with AGWP, demonstrating a lack of relationship between carbon dynamics and stem dynamics for these sites, also found for a larger number of plots and shown in Vilanova et al., (2018) and chapter 2.

DIFFERENCES IN FUNCTIONAL TRAIT COMPOSITION AMONG SITES

Using both the arithmetic and community weighted means, clear differences between plots and sites for most traits studied were found (Figure 2; Table S4). While some plots are statistically similar between both sites, particularly in the case of leaf dry matter content (LDMC) and wood density (WD), lowland and montane forests in Western Venezuela appear to be fairly different with regards to their trait composition. The trait variation and range of values in the dataset approaches that reported in other studies where samples have been collected across a global range of terrestrial and aquatic ecosystems (Kattge et al., 2011) (Tables S3 and S4).

The more evident contrasts occurred in the case of chlorophyll content (Chlor), specific leaf area (SLA), leaf mass per area (LMA) and both nitrogen and phosphorous content in leaves. Traits such as SLA and leaf nutrients (i.e. Leaf_N, Leaf_P) were much higher in their unweighted (Figure 2) and weighted mean values (Table S4) for the lowland forests. In contrast, LMA was higher at the montane forests, in combination with higher leaf thickness (L_th) and a relatively higher LDMC. The largest variation was found for leaf area (LA) within both sites. For instance, at high elevation, large trees of the species *Retrophyllum rospigliosii* (Pilg.) C.N. Page (Podocarpaceae) had, on average, very small leaves (Mean LA = 0.46 cm^2) compared to large compound leaves from *Ruagea pubescens* H. Karst. (Meliaceae) (Mean LA = 996.9 cm^2). In the case of the lowland plots, the smallest leaves reported are for *Brosimum alicastrum* Sw. (Moraceae) (mean LA of 20.9 cm^2) while the leaves of *Cecropia peltata* L. (Urticaceae) are the largest (Mean LA = 914.6 cm^2) (Table S3).

MULTIVARIATE DISTRIBUTION OF FUNCTIONAL TRAITS

The first two axes of the principal component analysis (PCA) explained 61.9 % of the variation, with a total of 74.4% explained by the first three. The first axis captured 42.02 % and was negatively correlated with leaf area (LA), SLA, Leaf_N and Leaf_P, while being positively correlated with Chlor, L_th, LDMC, LMA, $\text{Leaf}_\text{N:P}$ and wood density (WD). The second axis described 19.86 % of the variation and was positively correlated with Chlor, L_th, LA, LMA, and Leaf_P, and negatively correlated with LDMC, SLA, Leaf_N and $\text{Leaf}_\text{N:P}$ (Table 2). Although there is some level of site-convergence in the location of some species in the multivariate space, there is a clear distinction between both sites along these two axes of variation (Figure 3), with species from lowland forests mostly located on the acquisitive side of the trait space. Overall, each one of five traits (LMA, SLA, $Leaf_P$, L_{th}, LDMC) explained over 10% of the variation in the first two axes of the PCA (Figure S3).

Table 2. Loadings and variation explained by three major axes of variation using ten functional traits for 12 permanent plots in Western Venezuelan forests. In bold the traits with loadings above 0.3 for each PCA axis.

PCA variable / PCA Axes	**PC1**	**PC2**	**PC3**
Chlorophyll content (Chlor)	**0.372**	0.053	0.142
Leaf thickness (L_{th})	0.292	**0.451**	0.010
Lead dry matter content (LDMC)	0.269	**-0.419**	-0.085
Leaf area (LA)	-0.140	**0.342**	**0.345**
Specific leaf area (SLA)	**-0.423**	-0.120	-0.108
Leaf mass per area (LMA)	**0.435**	0.230	0.048
Nitrogen in leaves ($Leaf_N$)	**-0.376**	-0.018	**0.405**
Phosphorus in leaves ($Leaf_P$)	**-0.405**	0.211	-0.222
$Leaf_{N:P}$	0.040	**-0.322**	**0.764**
Wood density (WD)	0.093	**-0.535**	-0.207
Standard Deviation	2.050	1.409	1.121
Proportion of Variance	0.420	0.198	0.126
Cumulative Proportion	0.420	0.618	0.744

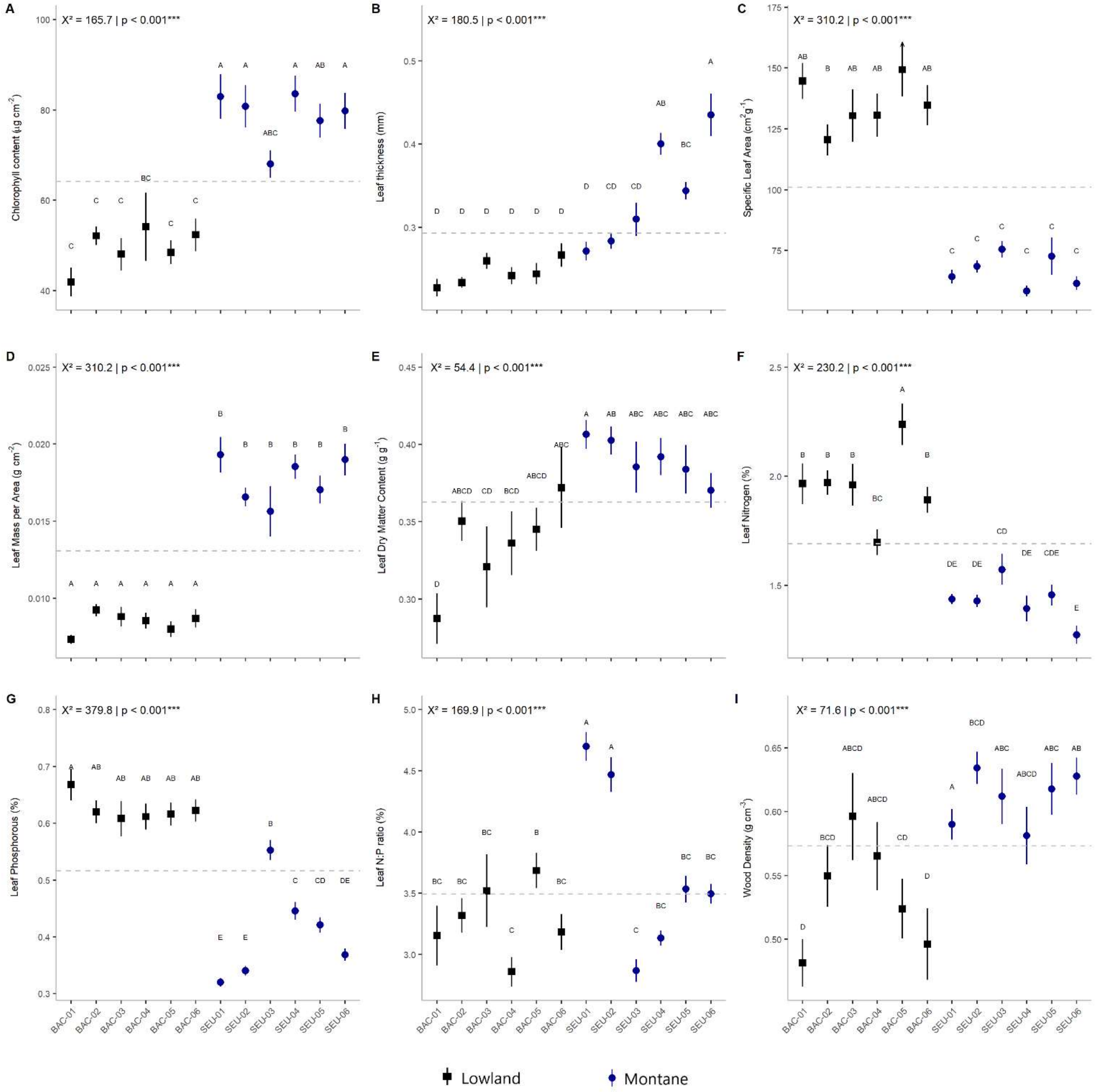


Figure 2. General differences in the unweighted arithmetic means ± standard error of the mean from chi-squared Kruskal-Wallis tests for nine functional traits in 12 forest plots in montane and lowland forests in western Venezuela. Square symbols depict lowland forest plots while circles montane forest plots. For visualization purposes, Leaf Area (LA) is not included but follows a similar trend as SLA. Gray dotted line represented the overall mean of each trait for all plots combined.

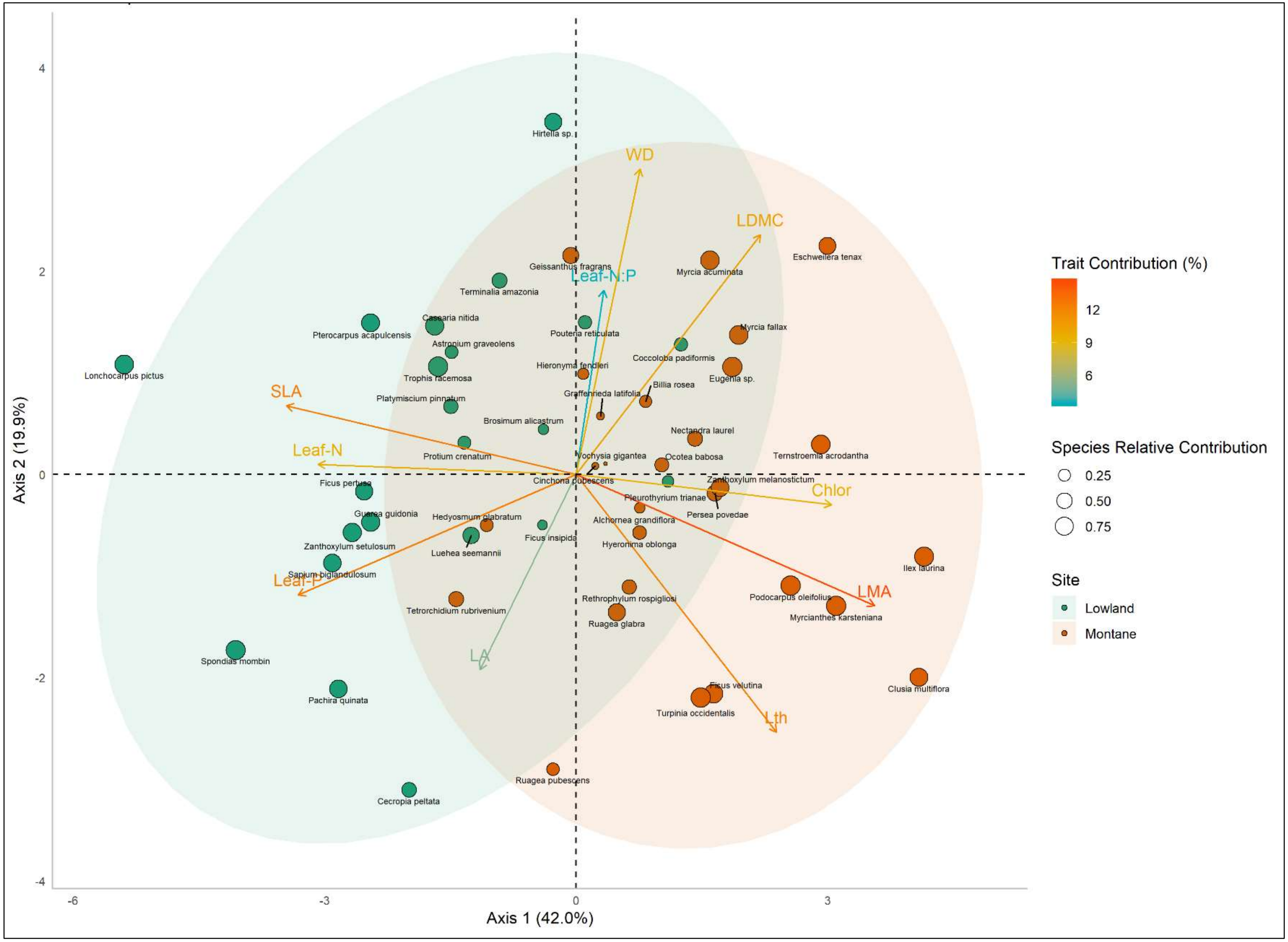


Figure 3. Principal component analysis showing the distribution of 50 tree species and 10 functional traits in lowland and montane forests of Western Venezuela. Green circles depict the species from lowland forests and red circles the species in montane forests. Colors in trait vectors represent the contribution (%) to the variance in the first two axes. Circle size indicates the contribution of each species to the variation in the first two axes of the PCA. For more details on the PCA analysis see Figure S3.

RELATIONSHIPS BETWEEN SPECIES TRAITS AND RELATIVE GROWTH RATES

Relative growth rates (RGRs) were, on average, higher in the lowland forests (5.61 ± 1.26 mm year^{-1} – 95% CI; n = 22 species), compared to the high elevation plots (2.19 ± 0.56 mm year^{-1}; n = 28 species). Using the scores of the principal component analysis I found that RGRs were negatively and significantly correlated with the first PCA axis ($\tau = -0.33$, $p < 0.001$), but with no consistent trend among sites. The relationship with PCA 2 was positive and consistent within sites, yet not significant ($\tau = 0.13$, $p = 0.37$) (Figure 4).

With regards to the relationship between RGRs and functional traits for all species in both sites, I see a positive and significant relationship with SLA ($\tau = 0.31$, $p = 0.019$), Leaf$_N$ ($\tau = 0.24$, $p = 0.004$) and Leaf$_P$ ($\tau = 0.39$, $p < 0.001$), whereas chlorophyll content ($\tau = -0.29$, $p = 0.038$), LMA ($\tau = -0.31$, $p = 0.003$) and WD ($\tau = -0.23$, $p = 0.021$) were all significantly negatively correlated with RGRs. Yet, only leaf nutrients and wood density showed partial consistency at both sites in the overall trends. Other traits (i.e. L$_{th}$, LDMC, LA and Leaf$_{N:P}$) did not have a significant effect on RGRs.

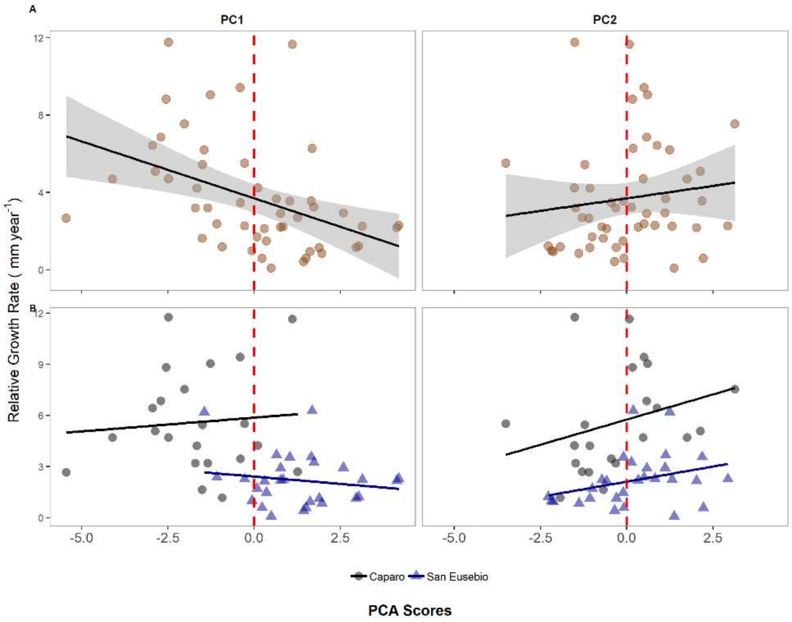


Figure 4. Relationships between relative growth rates for 50 tree species with the scores of two Principal Components axes in two contrasting forests of Western Venezuela. A) Relationship with no site distinction; B) Correlations by site. Trend lines are from simple linear models. Red dashed line indicates the "zero" value for the scores in each axis. For details on the direction of the vectors and loadings see Figure 3 and Table 2.

CWMS OF TRAITS, SOILS, FUNCTIONAL DIVERSITY AND EFFECTS ON RESPONSE VARIABLES

TURNOVER RATES

The community weighted means (CWMs) of three traits were significantly correlated (Kendall tau-based) with recruitment rates, with L_{th} and LMA having negative correlations and $Leaf_N$ positively correlated with *r* (Table S5). Yet, only the CWM of $Leaf_N$ was retained as a significant predictor in the mixed model analysis (Figure 4; Table 3). The CWMs of six traits were significantly correlated with mortality rates. Chlorophyll content and LMA had negative relationships with *m*, whereas LA, SLA, $Leaf_N$, and $Leaf_P$ appeared to be positively affecting *m* (Table S5). Again, when these predictors were included in mixed models, the only trait that showed a significant effect on mortality rates was the CWM of $Leaf_N$ (Table 3). Additional variables, including stem density and every soil parameter showed a significant correlation with mortality rates, with the total number of trees per plot having a negative association with *m*, whereas soil pH and phosphorous (P) in soil had a positive one. Aluminium (Al), nitrogen (% N) and carbon (% C) contents in soil had a negative correlation with mortality (Table S5), and only soil P and stem density were retained in the final mortality models (Figure 5).

ABOVEGROUND BIOMASS (AGB)

The CWMs of three traits (L_{th}, SLA, $Leaf_N$) had a significant correlation with AGB, with leaf thickness being the only one positively affecting AGB. The analysis of different mixed models showed, however, that the CWMs of LMA and $Leaf_N$ were the only traits retained as significant predictors of AGB. Carbon content in soil had a positive association with AGB, whereas the amount of phosphorous was negatively correlated with total AGB (Table S5). From the stand point of the mixed models tested, both carbon and phosphorous in soils continued to be important predictors of AGB (Figure 5; Table 3).

ABOVEGROUND WOODY PRODUCTIVITY (AGWP)

Kendall-tau (τ) correlations indicates negative and significant relationships between the CWMs of L_{th} and LMA with AGWP, while those from LA, $Leaf_N$ and $Leaf_P$ had a positive and significant relationship with productivity. Yet the CWM_{LMA} was not retained in the final model as a significant predictor. Two functional diversity indexes appeared for the first time having significant relationships with AGWP, with functional richness (F_{Ric}) positively affecting AGWP and evenness (F_{eve}) having an opposite effect (Table S5; Figure S4). Yet, the final model obtained for AGWP had the lowest R^2_m among all response variables considered (Figure 5; Table 3).

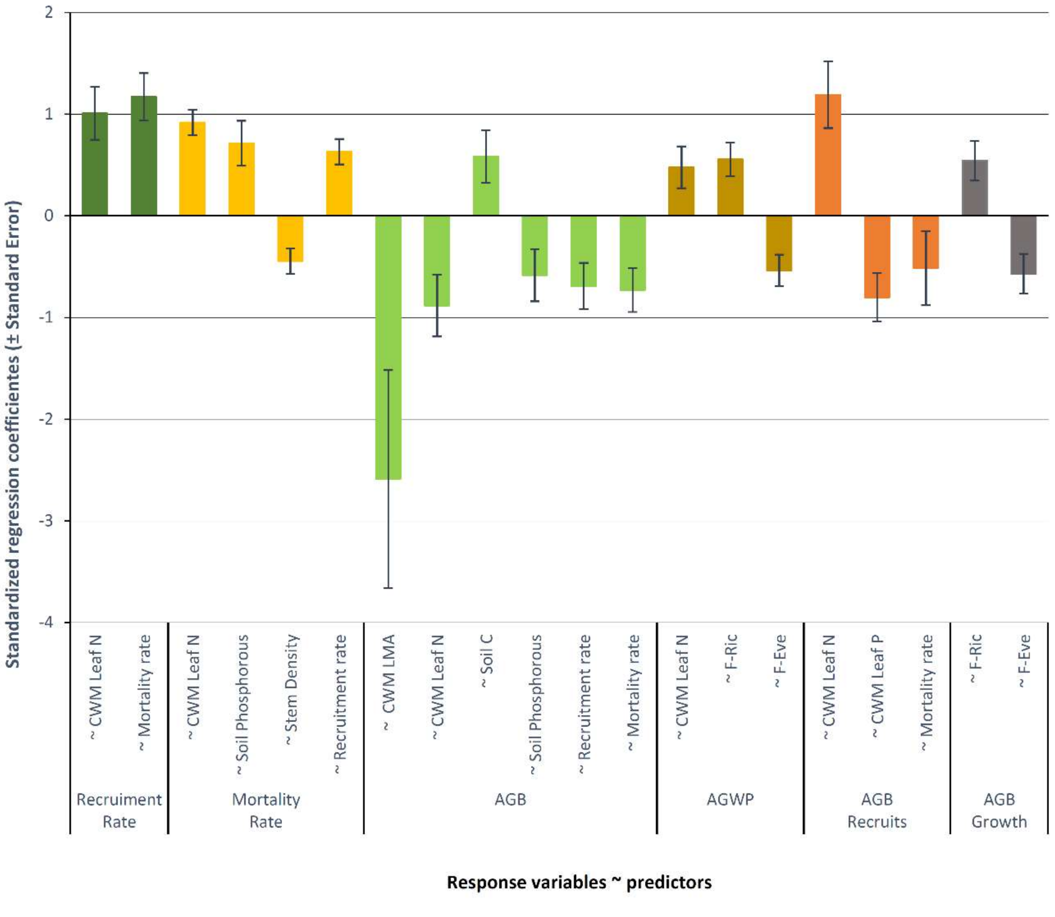


Figure 5. Standardized coefficients obtained from the 'best' models used to analyze the relationships between several predictors and four ecosystem processes in lowland and montane forests in Western Venezuela. The colored bars represent the standardized regression coefficients ± standard errors for each response variable (dark green: recruitment rates; orange: mortality rates; light green: AGB; dark green: AGWP). The coefficients from the predictors can be compared directly among each other, with higher values (positive or negative) having a much stronger relationship with each response. Only significant effects are included (see Table 3 for more information).

Table 3. Standardized coefficients from the ‘best’ linear mixed models selected using plot as a random effect to explain recruitment (*r*) and mortality (*m*) rates, aboveground biomass (AGB), and aboveground woody productivity (AGWP) in lowland and montane forests in Western Venezuela. The table is divided in three major groups of predictors: CWMs of functional traits and functional diversity indexes; turnover rates and forest structure; soil parameters. Significance levels (*p*-values), marginal (m) R^2_m for fixed effects only, and conditional (c) R^2_m for both fixed and random effects, as well as the corrected Akaike Information Criterion (AIC_c) are given.

Predictor	**Recruitment Rate (*r*)**		**Mortality Rate (*m*)**		**AGB**		**AGWP**	
	β-Coef	*p-value*	β-Coef	*p-value*	β-Coef	*p-value*	β-Coef	*p-value*
CWM $_{Chlor}$								
CWM $_{Lth}$								
CWM $_{LA}$								
CWM $_{SLA}$								
CWM $_{LMA}$					- 2.588	0.046		
CWM $_{LDMC}$								
CWM Leaf$_P$								
CWM Leaf$_N$	1.007	0.007	0.917	<0.001	- 0.882	0.030	0.476	0.040
CWM Leaf$_{N:P}$								
CWM $_{WD}$								
F$_{Ric}$							0.555	0.017
F$_{Eve}$							- 0.538	0.005
F$_{Div}$								
F$_{Dis}$								
r			0.630	0.001	- 0.692	0.013		
m	1.171	< 0.001			- 0.730	0.007		
Stem Density			- 0.445	0.006				
Soil_C					0.582	0.047		
Soil_Pho			0.713	0.009	- 0.584	0.046		
Soil_Al								
Soil_eCEC								
R^2_m	0.72		0.83		0.64		0.34	
R^2_c	0.97		0.98		0.96		0.92	
AIC_c	2.93		27.40		115.10		32.16	

DISCUSSION

MARKED DIFFERENCES IN STAND LEVEL PROCESSES AND TRAIT COMPOSITION AMONG SITES

In Western Venezuela, lowland seasonal forests and montane forests are markedly different in terms of stand-level processes (i.e. turnover rates, aboveground biomass and woody productivity). Faster dynamics (i.e. higher turnover rates) and higher productivity but lower AGB characterize the lowland forests while opposite trends are more common at higher elevations (Vilanova et al., 2018) (Figure S2). Whereas annual rainfall and seasonality (i.e. number of dry months) do not differ greatly between the two sites, annual mean temperature, elevation, and soil fertility do (Tables S1-S2). Thus, I expected strong differences in their species composition, hence unweighted and weighted mean trait values (Figure 2; Table S4), and the multivariate trait composition (i.e. trait space – Figure 3) at each site were also predicted to be statistically different (Figure 1).

The principal component analysis allowed for the visualization of the multivariate trait composition space at both sites (Table 2, Figure 3) indicating a strong influence of the so called 'leaf economics spectrum'(Wright et al., 2004), showing a tradeoff between investment in leaves with LMA, SLA, Leaf_P and L_th explaining most of the variation in the first two axes (Figure S3). One end of this spectrum comprises species mostly associated with the lowland forests, with potential for faster return on investments of nutrients with traits such as high leaf nutrient concentrations, low LMA (i.e. high SLA), and comparatively thinner leaves. These were all hypothesized traits of lowland forests in the original conceptual model (Figure 1), thus I expected such traits to be related to high rates of photosynthesis and respiration, short leaf lifetimes and low dry-mass investment per leaf area that are common in these conditions (Westoby et al., 2002; Wright et al., 2010; Gibert et al., 2016). In fact, these results seem to mirror the overall patterns in average growth rates found for both sites reported earlier.

On the opposite side of the spectrum, in the cooler, cloudier, lower fertility montane forests, species' traits seem to be predominately related to these conditions (e.g. low SLA, high LMA, L_th, WD, and low values for Leaf_N, Leaf_P). Montane species are typically characterized by long leaf lifetimes, expensive high-LMA leaf construction, low nutrient concentrations, and low rates of photosynthesis and respiration (Wright et al., 2004), indicating a slower return of investment. Leaf area has been found to be especially small in cold, high-elevation regions generally in response to nighttime constraints where larger leaves are more prone to frost damage (Dolph & Dilcher 1980; Wright et al., 2017), and in which thicker leaves and consequently higher LMA often imply a slower photosynthetic capacity per unit of leaf mass (Reich et al., 1997; Westoby et al., 2002). Due to the lack of detailed climatic information for each plot, I did not focus on the climate-trait relationships in this study. However, both unweighted and basal area weighted values of traits such as LMA and L_{th} were higher in the high elevation plots used here (Figure 2; Table S4). This corresponds with the increase in LMA with elevation found in studies using field and remote sensing data, and individual based model simulations as well in tropical forests of South America (Asner and Martin, 2016; Fyllas et al., 2017), with this effect likely regulated by temperature rather than by other factors such as moisture or solar radiation (Asner et al., 2014).

In the analysis of $Leaf_N$ and $Leaf_P$, soil nutrient content is the first and most obvious factor to consider. While lowland plots had a surprising lower percentage of nitrogen in soils compared to montane forests, phosphorous content was considerably higher in the alluvial lowland forests (Table S2). It has been shown that levels of phosphorous (P) are a stronger driver compared to nitrogen (N) for leaf nutrient concentration, and available P can increase the nutrient uptake and concentration in leaves (Maire et al., 2015). Moreover, P concentrations of upper-canopy foliage are often correlated with SLA (Townsend et al., 2007) as found in this study (Figure 3).

Only for two of the plots at the montane site, N:P ratios were significantly higher than those from the lowland plots (Figure 2; Table S4). Low levels in $Leaf_{N:P}$ have been associated with slow leaf-specific growth rates (Westoby & Wright, 2006), in agreement with the evidence showing that species occurring on nutrient-poor soils tend to shift toward higher average LMA and longer leaf lifespan than those species growing on more fertile soils (Westoby et al., 2002), conditions that were in fact observed in the montane forest plots. On the other hand, leaf economic traits related to resource acquisition such as SLA, $Leaf_N$ and $Leaf_P$ are positively correlated with soil nutrient content and these relationships can be stronger than those seen with climatic gradients (Ordoñez et al., 2009; Liu et al., 2012).

From the stand point of stem traits, I only focused here on wood density (WD), and this trait appears to be less significant in explaining the overall variations in trait composition (Figure S3). While WD was significantly different among all plots (Figure 2), the CWM of WD was similar between both sites (Table S4). The declining pattern of WD with elevation found elsewhere (c.f. Swenson and Enquist, 2007; Chave et al., 2009) was not observed here. However, in lowland tropical forests, species with higher wood density have been associated predominately with regions with low-fertility and weathered soils such as the Guiana Shield (Baker et al., 2004; ter Steege et al., 2006; Johnson et al., 2016), where it is linked to a greater expense per stem volume and to greater mechanical strength (Westoby & Wright, 2006; Chave et al., 2009).

In summary, the multi-trait space was considerably different between sites in agreement with the original hypothesis of environmental and adaptation constraints driving the divergence in trait composition between these low (i.e. montane forests) and high (i.e. lowland forests) resource environments. A higher dominance of conservative traits was found for the montane forests where ecological strategies that increase structural investment at the cost of decreased resource acquisition and demographic rates are common (Liu et al., 2012). In contrast, species with traits related to structurally inexpensive leaves, often with high specific leaf areas, higher nutrient concentration and lower wood density dominated the trait composition in the lowland plots.

THE RELATIONSHIP BETWEEN SPECIES’ GROWTH RATES AND TRAITS IS NOT CLEAR

Functional traits were hypothesized to accurately predict plant performance. Thus, plant growth should increase with resource availability (light, water, soil nutrients) and with traits that enhance resource acquisition (e.g. high specific leaf area – SLA, low wood density – WD). While higher growth rates for the species in the lowland plots were indeed higher with an almost two-fold difference in comparison with the montane plots (Figure 4), the relationship between RGRs and the average values of functional traits was not clear.

At first, regardless of site and when all traits were grouped into a principal component analysis (Figure 4A) it can be seen that species with nutrient-poor, thick, relatively heavy and small leaves, and to a lesser extent with denser wood stems, perform less favorably with regards to their growth. Moreover, six traits (i.e. Leaf chlorophyll content, SLA, LMA, Leaf_N, Leaf_P and WD) were significantly linked to RGRs when data was not classified by site, in agreement with studies showing some of these traits as important for plant performance (e.g. Wright et al., 2004; Poorter and Bongers 2006; Swenson and Enquist, 2007; Kunstler et al., 2016). However, while growth was expected to correlate positively, for instance, with a trait such as SLA since is indicative of the efficiency of biomass investment for light interception (see Poorter et al., 2008), there is an ambiguous trend when data is analyzed by site. On one hand, a negative slope in the case of lowland plots is evident, largely driven by the presence of a slow-growth late successional yet with high SLA legume species (*Lonchocarpus pictus* Pittier) characterized by large compound leaves but with high mean WD (0.74 g cm^{-3}). On the other, an almost flat slope for the montane plots was found for the RGR-SLA relationship. Similarly, with LMA being the inverse of SLA, a comparable trend was observed in agreement with studies that have shown LMA negatively affects RGRs and productivity (Westoby et al., 2002), but yet again, an opposite trend than the one expected specifically for the lowland plots was found.

SLA was shown to be a good predictor of growth and survival of seedlings of 13 tropical species under controlled conditions (Kitajima, 1994) or for the height growth of saplings of 53 tree species in the field (Poorter & Bongers, 2006). Yet, in the case of adult plants, this correlation has mostly been weaker or totally absent (Poorter et al., 2008; Wright et al., 2010; Prado-Junior et al., 2017) suggesting that, at least for some cases, trait–growth correlations may change systematically with plant size (Wright et al., 2010; Paine et al., 2015; Gibert et al., 2016; Falster et al., 2018). Furthermore, in the same montane study site used here, Quevedo-Rojas et al. (2016) found that the juveniles of 15 out of the 20 most important tree species had a non-random spatial distribution in relation to the percentage of canopy openness. This might indicate that low canopy openness dominates montane forests and despite the scattered tree-fall gaps present, light partitioning seems to be less relevant in determining the tree community structure at the juvenile stage. At least for this site, I then might expect that the almost flat trend in the SLA and LMA-growth relationship for large trees could be explained by a different factor (or group of them) other than light availability.

Another important reason for the non-conclusive evidence for a relationship between RGRs and traits in tropical forests that has been recently discussed has to do with whether these analyses are conducted considering the rates of individual trees or at the species level (Poorter et al., 2018; Yang et al., 2018; Worthy and Swenson, 2019). When an additional principal component analysis was conducted using the growth rate data from the 125 individuals instead of using species identity, there was a consistent trend regardless of site with the scores of the first PCA (results not shown here), which brings up additional questions regarding the relative low sample size used in the study, particularly for the lowland plots. The results from a power analysis suggest that if we want to reliably distinguish the species in their systems on the basis of leaf functional traits, sample sizes of 10 or greater per species sampled are likely needed (Hulshof and Swenson 2010), which implies additional factors to consider when conducting field work to collect functional trait data.

The cases of WD, $Leaf_N$, and $Leaf_P$ were different from previous results found for SLA and LMA in their relationship with growth rates. In fact, these three traits showed consistency among both sites and the species with nutrient-rich leaves showed a better growth performance, and the species with a high WD had slower growth rates with these trends being even more clear at the individual tree scale (results not shown here). The fact that the growth-WD relationship was consistent, not only at the individual and species level, but also for both sites is not surprising since this trait have been shown to be negatively correlated with growth rate at all stages of development after germination (Wright et al., 2010; Francis et al., 2017; Philipson et al., 2014). Greater construction costs of woody tissues imply that species with dense wood grow more slowly than those with soft wood (Chave et al., 2009), as oppose to low WD species with large vessel diameters that can enhance hydraulic conductance and water transport capacity, and hence, photosynthetic rates and comparatively higher growth rates (Swenson and Enquist, 2007; Poorter et al., 2008).

COMMUNITY WEIGHTED MEANS (CWMS) OF TRAITS AND COMMUNITY-LEVEL PROCESSES

CWMs of traits were reasonable bivariate predictors of turnover rates, AGB, and AGWP, with CWM_{Lth}, CWM_{SLA}, CWM_{LMA}, and CWMs of Leaf_{N} and Leaf_{P}, being overall the most important traits across all responses (Table S5). However, the CWM of Leaf_{N} appeared to be important, though in different ways, for all the responses in accord with the *biomass-ratio hypothesis* (Grime 1998) in which ecosystem processes are expected to be driven by the (traits of the) most abundant species in the community (Figure 5; Table 3). Moreover, there was a clear consistency at both sites in the relationship between the CWM of Leaf_{N} and all responses: turnover rates and AGWP were positively affected by the CWM of Leaf_{N}, whereas total AGB was negatively related with this trait (Figure S4, Table S5).

The importance of Leaf_{N} for both recruitment and mortality rates is consistent with the evidence showing nitrogen as a key element for plant growth and productivity (e.g. Vitousek and Sanford, 1986; Wright et al., 2011) and thus may enhance AGWP at the community level in agreement with the positive relationship between turnover and productivity shown at larger scales (Stephenson and van Mantgem 2005). For example, leaf nitrogen status was an important driver of the increase in net primary productivity in the analysis of ten contrasting sites in the Amazon (Aragão et al., (2009). Simultaneously, low AGWP is often associated with an overall high AGB as observed in the central Amazon and Guiana Shield regions (Malhi et al., 2006; Vilanova et al., 2018). Thus, the negative effect of the CWM of Leaf_{N} on total AGB therefore can be linked to a pattern of relatively slow-growing dominant Montane species.

The results from the mixed model analysis shows that CWM_{LMA} had a significant relationship with AGB (Table 3; Figure 5) consistent with studies showing that leaf mass per area and not total leaf area drive the differences in the AGB distribution among most woody plant functional types (Duursma & Falster, 2016). Yet, in all models tested, CWM_{LMA} continuously appeared negatively associated with total AGB in contradiction with the positive correlation found in the bivariate $\text{AGB}\sim\text{CWM}_{\text{LMA}}$ approach (Table S5) and with the original hypothesis for this trait. A positive effect of LMA over AGB is visible for the lowland plots, so the negative trend seems mostly driven the high elevation site (Figure S4-D). These results indicate that the power of this trait as a predictor of AGB might depend, on additional factors including plant size (Gibert et al., 2016; Falster et al., 2018), and phylogenetic variation (Neyret et al., 2016), which merit additional research.

The positive effect of functional richness (F_{Ric}) on AGWP suggest that, at least for the lowland forests with much higher F_{Ric} values compared to montane forests (Table S4), there is a higher efficiency in the use of available resources. The increased efficiency may be tied to a higher niche differentiation, thus increasing biomass productivity in accord with the *niche complementarity hypothesis* (Mason et al., 2005; Prado-Junior et al., 2016). Functional evenness, on the other hand, expresses the degree to which the biomass of a community is distributed to allow effective utilization of the entire range of resources available in the niche space (Mason et al., 2005; Finegan et al., 2015). In this study, though fairly similar between sites, I found an increase in the value of F_{Eve} index negatively affected AGWP at both sites (Figure 5; Figure S4-D). Assuming that resource availability is even throughout the niche space, higher functional evenness indicates that some parts of the niche space, while occupied, are under-utilized, which will tend to decrease productivity (Mason et al., 2005). Yet, these effects appear to be relatively low as evidenced by the low value in the standardized coefficients for both F_{Ric} and F_{Eve}, and the fact that the R^2_m was also low, implying that other site-related effects, different than functional traits might at play with regards to AGWP (Table 3; Figure 5).

Evidence that fertility is driving AGWP in these sites was not found in this study. Despite a positive and significant correlation between the CWM of $Leaf_P$ and AGWP (Table S5), bivariate correlations (Figure S4) or mixed models (Table 3) did not show the initially hypothesized effect of a higher nutrient content in soils positively influencing AGWP as per the *soil fertility hypothesis* (Wright et al., 2011; Quesada et al., 2012). I suggest this might be an effect of the low sample size as several studies have reported a positive effect of soil phosphorous on productivity, both in controlled conditions (e.g. Wright et al., 2011), or directly based on measured data in multiple tropical sites (e.g. Aragão et al., 2009; Quesada et al., 2012).

The positive effects of soil phosphorous on mortality rates are in line with the large-scale patterns seen for Amazonian forests where higher levels of competition and disturbance shape community structure together on more fertile soils (Quesada et al., 2012). Here, fast-growing species are better adapted and tend to dominate the community because nutrient availability is not a limiting factor to growth, and competition for light is high in comparison with less fertile sites (de Toledo et al., 2012). Indeed, higher mortality rates were found in the lowland plots (Figure S2; Table S4) where soil fertility is also considerably higher than montane forests (Table S2). It is conceivable that because trees produce more fine roots in poor soils to maximize nutrient uptake (de Toledo et al., 2012), such trees may be less prone to uprooting events. Such an effect may interact with the higher wood density of trees in poorer soils, with both factors simultaneously enhancing the capacity of stems to resist uprooting events in poor soils better than in rich soils (Chao et al., 2008; de Toledo et al., 2012; Vilanova et al., 2018). However, to fully uncover the connections between soil fertility and mortality rates we would need a more in-depth consideration of additional parameters, including soil water, slope effects, rooting depth and topography.

CONCLUSION

This study describes large structural and dynamic contrasts between lowland and montane forests in western Venezuela and shows how these are both mirrored by and closely associated with species functional differences. First, lowland seasonal forests are, on average, considerably more productive and more dynamic than those sites at higher elevation. The montane forests by contrast, attained higher levels of aboveground biomass. Second, large, significant, and coherent differences in trait composition across multiple traits were revealed. Multiple trait values, including both unweighted and plot-based weighted means of SLA, $Leaf_N$, $Leaf_P$, and a much higher value of functional richness, were all closely associated with the more productive environments (i.e. lowland forests). On the opposite side of the trait space, higher values of both average and weighted means of conservative-type of traits (i.e. LMA, L_{th}, $Leaf_{N:P}$, and WD) were more prevalent in the high elevation forests in the Andes. And third, at the community scale, this analysis suggests that turnover rates, aboveground biomass and woody productivity are driven by a combination of different factors where species' traits were important predictors. Here, the CWMs of several traits mixed with structural, dynamic and soil predictors all helped to explain the differences between lowland seasonal and high elevation montane forests of Western Venezuela.

Functional trait approaches have become popular in recent years, and for different forest-types beyond the tropics, as potential tools to better predict the effects of global change on forest ecosystems. This is likely to continue, especially with the increasing number of information being collected to organize massive and large-scale databases of traits (e.g. TRY database - Kattge et al., 2011; BAAD database - Falster et al., 2015; COMPADRE - Salguero-Gómez et al., 2015). However, especially in some of the most biodiverse areas of the world such as Venezuela, information remains very sparse. Additional efforts are urgently needed to improve this situation – across species, across multiple sites, and over time – in order to fully understand the potential effects of climate changes on tropical forest dynamics and function.

SUPPORTING INFORMATION.

Table S1. General description of the 12 forest plots used in this study. BAC = Barinas state-Caparo (lowland) | SEU = San Eusebio (montane).

Plot Code	**State**	**Latitude Decimal**	**Longitude Decimal**	**Date Established (decimal)**	**Last Census Date**	**Monitoring period (years)**	**No. of Censuses**	**Altitude (masl)**	**Mean Annual Temp. (ºC)**	**Avg. Min Temp (ºC)**	**Mean Annual Precipitation (mm year^{-1})**	**AET (mm year^{-1})** [a]	**PET (mm year^{-1})** [a]	**WA (mm year^{-1})** [a]	**Climatic Water Deficit (CWD)** [b]
BAC-01	Barinas	7.46	-71.01	1991.28	2016.30	25.02	13	141	26.8	20.5	1776	1298	1734	42	-427.66
BAC-02	Barinas	7.46	-71.01	1991.86	2016.30	24.44	12	143	26.8	20.5	1776	1298	1734	42	-427.66
BAC-03	Barinas	7.46	-71.01	1991.28	2016.30	25.02	10	144	26.8	20.5	1776	1298	1734	42	-427.66
BAC-04	Barinas	7.46	-71.01	1991.86	2016.31	24.45	12	138	26.8	20.5	1776	1298	1734	42	-427.66
BAC-05	Barinas	7.47	-71.02	2001.26	2016.31	15.05	9	142	26.8	20.5	1776	1298	1735	41	-423.66
BAC-06	Barinas	7.47	-71.02	1996.31	2016.31	20.00	10	140	26.8	20.5	1776	1298	1735	41	-423.66
SEU-01	Merida	8.66	-71.40	1968.81	2016.25	47.44	28	2318	14.3	6.9	1326	1103	1323	3	-266.39
SEU-02	Merida	8.62	-71.40	1968.81	2016.25	47.44	28	2312	14.3	6.9	1326	1077	1423	-9	-265.62
SEU-03	Merida	8.64	-71.41	1961.51	2016.26	54.75	34	2421	14.3	6.9	1326	1039	1281	45	-251.86
SEU-04	Merida	8.64	-71.41	1968.60	2016.27	47.67	27	2321	14.3	6.9	1326	1039	1281	45	-251.86
SEU-05	Merida	8.64	-71.40	1961.78	2016.26	54.48	33	2449	14.3	6.9	1326	1071	1297	29	-253.76
SEU-06	Merida	8.63	-71.40	1967.52	2016.26	48.74	26	2452	14.3	6.9	1326	1009	1270	56	-261.46

[a] Actual and potential evapotranspiration (AET and PET) data extracted from the were extracted from the Geospatial Database CGIAR Consortium for Spatial Information (Zomer et al., 2008) at http://www.cgiar-csi.org/data. Water availability (WA) = Mean annual precipitation – PET.

[b] Climatic Water Deficit (CWD) as in Chave et al., (2014) was obtained from a global climate layer for the long-term average of CWD at 2.5 arc-minute resolution. See: http://chave.ups-tlse.fr/pantropical_allometry.htm. This factor is measured as the difference between rainfall and evapotranspiration during dry months only and is, by definition, negative. CWD=0 means not seasonally water-stressed; in contrast, sites with very negative CWD values are strongly seasonally water-stressed.

Table S2. General description of soils in the 12 forest plots used in this study. eCEC= cation exchange capacity. BAC = Barinas state-Caparo (lowland) | SEU = San Eusebio (montane).

Plot	% Sand	% Silt	% Clay	pH (H_2O)	pH (KCl)	%N	%C	P (mg/kg)	Al (mg/kg)	Ca (mg/kg)	K (mg/kg)	Mg (mg/kg)	Na (mg/kg)	eCEC mmol/kg
BAC-01	13.10	78.40	8.44	5.01	4.22	0.24	2.65	19.01	159.98	854.97	96.37	202.65	11.88	80.09
BAC-02	3.68	87.00	9.37	5.54	4.83	0.26	2.45	10.97	42.83	1386.25	80.83	301.33	7.63	101.12
BAC-03	14.30	78.00	7.76	5.16	4.46	0.29	2.98	18.55	68.99	1174.21	110.34	232.09	18.73	88.99
BAC-04	6.08	85.30	8.63	5.53	4.77	0.18	1.91	20.58	67.79	969.65	89.91	142.96	3.51	70.13
BAC-05	3.38	86.00	10.60	4.92	4.00	0.14	1.34	35.96	117.63	340.52	51.63	81.37	2.97	38.21
BAC-06	47.20	48.96	3.80	5.71	4.96	0.17	1.62	9.30	45.20	809.30	63.08	93.64	12.73	55.28
SEU-01	5.29	85.75	8.99	3.89	3.42	0.77	10.19	4.22	1538.41	54.53	264.86	136.81	13.34	192.26
SEU-02	2.03	87.40	10.60	3.82	3.27	0.64	8.13	0.62	1371.04	60.64	230.56	122.89	13.73	171.97
SEU-03	14.30	78.80	6.96	3.81	3.24	0.54	8.20	4.97	845.96	222.12	164.71	114.35	13.73	119.30
SEU-04	16.70	78.80	4.60	3.96	3.35	0.74	12.65	5.90	592.75	993.63	180.79	150.03	10.69	132.87
SEU-05	15.50	77.40	7.18	3.78	2.91	0.54	10.29	6.10	320.67	93.82	123.32	48.33	5.84	47.70
SEU-06	11.20	77.50	11.20	3.92	2.97	0.20	5.26	5.83	198.58	42.91	67.49	21.81	5.49	27.96

Table S3. Average values for 10 functional traits and average relative growth rates (RGRs) for 50 of the most important (Basal area-based) tree species in two contrasting forest sites in Western Venezuela. (Caparo lowland forests = 22 species; San Eusebio montane forests = 28 species).

Site	*Species*	*Family*	*Chlor* ($\mu g\ cm^{-2}$)	L_{th} (*mm*)	*LDMC* ($g\ g^{-1}$)	*LA* (cm^2)	*SLA* ($cm^2\ g^{-1}$)	*LMA* ($g\ m^{-2}$)	$Leaf_N$ (*%*)	$Leaf_P$ (*%*)	$Leaf_{N:P}$ (*%*)	*WD* ($g\ cm^{-3}$)	*RGR* ($mm\ year^{-1}$)
Caparo	*Astronium graveolens* Jacq.	Anacardiaceae	26.07	0.18	0.40	130.06	98.10	104.25	1.72	0.69	2.49	0.87	5.44
Caparo	*Brosimum alicastrum* Sw.	Moraceae	55.78	0.29	0.43	20.91	104.61	98.52	1.58	0.53	2.97	0.60	3.46
Caparo	*Casearia nitida* Jacq.	Salicaceae	66.56	0.22	0.38	26.64	142.99	69.81	2.49	0.55	4.52	0.67	3.19
Caparo	*Cecropia peltata* L.	Urticaceae	49.44	0.41	0.26	914.58	84.12	117.80	2.75	0.57	4.82	0.30	7.54
Caparo	*Coccoloba padiformis* Meisn.	Polygonaceae	132.22	0.23	0.44	80.40	79.61	127.10	1.54	0.47	3.28	0.80	2.70
Caparo	*Ficus insipida*Willd.	Moraceae	70.23	0.27	0.34	65.13	85.09	119.45	1.93	0.47	4.10	0.38	9.41
Caparo	*Ficus pertusa* L.f.	Moraceae	45.86	0.18	0.30	37.95	174.08	57.44	1.79	0.60	2.98	0.41	8.81
Caparo	*Guarea guidonia* (L.) Sleumer	Meliaceae	44.50	0.20	0.32	185.96	108.21	89.37	2.24	0.80	2.80	0.57	4.71
Caparo	*Hirtella* sp.	Chrysobalanaceae	55.28	0.18	0.66	25.97	165.11	61.62	1.61	0.40	4.03	0.78	5.51
Caparo	*Lonchocarpus pictus* Pittier	Fabaceae	25.37	0.17	0.31	234.79	286.89	34.58	3.05	0.85	3.58	0.74	2.66
Caparo	*Luehea seemannii* Triana & Planch.	Malvaceae	52.60	0.27	0.39	112.33	101.60	99.70	1.96	0.63	3.11	0.42	9.05
Caparo	*Pachira quinata* W.S. Alverson	Malvaceae	20.60	0.32	0.17	124.54	144.45	68.57	1.51	0.76	1.98	0.42	5.08
Caparo	*Platymiscium pinnatum* (Jacq.) Dugand	Fabaceae	62.26	0.30	0.35	227.23	112.10	88.54	2.63	0.58	4.53	0.72	1.63
Caparo	*Pleurothyrium trianae* (Mez) Rohwer	Lauraceae	101.21	0.36	0.51	46.87	64.08	157.01	2.00	0.52	3.84	0.47	11.65
Caparo	*Pouteria reticulata* (Engl.) Eyma	Sapotaceae	63.57	0.23	0.51	37.78	92.27	114.16	1.51	0.57	2.70	0.79	4.24
Caparo	*Protium crenatum* Sandwith	Burseraceae	36.32	0.17	0.40	174.01	123.27	84.59	1.37	0.53	2.58	0.54	3.19
Caparo	*Pterocarpus acapulcensis* Rose	Fabaceae	48.90	0.20	0.46	79.95	155.52	64.79	2.87	0.63	4.56	0.59	11.76
Caparo	*Sapium glandulosum* (L.) Morong	Euphorbiaceae	68.93	0.25	0.25	38.69	137.64	72.37	2.84	0.78	3.63	0.41	6.42
Caparo	*Spondias mombin* L.	Anacardiaceae	35.48	0.23	0.19	270.03	212.43	47.10	1.89	0.80	2.36	0.38	4.69
Caparo	*Terminalia amazonia* (J.F. Gmel.) Exell	Combretaceae	56.17	0.22	0.36	41.02	110.61	91.66	2.35	0.40	5.86	0.67	1.18
Caparo	*Trophis racemosa* (L.) Urb.	Moraceae	44.57	0.23	0.38	39.84	119.30	83.33	2.31	0.58	3.98	0.66	4.21
Caparo	*Zanthoxylum setulosum* P. Wilson	Rutaceae	33.96	0.19	0.34	210.77	139.57	72.40	1.86	0.74	2.51	0.47	6.85
San Eusebio	*Alchornea grandiflora* Müll. Arg.	Euphorbiaceae	65.69	0.33	0.41	37.91	63.45	162.29	1.74	0.39	4.40	0.38	2.21
San Eusebio	*Billia rosea* (Planch. & Linden) C. Ulloa & P. Jørg.	Sapindaceae	63.35	0.21	0.44	128.32	67.98	156.62	1.17	0.43	2.78	0.69	2.22
San Eusebio	*Cinchona pubescens* Vahl	Rubiaceae	55.26	0.30	0.37	118.54	71.42	139.25	1.70	0.41	4.18	0.54	0.59
San Eusebio	*Clusia multiflora* Kunth	Clusiaceae	140.23	0.57	0.36	96.68	64.31	311.60	0.81	0.36	2.24	0.68	2.17

San Eusebio	*Eschweilera tenax* (Moritz ex O. Berg) Miers	Lecythidaceae	125.77	0.24	0.49	34.80	50.38	220.19	1.51	0.23	6.54	0.71	1.23
San Eusebio	*Eugenia* sp.	Myrtaceae	83.09	0.30	0.45	17.50	61.04	166.44	1.19	0.33	3.66	0.74	1.14
San Eusebio	*Ficus velutina* Humb. & Bonpl. ex Willd.	Moraceae	71.63	0.49	0.37	50.91	48.26	205.84	1.23	0.49	2.50	0.39	3.56
San Eusebio	*Geissanthus fragrans* Mez	Primulaceae	70.70	0.08	0.44	20.58	103.72	97.19	1.52	0.32	4.76	0.58	0.99
San Eusebio	*Graffenrieda latifolia* (Naudin) Triana	Melastomataceae	69.57	0.30	0.28	65.91	93.43	117.18	1.57	0.32	4.97	0.63	2.13
San Eusebio	*Hedyosmum glabratum* (Ruiz & Pav.) G.Don	Chlorantaceae	56.35	0.32	0.26	28.14	113.68	88.11	1.93	0.47	4.10	0.45	2.37
San Eusebio	*Hieronyma fendleri* Briq.	Phyllanthaceae	71.47	0.10	0.35	17.91	71.17	142.93	1.44	0.43	3.33	0.64	1.70
San Eusebio	Hieronyma oblonga (Tul.) Müll.Arg.	Phyllanthaceae	74.18	0.40	0.31	42.44	73.02	135.98	1.43	0.43	3.38	0.60	2.91
San Eusebio	*Ilex laurina* Kunth	Aquifoliaceae	134.81	0.46	0.52	42.04	35.10	284.93	0.98	0.35	2.80	0.58	2.29
San Eusebio	*Myrcia acuminata* (Kunth) DC.	Myrtaceae	55.90	0.23	0.50	12.52	58.38	167.85	1.26	0.30	4.21	0.81	0.94
San Eusebio	*Myrcia fallax* (Rich.) DC.	Myrtaceae	90.35	0.30	0.47	16.82	58.49	173.27	1.31	0.37	3.67	0.82	0.85
San Eusebio	*Myrcianthes karsteniana* (O.Berg) McVaugh	Myrtaceae	105.82	0.48	0.44	38.77	39.05	256.40	1.12	0.41	2.73	0.55	2.25
San Eusebio	*Nectandra laurel* Klotzsch ex Nees	Lauraceae	100.77	0.31	0.48	26.64	58.41	173.44	1.86	0.43	4.31	0.50	0.43
San Eusebio	*Ocotea macropoda* (Kunth) Mez	Lauraceae	72.37	0.23	0.38	96.20	55.03	195.42	1.51	0.38	4.01	0.51	3.55
San Eusebio	*Persea povedae* W.C. Burger	Lauraceae	50.75	0.40	0.44	85.88	55.88	183.98	1.16	0.32	3.61	0.55	6.28
San Eusebio	*Podocarpus oleifolius* D.Don	Podocarpaceae	86.46	0.44	0.44	5.36	42.33	234.94	1.21	0.38	3.25	0.45	2.93
San Eusebio	*Retrophyllum rospigliosii* (Pilg.) C.N.Page	Podocarpaceae	60.38	0.42	0.33	0.46	74.17	147.71	1.29	0.49	2.78	0.52	3.67
San Eusebio	*Ruagea glabra* Triana & Planch.	Meliaceae	86.96	0.35	0.34	137.67	53.93	188.41	1.93	0.58	3.32	0.47	0.08
San Eusebio	*Ruagea pubescens* H.Karst.	Meliaceae	90.83	0.31	0.34	996.98	92.30	264.79	2.00	0.60	3.33	0.47	2.27
San Eusebio	*Ternstroemia acrodantha* Kobuski & Steyerm	Pentaphylacaceae	69.98	0.45	0.46	12.13	43.11	232.56	1.09	0.27	4.02	0.69	1.16
San Eusebio	*Tetrorchidium rubrivenium* Poepp.	Euphorbiaceae	76.45	0.33	0.27	38.81	83.48	119.04	2.56	0.74	3.45	0.47	6.20
San Eusebio	*Turpinia occidentalis* (Sw.) G.Don	Staphyleaceae	83.68	0.47	0.35	94.33	49.20	210.11	1.51	0.46	3.27	0.34	0.59
San Eusebio	*Vochysia gigantea* Stafleu	Vochysiaceae	45.58	0.28	0.28	20.69	77.07	138.46	1.40	0.28	5.25	0.44	1.48
San Eusebio	*Zanthoxylum melanostictum* Schltdl. & Cham.	Rutaceae	65.93	0.38	0.40	94.69	51.75	208.81	1.38	0.33	4.19	0.59	3.24

Table S4. Average turnover rates (*r*: recruitment; *m*: mortality), mean aboveground biomass (AGB), mean aboveground woody productivity (AGWP), CWMs of ten functional traits and four functional diversity indexes for 12 plots in two contrasting forests in western Venezuela. Chlor: Chlorophyll content; L_{th}: leaf thickness; LDMC: Leaf dry matter content; LA: Leaf Area; SLA: Specific Leaf Area; LMA: Leaf Mass per Area; $Leaf_N$: Leaf nitrogen; $Leaf_P$: Leaf phosphorous; WD: Wood density; F_{Ric}: Functional richness; F_{Eve}: Functional evenness; F_{Div}: Functional divergence; F_{Dis}: Functional dispersion.

Plot Code**	***r*** **(% year^{-1})**	***m*** **(% year^{-1})**	**AGB (Mg C ha^{-1})**	**AGWP (Mg C ha year^{-1})**	**CWM Chlor (µg cm^{-2})**	**CWM L_{th} (mm)**	**CWM LA (cm^2)**	**CWM SLA (cm^2 g^{-1})**	**CWM LMA (g cm^{-2})**	**CWM LDMC (g g^{-1})**	**CWM $Leaf_N$ (%)**	**CWM $Leaf_P$ (%)**	**CWM $Leaf_{N:P}$ (%)**	**CWM WD (g cm^{-3})**	**F_{Ric}**	**F_{Eve}**	**F_{Div}**	**F_{Dis}**
BAC-01	2.37	3.13	106.78	3.23	31.71	0.26	171.94	164.31	0.006	0.21	1.77	0.74	2.47	0.42	0.89	0.60	0.91	1.80
BAC-02	3.45	3.70	95.28	2.77	58.43	0.23	70.56	113.35	0.009	0.35	2.08	0.59	3.71	0.55	5.48	0.75	0.85	2.46
BAC-03	2.36	2.76	191.79	2.86	41.54	0.27	103.9	125.89	0.008	0.31	1.65	0.66	2.65	0.58	0.69	0.69	0.96	2.75
BAC-04	1.96	2.30	127.17	1.90	40.60	0.28	89.69	127.74	0.008	0.29	1.61	0.64	2.61	0.50	1.64	0.86	0.70	2.19
BAC-05	3.60	3.65	69.65	3.04	48.89	0.26	196.52	133.68	0.008	0.37	2.02	0.59	3.41	0.54	12.48	0.69	0.76	2.79
BAC-06	2.30	2.67	136.58	3.99	53.39	0.26	138.56	118.98	0.010	0.37	1.71	0.62	2.82	0.56	19.51	0.66	0.77	2.95
SEU-01	2.20	1.33	159.93	2.56	79.40	0.30	42.31	66.66	0.017	0.39	1.46	0.33	4.65	0.60	3.42	0.64	0.85	2.74
SEU-02	1.90	1.10	130.36	2.27	84.78	0.30	52.92	65.68	0.018	0.40	1.47	0.33	4.69	0.62	3.97	0.76	0.79	2.84
SEU-03	1.55	1.17	211.66	2.53	68.38	0.35	107.04	72.38	0.016	0.36	1.41	0.47	3.11	0.59	0.14	0.58	0.65	2.29
SEU-04	2.45	1.87	184.32	2.72	74.33	0.37	23.68	70.18	0.015	0.34	1.63	0.52	3.17	0.55	0.03	0.69	0.77	2.58
SEU-05	1.63	1.56	170.81	1.98	75.95	0.34	74.43	59.28	0.019	0.41	1.36	0.37	3.72	0.58	1.40	0.72	0.79	2.28
SEU-06	1.80	1.76	169.63	1.81	81.68	0.40	38.55	63.43	0.019	0.38	1.25	0.39	3.25	0.59	2.05	0.79	0.74	2.43

** BAC = Lowland forests – Caparo | SEU = Montane Forests – San Eusebio

Table S5. Relationships between CWMs of traits, functional diversity indexes, turnover rates, AGB components, structure and soils with seven response variables related to dynamics, structure and function of two contrasting forests in western Venezuela. Values are Kendall-tau (τ) correlations, in **bold** those with $p < 0.05$.

Predictor	**Recruitment Rate**		**Mortality Rate**		**AGB Rec**		**AGB Mort**		**AGB Growth**		**AGB**		**AGWP**	
	Tau	*p-value*	*Tau*	*p-value*	*Tau*	*p-value*	*Tau*	*p-value*	*Tau*	*p-value*	*Tau*	*p-value*	*Tau*	*p-value*
CWM $_{CHLOR}$	-0.30	0.213	**-0.52**	**0.005**	0.24	0.927	0.03	0.431	-0.36	0.167	0.15	0.183	-0.45	0.120
CWM L_{th}	**-0.58**	**0.027**	-0.61	0.007	-0.27	0.144	0.18	0.217	-0.27	0.216	**0.55**	**0.013**	**-0.48**	**0.045**
CWM $_{LA}$	0.18	0.189	**0.33**	**0.027**	0.00	0.650	-0.03	0.972	0.36	0.118	-0.27	0.079	**0.39**	**0.039**
CWM $_{SLA}$	0.48	0.078	**0.52**	**0.001**	-0.12	0.705	-0.09	0.471	0.42	0.146	**-0.33**	**0.040**	0.58	0.058
CWM $_{LMA}$	**-0.48**	**0.040**	**-0.52**	**0.000**	0.06	0.619	0.09	0.398	-0.42	0.116	0.33	0.053	**-0.58**	**0.049**
CWM $_{LDMC}$	-0.30	0.668	-0.45	0.124	0.24	0.408	0.09	0.622	-0.36	0.397	0.09	0.488	-0.27	0.434
CWM $Leaf_N$	**0.70**	**0.000**	**0.67**	**0.000**	**0.27**	**0.031**	-0.12	0.639	0.39	0.242	**-0.48**	**0.005**	**0.61**	**0.044**
CWM $Leaf_P$	0.33	0.143	**0.61**	**0.002**	-0.27	0.928	0.00	0.801	0.39	0.068	-0.12	0.239	**0.48**	**0.055**
CWM $Leaf_{N:P}$	-0.09	0.971	-0.36	0.138	0.52	0.175	-0.18	0.702	-0.39	0.161	-0.06	0.858	-0.24	0.340
CWM $_{WD}$	-0.42	0.372	-0.58	**0.047**	0.18	0.577	-0.15	0.847	-0.30	0.410	0.27	0.114	-0.33	0.352
FRic	0.21	0.156	0.12	0.180	0.33	0.425	0.00	0.421	**-0.09**	**0.049**	-0.55	0.097	**0.18**	**0.015**
FEve	-0.03	0.961	0.06	0.927	0.21	0.904	-0.30	0.205	**-0.58**	**0.037**	-0.18	0.473	**-0.42**	**0.045**
FDiv	0.30	0.292	0.15	0.194	0.42	0.190	-0.15	0.404	0.12	0.642	-0.09	0.615	0.33	0.308
FDis	0.18	0.431	-0.03	0.845	0.36	0.209	-0.09	0.760	0.12	0.476	-0.03	0.987	0.33	0.344
Rec Rate			**0.55**	**0.000**	**0.3**	**0.004**	-0.03	0.575	0.24	0.686	**-0.24**	**0.012**	0.36	0.175
Mort Rate	**0.55**	**0.000**			0.03	0.062	0.06	0.505	0.15	0.507	**-0.52**	**0.007**	0.33	0.172
AGWP	0.36	0.175	0.33	0.172	0.15	0.494	0.24	0.311	**0.64**	**0.000**	-0.09	0.612		
AGB Rec	**0.3**	**0.004**	0.03	0.062			-0.24	0.339	-0.21	0.611	-0.21	0.072	0.15	0.494
AGB Mort	-0.03	0.575	0.06	0.505	-0.24	0.339			0.3	0.153	0	0.690	0.24	0.311
AGB Growth	0.24	0.686	0.15	0.507	-0.21	0.611	0.3	0.153			0.03	0.898	**0.64**	**0.000**
Density	-0.39	0.076	**-0.55**	**0.002**	0.24	0.881	0.03	0.767	-0.36	0.077	0.06	0.359	-0.42	0.069
Soil_pH	0.52	0.059	**0.48**	**0.003**	0	0.704	-0.15	0.421	0.36	0.084	-0.24	0.155	0.42	0.058
Soil_Nit	-0.3	0.122	**-0.52**	**0.010**	0.09	0.716	-0.06	0.618	-0.03	0.582	0.39	0.087	-0.21	0.492
Soil_C	-0.39	0.070	**-0.48**	**0.003**	-0.06	0.506	0.15	0.274	-0.12	0.391	**0.48**	**0.047**	-0.3	0.263
Soil_Pho	0.33	0.053	**0.73**	**0.009**	-0.06	0.322	0.03	0.278	0.18	0.714	**-0.42**	**0.046**	0.36	0.460
Soil_Al	-0.45	0.152	**-0.67**	**0.011**	0	0.851	0.03	0.809	-0.12	0.517	0.36	0.303	-0.24	0.475
Soil_eCEC	-0.06	0.472	-0.27	0.165	0.09	0.932	-0.18	0.523	0.15	0.941	0.15	0.379	-0.15	0.967

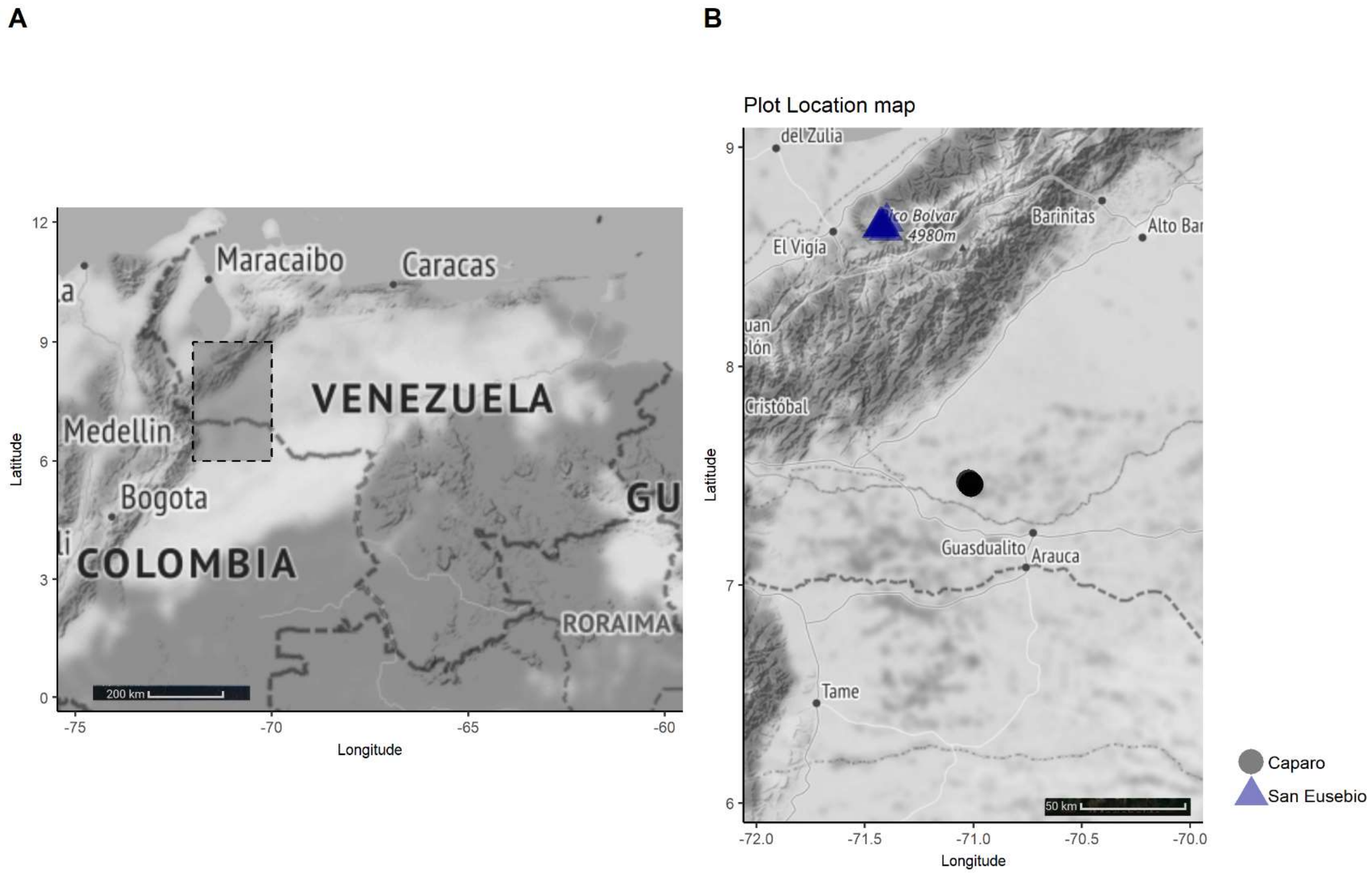


Figure S1. Location of 12 permanent plots in western Venezuela. Plots are almost contiguous at each site, so symbols overlap in B).

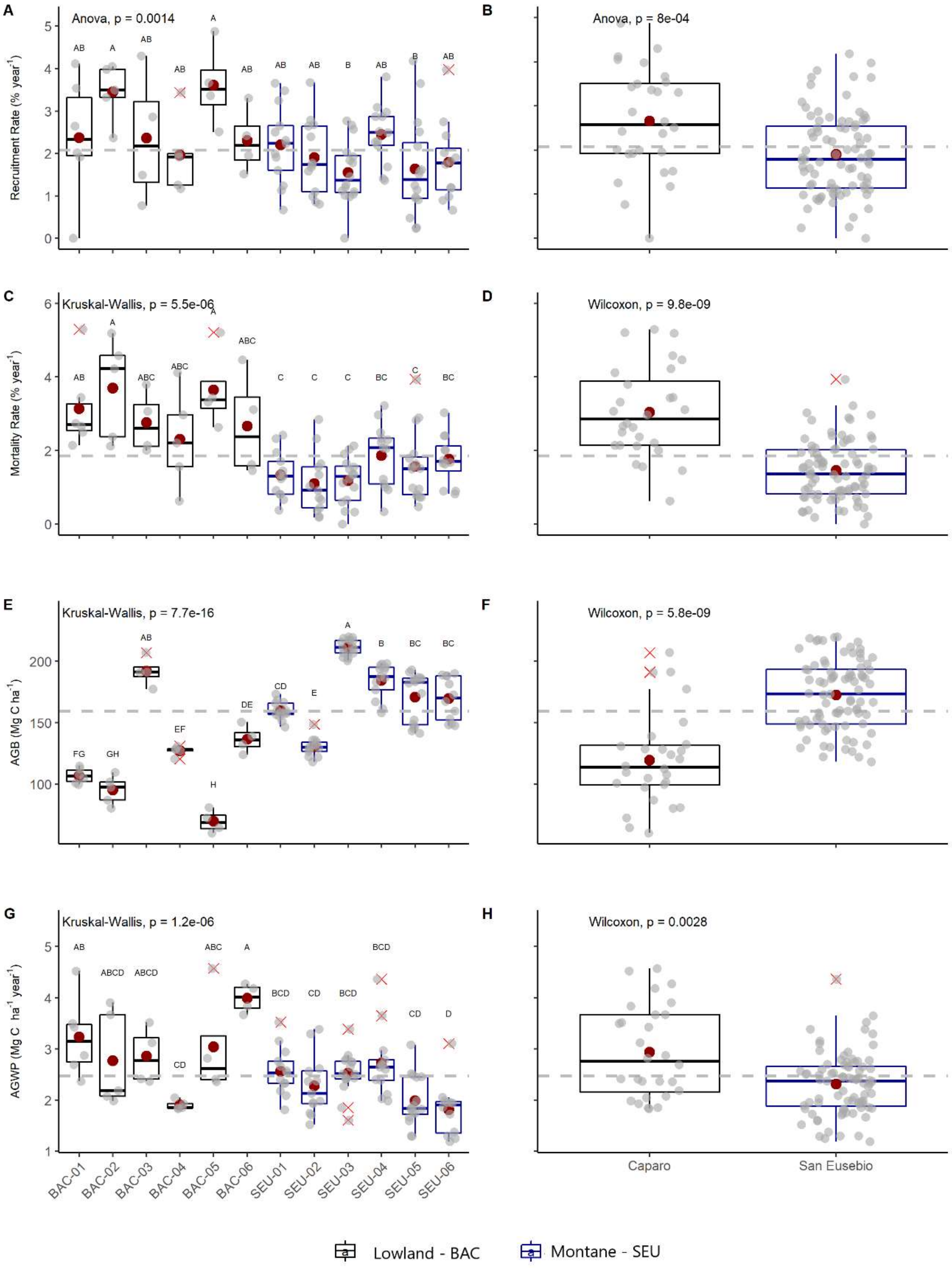


Figure S2. Boxplots showing general differences in four processes between plots (right column) and sites (left column) in two contrasting forests in western Venezuela. A-B) Recruitment rates; C-D) Mortality rates; E-F) Aboveground biomass (AGB); G-H) Aboveground woody productivity AGWP). Red circle shows the average value per plot and per site. Dashed gray line is the general mean for plots and sites. Letters indicate results from pos-hoc tests when significant differences were found.

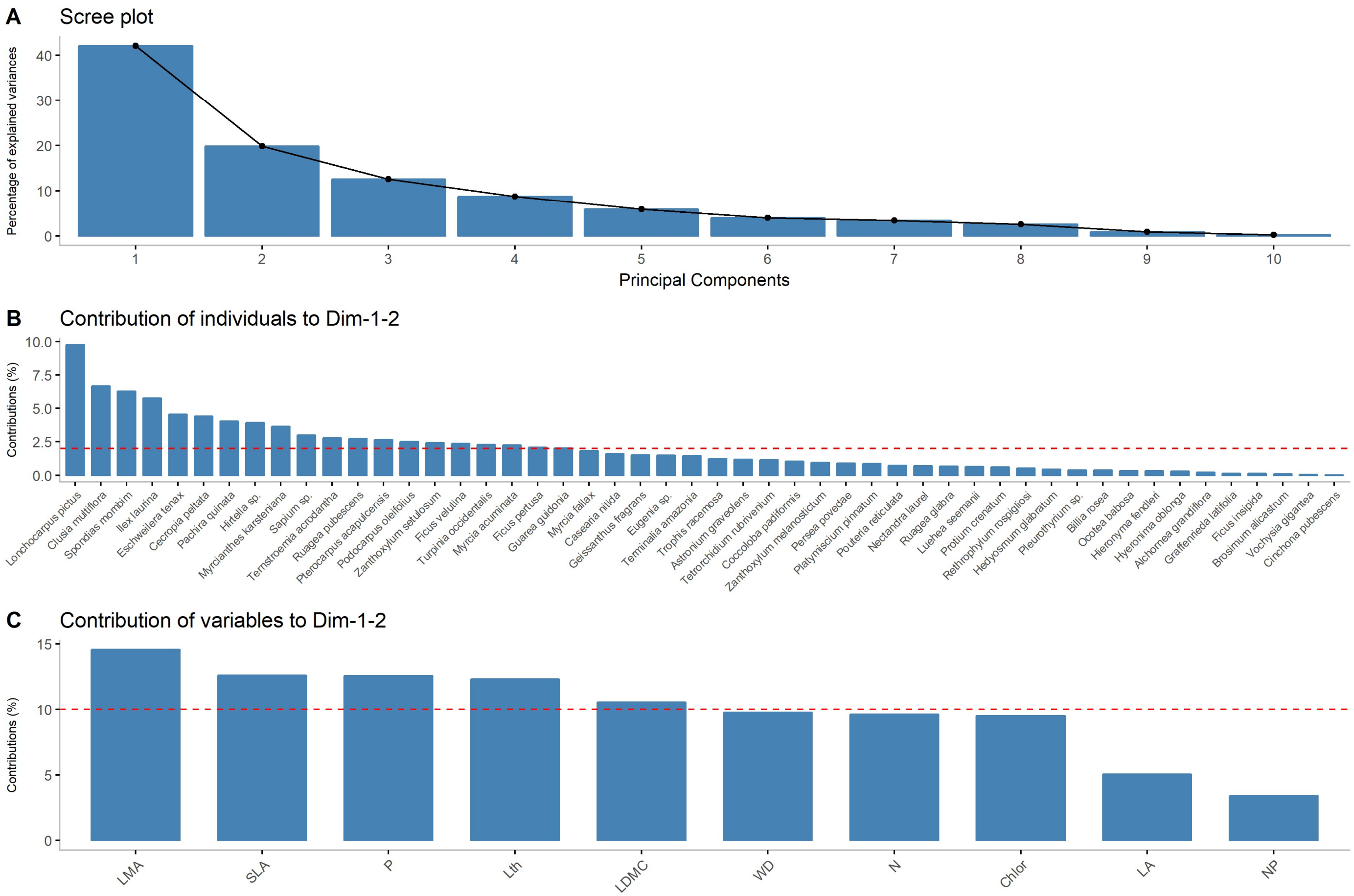


Figure S3. Decomposition of the Principal component analysis conducted in this study. A) Graphic of the percentage of the explained variance from 10 axes of variation; B) Relative contribution of species to the first two axes of variation; C) Relative contribution of traits to the first two axes of variation.

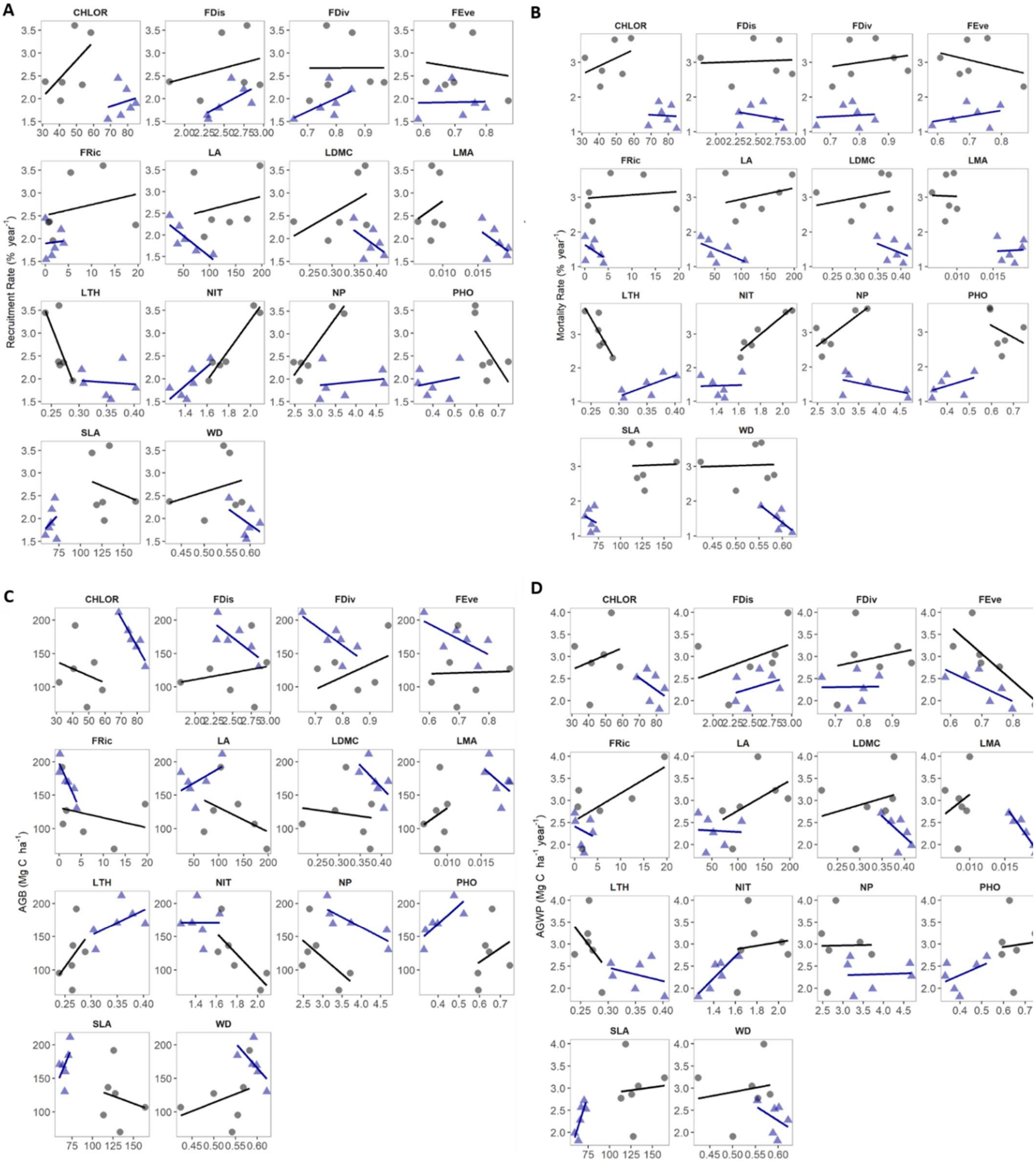
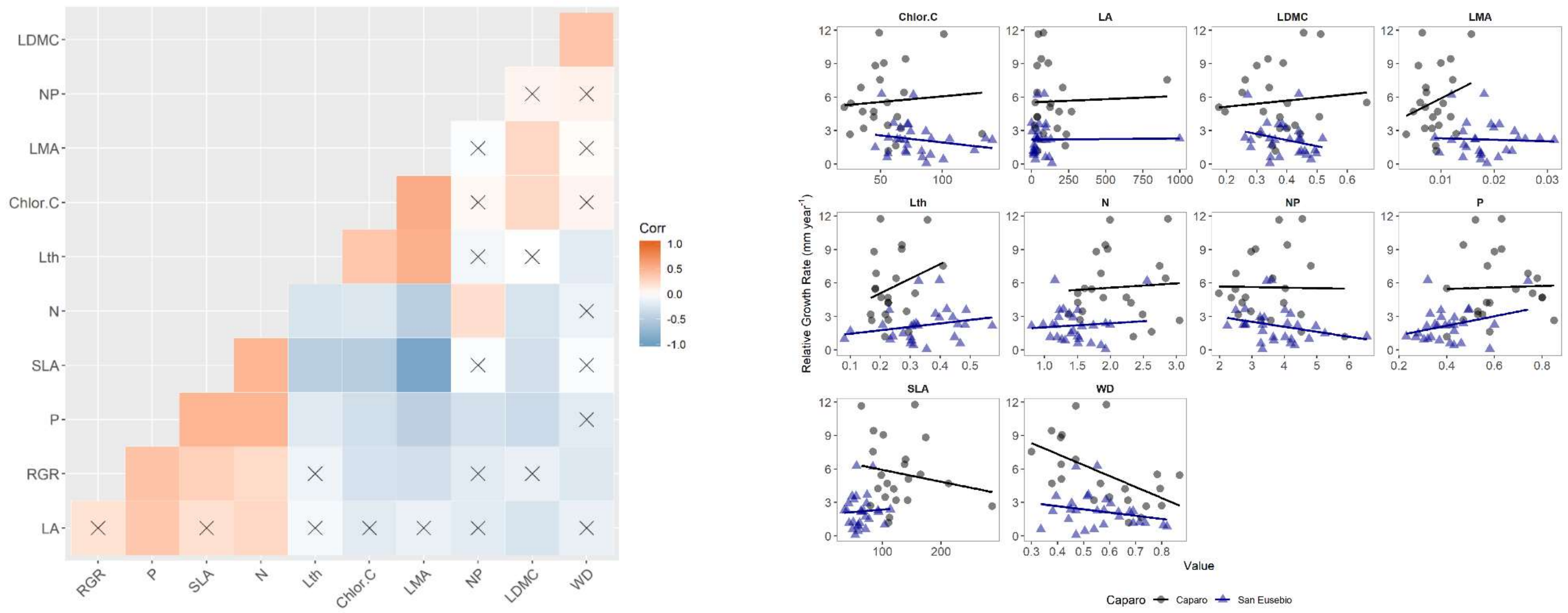


Figure S4. Relationships between recruitment (A), mortality (B), AGB (C), and AGWP (D) with CWMs of 10 functional traits and four functional diversity indexes for two contrasting forest sites in western Venezuela. Black circles indicate lowland plots in Caparo Forest Reserve, while blue triangles indicate plots at high elevation forests in San Eusebio.



A

B

Figure S5. Relationships between the relative growth rate with 10 functional traits measured and estimated for 50 tree species from two contrasting forests in Western Venezuela. A) Kendal-tau (τ) correlation matrix between pairs of trait average values and with RGRs. “X” implies not significant ($p < 0.05$) correlations between pairs of variables; B) Relative growth rates of 50 tree species and its relationships with 10 functional traits by site.

Caparo river and Western plains forests in Venezuela

Photo: Emilio Vilanova

CHAPTER 5

FINAL SYNTHESIS AND CONCLUSIONS

CHAPTER 5. FINAL SYNTHESIS AND CONCLUSIONS

Throughout the course of this project, I employed different approaches and methods to study the dynamics and structure of Venezuelan tropical forests. In doing this, several research questions were asked with regards to the potential existence of patterns in tree turnover, aboveground biomass (AGB) and woody productivity (AGWP) for a group of permanent forest plots that are representative of different mature forest-types in this northern portion of South America. I focused on these components of forest ecology since they are all important for the stability of any forest ecosystem (Pan et al., 2013), especially with regards to the function that forests do, and more importantly for understanding the potential impacts of climate change. In this last chapter I present a summary of the main findings and explain some of the identified limitations and advantages of the project to provide a context for a better understanding of the results and its potential implications for the conservation and management of Venezuelan tropical forests.

A MATTER OF SCALE?

As Simon Levin highlighted in his classical paper entitled "*The Problem of Pattern and Scale in Ecology*" (Levin, 1992), the mechanisms that might be influential in some of the processes analyzed in this project operate at different scales. Studying how tree populations might change over time (i.e. mortality and recruitment) in response to different biotic and abiotic factors, and moreover how these variations are linked to other processes such as carbon absorption (i.e. productivity) often require the interfacing of phenomena that occur on very different scales of space, time, and ecological organization (Levin, 1992). Thus, in **Chapter 1** the spatial scale of the project was presented as a partial overlapping between the individual tree to stand levels (i.e. community scale) while spanning from a few years up to almost five decades from the stand point of time. This temporal timeframe usually corresponds to the typical lifespan of many tropical trees and could serve to detect how trees acclimate to atmospheric changes, but might be shorter than the time needed to adequately investigate the return time of large-scale disturbance events that drive tropical forest dynamics (Zudeima et al., 2013). Nevertheless, analyzing multi-census data up to five decades is rare in the scientific literature regarding tropical forest ecology.

Deciphering unambiguous trends in tropical forest dynamics, especially those linked with global change, remains complicated because of the high levels of variability among and within tropical forest plots, the main source of data for many of these studies (Wagner et al., 2010). Differences among tree populations can become more difficult to detect as variance within a tree population increases, and often larger plot sizes than those used in this project are needed to provide robustness and statistical confidence in conclusions (Hall, 1998). As it was discussed in **Chapter 3**, some of the findings regarding the potential alterations in turnover and biomass change in tropical forests (e.g. Phillips & Gentry, 1994; Phillips et al., 2004) remained contentious mostly due to issues related to the plot size and the statistical treatment of multiple census intervals (Phillips et al. 2002; Sheil et al. 1996; Kohyama et al., 2018) that are used for this type of analysis. In this regard, some studies have shown that the type of sampling required to determine if sites differ in structure is not the same as needed to determine if sites differ in dynamics (Hall, 1998; Wagner et al., 2010). Consideration to anthropological aspects that could explain some of the patterns with regards of potential influence of pre and post-Columbian communities in today's forest dynamics should also be part of the conversation. **Nevertheless, with regards to the investigation of stem turnover and productivity (i.e. growth) the continuous monitoring of different sites for periods that span up to 50 years represents an important strength of this study that is worth highlighting. With the use of proper and standardized approaches (e.g. Lewis et al., 2004; Talbot et al., 2014) to deal with multiple census intervals, the estimates reported in this project are robust and comparable to other studies.**

In order to reduce the levels of uncertainty in the estimations of aboveground biomass (AGB), and thus the degree of confidence in the temporal changes in AGB of this study we would require several improvements that are discussed later in this section. In essence, these are related to expand the spatial coverage of the plot network in the studied regions in Venezuela, not only where we currently have data available, but also including other areas where we currently lack field data such as the mature stands in the very dry forests of the northwest portion of the country, along with several types of mangrove ecosystems in different portions along the coastal margins of the Caribbean sea.

HOW TURNOVER, BIOMASS AND PRODUCTIVITY VARY ACROSS DIFFERENT FOREST-TYPES?

In the early 2000's, Phillips et al. (2004) showed that there are clear spatial variations at larger scales in tree turnover in lowland Amazonian forests with more dynamic areas located to the Western region of the basin. Moreover, these differences are partially mirrored in the spatial variations in woody productivity (Baker et al., 2004; Quesada et al. 2012), and aboveground biomass (Malhi et al., 2006; Poorter et al., 2015; Vilanova et al., 2018). At larger scales, lowland forests in Western Amazonia are typically more productive but might store less carbon than those in the Eastern portion, including the Guiana Shield, where a higher carbon density in the aboveground vegetation has been reported (Malhi et al., 2006; Avitabile et al., 2016; Johnson et al., 2016). Thus, in **Chapter 2**, I wanted to confirm if these patterns hold at a sub-regional scale (country-level) while also including sites at higher elevations in the Andes to the West of the country that have been often excluded from many studies focusing on tropical forest dynamics. Indeed, forests of the Guiana Shield in Venezuela are areas with a much higher carbon storage capacity compared to other forest-types. Interestingly, despite its rather slow dynamics in terms of recruitment and mortality rates, these areas can also achieve higher levels of woody productivity, in some cases higher than the "fast" dynamic forests of the lowland Western Plains, a much fertile and younger bioregion. These findings were not expected and highlights the crucial role that species composition might play in combination with resource availability that will require further research in the future. Furthermore, another interesting finding coming out from this analysis is that forests in the Andes, especially those at higher elevations with much lower soil fertility than their counterparts in the lowland Western Plains, might be closer to the Guiana Shield forests with regards to their dynamics (i.e. low turnover rates) and carbon storage capacity (i.e. low productivity and high aboveground biomass – AGB - stocks). **Finally, at the scale of this project, woody productivity and stem dynamics (i.e. turnover rates) were found to be totally**

uncorrelated which seems to indicate that while mortality and recruitment can influence the total AGB in neotropical forests (e.g. Johnson et al., 2016), the rate at which carbon is stored (i.e. woody productivity) seems to be more a response of environmental drivers such as length of dry season and soil fertility.

WHAT HAPPENED WITH THE STRUCTURE AND FUNCTION OF VENEZUELAN FORESTS IN THE LAST FEW DECADES?

With more spatial and temporal coverage incorporated in the analysis compared to early studies (e.g. Phillips & Gentry, 1994; Phillips et al., 1996; Phillips et al., 2004), Brienen et al. (2015) showed for the 1980-2010 period that there has been temporal variation in the CO_2 sequestration capacity of lowland Amazonian forests, and that this capacity has been decreasing, likely as a response of global change and the increased frequency and severity of ENSO-driven droughts (Feldspauch et al., 2016). One of the interesting findings of this study was that the so called “changing ecology” of tropical forests (Lewis, 2009a), where the carbon sink capacity of tropical forests both in the neo and paleo tropics (Baker et al., 2004; Lewis et al. 2009b) was found to be positively influenced by increasing rates of turnover is now being weakened due to a decoupling phenomenon with much higher rates of tree mortality compared to recruitment, especially during the first decade of the 21st (twenty-first) century.

In **Chapter 3**, I conducted a temporal analysis of turnover rates, and woody productivity for the network of long-term Venezuelan plots as an independent examination of the Brienen et al. (2015) study in which I incorporated almost 50 years of additional data coming from the Andean forests. Besides adding information from montane ecosystems, a novel aspect of this research was the attempt to quantify the causal mechanisms behind the trends found for these processes. Despite the limited size of the dataset and the stochastic nature that characterize forest dynamics, **I consider this to be an important step towards a better understanding of the causal mechanisms of change in tropical forests that can feed other empirical or modeling studies where the factors that could affect the structure and dynamics of forests in the future are being addressed**. Overall, throughout different periods and regions, an increase in turnover rates was found, with mortality exceeding recruitment, hence, a decline in woody productivity was also found. Yet, this decline appears to be not strong enough so the changes in aboveground biomass are negligible, and for most of the period considered Venezuelan plots seemed to be acting as carbon sink.

WHAT ARE THE MAIN DRIVERS OF CHANGE IN VENEZUELAN TROPICAL FORESTS?

In studying the potential drivers of change in the dynamics of turnover and structure in Venezuelan forests, I first focused on analyzing what happened historically with regards to climate patterns in the last 100 years, thanks to the availability of georeferenced data from the Climate Research Unit (CRU) at University of East Anglia (Harris et al. 2014). Increasing trends in temperature were ubiquitous in all plots, with similar results observed for the Maximum Climatic Water Deficit (MCWD – *sensu* Aragão et al. 2007) and annual evapotranspiration, indicating a worrying trend towards a warmer and drier future. I found that different factors could be explaining the tendencies observed in the selected response variables. For example, temperature was a preeminent driver of mortality, while competition (i.e. increasing trends in stand density and growth) appears to be responsible for recruitment. There was a mix of factors between competition factors and temperature driving the results of aboveground woody productivity, with the latter likely having a larger influence via reduced growth overall. **Putting these results together, the main message from this research is that in the last 30-40 years, mature forests in Venezuela may have experienced concerted changes in their structure and turnover patterns, and these alterations are occurring beyond lowland forests, and montane sites in the Andes also seems to be experiencing similar changes, where climate change, via higher temperatures appears to be a fundamental factor for these alterations**.

HOW FUNCTIONAL DIVERSITY INTERACTS WITH THE ENVIRONMENT TO PREDICT TURNOVER AND STRUCTURE OF VENEZUELAN TROPICAL FORESTS?

In alignment with the main thematic area of this project, in the last research component of this project (**Chapter 4**), I used a local-scale framework to test different hypotheses regarding the relationships between stem turnover, aboveground biomass and productivity with different predictors including soil fertility, climate factors and functional diversity in two contrasting forests of Western Venezuela. **One of the novel aspects of this component was the use, for the first time in the context of forest research in Venezuela, of directly measured data for a group of traits that have been shown to be important to understand the mechanisms of species growth and mortality** (Diaz & Cabido, 2001; Perez-Harguindeguy et al., 2013; Violle et al., 2007).

The results found demonstrate that there is a notorious contrast in the multi-trait space among both sites studied, in coordination with the hypothesis that functional diversity might be more relevant than species richness for the structure and dynamics of tropical forests. Conservative-type traits are more dominant in the cooler, cloudier and less fertile environment of the high elevation forests in the Andes, while acquisitive-type traits are more common in the lowland, warmer and seasonal forests in the Western Plains region. The traits were partially useful descriptors of the processes considered, and the community weighted mean of Leaf Nitrogen appears to be a key trait to understand the differences across montane to lowland forests in this part of South America. While additional data is always needed, especially to strengthening the explanatory power of the analysis by increasing the number of traits and the number of samples, I strongly believe these results are relevant for at least two reasons. First, the description of the diverse environmental gradient of Venezuelan forests, including the distribution of functional traits for the constituent species is an interesting addition to the knowledge of a relatively poorly studied region/country. In addition, I am contributing with trait data from a rather unexplored set of sites that could be used in the future for other large-scale studies and will definitely help growing the current availability of trait data for future scientific research. **I consider the results to be of wide interest for ecologists, forest managers and policy makers**

interested in the current structure of tropical forests, as well as vegetation modelers aiming to predict forest responses to climate change.

A WAY FORWARD FOR THE STUDY OF FOREST ECOLOGY IN VENEZUELA

As shown in Chapter 1, **a pioneering effort to study a variety of forest-types in Venezuela started early in the twentieth century through the installation of numerous field plots (Veillon, 1985), with some sites already capturing continuous information for more than 50 years, making these the longest known records for the neotropics**. Among other reasons, a core element of this initiative was to support with field-data the initial implementation of forest management practices that were starting in the Western Plains region around 1970's with the allocation of the first logging concession (Kammeshedit et al., 2001; Vilanova et al., 2012). The characteristics of the management practices in natural forests in Venezuela have been addressed elsewhere (Torres-Lezama et al., 2008; Vilanova & Sabogal, 2012), but is worth highlighting that among the different factors contributing to the limited success of this process, underestimating the importance the data collected from some of the sites used in this project to determine, for instance, sustainable cutting cycles and thus implement better silvicultural plans for natural regeneration, was one of the most important failures (Kammeshedit et al., 2001; Vilanova & Sabogal, 2012).

Despite the loss of some of these sites due to deforestation and degradation, or simply due to lack of continuous funding and personnel, different teams of skilled researchers, technicians, students and local communities have been able to maintain and continue these efforts despite numerous limitations. An important enhancement to this monitoring program occurred with the active participation within the RAINFOR project (www.rainfor.org) which started in 2004 and was finally consolidated in 2009 when the majority of the plot data was incorporated in the forestplot.net database. This involvement certainly represented an important progress towards the expansion of our knowledge of neotropical forests and facilitated the interaction and collaboration of our national research community and multiple partners aiming at answering different questions about these ecosystems. In addition, other sites, mostly via single-census plots not included in the same network and managed by different researchers and institutions also exist and offer an opportunity to increase the coverage of research sites in Venezuelan forests.

In comparison with recent large-scale studies (e.g. Brienen et al., 2015; Esquivel-Muelbert et al., 2018) that focused on the ecology of Amazonian forests, for this project I used a relatively small dataset to offer an updated perspective on important ecological processes in the context of Venezuelan forests to improve our current understanding of forest dynamics and its relationships with environmental factors. **Nevertheless, although there are several limitations that have been addressed in each chapter/study that conform this dissertation, an important one has to do with the accurate characterization of the disturbance regime where these plots are located**. We know relatively well that gap-phase dynamics is probably the main driver of disturbance and associated changes in structure within mature tropical forests (Chazdon, 2014). Yet, a more accurate description of the historical patterns of disturbance is lacking to further test some of the results found here.

Certainly, long-term monitoring (i.e. decades to centuries) is a much necessary approach to detect patterns and underlying mechanisms. However, with a multi-scale approach that includes not only maintaining and continuing the long-term monitoring of the current plot-network with new sites, but also incorporating novel techniques such as remote sensing tools (e.g. LANDSAT, LiDAR) to address large-scale responses including the role of deforestation and degradation processes that are common in Venezuela (Pacheco et al., 2017), we could find ourselves gathering a more comprehensive type of data. In addition, local-scale (i.e. tree-level) experiments are urgently needed to understand the physiological mechanisms of a diverse set of forest-types to better understand the effects of climate change and other disturbance forces, which can include manipulative field experiments, and well-validated simulation models to improve predictions of forest responses to global change (Zudeima et al. 2013).

A MONITORING PLAN TO DOCUMENT THE DYNAMICS OF VENEZUELAN FORESTS

A global analysis conducted by Romijn et al. (2015) revealed several deficiencies regarding Venezuela's capacity to undertake an effective national-level program of forest monitoring to address several aspects of forests including deforestation, land-use change, and climate change. Lack of sufficient human and funding resources, limited coordination at different institutional levels, and sufficient access to modern technology to complement on-the-ground activities with remote sensing tools were detected as important limitations. It is not hard to imagine that with the ongoing institutional, economic and humanitarian crisis, many of these activities have been simply abandoned or suspended, which highlights the enormous value that the network of forest plots currently possesses.

From the stand point of natural resource management, a potential national monitoring program would be based on periodical assessments of selected variables of forest ecosystems, whether these are related to metrics of deforestation or degradation, or about some of the processes studied in this project (i.e. turnover, biomass, productivity). Furthermore, I see this plan focusing on areas beyond mature forests but also expanding the coverage to other human-disturbed areas where secondary forests are still valuable resources to provide a myriad of ecosystem services that needs to be properly quantified. Overall, a comprehensive plan to monitor the dynamics and ecology of Venezuelan forests is justified by at least three main reasons:

1) Collecting standardized data will facilitate decision-making process with regards to policies for sustainable forest management, conservation of biodiversity, people's livelihood, and ecosystem services;
2) A monitoring program for Venezuelan forests could promote training efforts for all stakeholders interested in the fate of forest ecosystems and in the services forests currently provide in the context of future climate change;
3) To have an adaptable and functional program of forest monitoring at different scales could yield important benefits for the planning, action, evaluation and learning processes that should be part of any institution linked to Venezuelan forests.

FINAL CONCLUSIONS

Venezuela is one of the most biologically diverse countries on earth. Yet, a high proportion of its ecosystems, especially forests, are threatened by different drivers that may compromise the services these provide while enhancing climate change through the emissions of carbon. The findings of this project represent a body of knowledge regarding the ecology and dynamics of different areas, some of which seem to be already experiencing the effects of increasing temperatures resulting in higher rates of tree mortality and a reduction in productivity. However, in some cases, these areas are not only still acting as carbon sinks mitigating the effects of climate change, but they also constitute large reservoirs of carbon and habitat for biodiversity making them highly important for a sustainable future.

Globally, several approaches have been proposed to increase the climate change mitigation potential of tropical forests and/or maintain their high levels of biodiversity. I strongly believe that the results presented in this dissertation project may have important connections and implications to initiatives such as reducing carbon emissions from deforestation and forest degradation, sustainable forest (or land) management for timber and nontimber forest products and increasing forest cover by forest landscape restoration. Each chapter in this dissertation contains information to feed and improve decision making processes at different levels but addressing the nature and characteristics of each initiative deserves further attention and additional space beyond this thesis. However, should Venezuela be able to find a solution to the ongoing humanitarian crisis that is affecting the stability of the entire nation, I see the results and conclusions of my research as important elements for a better future of Venezuelan tropical forests, its research community and overall the country.

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Emilio Vilanova Short Bio – November 2019

Emilio Vilanova has a forest engineering degree from the Universidad de Los Andes (ULA), Venezuela from 2003, and a Master in Forest Management from 2007 from the same institution. Between 2008 and 2013, before joining the PhD Program, he was part of the Research staff at the Institute of Forest Research and Development (INDEFOR) at ULA where he led a Senior-level course in Forest Management for 5 years. In Venezuela, he also co-led a Tropical Silviculture class for four years and collaborated as a temporary lecturer in a graduate-level course on Tropical Forest Ecology for two years. Between 2011 and 2012 he worked as a forest consultant for the UN-FAO Forestry office to prepare a national-level report of the state of the art of Silvicultural practices in Venezuela within a regional study conducted in all Amazonian countries. First as a graduate student in 2004 and later as the principal investigator he has been (and still is) part of the Amazon Forest Inventory Network (RAINFOR project) and the Amazon Tree Diversity Network (ATDN) both international networks to study the ecology of forests in the neotropics and its implications for conservation, management and climate change. As a research assistant at the Center for Sustainable Forestry at Pack Forest in Washington state between 2014 and 2018 he contributed to several projects linked to forest ecology and silviculture of Pacific Northwest forests and helped during the summer and spring internship programs there. In 2018, he worked as a lecturer for the Fall-edition of the Applied Forest Ecology course (Silviculture) at the University of California – Berkeley. His primary interests are forest ecology and sustainable management with an emphasis on tropical forests. As a lead author or coauthor he has more than 30 publications in different scientific journals.

More info:

http://emiliovilanova.com

A beautiful view of the majestic tropical rainforest of the Guiana Shield

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