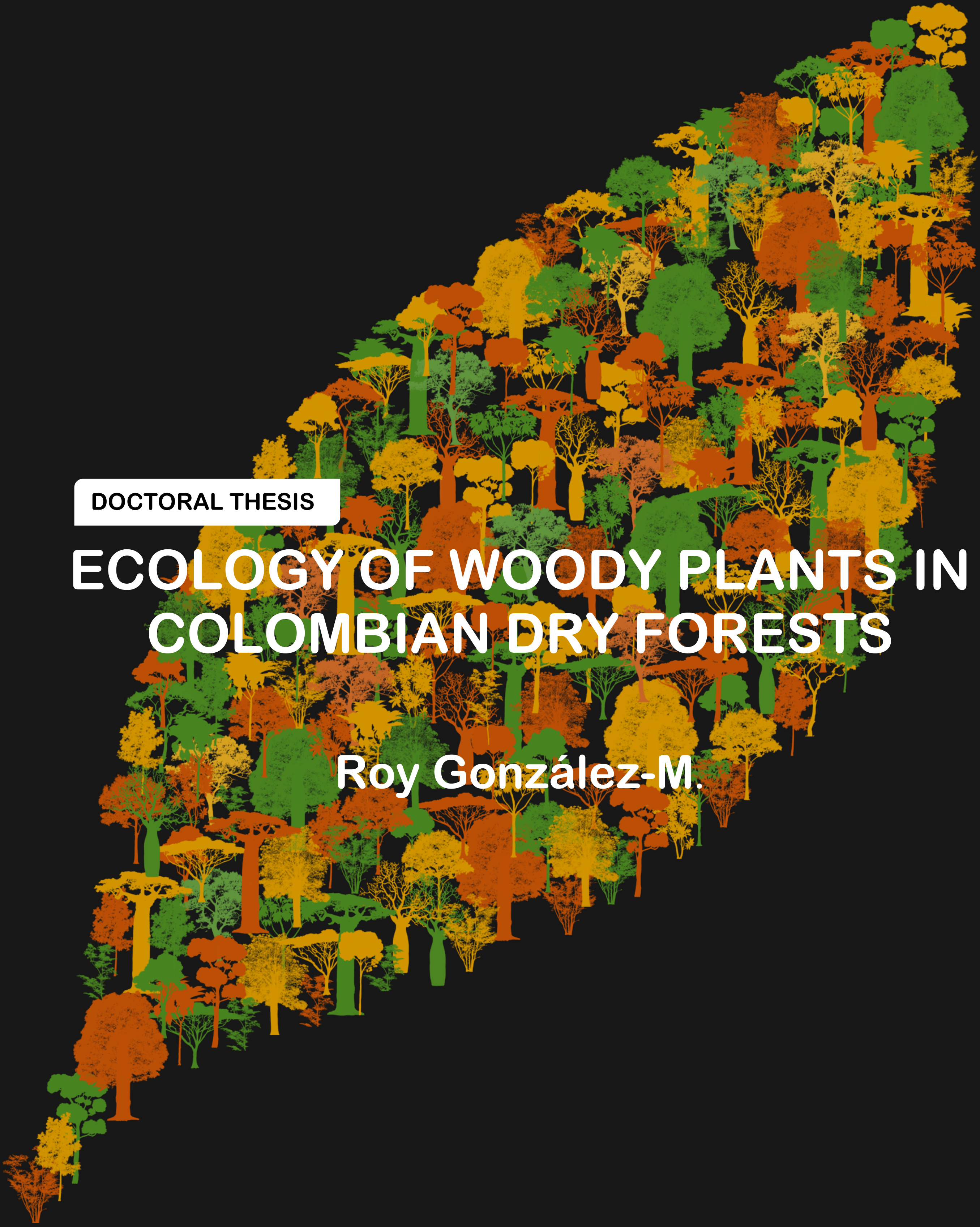

DOCTORAL THESIS

ECOLOGY OF WOODY PLANTS IN COLOMBIAN DRY FORESTS

Roy González-M.

ECOLOGY OF WOODY PLANTS IN COLOMBIAN DRY FORESTS

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This research was conducted under the auspice of the Colombian tropical dry forests research and monitoring agenda from the Instituto de Investigación de Recursos Biológicos Alexander von Humboldt.

Ecology of woody plants in Colombian dry forests

Importance of environmental harshness and plant community attributes on ecosystem processes

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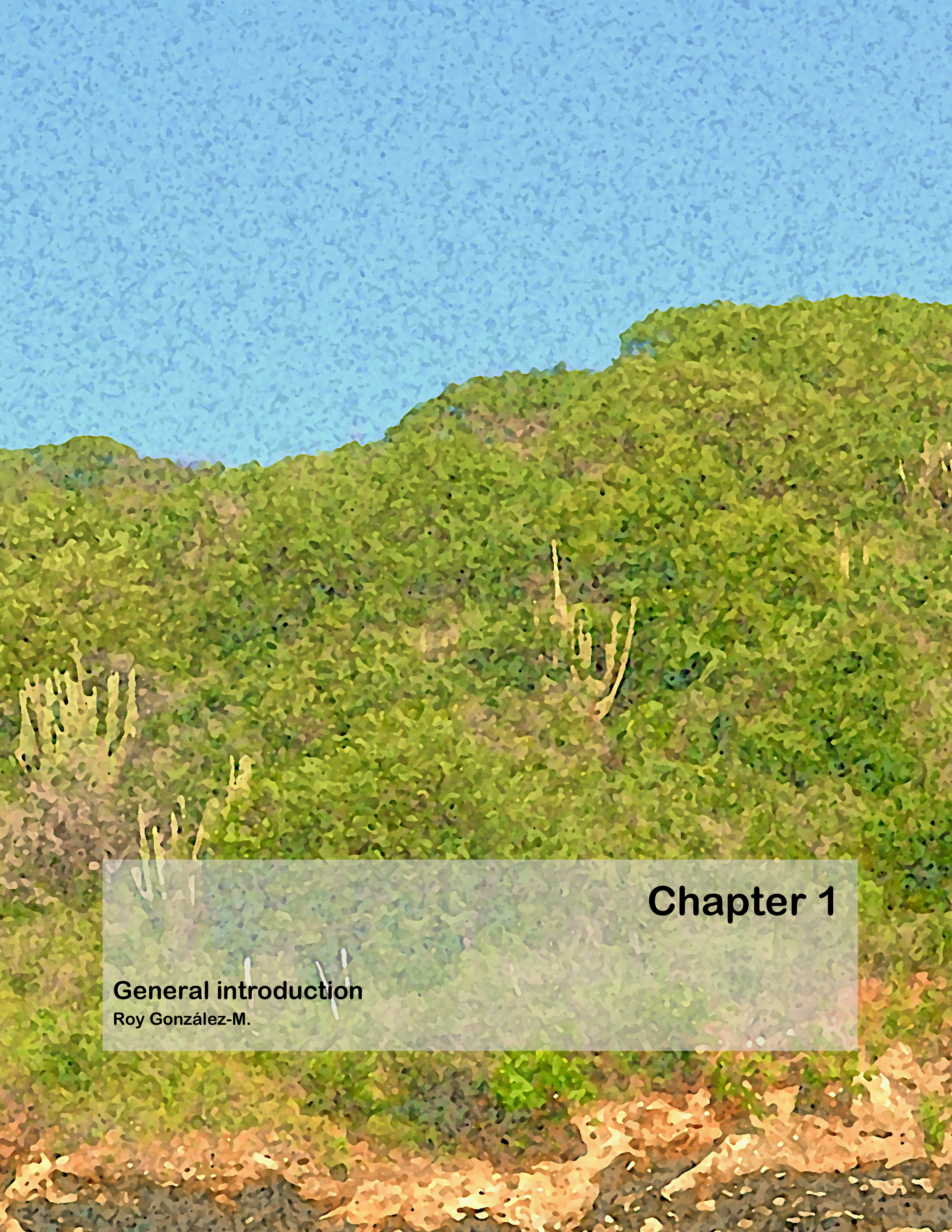


Chapter 1

General introduction

Roy González-M.

Tropical dry forests: a general context

Tropical dry forests (TDF) are widely distributed around the world, representing 42% of all tropical forests (Brown & Lugo 1982), with 54.2% of them located in South America (Miles *et al.* 2006). However, this ecosystem has been historical exposed to strong human transformation (Rodríguez *et al.* 2008; Portillo-Quintero & Sánchez-Azofeifa 2010; Linares-Palomino *et al.* 2011), to the point of being listed as a critically endangered ecosystem in South America, and under a high probability of collapse in the next 50 years (Rowland *et al.* 2019). In South America, TDF are typically characterized by a mean annual rainfall lower than 2000 mm and a marked rainfall seasonality given by 3-6 months with precipitation below 100 $mm \cdot month^{-1}$, when potential evapotranspiration exceeds precipitation (Murphy & Lugo 1986; Mooney *et al.* 1995; Murphy & Lugo 1995; Dirzo *et al.* 2011). Across the continent, TDF occur in the lowlands and are distributed in 11 floristic groups (DRYFLOR *et al.* 2016) where rainfall seasonality and biogeography are recognized, at least for at a regional scale, as the main determinants of their floristic relationships, diversity and ecology (Pennington *et al.* 2009; Linares-Palomino *et al.* 2011; Hulshof *et al.* 2014). However, there are different studies highlighting the needs for evaluating the role of other environmental factors such as temperature, isothermality, soil nutrient and water storage, among others, in driving diversity, structure and ecological processes of TDF (Ferreira-Nunes *et al.* 2014; Neves *et al.* 2015). Likewise, recent studies called the attention about considering the legacy of the human footprint and the consequences of climatic anomalies on changes in the diversity and functioning of TDF (Portillo-Quintero & Sánchez-Azofeifa 2010; Allen *et al.* 2015, 2017a) that will improve conservation strategies in South America (Sánchez-Azofeifa *et al.* 2005b; García & González-M 2019).

Colombian TDF provide a unique opportunity to address these gaps of knowledge and advance research guidelines for their conservation. First, the geographic location of Colombian TDF represents the three main forests types of this ecosystem in South America (*i.e.*, forests in the Caribbean lowlands region, forests in the Inter Andean region, and forests in dry Savannas, **Figure 1**; Pennington *et al.* 2006, 2009; DRYFLOR *et al.* 2016) representing important floristic distinctiveness within the country but high floristic representativeness across the region. Second, Colombian TDF are under the influence of the intertropical convergence zone (Asmerom *et al.* 2020) and biogeographically isolated by the three central Andean mountains of Northern South America (**Figure 1**, Pizano & García 2014) with strong variations in the climatic and soil conditions. Therefore, differences in environmental controls on diversity, structure and ecology can be expected. Third, Colombian TDF are not an exception in the global context and have suffered intense conversion to pastures and agriculture (Bianchi & Haig 2013; Pizano & García 2014). In fact, the human footprint has caused that less than 10% of their original extent remain (García *et al.* 2014), with more than 60% of the forested areas corresponding to secondary and young forests (Andrade-Erazo *et al.* 2019); this may drive differences in plant diversity, forests structure and ecological dynamics. Four, Colombian TDF are located in the area of cyclic occurrence of El Niño Southern Oscillation that promotes recurrent drought anomalies and should drive ecological changes in this ecosystem (**Figure 1**, Holmgren *et al.* 2001; Kogan & Guo 2017). Despite its ecological value, as well as the relatively recent interest of ecologists and conservationists (Pizano *et al.* 2017), Colombian TDF remain widely understudied. This overarching objective of this thesis was to generate a deeper understanding of the ecology of TDF, which will favor its conservation.

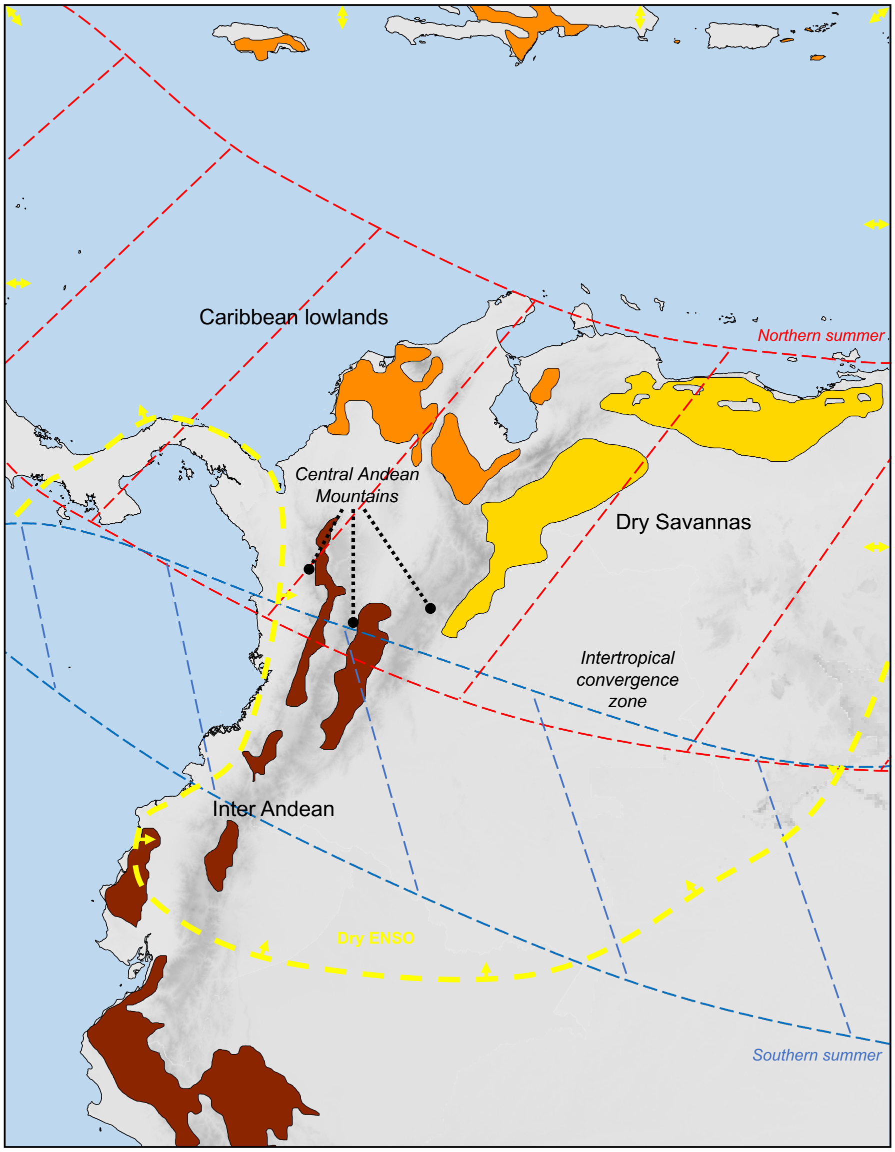


Figure 1. Tropical dry forests formations in Northern South America corresponding to the Caribbean lowlands region (orange), the Inter Andean region (brown), and dry Savannas (yellow area). Adapted from Pennington *et al.* (2009) and DRYFLOR *et al.* (2016). Intertropical convergence zone for the Northern summer (hatched area in red) and Southern summer (hatched area in blue). Adapted from Asmerom *et al.* (2020). 'El Niño' dry phenomenon in Northern South America (hatched area in yellow). Adapted from (Holmgren *et al.* 2001).

Environmental harshness in TDF

Environmental harshness is considered as the abiotic factors, or combinations of them, filtering species from communities and driving patters of diversity and structure across gradients (Marks, Muller-Landau & Tilman, 2016; Whittaker, 1965). Overall, rainfall seasonality is considered the main abiotic factors determining harsh conditions in TDF (Murphy & Lugo 1986; Allen *et al.* 2015, 2017a), and a wide number of researches have demonstrated that the frequency, timing and intensity of precipitations strongly control floristic turnover, diversity and forest structure of TDF (Murphy & Lugo 1986; Gillespie *et al.* 2000; Neves *et al.* 2015; Le Bagousse-Pinguet *et al.* 2017). The underlying assumption is that water limitations impose restrictions on species that are non-adapted to cope with those limitations (Chaves *et al.* 2002). For instance, variation in annual precipitations exert a control on floristic composition across the South American Dry Diagonal (Neves *et al.* 2015), TDF species richness decreases with reductions in precipitation in Perú (Muenchow *et al.* 2013), and the richness of deciduous species increases with the severity of the dry season in Central Africa (Ouédraogo *et al.* 2016).

Nevertheless, plant species do not only respond to water constraints in TDF (Peña-Claros *et al.* 2012; Ouédraogo *et al.* 2016) and variables such as temperature, isothermality, solar radiation, soil fertility, among others, have been found to exert important controls on species composition, diversity and forests structure of this ecosystem (Gillespie *et al.* 2000; Peña-Claros *et al.* 2012; Muenchow *et al.* 2013; Neves *et al.* 2015). For instance, TDF of Mexico that had low soil water retention capacity and high intensities of solar radiation had low density of stems and an increase in small diameter trees species (Galicia *et al.* 1999). These results reflect the importance of the climate-soils interactions in shaping harsh environments in TDF. Likewise, soil fertility as a source of nutrients supporting plant energy, physiological responses and performance (Kreft & Jetz 2007; Laliberté *et al.* 2013) is an important control on forest communities (García-Palacios *et al.* 2012). For example, in Peruvian TDFs the content of potassium and sodium also explained species turnover along a precipitation gradient (Muenchow *et al.* 2013), in TDF of central Africa, Western India and South America as an increase in nutrient availability increased the presence of species with high fertility requirements and the size of individuals trees (Nirmal Kumar *et al.* 2011; Peña-Claros *et al.* 2012; Ouédraogo *et al.* 2016). Thus, the concept of environmental harshness needs to be revisited and consider other harsh conditions such as low soil fertility.

In addition, recent studies have suggested that changes in the land-cover have important consequences in determining plant community attributes due to their relation with the loss of habitat provisioning and raise barriers for dispersal processes (Lindborg & Eriksson 2004; Evelin *et al.* 2009; Stein *et al.* 2014). Factors such as the fraction of forest and secondary vegetation in the area, patch diversity, (*e.g.* number of cover types) and patchiness (*e.g.* density, mean patch size) are generally considered important drivers of changes in species composition, diversity and forest structure (McGarigal & Marks 1995; Zhi-yun *et al.* 1999; Lindborg & Eriksson 2004; Baynes *et al.* 2016). For instance, land cover transformation may increase habitat heterogeneity and promote local species richness (Stein *et al.* 2014), while forest cover fragmentation has found to reduce tree density in tropical forest as the result of habitat loss and isolation (Baynes *et al.* 2016). It is well known that TDF typically occur as small fragments due to historical land-cover transformation (Portillo-Quintero & Sánchez-Azofeifa 2010), which should have effects on forest diversity and structure (Muenchow *et al.* 2013). Surprisingly, despite the high levels of transformation there are not studies that have explored the effects of land-cover on vegetation attributes in Colombian TDF. In this context, it is critical to deepen our understanding of the role that land-cover transformation plays as part of the factors determining environmental harshness for TDF in the Anthropocene.

From patterns to a mechanistic understanding of the ecology of TDF

Diversity and forests structure show directional shifts with environmental harshness. Globally, plant diversity have been found to decrease with climate severity (Kreft & Jetz 2007), soil nutrient limitations (Laliberté *et al.* 2014; Wan *et al.* 2018) and land-cover transformation (Gerstner *et al.* 2014); less is known of forests structural changes. However, understanding the mechanisms behind these patterns of changes is a challenging task that needs to consider the autecology of species and its relationships with the environmental harshness. Trait-based ecology provides a conceptual framework that could identify mechanisms, under the assumption that traits confer different abilities to cope with the certain environmental conditions; e.g., species with low water-stress tolerance may be filtered out of a community (Cornwell & Ackerly 2009; Kraft *et al.* 2015). Therefore, shifts in species composition along environmental harshness gradients in dry ecosystems could be explained by a filtering of species with traits that are not adapted to tolerate stress (Bernard-Verdier *et al.* 2012; Wigley *et al.* 2016; Le Bagousse-Pinguet *et al.* 2017).

In TDF filtering effects are mainly studied in the context of water constraints, with an emphasis on hydraulic traits (Markesteijn *et al.* 2011b; Méndez-Alonzo *et al.* 2012; Pineda-García *et al.* 2013). Water-stressed environments are expected to favor the dominance of species with conservative traits related to high hydraulic safety and, therefore, lower drought-induce mortality (*e.g.* high wood density or narrow vessels; Markesteijn *et al.* 2011; Méndez-Alonzo *et al.* 2012; Pineda-García *et al.* 2015). Yet, these environments could also favor species with acquisitive traits that avoid water constraints (e.g. deciduous species; Pineda-García *et al.* 2015; Méndez-Toribio *et al.* 2017). Less is known about the effects of harsh soil conditions on TDF trait variation. However, some studies suggest that infertile soils decreases the dominance of species with acquisitive traits (*e.g.*, deciduous species), because these species have high leaf turnover rates and high leaf nutrient concentrations (Peña-Claros *et al.* 2012; Ouédraogo *et al.* 2016). In addition, there is no certainty in how other climatic factors, or their interaction with soil fertility, determine differences in traits across environmental harshness gradients in TDF.

Moreover, despite the recognized importance of land-cover transformation as an axis of environmental harshness in TDF, to the best of our knowledge no studies have focused on the trait / land-cover transformation in these forests. However, there are many possible effects of land-cover transformation on species traits, and consequently on the diversity and structure of TDF. For instance, species with seed traits related to vertebrate-dispersion tend to decreases with fragmentation, as the result of a loss of dispersal vectors in small fragments (Cordeiro & Howe 2001). Likewise, there is evidence that land-cover transformation causes changes in the local environmental conditions for species establishment and their persistence. For example, high fragmentation levels decrease the continuity and size of forests causing higher wind exposure and temperature, inducing high mortality of species that are not adapted to more stressful conditions (Cagnolo *et al.* 2006; Laurance & Curran 2008). Therefore, it is important to develop conceptual frameworks that deepen our understanding of the ecological mechanisms that explain patterns of species diversity and forest structure under environmental harshness as the combined effects of climate severity, soil fertility limitations and land-cover transformation.

Xylem anatomy traits as descriptors of hydraulic vulnerability in TDF

Plants exposed to harsh conditions, in particular those causing water-stress, can be adapted to maintain their function and avoid mortality (McDowell 2011; Feng *et al.* 2016). Hydraulic vulnerability, understood as the risk of failure in the water distribution system in a plant due to cavitation, is one of the most commonly cited mechanisms that explains plant mortality under intense water-stress because it reduces water supply to the leaves for photosynthesis (McDowell *et al.* 2008; Bartlett *et al.* 2012; Venturas *et al.* 2016).

Of the different traits that can be used to evaluate hydraulic vulnerability of species the most commonly used is hydraulic conductivity (Bartletta *et al.* 2016). This trait measures water transport capacity, with important consequences for water stress tolerance, cavitation risks and xylem damage (Brodribb *et al.* 2003; Santiago *et al.* 2004b; Lenz *et al.* 2006; Bartlett *et al.* 2012). A large body of literature on hydraulic conductivity has shown that there is a tradeoff between hydraulic safety and hydraulic efficiency (Méndez-Alonzo *et al.* 2012; Meinzer & McCulloh 2013; Bartletta *et al.* 2016; Gleason *et al.* 2016). This hypothesis states that species with high hydraulic safety, *e.g.*, more negative water potential values before loss of conductivity, at the expenses of low water transport capacity, have low risk of suffering embolisms and cavitation, and consequently, low risk of dying under water-stress (Bartletta *et al.* 2016; Gleason *et al.* 2016). In contrast, species with high hydraulic efficiency have a higher risk of dying under water-stress conditions due higher risks of embolisms formation and loss of conductivity (Chaves *et al.* 2002; Markesteijn 2010).

It has been suggested that both extremes of this continuum correlate with the evergreen–deciduous leaf habit in TDF species, where evergreen species appear to be on the high hydraulic safety end while deciduous species should be on the high hydraulic efficiency end (Méndez-Alonzo *et al.* 2012; Pineda-García *et al.* 2015). Although it is generally expected that this continuum influences TDF demography processes (Markesteijn 2010; Markesteijn *et al.* 2011a, b), it is recognized that plants have multiple combinations of traits which may cause a decoupling from the expected hydraulic safety-efficiency trade-off or leaf phenology habits (Fortunel *et al.* 2012; Bartletta *et al.* 2016; Gleason *et al.* 2016). The xylem anatomy traits are considered important descriptors of these possible combinations, with the capacity of disentangling decoupling in the hydraulic safety-efficiency trade-offs and differences in the demography of plants in TDF (*e.g.*, *biohydraulics designs* and *biomechanics resistance*, Sobrado 1997; Jacobsen *et al.* 2012; Beeckman 2016). For instance, water-stress tolerance is suggested to be associated with bio-hydraulic designs, where differences in size and density of vessels producing differences in hydraulic safety may be countered with high fractions of fiber and rays (Sobrado 1997; Jacobsen *et al.* 2012; Beeckman 2016). Thus, species having larger vessels, also expected to have high cavitation risks, may reinforced these vessels with high investments in cellular wall thickness (*i.e.*, fiber and ray fractions; Hacke *et al.* 2001; Méndez-Alonzo *et al.* 2012; Beeckman 2016). However, there are no studies evaluating the hydraulic safety-efficiency trade-offs based on the conceptual framework of coordination with xylem anatomical traits, which may be important for advancing a comprehensive understanding of hydraulic vulnerability in TDF, as well as, its effect on species dynamics and ecosystem processes (*e.g.* net primary productivity).

Influence of El Niño–Southern Oscillation in TDF

Despite of the expected effects of environmental harshness on TDF, extreme dry conditions have also important controls on their functioning (Allen *et al.* 2010, 2015, 2017a). However, the study of extreme drought events and the functional responses of species are still poorly understood for this ecosystem (Powers *et al.* 2020). El Niño Southern Oscillation (El Niño) is considered one of most influencing climatic events affecting the dynamic and function of ecosystems in the tropics (Holmgren *et al.* 2001). During El Niño events, severe droughts have occurred in Northern Latin America (Holmgren *et al.* 2001; Allen *et al.* 2010), which have been associated to increase tree mortality rates (Sheil & Phillips 1995; Williamson *et al.* 2000; Nepstad *et al.* 2007). The 2015-6 El Niño ($ENSO_{2015}$) was recognized as the stronger event of the past 36 years (Anyamba *et al.* 2019; Powers *et al.* 2020), and was even stronger than the event of 1997–1998 (Kogan & Guo 2017). According to the National Oceanic and Atmospheric Administration (NOAA, *http://www.cpc.ncep.noaa.gov/*), warm episodes associated to $ENSO_{2015}$ started on October 2014 and lasted until June 2016. In Colombia, according to the Institute of Hydrology, Meteorology and Environmental Studies (IDEAM, *http://www.ideam.gov.co/*), $ENSO_{2015}$ caused an extreme drought event for a whole year, from April 2015 to March 2016, with peaks in May 2015 and January 2016. However, there are no known studies that have explored how this extreme drought event could have affected tree dynamics TDF in Colombia.

Although plants in TDF have different strategies to survive the frequent water constraints due to recurring annual drought periods (Markesteijn *et al.* 2011a; Méndez-Alonzo *et al.* 2012), extremely dry events such as El Niño could induce abnormal mortality rates (Williamson *et al.* 2000; Chazdon *et al.* 2005; Nepstad *et al.* 2007) particularly for hydraulically vulnerable species (Powers *et al.* 2020). Yet, there are relatively few studies exploring this issue (Allen *et al.* 2017a). In Ecuador the drought event "La Niña 2011" was related to an absence of radial increments in deciduous trees (Spannl *et al.* 2016). In Costa Rica, species with low hydraulic safety margins exhibited high mortality rates under $ENSO_{2015}$ with respect to those with high hydraulic safety margins (Powers *et al.* 2020). However, and in contrast to this evidence, species with high hydraulic safety margins showed high mortality rates during California's drought of 2014, while species with low hydraulic safety margins but with deep roots were less affected (Venturas *et al.* 2016). These contrasting results, reinforce the need for more explorations of the trait-ENSO relationships for a predictive approach of the magnitude of this phenomenon in TDF and recommendation for future climatic change scenarios.

In terms of ecosystem dynamics and processes, it is well known that strong climatic disturbances increase mortality (Condit *et al.* 1995; Venturas *et al.* 2016) and reduce biomass storage (Rolim *et al.* 2005; Allen *et al.* 2010). In dry ecosystems the most important factor explaining variation in biomass is precipitation (Holmgren *et al.* 2001; Ogaya & Peñuelas 2007; Becknell *et al.* 2012; Spannl *et al.* 2016). Thus, an extreme drought event such as $ENSO_{2015}$, should cause important reductions in above-ground standing biomass and in net above-ground biomass gain (i.e., stem growth) due to higher tree mortality (Venturas *et al.* 2016; Powers *et al.* 2020), low tree growth rates (Rodríguez *et al.* 2005; Spannl *et al.* 2016) and low tree recruitment (Nepstad *et al.* 2007). However, I am not aware of studies that have evaluated the effects of an El Niño event in tree mortality, growth and net biomass change in Colombian TDF.

Aim of this thesis

Our understanding of the abiotic factors determining environmental harshness and its influence on ecological patterns is still limited in TDF. Therefore, the focus of my study was to determine what environmental conditions are driving species composition and diversity, forest structure, functional trait composition and dynamics of ecosystem processes of dry forest tree communities in Colombia (**Figure 2**).

The specific objectives of the present thesis were:

(1) To evaluate how climate, soil, and land-cover factors vary among Colombian TDF, characterizing the 'environmental harshness' of this ecosystem.

(2) To explore how plant community attributes (*e.g.*, species composition and diversity, forests structure, and trait community composition) vary along gradients of environmental harshness in Colombian TDF.

(3) To evaluate the functional strategies of TDF tree species in response to gradients of environmental harshness and the extreme drought $ENSO_{2015}$ in Colombia.

(4) To explore how standing biomass and biomass demographic changes are related to the extreme drought $ENSO_{2015}$ in Colombia.

(5) To translate the ecological comprehension of Colombian TDF to the information sources for decision-makers in conservation.

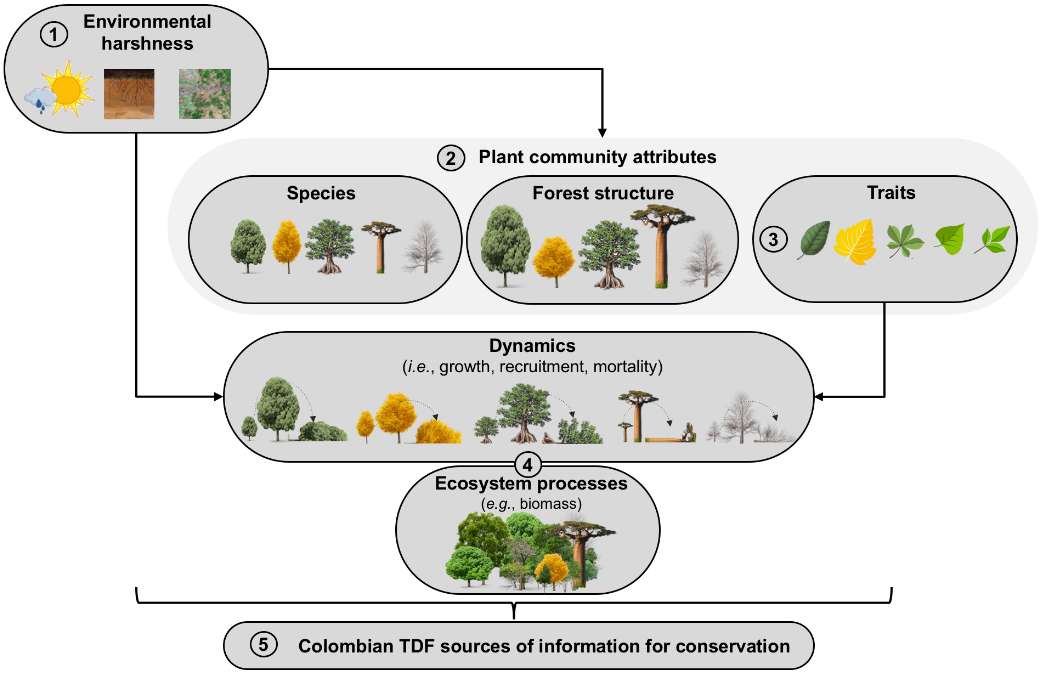


Figure 2. Conceptual framework delineating the principal aim and specific objectives of this thesis.

Thesis outline

This thesis consists of 7 chapters: a general introduction (**Chapter 1**), four research chapters (**Chapter 2-5**), three infographic offprints (**Chapter 6**) and the general discussion (**Chapter 7**), showing how climatic and soil conditions, and land-cover transformation determine differences in floristic composition, species diversity, forests structure, trait community composition, standing biomass and biomass demographic changes in TDF.

Chapter 2 evaluates how climate and soil conditions vary across six geographic regions of TDF in Colombia, based on an extensive field work covering all 571 forests floristic surveys across the country. Additionally, this chapter describes the status of land-cover transformation and successional stages of TDFs across these regions, and the main anthropogenic pressures impacting their conservation.

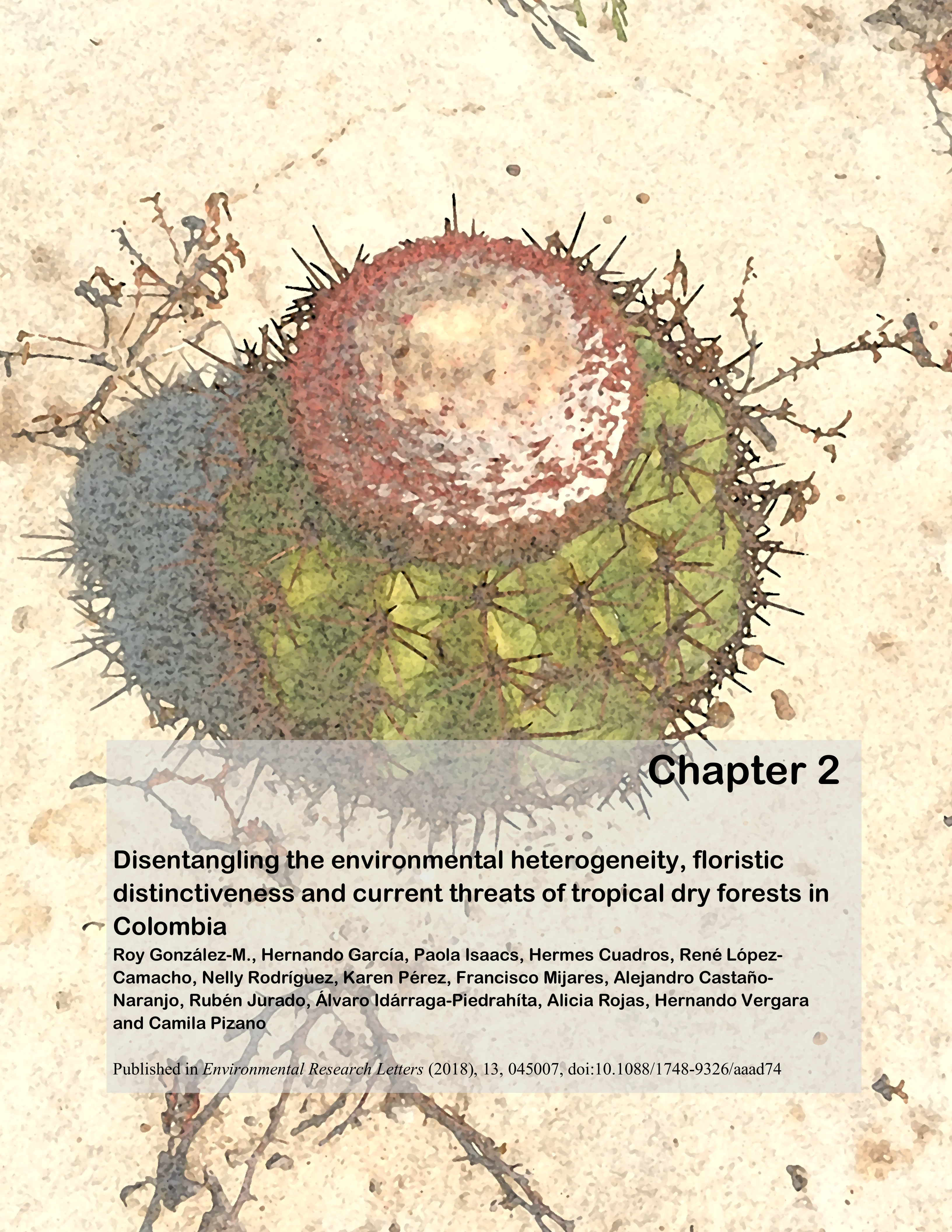
Chapter 3 analyzes the effects of environmental harshness on TDF plant community attributes based on a network of 1 ha permanent plots installed across the country. First, this chapter evaluates how environmental harshness is reflected into climate severity, differences in soil fertility and land-cover transformation and if these axes of environmental harshness determine changes in species diversity and forests structure in TDF. Second, the chapter explores if functional groups with different strategies to overcome stressful conditions (*e.g.*, deciduous and legumes species) exhibited different patterns of changes across the environmental harshness.

Chapter 4 explores the trait-environment and trait-biomass productivity relationships in Colombian TDF based on the evaluation on different organization ecological scales (*e.g.*, individuals, populations, species and communities). This chapter compares the ability of different sampling methods (varying the level of species and abundances representativeness and trait variability) to correctly detect these relationships.

Chapter 5 aim is to identify the functional mechanisms that can explain species sensitivity to the extreme $ENSO_{2015}$ in TDF of Colombia. To do that, this chapter first explores the functional trait space of TDF tree species based on an extensive sampling of 15 leaf and hydraulic functional traits in 338 species recorded in 11 1-ha permanent plots. Second, it evaluates how this space is related to the hydraulic safety-efficiency trade-off and tissue investment for this ecosystem. Third, it analyzes if the species occupation across this space is related to biomass demographic changes under the extreme drought.

Chapter 6 consists of three infographic offprints with (i) the distribution and conservation status of TDF in Colombia, (ii) the permanent plots monitoring network of TDF in Colombia, and (iii) the functional trait data sampled for this ecosystem in the country. These offprints are part of the annual reports for the biodiversity status and trends in Colombia, transmitting the principal information in biodiversity to decision-makers in conservation.

Chapter 7 presents the general discussion and summary of this thesis.



Chapter 2

Disentangling the environmental heterogeneity, floristic distinctiveness and current threats of tropical dry forests in Colombia

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Abstract

Tropical dry forests (TDFs) have been defined as a single biome occurring mostly in the lowlands where there is a marked period of drought during the year. In the Neotropics, dry forests occur across contrasting biogeographical regions that contain high beta diversity and endemism, but also strong anthropogenic pressures that threaten their biodiversity and ecological integrity. In Colombia, TDFs occur across six regions with contrasting soils, climate, and anthropogenic pressures, therefore being ideal for studying how these variables relate to dry forest species composition, successional stage and conservation status. Here, we explore the variation in climate and soil conditions, floristic composition, forest fragment size and shape, successional stage and anthropogenic pressures in 571 dry forest fragments across Colombia. We found that TDFs should not be classified solely on rainfall seasonality, as high variation in precipitation and temperature were correlated with soil characteristics. In fact, based on environmental factors and floristic composition, the dry forests of Colombia are clustered in three distinctive groups, with high species turnover across and within regions, as reported for other TDF regions of the Neotropics. Widely distributed TDF species were found to be generalists favored by forest disturbance and the early successional stages of dry forests. On the other hand, TDF fragments were not only small in size, but highly irregular in shape in all regions, and comprising mostly early and intermediate successional stages, with very little mature forest left at the national level. At all sites, we detected at least seven anthropogenic disturbances with agriculture, cattle ranching and human infrastructure being the most pressing disturbances throughout the country. Thus, although environmental factors and floristic composition of dry forests vary across regions at the national level, dry forests are equally threatened by deforestation, degradation and anthropogenic pressures all over the country, making TDFs a top priority for conservation in Colombia.

Key words: anthropogenic pressures, climate, floristic composition, forest fragments, soils, successional stages, tropical dry forest.

Introduction

Tropical dry forests (TDFs) occur in America, Asia and Africa, where mean annual temperature is greater than 17 °C, annual rainfall ranges from 250–2000 mm and potential evapotranspiration is higher than precipitation (Holdridge 1967; Murphy & Lugo 1986; Kalacska *et al.* 2004; Dirzo *et al.* 2011). However, climatic limits of dry ecosystems are still unclear, as the dry biome occurs across different rainfall regimes (*e.g.* dry savannas can have up to 2500 mm rainfall·year^{-1}, Lehmann *et al.* 2011) and vary dramatically in soil conditions (Rundel & Boonpragob 1995; Sampaio 1995) and elevation. Therefore, TDFs are generally defined by their seasonality, with 3–6 dry months (precipitation < 100 mm·month^{-1}, Portillo-Quintero & Sánchez-Azofeifa 2010), which determines the deciduous phenology of many woody plants, and the biological cycles of these forests as a whole (Pennington *et al.* 2009; Dirzo *et al.* 2011). In terms of floristic composition, TDFs strongly differ between South America, Africa and Asia (Dexter *et al.* 2015), and have a high plant species turnover across the Neotropics, where species of different floristic groups are commonly restricted to a single region (DRYFLOR *et al.* 2016).

Although TDFs are used to represent 42% of all the worlds' tropical forests (Brown & Lugo 1982), only 1000 000 km^2 are left worldwide (Miles *et al.* 2006; Portillo-Quintero & Sánchez-Azofeifa 2010; Powers *et al.* 2011), with more than 50% left in South America (Miles *et al.* 2006). These forests have been recognized as highly endangered ecosystems (Murphy & Lugo 1986; Janzen 1988b). However, research in the tropics has been concentrated on more humid forests (Powers *et al.* 2011; Sánchez-Azofeifa & Portillo-Quintero 2011). This imbalance in knowledge has also been reflected in a general absence of studies that assess the different environmental conditions under which dry forests occur, and their degree of degradation and fragmentation across Latin America (Sánchez-Azofeifa *et al.* 2005a; Portillo-Quintero & Sánchez-Azofeifa 2010; Sánchez-Azofeifa & Portillo-Quintero 2011). For instance, recent studies showed high floristic turnover among different regions in the Neotropics (DRYFLOR *et al.* 2016), but little is known on how differences in species composition may be related to climate and soil factors.

Accurate measurements of TDF extent and successional status are key tools for the conservation and landscape planning for these forests (Hesketh & Sánchez-Azofeifa 2014), and are necessary for addressing their ecological importance and as providers of ecosystem services (Calvo-Rodriguez *et al.* 2017). The only analysis of TDF cover at the global scale revealed that deforestation was six times higher in Latin America (12%) compared to Asia and Africa (2%) between 1980 and 2000 (Miles *et al.* 2006). Similarly, Olson *et al.* (2001) and Portillo-Quintero & Sánchez-Azofeifa (2010) showed that 66% of dry forest in Latin America has been lost due to deforestation, and only 4.5% is subject to protection. At the regional level, similar efforts to map the distribution and loss of TDFs have been published for Mexico (Trejo & Dirzo 2000; Sánchez-Azofeifa *et al.* 2009), Puerto Rico (Martinuzzi *et al.* 2013), Venezuela (Fajardo *et al.* 2005) and the Antilles (Helmer *et al.* 2008). However, few studies have evaluated the successional status and anthropogenic pressures of dry forests in the field (e.g. Larkin *et al.* 2012), which is key information for addressing their real conservation status. Furthermore, few studies have explored how in addition to fragmentation and successional status of dry forests, environmental conditions and species composition vary across different regions, which is crucial for implementing more effective conservation and management plans for TDFs.

In Colombia, TDFs originally covered 8'882 854 ha, but around 90% of its cover was replaced by pastures, agricultural fields, and urbanization by the end of the 20th century (Etter *et al.* 2008; García *et al.* 2014). In fact, only 8% (720 000 ha) of TDF original cover is left in land mosaics in which successional forest covers at least 30% of the territory (384 416 ha) (García *et al.* 2014). This means that less than 4% of the original TDFs remain as mature forests. Moreover, only 5% of what is left is preserved in protected areas (García *et al.* 2014). Given this critical situation and the lack of information on the conservation status of this ecosystem in Colombia (Fernández-Méndez *et al.* 2013; Pizano *et al.* 2014a), the purpose of this study was to evaluate the variation of environmental conditions, floristic composition and conservation status of TDFs at the national level by doing extensive field surveys. Specifically, we intended to answer the following three questions: (1) How do environmental conditions and floristic composition of TDFs vary across six geographic regions? (2) What are the land-cover status and successional stages of TDFs across these regions? (3) Which are the main anthropogenic pressures impacting dry forests? This information will not only contribute to our understanding of the abiotic, biotic and anthropogenic factors that shape dry forests in Colombia, but can support better founded conservation and management strategies for this highly endangered ecosystem.

Methods

Study area

In Colombia, TDFs occur across altitudinal and climatic gradients and in transitions from humid forests to savannas (Pizano *et al.* 2014a). Therefore, we used the broad definition of TDFs being lowland to mid-elevation (up to 1200 masl) forests that experience at least three months of drought (<300 mm total rainfall,

~100 mm·month^{-1}) (Mooney *et al.* 1995). We used the 1:100 000 scaled national map of TDFs (Corzo & Delgado 2012) to randomly select 571 existing forest fragments (sites) within TDF landscapes in six geographic regions of Colombia suggested by (Pizano *et al.* 2014b) (**Figure 1, Supporting Information Table S1**). We excluded areas that appeared as dry forests in the national map, but were confirmed as not being TDFs by local experts. The number of sample sites was proportional to the extent of TDFs for each region, and it was validated by a field team of botanists, ecologists and spatial analysts.

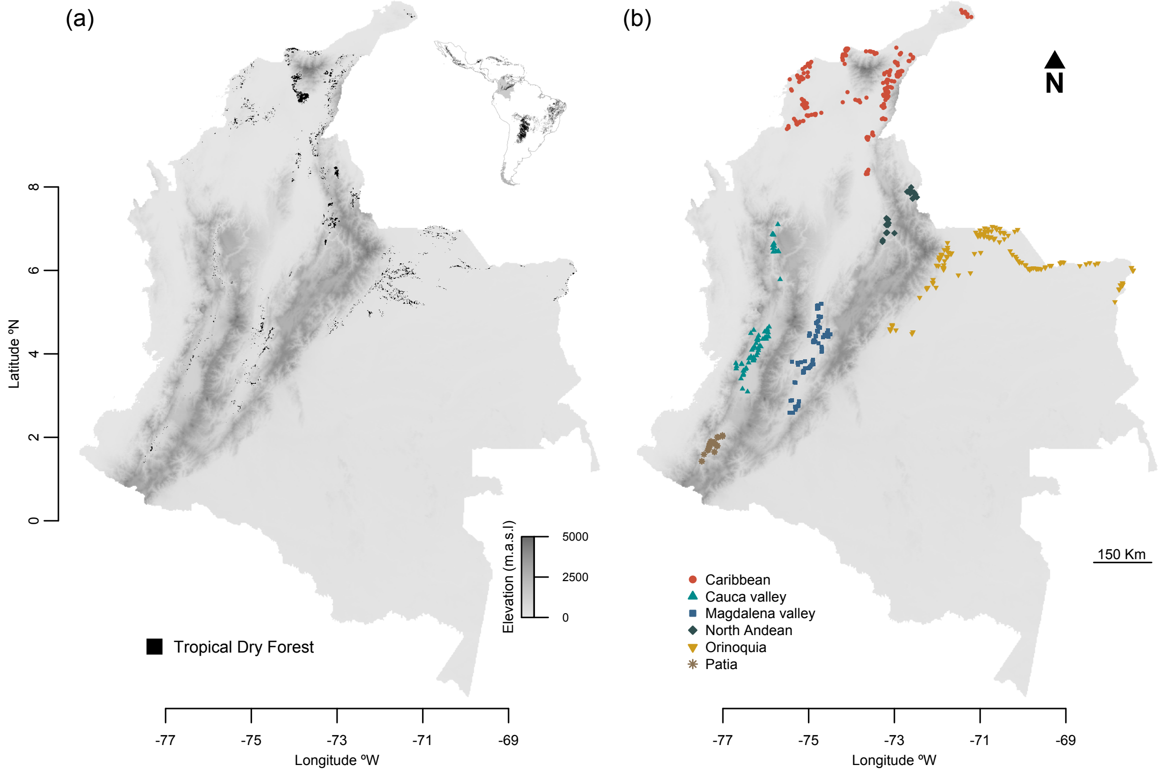

Figure 1. Current extent and distribution (a), and field sample sites across six regions of TDFs in Colombia (b), as defined by (Pizano *et al.* 2014b).

Environmental variables

Climatic variables for TDF regions were estimated using the national climatic model developed by the Instituto de Hidrología, Meteorología y Estudios Ambientales and Instituto Humboldt of Colombia, based on 2046 weather stations around the country (monthly data in a resolution of 90 m Selected climatic variables included mean annual temperature (MAT ºC), total annual precipitation (TAP mm), total precipitation in the driest period (rainfall ≤ 300 mm in three continuous months (~100 mm·month^{-1}); TPdriest mm), number of dry seasons when precipitation is < 300 mm (drySeason: 1 or 2 periods·year^{-1}) and number of dry months where precipitation is < 100 mm (dryMonths: 1 to 12 months·year^{-1}) (**Table S1**). Soil variables included pH (in H_2O), soil organic carbon content (OCarbon g·kg^{-1}), sand content (% particles > 50-2000 µm), silt content (% particles 2-50 µm) and clay content (% particles < 2 µm, bulk density (BulkDens kg·m^{-3}), cation exchange capacity (CEC cmol$_c$·kg^{-1}), and absolute depth to bedrock (Bedrock cm). Soil variables where obtained from the global soil information system (SoilGrids 1–km, Hengl *et al.* 2014) (**Table S1**).

Field sampling data

Field sampling was done between August 2013 and October 2014. Field teams collected the following information at each site: geographic coordinates (Lat./Long. decimal), altitude (m), presence of vascular plant species, successional stage of forest fragments, and the anthropogenic pressures present inside the forest fragment as well as in the surrounding matrix. For plant species data collection, field teams ran a linear transect inside each forest fragment sampled, in which plant species were sampled, photographed and identified by local botanists who also collected reference specimens. All plants of height ≥ 1.3m were sampled including palms, shrubs, lianas and cacti. For plants with dubious identity, 1–3 specimens were collected for taxonomic identification (**Table S2**). All specimens were processed in a local herbarium (**Table S2**) and homologated based on duplicates in the Federico Médem Herbarium in Bogotá using the APG III classification system (Haston *et al.* 2009).

Quantifying land-cover metrics

Forest fragment size and shape were quantified based on dry forest patches interpreted from a Landsat 8 Mosaic 2014 of TDF distribution published by the Humboldt Institute (15 × 15 m resolution) and developed following global models and protocols for image processing using remote sensing techniques (Xu & Becker 2012). Remote sensing resolution was improved using Google EarthPro© images from 2014–2015 (Yu & Gong 2012). Each fragment was mapped by visual interpretation, keeping a fixed digitalization height of 1500 m. This fixed scale assured fragment size and shape was correctly compared between and within regions. All 571 sample sites were re-interpreted using this method for land-cover metric evaluation during the field-sampling period. 77 sites were excluded from the analyses due to cloudiness in the images.

Successional stages and anthropogenic pressures

Botanists classified TDF successional stages in the field in four categories: no-forest (in some areas forest fragments had a different size or shape to those in the map due to difference in scale), early, intermediate, and late, based on the physiognomy and structural data including visually estimated canopy height and stem density, and the presence of pioneer and late successional species (Kalacska *et al.* 2004; García Millán *et al.* 2014). Early successional forests were characterized by low stem density, open vegetation, dominance of pioneer species, and a canopy height of 10 m. Intermediate forests were defined as more dense vegetation in which intermediate-successional species were common, there was a second layer of young trees, a dense understory, and mature trees up to 15 m in height. Finally, late forests were distinguished by a multi-layer and heterogeneous canopy of more than 15 m in height with emergent trees, the presence of late-successional species, and a more open understory (Kalacska *et al.* 2004; García Millán *et al.* 2014). At each sample site, anthropogenic pressures were recorded and categorized according to their impact level from the lowest to the highest as follows: ecotourism (1), hunting (2), non-timber forest product extraction (3), selective logging (4), cattle herding inside the forest (5), intensive logging (6), agriculture (7), cattle ranching (8), human infrastructure (9), hydrocarbons (10), fire (11), clear-cut mining (12) and erosion (13). Cattle herding inside the forest was classified as a different pressure to cattle ranching because herding means cattle browse in the understory of TDFs (particularly during the dry season), while forests are clear-cut for the establishment of cattle ranches. Categories 1–5 and fire were recorded based on interviews with local people, while all other pressures were visually assessed.

Data analyses

We ran a principal component analysis (PCA) to analyze environmental heterogeneity of TDFs across Colombia, reduce climate-soil dimensionality, and identify the principal axes of variation across regions. We also used the unweighted pair-group Simpson dissimilarity index ($D_{Simpson}$) to evaluate plant species turnover across TDF field sites, as other authors have suggested this is an effective measure of geographical regionalization (Kreft & Jetz 2010) and floristic clustering of TDFs at different geographic scales (Dexter *et al.* 2015; DRYFLOR *et al.* 2016). $D_{Simpson}$ ranges between 0 and 1, where values close to the unit indicate maximum floristic dissimilarity. We then used the $D_{Simpson}$ distance matrix as the basis for ordination of TDFs in regions using non-metric multidimensional scaling (NMDS, Borcard *et al.* 2011). To test if TDF regions had significantly different mean $D_{Simpson}$, we used the analysis of similarity test (ANOSIM, Clarke 1993). Finally, we computed a redundancy analysis (RDA, with Hellinger transformation) to address how differences in species composition may be related to soil and environmental conditions, for which R^2 and adjusted R^2 were calculated to identify the percentage of the explained variance (Borcard *et al.* 2011). The significance of the canonical axes in RDA was tested by a one-way analysis of variance (ANOVA) following (Legendre *et al.* 2011).

Total fragment size (area in hectares) was estimated based on land-cover data for each TDF region, as a key metric for estimating patch occupancy and conservation status in the landscape (McGarigal & Marks 1995; Hill & Curran 2003). We also used land-cover data to calculate the shape index as the perimeter/area ratio. This index is defined as the fragment narrowing shape by which a theoretical zero value indicates an infinitely large perimeter around an infinitesimally small area (Moser *et al.* 2002; Berry 2007). Hence, a lower value in the index indicates a more irregularly shaped form of forest fragments resulting from land-cover transformations. A one-way ANOVA and a post-hoc Tukey test were performed to compare forest fragment size (area) and shape index (perimeter/area ratio) across the six regions. Both metrics were $\log_{10}$-transformed to fit the assumption of normality.

Forest successional status relative frequency (%) was estimated as the sum of sites (s) in which we reported each successional category (C) divided by the total number of sites measured for each region (R) multiplied by 100: $F = 100 \times \sum_{i=1}^{s} C_i / \sum_{i=1}^{s} R_i$, a descriptive summary of the successional status of TDF fragments in each region. We also estimated the relative frequency (%) of each anthropogenic pressure inside forest fragments and in the surrounding matrix across regions (anthropogenic pressures: 1-13; see before). To evaluate the impact of pressures and differences across the six regions, we performed a non-parametric one-way ANOVA (Kruskal–Wallis; Sokal & Rohlf 1995; McDonal 2014), and a multiple pair comparisons test (Posthoc Kruskal-Nemenyi test; Dunn 1964; Pohlert 2016), using the mean ranks of pressures per region as the level of impact. In both analyses, values higher than 6.5 indicate a high level of anthropogenic pressures for a TDF region.

All statistical analyses were performed using the statistical program R (R Development Core Team 2005, version 3.2.2). We used the package 'vegan' (Oksanen *et al.* 2007) for estimating the Simpson dissimilarity index, the NMDS and RDA, and 'PMCMR' package for calculating the Posthoc Kruskal-Nemenyi test (Pohlert 2016). For information on how many forest sampling sites were used for each analysis, please see **Table S3.**

Results

TDFs in Colombia occur in areas with high environmental and soil variation (**Figure 2a**), with a mean annual temperature of 26.5 ± 1.6 °C, mean annual precipitation of 1575.1 ± 596.9 mm, and one to two annual dry seasons with a total precipitation of 115.3 ± 65.4 mm (~3 months continuous < 100 mm month^{-1}) (**Table S1**). Soils varied from low fertility (pH < 5.5, CEC = 11.3 ± 4.1 cmol$_c$ kg^{-1}), high sand content (> 40%) and low organic carbon content (< 13 g kg^{-1}), to fertile due to high cation exchange capacity (> 20 cmol$_c$·kg^{-1}), and higher content of finer textures (clay content > 30%) and organic matter (>20 cmol$_c$ kg^{-1}) (**Table S1**). Dry forest vegetation clustered in six different groups ($P < 0.001$), with a clear overlap between inter-Andean valley regions (**Figure 2b**). Sites across the six TDF regions showed high floristic dissimilarity (mean $D_{Sipmson} = 0.89$, median $D_{Sipmson} = 0.92$), as 73.3% of plant species were found only in one region, 13.8% of species were shared between two regions, and 1.3%–4.3% species were found in 3–5 regions (**Table S2**). In fact, only three species were found in all six regions (*Guazuma ulmifolia, Ceiba pentandra* and *Ochroma pyramidale*, Malvaceae), and the most frequently detected species varied in each region (**Table S2**). Correspondingly, we found a high floristic dissimilarity within regions, which ranged from 0.67 in Patía to 0.88 in the North Andean region in the median of $D_{Sipmson}$.

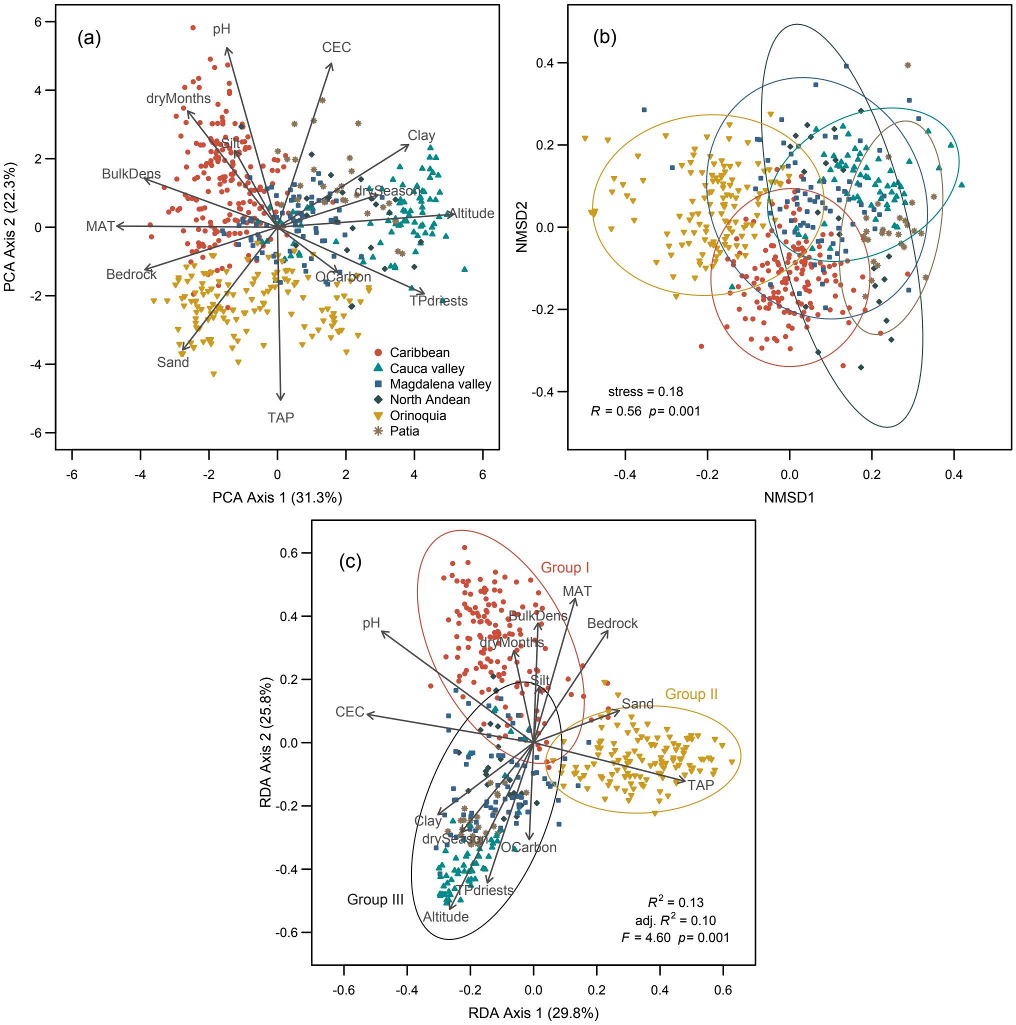

Figure 2. Variation in TDF environmental and soil conditions (a), plant species composition (b), and their correlation (c) across six TDF regions in Colombia. (a) Ordination space of environmental conditions (PCA, soil-climate variables, $N = 558$); (b) ordination space of TDF floristic composition (NMDS, $N = 464$) using the Simpson

dissimilarity index as distance between pair-sites; and (c) RDA fitted for the floristic composition and climate-soil conditions (RDA, $N = 456$). Ellipses represent 95% confidence intervals for all analyses

TDFs clustered in three main floristic groups associated to climate-soil conditions ($P = 0.001$, **Figure 2c**): (1) the Caribbean, with high soil fertility (mean pH > 6.3, CEC > 20 cmol$_c$ kg^{-1}), the longest dry season (5.0 ± 1.7 months per dry period, TPdriest ~1–155 mm) and high aridity due to high temperatures (MAT = 27.3 ± 0.9 °C) (**Figure 2c**, **Table S1**); (2) the Orinoquía, with total annual precipitation above 2367 mm, but dry season (3.9 ± 0.8 months) precipitation of only 40–231 mm, and soils with the highest sand content (40.4 ± 7.4%) and the lowest fertility (pH < 5.3, CEC 11.3 ± 4.1 cmol$_c$ kg^{-1}) (**Figure 2**, **Table S1**, and **S3**) the inter-Andean valleys with high soil fertility (CEC > 19.6 cmol$_c$ kg^{-1}, clay content > 36.5%) and the highest total precipitation during the driest period (45–298 mm), with two annual dry seasons (**Figure 2**, **Table S1**), and valleys with different altitudes (Cauca Valley = 375–1211 m, Magdalena Valley = 227–906 m, North Andean = 188–1154 m and Patía = 555–953 m; **Figures 2a-c** and **Table S1**). Environmental and soil factors explained 13% (R^2) and 10% (*adjusted* R^2) of the variation in species composition (**Figure 2c**), with a large proportion of unexplained variance.

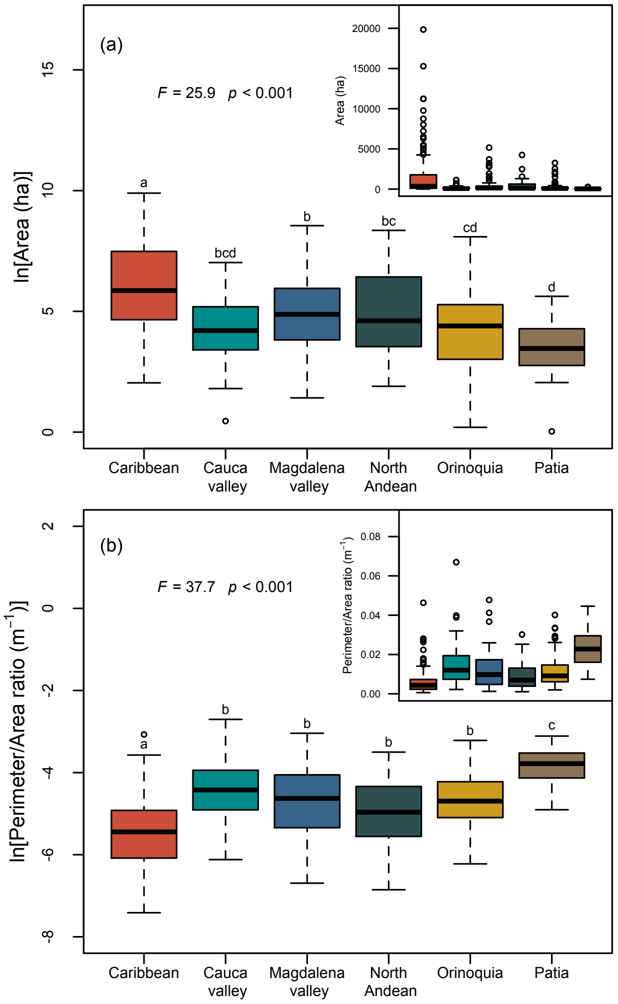

Figure 3. Fragment size in hectares (a) and shape index (perimeter/area) (b) for six regions of TDFs in Colombia. Different letters indicate statistically significant differences between groups ($P < 0.05$). The upper-right boxes show the forest fragment size and shape index without log transformation.

A total of 332 342 ha of TDFs were mapped and validated in the field (494 forest fragments). Forest fragment size had a median of 115.2 ha and a perimeter/area ratio index of 0.008 at the national level (**Figure 3a**). The largest forest fragments where found in the Caribbean, where fragment size showed high variation (mean A = 1530.4 ± 2840.4 ha), followed by the Cauca and Magdalena Valleys, North Andean and Orinoquía (**Figure 3a**). The smallest forest fragments were found in the Patía Valley, where average fragment size was 56.9 ± 63.9 ha (**Figure 3a**). In general, all forest fragments across the six regions had high narrowing values as a result of large perimeters around low area per patch (median shape index 0.004–0.025, **Figure 3b**). In the Caribbean, although fragments were the biggest, they also had the highest narrowing, indicating high levels of transformation (median shape index 0.004, **Figures 3a** and **3b**). In contrast, the Patía region had the lowest fragment narrowing (median shape index 0.023, **Figures 3a** and **3b**) as a result of low forest patch size and regularly shaped fragment shapes. In terms of successional stages, except for the Orinoquía region, the relative frequency of late successional forests (mature forests) was lower than 7% for all regions (**Figure 4**). An extreme case was the Patía region, where no mature forests could be found (**Figure 4**). Correspondingly, dry forests in all regions were at either early (~31%–50%) or intermediate succession (~21%–63%), but in Orinoquía, where no early successional forests were found, and TDFs were either intermediate or mature (**Figure 4**).

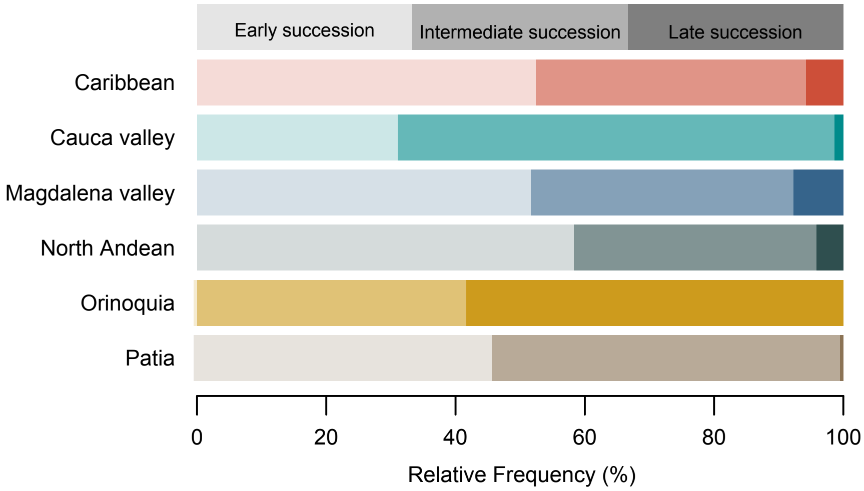

Figure 4. Relative frequency of three successional stages of dry forest fragments registered at each field sample site across six regions in Colombia

Anthropogenic pressure mean rank was higher than 6.5 inside the forest (7.2) and in the surrounding matrix (8.2) across all regions, except inside the forests in the Caribbean and Orinoquía regions (**Figure 5**). In order of importance, the most frequent pressures for all regions inside the forests were: selective logging (reported presence 175, total represented percentage = 30.6%), herding (160, 28.0%), human infrastructure (150, 26.3%) and hunting (110, 19.3%). In contrast, the most frequently reported pressures in the surrounding matrix were: cattle-ranching (327, 57.3%), human infrastructure (314, 54.9%), agriculture (148, 25.9%) and fire (92, 16.1%). The Magdalena Valley, North Andean and Patía regions were the most threatened by high-impact levels inside the forest (Mean rank > 8.1, **Figure 5a**), while high impact levels were present in the surrounding matrix of all regions (Mean rank > 8.2, **Figure 5b**), with the highest in the Patía region.

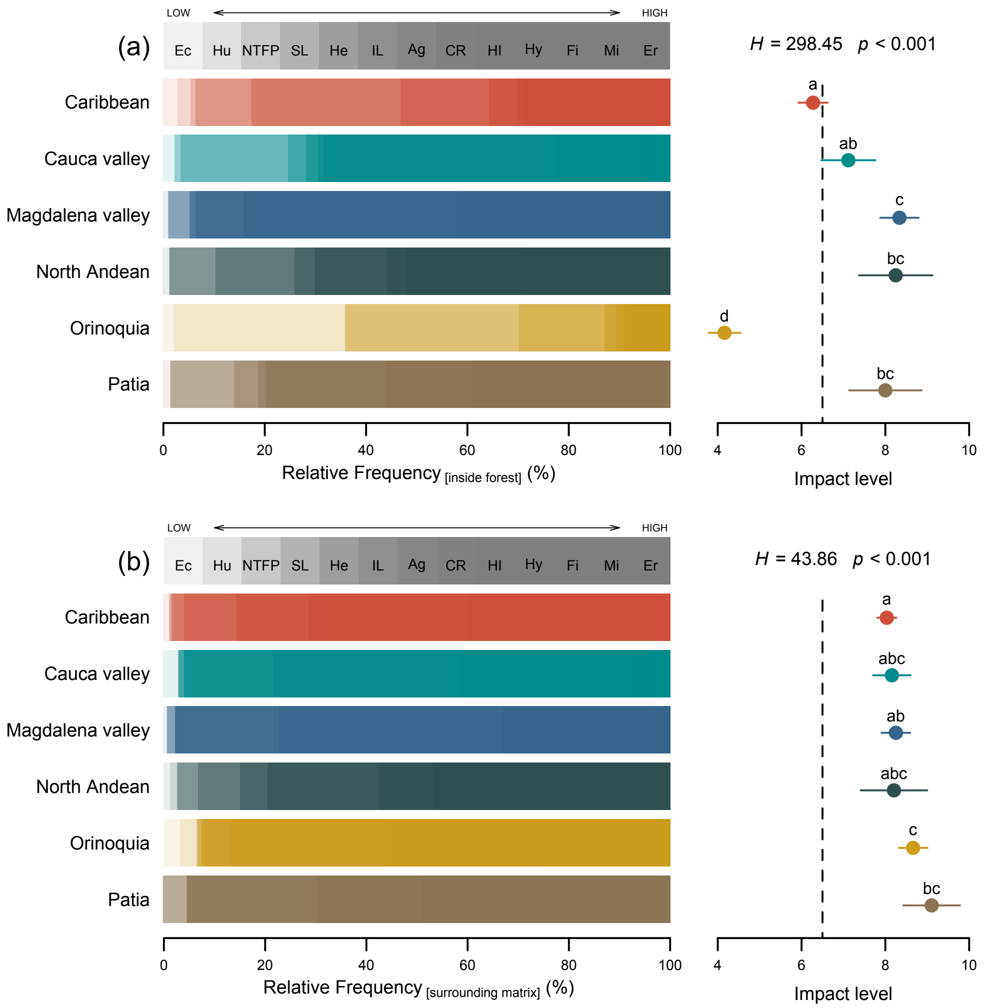

Figure 5. Frequency of anthropogenic pressures and their impact inside dry forest fragments (a) and in the surrounding matrix (b) in six regions of Colombia (N = 457). The arrows indicate the level of impact for each pressure from low (ecotourism (Ec), hunting (Hu), extraction of non-timber forest products (NTFP), selective logging (SL), herding inside the forest (He)) to high (intensive logging (IL), agriculture (Ag), cattle ranching (CR), human infrastructure (HI), hydrocarbons (Hy), fire (Fi), clear-cut mining (Mi), and erosion (Er)). Values higher than 6.5 (dashed line) in the plots indicate the presence of a high number of pressures in a given region based on the mean ranks (Kruskal–Wallis test, H). Different letters indicate statistically significant differences between groups ($P < 0.05$).

Discussion

Floristic distinctiveness matches environmental heterogeneity of TDF in Colombia

TDFs are commonly defined as a single biome characterized by a strong seasonality in precipitation (Pennington *et al.* 2009; Portillo-Quintero & Sánchez-Azofeifa 2010). However, these forests vary significantly in rainfall seasonality (Murphy & Lugo 1986, 1995; Gentry 1995; Pennington *et al.* 2009), soil nutrients, soil texture (Peña-Claros *et al.* 2012), soil water storage (Neves *et al.* 2015), frost (Pennington *et al.* 2006b) and altitude (Gentry 1995). Correspondingly, TDF plants have been modeled as metacommunities historically adapted to dry conditions (Pennington *et al.* 2009) with high species turnover and endemism as a result of historical fragmentation, dispersal limitation (Linares-Palomino *et al.* 2011; Neves *et al.* 2015) and environmental controls (Neves *et al.* 2015; Williams *et al.* 2017).

We found that TDFs in Colombia cannot be defined solely on rainfall parameters such as total annual precipitation (as defined in methods), mean annual temperature (as defined in methods), TAP or MAT/TAP ratio (Murphy & Lugo 1986; Gentry 1995; Pennington *et al.* 2009). Taken together, all environmental variables measured across six TDF regions (**Table S1**) grouped dry forests in three clusters: the Caribbean, the Orinoquía, and the inter-Andean valleys (**Figure 2a**). The Caribbean experiences the longest and harshest dry season with high MAT and low precipitation, similar to TDFs in Venezuela (Fajardo *et al.* 2005) and Central America (Murphy & Lugo 1986; Gentry 1995), but contain mostly fertile soils, as a result of low nutrient leaching (Fajardo *et al.* 2005). In contrast, the Orinoquía had a high TAP and low soil fertility as the result of high nutrient leaching (Malagón-Castro 2003) and high sand content, resulting in low soil water storage during the dry season (Medina & Silva 1990; Dezzeo *et al.* 2008), an important determinant of dry forests across the Neotropics (Dezzeo *et al.* 2008; Peña-Claros *et al.* 2012; Neves *et al.* 2015). Finally, the inter-Andean valleys had the highest soil fertility and a high variation in rainfall during the dry season (**Table S1**), with two annual dry seasons determined by Colombia's mountainous geography (Fernández-Méndez *et al.* 2013). In addition to these marked differences in climate and soils, these three regions differed in altitude (**Table S1**).

Matching the variation in environmental conditions, we found that 73.3% of TDF plant species were only found in one region, and that the floristic composition of dry forests in Colombia is clustered in the same three groups: the Caribbean and the inter-Andean valleys (Patía, Cauca and Magdalena Valleys and North Andean), as suggested by (DRYFLOR *et al.* 2016), and the Orinoquía ($P < 0.001$), a region where TDFs have been poorly studied, but has been suggested as a separate floristic entity by Espinal & Montenegro (1977) and Pizano *et al.* (2014b) (**Figures 2b-c**). In fact, environmental and soil factors explained 13% of the variation in plant species composition (**Figure 2c**). Similar to other dry forests in the Neotropics, we found high species turnover for both across and within regions (Linares-Palomino *et al.* 2011; Neves *et al.* 2015; DRYFLOR *et al.* 2016; Williams *et al.* 2017), as well as high levels of endemism across TDF regions. Floristic composition in the Caribbean appears to be correlated with soils with a high pH and high bulk density, high mean annual temperature, and the longest dry season (**Figure 2c**). Meanwhile, the presence of plants in the inter-Andean valleys was correlated with soils with high clay and organic carbon content, two dry seasons, and the highest altitudes (**Figure 2c**). For example, *Trichilia carinata* and *Trichilia oligofoliolata* are restricted to the Magdalena Valley, although locally abundant (González-M et al 2016) (**Table S2**). Finally, dry forests of the Orinoquía, with the most unique flora, are characterized by sandy soils and the highest precipitation (**Figure 2c**). This supports the hypothesis that TDFs in northern South America were isolated from other dry areas due to geography barriers such as rainy formations (Amazonia and Chocó), and the Andes (Gentry 1982; Pennington *et al.* 2009). A caveat of our study is that we only sampled plant species of ≥ 1.3 m in height, therefore excluding species important for dry forests such as epiphytes and herbs (Linares-Palomino *et al.* 2009; Pizano *et al.* 2014b). On the other hand, although the correlation between environmental and soil conditions and floristic distinctiveness was clear, we failed to explained a large fraction (87%) of the variation in dry forest species composition (**Figure 2c**). However, as reported before, given the many factors that determine plant species composition, this is a usual result of studies on floristic composition over similar spatial scales with species presence-absence data (Guisan *et al.* 2011; Neves *et al.* 2015).

We also found that the most widespread dry forest species were generalists that are favored by forest disturbance and early successional stages (**Table S2**), as reported by previous studies (Uribe *et al.*

2001; López-Camacho *et al.* 2007; Castellanos-Castro & Newton 2015; Williams *et al.* 2017) for other TDFs (Newbold et al 2014), indicating the incipient successional status of dry forests at the regional level (Derroire *et al.* 2016). Furthermore, we found an introduced invasive species (*V. farnesiana*) among the most common species of TDFs throughout the country, suggesting that TDFs are also highly susceptible to invasion (Pizano *et al.* 2014a). This shows the importance of taking into account human land-cover disturbances as determinants of floristic composition and species turnover of TDFs (Larkin *et al.* 2012).

Successional status and current threats of TDF in Colombia

Previous studies using remotely sensed data have shown that TDFs are highly fragmented in the Neotropics (Fajardo *et al.* 2005; Miles *et al.* 2006; Rodríguez *et al.* 2008; Portillo-Quintero & Sánchez-Azofeifa 2010). However, field-collected information on forest fragment shape and size, successional stage, species composition and forest conservation status, is rare. Anthropogenic pressures in TDFs vary from hunting, selective logging and local clearing with fire (for agriculture and cattle ranching) to complete deforestation and soil desertification (Janzen 1988b, a; García *et al.* 2014), but are still fairly unexplored in the Neotropics. In particular, methods such as satellite image analysis are unable to detect subtle changes in the forest due to hunting, non-timber forest harvesting, selective logging, invasion of exotic species and understory thinning due to cattle herding (Peres *et al.* 2006).

In an extensive and unique field survey at the national level, we found that TDFs in Colombia are highly fragmented, narrowly shaped, and comprise mostly early and intermediate successional stages, with very little mature forest (**Figures 3** and **4**). At the national level, dry forest comprises very small and highly irregularly shaped forest fragments, with larger remnants only found in the Caribbean and the Magdalena Valley (**Figure 3**). Furthermore, of the 332 342 ha of TDFs mapped across six regions, between 31%–50% of the fragments contained early, ~21%–63% intermediate, and less than 7% mature forest (except for Orinoquía) (**Figure 4**).

On the other hand, high-impact disturbances such as human infrastructure and hunting were common inside dry forest fragments in all regions but Orinoquía, where lower-impact disturbances (cattle herding, hunting, non-timber forest product extraction, and ecotourism) were more important (**Figure 5a**). Similarly, pressures in the surrounding matrix included higher-impact disturbances such as cattle ranching, human infrastructure, agriculture and fire in all regions (**Figure 5b**). Orinoquía, an extensive area (285 440 km^2), had the least pressures inside the forest (**Figure 5a**), and was the only region where mature TDFs still exist (**Figure 4**). However, this is the new agricultural frontier as declared by the Colombian government, and therefore presented high-impact anthropogenic pressures in the surrounding matrix. Thus, in contrast to a tendency towards conservation, deforestation and degradation of TDFs, at the national level will probably tend to increase as a result of high-impact pressures detected in all regions. In particular, previous studies have shown that both high- and low-impact pressures may further degrade TDFs. For example, in the dry forests of Sonebhadra (India), an increase in human population led to increased illegal tree felling, extraction of non-timber resources and cattle herding, which led to significant declines in 52% of the population of all 65 forest plant species (Sagar & Singh 2004). Furthermore, degradation of TDFs may substantially increase carbon emissions, negatively impacting payment schemes such as the 'Reduced Emissions from Forest Deforestation and Degradation’ (REDD), one of the most advocated conservation strategies for TDFs (Portillo-Quintero *et al.* 2015). However, more extensive field work and satellite and remote sensing methods (Peres *et al.* 2006; García Millán *et al.* 2014; Li *et al.* 2017), as well as studies on the response of species to disturbance (Newbold *et al.* 2014), need to be done to better estimate the extent and impact of anthropogenic pressures on TDFs.

Conclusions

Although considered a biome, TDFs have been shown to differ both environmentally and floristically at the regional scale (Murphy & Lugo 1986; Gentry 1995; Murphy & Lugo 1995; Pennington *et al.* 2006b, 2009; Peña-Claros *et al.* 2012; Neves *et al.* 2015). In this extensive field survey in Colombia, we found that both environmental and floristic characteristics of TDFs varied significantly across regions, and grouped dry forests in three separate entities: the Caribbean, the inter-Andean valleys, and the Orinoquía region. In fact, we found a high species turnover across and within regions (Linares-Palomino *et al.* 2011; Neves *et al.* 2015; DRYFLOR *et al.* 2016), and high levels of regional endemism. At the same time, the most common dry forest tree species were generalists that are favored by forest disturbance and are common in early successional stages. Thus, disturbance is a key determinant of plant community composition in the dry forests of Colombia.

In addition to differences in environmental conditions and plant species across dry forest regions, our broad field study allowed us to verify that TDFs are highly fragmented, consisting of irregularly shaped forest fragments, and of mostly early and intermediate successional forests across the national level (Portillo-Quintero & Sánchez-Azofeifa 2010). Furthermore, anthropogenic pressures inside forest fragments and in the surrounding matrix were equally high across all regions of dry forest, with high-impact disturbance such as human infrastructure, fire, cattle ranching and agricultural plantations dominating TDFs across the country. Thus, the protection of TDF should be a priority in Colombia, where environmental, biotic, successional, and human dimensions need to be considered for assuring more effective management and conservation strategies of these unique forests.

Acknowledgments

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Supporting information

Table S1. Environmental conditions (climate and soils variables) for 571 dry forest fragments in six regions of TDF in Colombia

Geographic region	**Caribbean**	**Cauca valley**	**Magdalena valley**	**North Andean**	**Orinoquia**	**Patia**
Field samples (N)	202	88	80	25	146	30
Latitude (Lat. maximum | minimum, dec.)	12.24|8.31	7.1|2.04	5.2|2.58	7.99|6.69	7.05|4.48	2.05|1.43
Longitude (Long. maximum | minimum, dec.)	-71.21|-75.51	-75.39|-77.08	-74.49|-75.45	-72.47|-73.28	-67.43|-73.1	-77.01|-77.49
Altitude (Alt. maximum | mean | minimum, masl)	11|173|844	375|865|1211	227|412|906	188|623|1154	47|217|743	555|718|953
Mean annual temperature (MAT ± SD, ºC)	27.3 ± 0.9	24.2 ± 1.5	27.6 ± 1.1	25.3 ± 1.5	26.8 ± 1	24.7 ± 0.7
Total annual of precipitation (TAP ± SD, mm)	1260 ± 347	1359 ± 289	1391 ± 218	1263 ± 228	2367 ± 517	1199 ± 333
Total precipitation in driest period [3 months rainfall] (TPdriests. maximum | mean | minimum, mm)	1|69|155	75|178|298	86|162|261	106|191|290	48|102|231	45|109|296
Number of dry periods [3 months=1 period] (drySeason, unit)	1	1-2	1-2	2	1	1-2
Number of dry months [<100 month^{-1}] (dryMonths ± SD, unit)	5.0 ± 1.7	3.5 ± 0.8	3.3 ± 0.6	3.8 ± 1.6	3.9 ± 0.8	5.2 ± 2.2
pH [in H2O at depth 0.30 m] (pH)	6.3 ± 0.3	5.8 ± 0.2	6 ± 0.3	5.8 ± 0.3	5.3 ± 0.2	6.1 ± 0.2
Soil organic carbon content [fine earth fraction at depth 0.30 m] (OCarbon ± SD, g·kg^{-1})	13.3 ± 6.8	25.7 ± 10.4	16.2 ± 6.3	18.4 ± 7	20.7 ± 18.8	24.5 ± 6.2
Sand content [>50-2000 µm at depth 0.30 m] (Sand ± SD, %)	38.0 ± 3.9	36.5 ± 5.7	38.2 ± 3.8	37.5 ± 3.1	40.4 ± 7.4	35.2 ± 3.4
Silt content [2-50 µm at depth 0.30 m] (Silt ± SD, %)	27.5 ± 2.7	25.5 ± 2.3	25.3 ± 2.9	25.8 ± 2.4	25.7 ± 4.8	26.9 ± 2.7
Clay content [<2 µm at depth 0.30 m] (Clay ± SD, %)	34.5 ± 2.7	37.9 ± 5.2	36.5 ± 2.7	36.4 ± 3	31.8 ± 6.7	38.1 ± 3.3
Bulk density [fine earth at depth 0.30 m] (BulkDens ± SD, kg·m^{-3})	1.44 ± 0.05	1.34 ± 0.07	1.42 ± 0.05	1.38 ± 0.04	1.37 ± 0.2	1.34 ± 0.06
Cation exchange capacity of soil [at depth 0.30 m] (CEC ± SD, cmol$_c$·kg^{-1})	20.6 ± 4.1	21.5 ± 3.9	18.2 ± 2.6	19.6 ± 2.1	11.3 ± 4.1	21.3 ± 4
Absolute depth to bedrock (Bedrock, cm)	59.6 ± 32.5	19.7 ± 10.2	34.7 ± 12.6	19.6 ± 7.1	57.2 ± 23.1	18.6 ± 11.2

Table S2. Frequency of plant species in 464 dry forest field sample sites in six regions of TDF in Colombia: most frequent species inside a region (a), most frequent species between regions (b) and most frequent species for all field sample sites (c). The species most commonly found across TDF sites were *G. ulmifolia* (number of sites: *N* = 165), *Astronium graveolens* (*N* = 158), *Attalea butyracea* (*N* = 114), *Bursera simaruba* (*N* = 106), *Spondias mombin* (*N* = 103), *Platymiscium pinnatum* (*N* = 88), *Handroanthus chrysanthus* (*N* = 84) and *Vachellia farnesiana N* = 77). These species represent only 0.9% of the total 881 plant species found, and are shared across 16.6-18% of the total sites sampled in 4-6 regions. The most frequently detected species in each region varied as follows: in the Caribbean, *A. graveolens* (detected in 46.5% of sites) and *B. simaruba* (37.6%), in the Cauca valley, *G. ulmifolia* (50.5%) and *Pithecellobium dulce* (27.9%), in the Magdalena valley, *G. ulmifolia* (45%), *A. graveolens* (34%) and *A. butyracea* (34%), in the North Andean, *Prosopis juliflora* (40.0%), *Muntingia calabura* (36.0%) and *Cecropia peltata* (36.0%), in the Orinoquia, *Vitex orinocensis (*44.5%) and *A. butyracea* (43.8%) and in the Patia, *G. ulmifolia* (73%) and *Zanthoxylum fagara* (65.4%). Reference specimens: Caribbean (Herbarium DUGAND H. Cuadros 6439–6751), Cauca valley (Herbarium INCIVA A. Castaño-Naranjo 154–327, Herbarium HUA A. Idárraga-Piedrahíta 5748–5796), Magdalena valley (Herbarium UDBC R. López 15404–15669, J. Aguilar 2150-3214), North Andean (Herbarium CDMB A. Rojas 2146–2234), Orinoquia (Herbarium FMB F. Mijares 1192–1358, F. Castro-Lima 19344-19469), Patia (Herbarium UDENAR R. Jurado 1-19, 354-446, Herbarium CAUP B. Ramírez 23244–23426), TDF All regions (Herbarium FMB R. González-M 1058–2485). *Exotic species.

Family	Species	Growth form	Caribbean	Cauca valley	Magdalena valley	North andean	Orinoquia	Patia	All regions	All sites
Acanthaceae	*Aphelandra pulcherrima*	herbaceous	2						1	2
Acanthaceae	*Bravaisia integerrima*	tree	6						1	6
Acanthaceae	*Trichanthera gigantea*	tree		1			1	1	3	3
Achariaceae	*Lindackeria paludosa*	tree					1		1	1
Achariaceae	*Mayna odorata*	tree			3				1	3
Achatocarpaceae	*Achatocarpus nigricans*	tree	3	16	1				3	20
Anacardiaceae	*Anacardium excelsum*	tree	27	15	20	7			4	69
Anacardiaceae	*Astronium fraxinifolium*	tree	4						1	4
Anacardiaceae	***Astronium graveolens***	**tree**	**94**[a]	7	**27**[a]	2	28		**5**[b]	**158**[c]
Anacardiaceae	*Astronium* sp	tree					11		1	11
Anacardiaceae	*Cyrtocarpa velutinifolia*	tree					3		1	3
Anacardiaceae	*Mangifera indica*	tree	1		2				2	3
Anacardiaceae	*Mauria* sp	tree			1				1	1
Anacardiaceae	***Spondias mombin***	**tree**	29	2	11		**61**[a]		4	**103**[c]
Anacardiaceae	*Spondias radlkoferi*	tree	1	1					2	2
Anacardiaceae	*Tapirira guianensis*	tree					41		1	41
Annonaceae	*Annona edulis*	tree	1				3		2	4
Annonaceae	*Annona exsucca*	tree					1		1	1
Annonaceae	*Annona glabra*	tree	1						1	1
Annonaceae	*Annona jahnii*	tree					4		1	4
Annonaceae	*Annona mucosa*	tree		1	1				2	2
Annonaceae	*Annona muricata*	tree		5					1	5
Annonaceae	*Annona neovelutina*	tree					1		1	1
Annonaceae	*Annona rensoniana*	tree						3	1	3
Annonaceae	*Annona reticulata*	tree	2						1	2
Annonaceae	*Annona* sp	tree						2	1	2

Family	Species	Growth form	Caribbean	Cauca valley	Magdalena valley	North andean	Orinoquia	Patia	All regions	All sites
Annonaceae	*Annona* sp1	tree				2			1	2
Annonaceae	*Annona* sp2	tree		1	2				2	3
Annonaceae	*Annona* sp3	tree		1			7		2	8
Annonaceae	*Bocageopsis multiflora*	tree					2		1	2
Annonaceae	*Duguetia odorata*	tree					2		1	2
Annonaceae	*Duguetia riberensis*	tree					1		1	1
Annonaceae	*Guatteria maypurensis*	tree		1			2		2	3
Annonaceae	*Guatteria metensis*	tree					1		1	1
Annonaceae	*Guatteria recurvisepala*	tree					1		1	1
Annonaceae	*Guatteria rubrinervis*	tree					1		1	1
Annonaceae	*Oxandra espintana*	tree			2				1	2
Annonaceae	*Oxandra* sp	tree	1						1	1
Annonaceae	*Pseudomalmea* sp	tree			1				1	1
Annonaceae	*Sapranthus isae*	tree	2						1	2
Annonaceae	*Xylopia aromatica*	tree	4		9	3	13		4	29
Annonaceae	*Xylopia emarginata*	tree					1		1	1
Annonaceae	*Xylopia* sp	tree					2		1	2
Annonaceae	*Xylopia* sp1	tree				1			1	1
Apocynaceae	*Asclepias* sp	herbaceous			1				1	1
Apocynaceae	*Aspidosperma cuspa*	tree	5						1	5
Apocynaceae	*Aspidosperma polyneuron*	tree	56		4				2	60
Apocynaceae	*Aspidosperma spruceanum*	tree					2		1	2
Apocynaceae	*Cascabela thevetia**	shrub		3		2			2	5
Apocynaceae	*Forsteronia affinis*	liana		1					1	1
Apocynaceae	*Himatanthus articulatus*	tree					18		1	18
Apocynaceae	*Mandevilla lancifolia*	liana					1		1	1
Apocynaceae	*Mandevilla* sp	liana		1					1	1
Apocynaceae	*Odontadenia macrantha*	tree					1		1	1
Apocynaceae	*Plumeria alba*	tree	4						1	4
Apocynaceae	*Plumeria pudica*	tree				2			1	2
Apocynaceae	*Prestonia* sp	liana	1						1	1
Apocynaceae	*Tabernaemontana amygdalifolia*	tree	1						1	1
Apocynaceae	*Tabernaemontana cymosa*	tree	12				1		2	13
Apocynaceae	*Tabernaemontana grandiflora*	tree	2		1				2	3
Apocynaceae	*Tabernaemontana* sp1	tree	1						1	1
Apocynaceae	*Thevetia ahouai*	tree	4						1	4
Apocynaceae	*Thevetia* sp	tree				1			1	1
Araceae	*Monstera adansonii*	liana					1		1	1
Araliaceae	*Aralia excelsa*	shrub	2						1	2
Araliaceae	*Dendropanax arboreus*	tree		1			2		2	3

Family	Species	Growth form	Caribbean	Cauca valley	Magdalena valley	North andean	Orinoquia	Patia	All regions	All sites
Araliaceae	*Dendropanax* sp	tree			1		1		2	2
Araliaceae	*Oreopanax acerifolius*	tree		5					1	5
Araliaceae	*Oreopanax* sp	tree		1					1	1
Araliaceae	*Schefflera bejucosa*	liana				1			1	1
Araliaceae	*Schefflera morototoni*	tree				1	17		2	18
Araliaceae	*Schefflera* sp	tree			1	2			2	3
Arecaceae	*Acrocomia aculeata*	palm	7				6		2	13
Arecaceae	*Acrocomia* sp	palm				1			1	1
Arecaceae	*Aiphanes aculeata*	palm					3		1	3
Arecaceae	*Aiphanes horrida*	palm					1		1	1
Arecaceae	*Astrocaryum jauari*	palm					1		1	1
Arecaceae	***Attalea butyracea***	**palm**	22	1	**27**[a]		**64**[a]		4	**114**[c]
Arecaceae	*Attalea maripa*	palm					8		1	8
Arecaceae	*Attalea microcarpa*	palm					1		1	1
Arecaceae	*Attalea* sp	palm			1				1	1
Arecaceae	*Bactris bidentula*	palm					1		1	1
Arecaceae	*Bactris gasipaes*	palm	3				2		2	5
Arecaceae	*Bactris gasipaes* var. *chichagui*	palm	1				1		2	2
Arecaceae	*Bactris major*	palm	4						1	4
Arecaceae	*Bactris pilosa*	palm			1				1	1
Arecaceae	*Chamaedorea linearis*	palm		1					1	1
Arecaceae	*Cocos nucifera*	palm	1		1				2	2
Arecaceae	*Copernicia tectorum*	palm	5						1	5
Arecaceae	*Desmoncus orthacanthos*	palm					2		1	2
Arecaceae	*Elaeis guineensis*	palm	3						1	3
Arecaceae	*Elaeis oleifera*	palm	3						1	3
Arecaceae	*Oenocarpus minor*	palm					4		1	4
Arecaceae	*Roystonea oleracea*	palm					2		1	2
Arecaceae	*Sabal mauritiiformis*	palm	13						1	13
Arecaceae	*Syagrus orinocensis*	palm					7		1	7
Arecaceae	*Syagrus sancona*	palm		1			10		2	11
Aristolochiaceae	*Aristolochia maxima*	liana			1				1	1
Aristolochiaceae	*Aristolochia* sp	liana		1					1	1
Asparagaceae	*Agave* sp	succulent		1					1	1
Asparagaceae	*Furcraea cabuya*	succulent		17					1	17
Asteraceae	*Calea sessiliflora*	herbaceous						1	1	1
Asteraceae	*Chromolaena laevigata*	shrub						1	1	1
Asteraceae	*Mikania* sp	shrub				1			1	1
Asteraceae	*Piptocoma discolor*	tree				4	14		2	18
Asteraceae	*Tessaria integrifolia*	tree		2				1	2	3

Family	Species	Growth form	Caribbean	Cauca valley	Magdalena valley	North andean	Orinoquia	Patia	All regions	All sites
Asteraceae	*Vernonanthura brasiliana*	tree						1	1	1
Asteraceae	*Vernonanthura phosphorica*	tree		9					1	9
Basellaceae	*Anredera floribunda*	liana			1				1	1
Bignoniaceae	*Amphilophium granulosum*	liana					1		1	1
Bignoniaceae	*Amphilophium paniculatum*	liana	1						1	1
Bignoniaceae	*Arrabidaea* sp	liana					1		1	1
Bignoniaceae	*Bignonia corymbosa*	liana					4		1	4
Bignoniaceae	*Bignonia pterocalyx*	liana	1						1	1
Bignoniaceae	*Bignonia* sp	liana		1					1	1
Bignoniaceae	*Fridericia mollissima*	liana	2						1	2
Bignoniaceae	*Fridericia pubescens*	liana					1		1	1
Bignoniaceae	*Gelseminum insigne*	tree					13		1	13
Bignoniaceae	*Godmania aesculifolia*	tree					4		1	4
Bignoniaceae	*Gonzalagunia cornifolia*	herbaceous						1	1	1
Bignoniaceae	*Handroanthus albus*	tree					1		1	1
Bignoniaceae	*Handroanthus billbergii*	tree	45				1		2	46
Bignoniaceae	***Handroanthus chrysanthus***	**tree**	30		5		41	8	4	**84**[c]
Bignoniaceae	*Handroanthus coralibe*	tree	5						1	5
Bignoniaceae	*Handroanthus guayacan*	tree					5		1	5
Bignoniaceae	*Handroanthus impetiginosus*	tree	1						1	1
Bignoniaceae	*Handroanthus ochraceus*	tree					4		1	4
Bignoniaceae	*Handroanthus ochraceus*	tree					9		1	9
Bignoniaceae	*Handroanthus serratifolius*	tree					6		1	6
Bignoniaceae	*Jacaranda copaia*	tree			2		6		2	8
Bignoniaceae	*Jacaranda obtusifolia*	tree					20		1	20
Bignoniaceae	*Jacaratia digitata*	tree					1		1	1
Bignoniaceae	*Roseodendron chryseum*	tree	1						1	1
Bignoniaceae	*Tabebuia orinocensis*	tree					1		1	1
Bignoniaceae	*Tabebuia rosea*	tree	12		8	1			3	21
Bignoniaceae	*Tanaecium tetragonolobum*	liana	1						1	1
Bignoniaceae	*Tecoma stans*	tree	2	5				1	3	8
Bixaceae	*Bixa urucurana*	shrub					3		1	3
Bixaceae	*Cochlospermum orinocense*	tree					15		1	15
Bixaceae	*Cochlospermum vitifolium*	tree	12				18		2	30
Boraginaceae	*Bourreria cumanensis*	tree	11						1	11
Boraginaceae	*Bourreria* sp	tree						1	1	1
Boraginaceae	*Cordia alba*	tree	42		1		1		3	44
Boraginaceae	***Cordia alliodora***	**tree**	25	2	1	1	16		**5**[b]	45
Boraginaceae	*Cordia bicolor*	tree	3				7		2	10
Boraginaceae	*Cordia curassavica*	tree				2		4	2	6

Family	Species	Growth form	Caribbean	Cauca valley	Magdalena valley	North andean	Orinoquia	Patia	All regions	All sites
Boraginaceae	*Cordia gerascanthus*	tree	2	1	2	1			4	6
Boraginaceae	*Cordia lanceolata*	tree						1	1	1
Boraginaceae	*Cordia macuirensis*	tree	1						1	1
Boraginaceae	*Cordia nodosa*	tree	4				1		2	5
Boraginaceae	*Cordia panamensis*	tree		1			1		2	2
Boraginaceae	*Cordia* sp	tree			1		5		2	6
Boraginaceae	*Cordia* sp1	tree		1					1	1
Boraginaceae	*Cordia* sp2	tree			4				1	4
Boraginaceae	*Cordia tetrandra*	tree					22		1	22
Boraginaceae	*Cordia thaisiana*	tree					5		1	5
Bromeliaceae	*Bromelia karatas*	succulent		2					1	2
Bromeliaceae	*Bromelia pinguin*	succulent	5						1	5
Bromeliaceae	*Bromelia* sp	succulent		2					1	2
Bromeliaceae	*Pitcairnia pruinosa*	succulent					1		1	1
Bromeliaceae	*Pitcairnia* sp	succulent		2					1	2
Bromeliaceae	*Tillandsia flexuosa*	succulent					5		1	5
Burseraceae	*Bursera glabra*	tree	8						1	8
Burseraceae	*Bursera graveolens*	tree	25		2	1			3	28
Burseraceae	***Bursera simaruba***	**tree**	**76**[a]	7	11	3	9		**5**[b]	**106**[c]
Burseraceae	*Bursera* sp	tree			2				1	2
Burseraceae	*Bursera tomentosa*	tree		1				1	2	2
Burseraceae	*Commiphora leptophloeos*	tree					1		1	1
Burseraceae	*Protium guianense*	tree					5		1	5
Burseraceae	*Protium heptaphyllum*	tree					18		1	18
Burseraceae	*Protium llanorum*	tree					3		1	3
Burseraceae	*Protium* sp	tree					1		1	1
Burseraceae	*Protium* sp1	tree		1					1	1
Burseraceae	*Protium subserratum*	tree					1		1	1
Burseraceae	*Protium tenuifolium*	tree			1				1	1
Burseraceae	*Tetragastris panamensis*	tree					7		1	7
Burseraceae	*Trattinnickia aspera*	tree					1		1	1
Burseraceae	*Trattinnickia rhoifolia*	tree					4		1	4
Burseraceae	*Trattinnickia* sp	tree					1		1	1
Buxaceae	*Buxus citrifolia*	shrub	1						1	1
Cactaceae	*Acanthocereus* sp	cactus				3			1	3
Cactaceae	*Acanthocereus* sp1	cactus			2				1	2
Cactaceae	*Acanthocereus tetragonus*	cactus	8				1		2	9
Cactaceae	*Cereus hexagonus*	cactus	2			3	1		3	6
Cactaceae	*Hylocereus megalanthus*	cactus		2					1	2
Cactaceae	*Melocactus curvispinus*	cactus	1		1				2	2

Family	Species	Growth form	Caribbean	Cauca valley	Magdalena valley	North andean	Orinoquia	Patia	All regions	All sites
Cactaceae	*Melocactus mazelianus*	cactus					1		1	1
Cactaceae	*Opuntia caracassana*	cactus	10			1			2	11
Cactaceae	*Opuntia dillenii*	cactus				3		5	2	8
Cactaceae	*Opuntia pittieri*	cactus		4					1	4
Cactaceae	*Opuntia* sp	cactus						1	1	1
Cactaceae	*Opuntia* sp1	cactus				3			1	3
Cactaceae	*Opuntia* sp2	cactus		1					1	1
Cactaceae	*Opuntia* sp3	cactus			1				1	1
Cactaceae	*Pereskia guamacho*	cactus	26						1	26
Cactaceae	*Pilosocereus colombianus*	cactus						1	1	1
Cactaceae	*Pilosocereus lanuginosus*	cactus						1	1	1
Cactaceae	*Pilosocereus* sp	cactus						5	1	5
Cactaceae	*Stenocereus griseus*	cactus	23			2			2	25
Cactaceae	*Stenocereus humilis*	cactus		1				1	2	2
Cactaceae	*Stenocereus* sp	cactus			5				1	5
Cactaceae	*Stenocereus* sp1	cactus				2			1	2
Calophyllaceae	*Caraipa llanorum*	tree					1		1	1
Cannabaceae	*Celtis iguanaea*	liana	2	1	3				3	6
Cannabaceae	*Trema micrantha*	tree		11		2			2	13
Capparaceae	*Belencita nemorosa*	shrub	9						1	9
Capparaceae	*Capparidastrum frondosum*	tree	4		5				2	8
Capparaceae	*Capparidastrum pachaca*	tree	9						1	9
Capparaceae	*Capparidastrum tenuisiliquum*	tree	1						1	1
Capparaceae	*Cleoserrata* sp	herbaceous		1					1	1
Capparaceae	*Cleoserrata speciosa*	herbaceous	1						1	1
Capparaceae	*Crateva tapia*	tree	28				1		2	29
Capparaceae	*Crescentia cujete*	tree			1			2	2	3
Capparaceae	*Cynophalla amplissima*	tree		4		1		9	3	14
Capparaceae	*Cynophalla flexuosa*	tree	3					1	2	4
Capparaceae	*Cynophalla hastata*	tree	1		1				2	2
Capparaceae	*Cynophalla linearis*	tree	5						1	5
Capparaceae	*Cynophalla verrucosa*	tree	5						1	5
Capparaceae	*Morisonia americana*	shrub	12						1	12
Capparaceae	*Quadrella indica*	tree	7	2	6				3	15
Capparaceae	*Quadrella odoratissima*	tree	25		13	3			3	41
Caricaceae	*Carica papaya*	tree						2	1	2
Caricaceae	*Vasconcellea cauliflora*	tree		2					1	2
Celastraceae	*Hippocratea volubilis*	liana	4		1				2	5
Celastraceae	*Prionostemma aspera*	liana		1					1	1
Celastraceae	*Schaefferia frutescens*	shrub	1						1	1

Family	Species	Growth form	Caribbean	Cauca valley	Magdalena valley	North andean	Orinoquia	Patia	All regions	All sites
Chrysobalanaceae	*Hirtella americana*	tree					1		1	1
Chrysobalanaceae	*Hirtella elongata*	tree					1		1	1
Chrysobalanaceae	*Hirtella racemosa*	tree					1		1	1
Chrysobalanaceae	*Licania alba*	tree					2		1	2
Chrysobalanaceae	*Licania apetala*	tree	1				24		2	25
Chrysobalanaceae	*Licania hypoleuca*	tree					1		1	1
Chrysobalanaceae	*Licania kunthiana*	tree					1		1	1
Chrysobalanaceae	*Licania micrantha*	tree					1		1	1
Chrysobalanaceae	*Parinari excelsa*	tree					3		1	3
Chrysobalanaceae	*Parinari pachyphylla*	tree	4						1	4
Clusiaceae	*Calophyllum brasiliense*	tree					1		1	1
Clusiaceae	*Clusia alata*	tree		2		2			2	4
Clusiaceae	*Clusia grandiflora*	tree					2		1	2
Clusiaceae	*Clusia latipes*	tree		4					1	4
Clusiaceae	*Clusia minor*	tree		1			3		2	4
Clusiaceae	*Clusia multiflora*	tree				1			1	1
Clusiaceae	*Clusia* sp	tree				1			1	1
Clusiaceae	*Clusia* sp1	tree			3				1	3
Clusiaceae	*Garcinia madruno*	tree			2		5		2	7
Combretaceae	*Buchenavia tetraphylla*	tree					6		1	6
Combretaceae	*Combretum aculeatum*	liana	1						1	1
Combretaceae	*Combretum fruticosum*	liana	6		2				2	8
Combretaceae	*Combretum* sp	liana	1						1	1
Combretaceae	*Terminalia amazonia*	tree					16		1	16
Combretaceae	*Terminalia oblonga*	tree					2		1	2
Connaraceae	*Connarus venezuelanus*	tree					13		1	13
Costaceae	*Dimerocostus strobilaceus*	herbaceous					1		1	1
Cyclanthaceae	*Carludovica palmata*	herbaceous	2	1					2	3
Dilleniaceae	*Curatella americana*	tree	10		10		1		3	21
Dilleniaceae	*Davilla kunthii*	shrub					1		1	1
Dioscoreaceae	*Dioscorea alata*	liana	1						1	1
Ebenaceae	*Diospyros sericea*	tree					1		1	1
Ebenaceae	*Diospyros* sp2	tree			1				1	1
Elaeocarpaceae	*Sloanea terniflora*	tree					6		1	6
Erythroxylaceae	*Erythroxylum citrifolium*	tree					1		1	1
Erythroxylaceae	*Erythroxylum haughtii*	tree						3	1	3
Erythroxylaceae	*Erythroxylum havanense*	tree	2						1	2
Erythroxylaceae	*Erythroxylum hondense*	tree	2						1	2
Erythroxylaceae	*Erythroxylum macrophyllum*	tree					2		1	2
Erythroxylaceae	*Erythroxylum suberosum*	tree					3		1	3

Family	**Species**	**Growth form**	**Caribbean**	**Cauca valley**	**Magdalena valley**	**North andean**	**Orinoquia**	**Patia**	**All regions**	**All sites**
Erythroxylaceae	*Erythroxylum williamsii*	tree					1		1	1
Euphorbiaceae	*Acalypha diversifolia*	tree		1			1		2	2
Euphorbiaceae	*Acalypha macrostachya*	tree						1	1	1
Euphorbiaceae	*Acalypha* sp	shrub		2					1	2
Euphorbiaceae	*Acalypha* sp1	shrub			1				1	1
Euphorbiaceae	*Alchornea discolor*	tree					14		1	14
Euphorbiaceae	*Alchornea* sp	tree			1				1	1
Euphorbiaceae	*Alchornea triplinervia*	tree					2		1	2
Euphorbiaceae	*Allophylus amazonicus*	tree					2		1	2
Euphorbiaceae	*Cnidoscolus aconitifolius*	herbaceous				1			1	1
Euphorbiaceae	*Cnidoscolus jaenensis*	herbaceous		1					1	1
Euphorbiaceae	*Cnidoscolus tubulosus*	herbaceous		3		1		2	3	6
Euphorbiaceae	*Cnidoscolus urens*	herbaceous	11						1	11
Euphorbiaceae	*Croton argenteus*	tree	1						1	1
Euphorbiaceae	*Croton ferrugineus*	tree						15	1	15
Euphorbiaceae	*Croton gossypiifolius*	tree		16		1	1		3	18
Euphorbiaceae	*Croton hibiscifolius*	tree						5	1	5
Euphorbiaceae	*Croton lechleri*	tree					3		1	3
Euphorbiaceae	*Croton leptostachyus*	tree				1		1	2	2
Euphorbiaceae	*Croton malambo*	tree	4						1	4
Euphorbiaceae	*Croton megalodendron*	tree					18		1	18
Euphorbiaceae	*Croton niveus*	tree	11						1	11
Euphorbiaceae	*Croton punctatus*	tree	1						1	1
Euphorbiaceae	*Croton rhamnifolius*	tree	1						1	1
Euphorbiaceae	*Croton schiedeanus*	tree		1					1	1
Euphorbiaceae	*Croton* sp	tree					3		1	3
Euphorbiaceae	*Croton* sp1	tree		8	18				2	26
Euphorbiaceae	*Croton* sp2	tree			1		7		2	8
Euphorbiaceae	*Croton* sp3	tree				4			1	4
Euphorbiaceae	*Euphorbia cotinifolia*	tree	5	17	1			1	4	24
Euphorbiaceae	*Euterpe precatoria*	tree				1	5		2	6
Euphorbiaceae	*Garcia nutans*	tree	2						1	2
Euphorbiaceae	*Hura crepitans*	tree	62	1					2	63
Euphorbiaceae	*Jatropha gossypiifolia*	shrub	1					3	2	4
Euphorbiaceae	*Mabea montana*	tree				1			1	1
Euphorbiaceae	*Mabea* sp	tree			3				1	3
Euphorbiaceae	*Mabea trianae*	tree					16		1	16
Euphorbiaceae	*Manihot carthaginensis*	tree	7						1	7
Euphorbiaceae	*Manihot esculenta*	shrub	2						1	2
Euphorbiaceae	*Manihot tristis*	tree					1		1	1

Family	Species	Growth form	Caribbean	Cauca valley	Magdalena valley	North andean	Orinoquia	Patia	All regions	All sites
Euphorbiaceae	*Maprounea guianensis*	tree					1		1	1
Euphorbiaceae	*Pera glabrata*	tree					1		1	1
Euphorbiaceae	*Ricinus communis*	shrub		1				1	2	2
Euphorbiaceae	*Sapium glandulosum*	tree					29		1	29
Euphorbiaceae	*Sapium jenmannii*	tree					2		1	2
Fabaceae	*Abarema jupunba*	tree					3		1	3
Fabaceae	*Abarema* sp	tree	1						1	1
Fabaceae	*Acacia mangium**	tree	1						1	1
Fabaceae	*Acacia pennatula*	tree		2				14	2	16
Fabaceae	*Acacia polyphylla*	shrub	1						1	1
Fabaceae	*Acacia* sp	tree			2	4			2	6
Fabaceae	*Albizia carbonaria*	tree				2			1	2
Fabaceae	*Albizia guachapele*	tree		12	23	2	7		4	44
Fabaceae	*Albizia niopoides*	tree	46	4			10		3	60
Fabaceae	***Albizia saman***	**tree**	28	10	6		1	3	**5**[b]	48
Fabaceae	*Albizia* sp	tree			1				1	1
Fabaceae	*Albizia subdimidiata*	tree					2		1	2
Fabaceae	*Anadenanthera peregrina*	tree					17		1	17
Fabaceae	*Andira inermis*	tree		1					1	1
Fabaceae	*Andira* sp	tree	1						1	1
Fabaceae	*Andira surinamensis*	tree					9		1	9
Fabaceae	*Apuleia leiocarpa*	tree					19		1	19
Fabaceae	*Bauhinia aculeata*	liana	2						1	2
Fabaceae	*Bauhinia guianensis*	liana	1						1	1
Fabaceae	*Bauhinia hymenaeifolia*	liana			1				1	1
Fabaceae	*Bauhinia petiolata*	tree			2				1	2
Fabaceae	*Bauhinia picta*	shrub				4			1	4
Fabaceae	*Bauhinia ungulata*	liana	1				7		2	8
Fabaceae	*Bentamantha* sp	shrub					1		1	1
Fabaceae	*Brownea ariza*	tree			2				1	2
Fabaceae	*Brownea rosa-de-monte*	tree	2						1	2
Fabaceae	*Brownea* sp	tree			1				1	1
Fabaceae	*Caesalpinia cassioides*	shrub						11	1	11
Fabaceae	*Caesalpinia coriaria*	tree	35						1	35
Fabaceae	*Caesalpinia ebano*	tree	2						1	2
Fabaceae	*Caesalpinia granadillo*	tree	5						1	5
Fabaceae	*Caesalpinia punctata*	tree	1						1	1
Fabaceae	*Caesalpinia* sp	tree	1						1	1
Fabaceae	*Calliandra magdalenae*	tree	7		1				2	8
Fabaceae	*Calliandra pittieri*	tree		7				16	2	23

Family	Species	Growth form	Caribbean	Cauca valley	Magdalena valley	North andean	Orinoquia	Patia	All regions	All sites
Fabaceae	*Calliandra purdiaei*	tree				3			1	3
Fabaceae	*Calliandra* sp	tree				3			1	3
Fabaceae	*Calliandra* sp1	tree			6				1	6
Fabaceae	*Calliandra trinervia var. carbonaria*	tree				1			1	1
Fabaceae	*Cassia fistula*	tree			2				1	2
Fabaceae	*Cassia grandis*	tree	1	1				2	3	4
Fabaceae	*Cassia moschata*	tree		1			24		2	25
Fabaceae	*Cassia* sp	tree			1	3			2	4
Fabaceae	*Centrolobium paraense*	tree	2						1	2
Fabaceae	*Chloroleucon mangense*	tree	11		2				2	13
Fabaceae	*Clathrotropis brachypetala*	tree					1		1	1
Fabaceae	*Clathrotropis macrocarpa*	tree					1		1	1
Fabaceae	*Clitoria dendrina*	shrub					4		1	4
Fabaceae	*Clitoria hermannii*	shrub					1		1	1
Fabaceae	*Copaifera pubiflora*	tree					44		1	44
Fabaceae	*Coursetia ferruginea*	tree	3						1	3
Fabaceae	*Coussarea* sp	tree					1		1	1
Fabaceae	*Coutarea hexandra*	tree	4					1	2	5
Fabaceae	*Crudia glaberrima*	tree					2		1	2
Fabaceae	*Cynometra bauhiniifolia*	tree					1		1	1
Fabaceae	*Dalbergia* sp	tree					1		1	1
Fabaceae	*Desmodium purpusii*	liana		2					1	2
Fabaceae	*Dioclea guianensis*	liana					1		1	1
Fabaceae	*Dioclea sericea*	liana						1	1	1
Fabaceae	*Dioclea* sp	liana			1				1	1
Fabaceae	*Diphysa carthagenensis*	tree	3						1	3
Fabaceae	*Dipteryx odorata*	tree					2		1	2
Fabaceae	*Entada polystachya*	liana	3						1	3
Fabaceae	*Enterolobium barinense*	tree					12		1	12
Fabaceae	*Enterolobium cyclocarpum*	tree	12	2			15		3	29
Fabaceae	*Enterolobium schomburgkii*	tree					3		1	3
Fabaceae	*Enterolobium* sp1	tree		3	4				2	7
Fabaceae	*Enterolobium timbouva*	tree					2		1	2
Fabaceae	*Erythrina fusca*	tree		2			15		2	17
Fabaceae	*Erythrina poeppigiana*	tree		19	2	4	4		4	29
Fabaceae	*Erythrina rubrinervia*	tree						1	1	1
Fabaceae	*Erythrina* sp	tree					1		1	1
Fabaceae	*Erythrina* sp1	tree				1			1	1
Fabaceae	*Erythrina* sp2	tree			1				1	1
Fabaceae	*Erythrina velutina*	tree	5						1	5

Family	Species	Growth form	Caribbean	Cauca valley	Magdalena valley	North andean	Orinoquia	Patia	All regions	All sites
Fabaceae	*Gliricidia sepium*	tree			2	1		10	3	13
Fabaceae	*Haematoxylum brasiletto*	tree	25			3			2	28
Fabaceae	*Hydrochorea corymbosa*	tree					8		1	8
Fabaceae	*Hymenaea courbaril*	tree	3				32		2	35
Fabaceae	*Hymenolobium petraeum*	tree					6		1	6
Fabaceae	*Inga alba*	tree					12		1	12
Fabaceae	*Inga cylindrica*	tree					1		1	1
Fabaceae	*Inga densiflora*	tree		3					1	3
Fabaceae	*Inga edulis*	tree	5				7		2	12
Fabaceae	*Inga fastuosa*	tree					2		1	2
Fabaceae	*Inga gracilifolia*	tree					1		1	1
Fabaceae	*Inga interrupta*	tree					2		1	2
Fabaceae	*Inga leiocalycina*	tree					1		1	1
Fabaceae	*Inga semialata*	tree		4		1			2	5
Fabaceae	*Inga* sp	tree		1			10		2	11
Fabaceae	*Inga* sp1	tree			6				1	6
Fabaceae	*Inga* sp2	tree		5					1	5
Fabaceae	*Inga* sp3	tree				4			1	4
Fabaceae	*Inga* sp6	tree			1				1	1
Fabaceae	*Inga spectabilis*	tree	1						1	1
Fabaceae	*Inga vera*	tree	1					2	2	3
Fabaceae	*Ipomoea pes-caprae*	liana	2						1	2
Fabaceae	*Leucaena glauca*	tree	1						1	1
Fabaceae	*Leucaena leucocephala*	tree		7	5	7		1	4	20
Fabaceae	*Libidibia ebano*	tree	6						1	6
Fabaceae	*Lonchocarpus pictus*	tree	1						1	1
Fabaceae	*Lonchocarpus punctatus*	tree	6						1	6
Fabaceae	*Lonchocarpus sanctae-marthae*	tree	16						1	16
Fabaceae	*Lonchocarpus violaceus*	tree	1						1	1
Fabaceae	*Luetzelburgia* aff. *andina*	tree		1					1	1
Fabaceae	*Machaerium arboreum*	tree	17				14		2	31
Fabaceae	*Machaerium biovulatum*	tree	12	1			6		3	19
Fabaceae	*Machaerium capote*	tree	7	9	7	1			4	24
Fabaceae	*Machaerium kegelii*	liana			1				1	1
Fabaceae	*Machaerium macrophyllum*	tree			2				1	2
Fabaceae	*Machaerium* sp	tree					2		1	2
Fabaceae	*Machaerium* sp1	tree	2		10				2	12
Fabaceae	*Machaerium* sp2	tree			6				1	6
Fabaceae	*Machaerium* sp3	liana	1						1	1
Fabaceae	*Machaerium* sp4	liana		1					1	1

Family	Species	Growth form	Caribbean	Cauca valley	Magdalena valley	North andean	Orinoquia	Patia	All regions	All sites
Fabaceae	*Machaerium* sp6	tree			1				1	1
Fabaceae	*Macrolobium multijugum*	tree					2		1	2
Fabaceae	*Mimosa albida*	shrub						1	1	1
Fabaceae	*Mimosa colombiana*	shrub					1		1	1
Fabaceae	*Mimosa* sp	shrub					1		1	1
Fabaceae	*Mimosa* sp1	shrub					1		1	1
Fabaceae	*Mimosa trianae*	tree					1		1	1
Fabaceae	*Muellera broadwayi*	tree	1						1	1
Fabaceae	*Myrospermum frutescens*	tree	7				2		2	9
Fabaceae	*Myroxylon balsamum*	tree		1					1	1
Fabaceae	*Ormosia macrocalyx*	tree					5		1	5
Fabaceae	*Parkia pendula*	tree					1		1	1
Fabaceae	*Parkinsonia aculeata*	tree				1			1	1
Fabaceae	*Parkinsonia* sp	tree				1			1	1
Fabaceae	*Peltogyne floribunda*	tree					10		1	10
Fabaceae	*Peltogyne purpurea*	tree	5						1	5
Fabaceae	*Peltogyne* sp	tree	1						1	1
Fabaceae	*Phanera guianensis*	liana					1		1	1
Fabaceae	*Piptadenia flava*	tree	45						1	45
Fabaceae	*Piptadenia gonoacantha*	tree	27						1	27
Fabaceae	*Piptadenia* sp	tree					3		1	3
Fabaceae	***Pithecellobium dulce***	**tree**	11	**26**^{a}	17	5		2	**5**^{b}	61
Fabaceae	*Pithecellobium lanceolatum*	tree	3	6	3			7	4	19
Fabaceae	*Pithecellobium roseum*	tree	13						1	13
Fabaceae	*Pithecellobium* sp	tree			7				1	7
Fabaceae	*Platycarpum orinocense*	tree					2		1	2
Fabaceae	***Platymiscium pinnatum***	**tree**	66	1	3	2	16		**5**^{b}	**88**^{c}
Fabaceae	*Platypodium elegans*	tree	1				1		2	2
Fabaceae	***Prosopis juliflora***	**tree**	39		8	**10**^{a}			3	57
Fabaceae	*Prosopis* sp	tree			1				1	1
Fabaceae	*Pseudosamanea* sp	tree				1			1	1
Fabaceae	*Pterocarpus acapulcensis*	tree	18				36		2	54
Fabaceae	*Pterocarpus officinalis*	tree	1				1		2	2
Fabaceae	*Pterocarpus rohrii*	tree	13		3		2		3	18
Fabaceae	*Pterocarpus* sp	tree		1					1	1
Fabaceae	*Schizolobium parahyba*	tree	2						1	2
Fabaceae	*Schizolobium sp*	tree			5	3			2	8
Fabaceae	*Senegalia glabra*	liana	4						1	4
Fabaceae	*Senegalia hayesii*	shrub	1						1	1
Fabaceae	*Senegalia macbridei*	liana					1		1	1

Family	Species	Growth form	Caribbean	Cauca valley	Magdalena valley	North andean	Orinoquia	Patia	All regions	All sites
Fabaceae	*Senegalia multipinnata*	tree				5			1	5
Fabaceae	*Senegalia riparia*	shrub					1		1	1
Fabaceae	*Senegalia* sp	tree	1						1	1
Fabaceae	*Senegalia* sp1	tree			3				1	3
Fabaceae	*Senegalia* sp2	tree	1						1	1
Fabaceae	*Senegalia tamarindifolia*	tree	1						1	1
Fabaceae	*Senna atomaria*	tree	9						1	9
Fabaceae	*Senna bacillaris*	tree				2			1	2
Fabaceae	*Senna bicapsularis*	tree	2						1	2
Fabaceae	*Senna fruticosa*	tree	1						1	1
Fabaceae	*Senna multijuga*	tree					1		1	1
Fabaceae	*Senna obtusifolia*	tree						7	1	7
Fabaceae	*Senna silvestris*	tree					2		1	2
Fabaceae	*Senna* sp	tree			3				1	3
Fabaceae	*Senna spectabilis*	tree		25					1	25
Fabaceae	*Stryphnodendron* sp	tree					1		1	1
Fabaceae	*Styphnolobium sporadicum*	tree		1					1	1
Fabaceae	*Swartzia arborescens*	tree					1		1	1
Fabaceae	*Swartzia dipetala*	tree					1		1	1
Fabaceae	*Swartzia pittieri*	tree					1		1	1
Fabaceae	*Swartzia robiniifolia*	tree		1					1	1
Fabaceae	*Swartzia simplex*	tree			1				1	1
Fabaceae	*Swartzia* sp	tree					8		1	8
Fabaceae	*Swartzia trianae*	tree			3				1	3
Fabaceae	*Tachigali guianensis*	tree					1		1	1
Fabaceae	*Tachigali* sp	tree					2		1	2
Fabaceae	*Uribea tamarindoides*	tree	2						1	2
Fabaceae	***Vachellia farnesiana***	**shrub**	46	8	4	6		13	**5**[b]	**77**[c]
Fabaceae	*Vachellia macracantha*	tree	1						1	1
Fabaceae	*Vachellia* sp	tree	1						1	1
Fabaceae	*Vachellia tortuosa*	tree	1						1	1
Fabaceae	*Vigna* sp	herbaceous			1				1	1
Fabaceae	*Zapoteca formosa*	tree	2						1	2
Fabaceae	*Zygia* sp	tree			7				1	7
Gentianaceae	*Adenolisianthus arboreus*	herbaceous					1		1	1
Goupiaceae	*Goupia glabra*	tree					2		1	2
Heliconiaceae	*Heliconia latispatha*	herbaceous	5	1					2	6
Hernandiaceae	*Gyrocarpus americanus*	tree	20	2					2	22
Hypericaceae	*Vismia baccifera*	tree				1	1		2	2
Hypericaceae	*Vismia lauriformis*	tree	2						1	2

Family	Species	Growth form	Caribbean	Cauca valley	Magdalena valley	North andean	Orinoquia	Patia	All regions	All sites
Hypericaceae	*Vismia macrophylla*	tree				1	1		2	2
Hypericaceae	*Vismia* sp	tree			2				1	2
Lacistemataceae	*Lacistema aggregatum*	tree	1	1			1		3	3
Lamiaceae	*Gmelina arborea**	tree	1						1	1
Lamiaceae	*Tectona grandis**	tree	2		1				2	3
Lamiaceae	*Vitex capitata*	tree					3		1	3
Lamiaceae	*Vitex compressa*	tree	1						1	1
Lamiaceae	*Vitex cymosa*	tree	7						1	7
Lamiaceae	***Vitex orinocensis***	**tree**					**65**[a]		1	65
Lamiaceae	*Vitex* sp	tree			4				1	4
Lauraceae	*Aniba* sp	tree					2		1	2
Lauraceae	*Cinnamomum triplinerve*	tree		4				1	2	5
Lauraceae	*Licaria applanata*	tree		1					1	1
Lauraceae	*Nectandra cuspidata*	tree					5		1	5
Lauraceae	*Nectandra membranacea*	tree		1					1	1
Lauraceae	*Nectandra pichurim*	tree					16		1	16
Lauraceae	*Nectandra purpurea*	tree						1	1	1
Lauraceae	*Nectandra* sp	tree			1				1	1
Lauraceae	*Nectandra* sp1	tree					4		1	4
Lauraceae	*Nectandra turbacensis*	tree	8						1	8
Lauraceae	*Ocotea bofo*	tree					8		1	8
Lauraceae	*Ocotea cernua*	tree		1			13		2	14
Lauraceae	*Ocotea guianensis*	tree				1			1	1
Lauraceae	*Ocotea longifolia*	tree					5		1	5
Lauraceae	*Ocotea schomburgkiana*	tree					1		1	1
Lauraceae	*Ocotea* sp	tree		2			1		2	3
Lauraceae	*Ocotea veraguensis*	tree		15	1				2	16
Lauraceae	*Persea caerulea*	tree		2					1	2
Lecythidaceae	*Eschweilera* sp	tree					2		1	2
Lecythidaceae	*Eschweilera tenuifolia*	tree					2		1	2
Lecythidaceae	*Gustavia augusta*	tree					1		1	1
Lecythidaceae	*Gustavia hexapetala*	tree			1		1		2	2
Lecythidaceae	*Gustavia* sp	tree			1				1	1
Lecythidaceae	*Gustavia superba*	tree	4						1	4
Lecythidaceae	*Lecythis minor*	tree	9						1	9
Loasaceae	*Mentzelia scabra*	herbaceous	1						1	1
Loranthaceae	*Gaiadendron punctatum*	tree				1			1	1
Lythraceae	*Lafoensia punicifolia*	tree	2	6					2	8
Malpighiaceae	*Bunchosia armeniaca*	tree		1					1	1
Malpighiaceae	*Bunchosia odorata*	tree	1						1	1

Family	Species	Growth form	Caribbean	Cauca valley	Magdalena valley	North andean	Orinoquia	Patia	All regions	All sites
Malpighiaceae	*Bunchosia pseudonitida*	tree		2				2	2	4
Malpighiaceae	*Bunchosia* sp2	liana			1				1	1
Malpighiaceae	*Byrsonima crassifolia*	shrub			3		3		2	6
Malpighiaceae	*Byrsonima crispa*	shrub					1		1	1
Malpighiaceae	*Byrsonima japurensis*	shrub					1		1	1
Malpighiaceae	*Byrsonima nitidissima*	shrub					3		1	3
Malpighiaceae	*Byrsonima* sp	shrub			1				1	1
Malpighiaceae	*Byrsonima spicata*	tree				1			1	1
Malpighiaceae	*Hiraea reclinata*	shrub	1						1	1
Malpighiaceae	*Hiraea* sp	liana	1						1	1
Malpighiaceae	*Malpighia glabra*	tree	9	1	3	1			4	14
Malvaceae	*Abutilon ibarrense*	shrub						5	1	5
Malvaceae	*Apeiba tibourbou*	tree					2		1	2
Malvaceae	*Cavanillesia chicamochae*	tree				1			1	1
Malvaceae	*Cavanillesia platanifolia*	tree	6						1	6
Malvaceae	***Ceiba pentandra***	**tree**	14	6	2	3	32	1	**5**[b]	58
Malvaceae	*Ceiba* sp	tree			1				1	1
Malvaceae	***Guazuma ulmifolia***	**tree**	43	**47**[a]	**36**[a]	7	13	**19**[a]	**5**[b]	**165**[c]
Malvaceae	*Hampea thespesioides*	tree			1				1	1
Malvaceae	*Helicteres baruensis*	tree	1						1	1
Malvaceae	*Helicteres* sp	shrub				2			1	2
Malvaceae	*Heliocarpus popayanensis*	tree				2			1	2
Malvaceae	*Luehea candida*	tree	1						1	1
Malvaceae	*Luehea seemannii*	tree		1	1		5		3	7
Malvaceae	*Luehea speciosa*	tree	2			1			2	3
Malvaceae	*Lueheopsis* sp	tree					1		1	1
Malvaceae	***Ochroma pyramidale***	**tree**	5	6	14	4	3	12	**5**[b]	44
Malvaceae	*Pachira nukakica*	tree					1		1	1
Malvaceae	*Pachira orinocensis*	tree					2		1	2
Malvaceae	*Pachira quinata*	tree	10						1	10
Malvaceae	*Pachira* sp	tree					6		1	6
Malvaceae	*Pavonia sepium*	herbaceous						1	1	1
Malvaceae	*Pseudobombax croizatii*	tree					1		1	1
Malvaceae	*Pseudobombax maximum*	tree	2						1	2
Malvaceae	*Pseudobombax septenatum*	tree	48	1	6		9		4	64
Malvaceae	*Sida jamaicensis*	herbaceous						2	1	2
Malvaceae	*Sida rhombifolia*	herbaceous						2	1	2
Malvaceae	*Sterculia apetala*	tree	50		1		23		3	74
Malvaceae	*Sterculia colombiana*	tree				1			1	1
Malvaceae	*Theobroma cacao*	tree			1				1	1

Family	Species	Growth form	Caribbean	Cauca valley	Magdalena valley	North andean	Orinoquia	Patia	All regions	All sites
Melastomataceae	*Acanthella sprucei*	herbaceous					1		1	1
Melastomataceae	*Bellucia grossularioides*	shrub				1			1	1
Melastomataceae	*Clidemia capitellata*	shrub						1	1	1
Melastomataceae	*Miconia albicans*	shrub						1	1	1
Melastomataceae	*Miconia holosericea*	shrub					1		1	1
Melastomataceae	*Miconia multispicata*	shrub					1		1	1
Melastomataceae	*Miconia* sp	shrub			6		2		2	8
Melastomataceae	*Miconia* sp1	tree				2			1	2
Melastomataceae	*Miconia* sp2	shrub			1				1	1
Melastomataceae	*Mouriri* sp	tree					1		1	1
Meliaceae	*Cedrela odorata*	tree	4	2		4	7		4	17
Meliaceae	*Guarea glabra*	tree					1		1	1
Meliaceae	*Guarea guidonia*	tree	4	7			20		3	31
Meliaceae	*Guarea* sp	tree			7				1	7
Meliaceae	*Ruagea glabra*	tree	3						1	3
Meliaceae	*Swietenia macrophylla*	tree	2						1	2
Meliaceae	*Trichilia acuminata*	tree	3						1	3
Meliaceae	*Trichilia carinata*	tree			3				1	3
Meliaceae	*Trichilia elegans*	tree			1				1	1
Meliaceae	*Trichilia hirta*	tree			1				1	1
Meliaceae	*Trichilia oligofoliolata*	tree			2				1	2
Meliaceae	*Trichilia pallida*	tree		4	4		2		3	10
Meliaceae	*Trichilia* sp	tree			6				1	6
Meliaceae	*Trichilia* sp1	tree	1						1	1
Moraceae	*Brosimum alicastrum*	tree	6	15			2		3	23
Moraceae	*Brosimum guianense*	tree					1		1	1
Moraceae	*Brosimum* sp	tree	1						1	1
Moraceae	*Brosimum* sp1	tree					7		1	7
Moraceae	*Brosimum* sp2	tree			1				1	1
Moraceae	*Clarisia biflora*	tree		1					1	1
Moraceae	*Ficus americana*	tree					2		1	2
Moraceae	*Ficus dendrocida*	tree	7				19		2	26
Moraceae	*Ficus insipida*	tree	4	11		2	19		4	36
Moraceae	*Ficus lyrata**	tree	1						1	1
Moraceae	*Ficus maxima*	tree				3			1	3
Moraceae	*Ficus nymphaeifolia*	tree					2		1	2
Moraceae	*Ficus obtusifolia*	tree		6			2	3	3	11
Moraceae	*Ficus pandurata*	tree	1						1	1
Moraceae	*Ficus pertusa*	tree					2		1	2
Moraceae	*Ficus* sp	tree			10				1	10

Family	Species	Growth form	Caribbean	Cauca valley	Magdalena valley	North andean	Orinoquia	Patia	All regions	All sites
Moraceae	*Ficus* sp1	tree		12					1	12
Moraceae	*Ficus* sp2	tree		1					1	1
Moraceae	*Ficus* sp3	tree					14		1	14
Moraceae	*Ficus* sp4	tree				5			1	5
Moraceae	*Ficus* sp5	tree						1	1	1
Moraceae	*Ficus trigona*	tree					1		1	1
Moraceae	*Ficus zarzalensis*	tree		1					1	1
Moraceae	*Helianthostylis sprucei*	tree			1				1	1
Moraceae	*Maclura tinctoria*	tree	20		10	1	6		4	37
Moraceae	*Maquira coriacea*	tree					5		1	5
Moraceae	*Poulsenia armata*	tree	1						1	1
Moraceae	*Pseudolmedia* sp	tree			1				1	1
Moraceae	*Pseudolmedia* sp1	tree					1		1	1
Moraceae	*Sorocea* sp	tree			1		1		2	2
Moraceae	*Sorocea sprucei*	tree	1				1		2	2
Moraceae	*Sorocea trophoides*	tree		1					1	1
Moraceae	*Trophis racemosa*	tree	3	1					2	4
Muntingiaceae	***Muntingia calabura***	**tree**	5	3	5	**9**[a]		3	**5**[b]	25
Musaceae	*Musa* x *paradisiaca**	shrub	3						1	3
Myristicaceae	*Virola sebifera*	tree					4		1	4
Myrtaceae	*Calyptranthes meridensis*	tree					1		1	1
Myrtaceae	*Campomanesia aromatica*	tree					1		1	1
Myrtaceae	*Capirona decorticans*	tree					2		1	2
Myrtaceae	*Eugenia biflora*	tree		9					1	9
Myrtaceae	*Eugenia lambertiana*	tree	1						1	1
Myrtaceae	*Eugenia monticola*	tree		5					1	5
Myrtaceae	*Eugenia procera*	tree	3	12	3				3	18
Myrtaceae	*Eugenia* sp	tree						6	1	6
Myrtaceae	*Eugenia* sp2	tree		3					1	3
Myrtaceae	*Eugenia* sp3	tree			3				1	3
Myrtaceae	*Eugenia* sp4	tree			1				1	1
Myrtaceae	*Myrcia fallax*	tree		1				3	2	4
Myrtaceae	*Myrcia multiflora*	tree	1						1	1
Myrtaceae	*Myrcia paivae*	tree					1		1	1
Myrtaceae	*Myrcia popayanensis*	tree		1					1	1
Myrtaceae	*Myrcia* sp	tree				1			1	1
Myrtaceae	*Myrcia splendens*	tree	1						1	1
Myrtaceae	*Myrcia sylvatica*	tree					1		1	1
Myrtaceae	*Myrcianthes leucoxyla*	tree	2						1	2
Myrtaceae	*Myrcianthes* sp	tree			5				1	5

Family	Species	Growth form	Caribbean	Cauca valley	Magdalena valley	North andean	Orinoquia	Patia	All regions	All sites
Myrtaceae	*Pseudanamomis umbellulifera*	shrub	1						1	1
Myrtaceae	*Psidium guajava*	tree		3				1	2	4
Myrtaceae	*Psidium guineense*	tree		8		2			2	10
Myrtaceae	*Psidium salutare*	tree						1	1	1
Myrtaceae	*Psidium sartorianum*	tree						3	1	3
Myrtaceae	*Psidium* sp	tree				2	4		2	6
Myrtaceae	*Syzygium jambos**	tree				1			1	1
Nyctaginaceae	*Guapira costaricana*	tree		2					1	2
Nyctaginaceae	*Guapira pacurero*	tree	5						1	5
Nyctaginaceae	*Guapira* sp1	tree		1					1	1
Nyctaginaceae	*Guapira uberrima*	tree	3						1	3
Nyctaginaceae	*Neea amplifolia*	tree	1						1	1
Nyctaginaceae	*Neea macrophylla*	tree			1				1	1
Nyctaginaceae	*Neea nigricans*	tree	1						1	1
Nyctaginaceae	*Neea* sp	tree	1						1	1
Nyctaginaceae	*Neea* sp1	tree		1			5		2	6
Nyctaginaceae	*Neea* sp2	tree	1						1	1
Nyctaginaceae	*Pisonia aculeata*	liana	2	2	1			1	4	6
Nyctaginaceae	*Pisonia nigricans*	tree	4						1	4
Nyctaginaceae	*Pisonia* sp	liana			3				1	3
Ochnaceae	*Cespedesia spathulata*	tree	1						1	1
Ochnaceae	*Ouratea* sp	tree					1		1	1
Olacaceae	*Heisteria acuminata*	tree					1		1	1
Opiliaceae	*Agonandra brasiliensis*	tree					9		1	9
Orchidaceae	*Vanilla planifolia*	succulent					1		1	1
Passifloraceae	*Passiflora edulis*	liana						2	1	2
Passifloraceae	*Passiflora sphaerocarpa*	liana		1					1	1
Peraceae	*Pera arborea*	tree					2		1	2
Petiveriaceae	*Seguieria americana*	liana	4						1	4
Phyllanthaceae	*Amanoa guianensis*	tree					1		1	1
Phyllanthaceae	*Hieronyma alchorneoides*	tree	1	1					2	2
Phyllanthaceae	*Hieronyma* sp	tree			1				1	1
Phyllanthaceae	*Margaritaria nobilis*	tree					1		1	1
Phyllanthaceae	*Phyllanthus acuminatus*	shrub		1			1		2	2
Phyllanthaceae	*Phyllanthus botryanthus*	shrub		1					1	1
Phyllanthaceae	*Phyllanthus elsiae*	shrub					4		1	4
Phyllanthaceae	*Phyllanthus salviifolius*	tree	1						1	1
Phyllanthaceae	*Phyllanthus* sp	tree			1				1	1
Picrodendraceae	*Piranhea trifoliata*	tree					1		1	1
Piperaceae	*Peperomia* sp	herbaceous						1	1	1

Family	Species	Growth form	Caribbean	Cauca valley	Magdalena valley	North andean	Orinoquia	Patia	All regions	All sites
Piperaceae	*Piper aduncum*	shrub	1	2		2		1	4	6
Piperaceae	*Piper marginatum*	shrub	2						1	2
Piperaceae	*Piper* sp	shrub		3	1	1			3	5
Piperaceae	*Piper* sp6	shrub			1				1	1
Poaceae	*Bambusa vulgaris*	shrub	2						1	2
Poaceae	*Guadua angustifolia*	shrub		23	9		4		3	36
Polygalaceae	*Securidaca* sp	tree	1						1	1
Polygonaceae	*Coccoloba acuminata*	tree	1						1	1
Polygonaceae	*Coccoloba caracasana*	tree	1				4		2	5
Polygonaceae	*Coccoloba coronata*	tree	1						1	1
Polygonaceae	*Coccoloba mollis*	tree					1		1	1
Polygonaceae	*Coccoloba obovata*	tree	1						1	1
Polygonaceae	*Coccoloba obtusifolia*	tree	3						1	3
Polygonaceae	*Coccoloba padiformis*	tree	2						1	2
Polygonaceae	*Coccoloba* sp	tree	1		6		1		3	8
Polygonaceae	*Coccoloba* sp1	tree	1		2				2	3
Polygonaceae	*Coccoloba* sp2	tree			1				1	1
Polygonaceae	*Coccoloba* sp4	shrub	1						1	1
Polygonaceae	*Ruprechtia cruegeri*	liana					2		1	2
Polygonaceae	*Ruprechtia ramiflora*	tree	16						1	16
Polygonaceae	*Ruprechtia* sp1	tree			1				1	1
Polygonaceae	***Triplaris americana***	**tree**	31	3	17	3	6		**5^b**	60
Polygonaceae	*Triplaris melaenodendron*	tree			4				1	4
Primulaceae	*Ardisia guianensis*	tree	1						1	1
Primulaceae	*Bonellia frutescens*	shrub	3						1	3
Primulaceae	*Geissanthus* sp	tree			5				1	5
Primulaceae	*Jacquinia armillaris*	shrub	1						1	1
Primulaceae	*Myrsine guianensis*	tree		12	2	4	1		4	19
Proteaceae	*Roupala montana*	tree					1		1	1
Proteaceae	*Roupala* sp	tree			2				1	2
Rhamnaceae	*Frangula goudotiana*	tree	2						1	2
Rhamnaceae	*Ziziphus jujuba*	tree	6						1	6
Rhamnaceae	*Ziziphus saeri*	tree	1						1	1
Rhamnaceae	*Ziziphus* sp	tree						1	1	1
Rhamnaceae	*Ziziphus strychnifolia*	tree			1				1	1
Rubiaceae	*Alseis blackiana*	tree			1				1	1
Rubiaceae	*Amaioua corymbosa*	tree					1		1	1
Rubiaceae	*Calycophyllum candidissimum*	tree	4						1	4
Rubiaceae	*Chiococca alba*	shrub	2	1					2	3
Rubiaceae	*Chomelia spinosa*	tree	1						1	1

Family	Species	Growth form	Caribbean	Cauca valley	Magdalena valley	North andean	Orinoquia	Patia	All regions	All sites
Rubiaceae	*Genipa americana*	tree	5	6			5		3	16
Rubiaceae	*Guettarda roupalifolia*	tree		1					1	1
Rubiaceae	*Guettarda* sp	tree					1		1	1
Rubiaceae	*Hamelia patens*	shrub	5						1	5
Rubiaceae	*Ladenbergia* sp	tree			1				1	1
Rubiaceae	*Palicourea rigida*	shrub					1		1	1
Rubiaceae	*Pittoniotis trichantha*	tree	1						1	1
Rubiaceae	*Pogonopus speciosus*	tree	5						1	5
Rubiaceae	*Psychotria carthagenensis*	shrub	2						1	2
Rubiaceae	*Psychotria micrantha*	shrub		2					1	2
Rubiaceae	*Randia aculeata*	tree	3				1		2	4
Rubiaceae	*Randia armata*	tree			2				1	2
Rubiaceae	*Randia dioica*	tree			1				1	1
Rubiaceae	*Randia obcordata*	shrub	18						1	18
Rubiaceae	*Randia pubistyla*	shrub	1						1	1
Rubiaceae	*Randia* sp	shrub			4				1	4
Rubiaceae	*Rosenbergiodendron formosum*	shrub	3						1	3
Rubiaceae	*Rudgea crassiloba*	tree					6		1	6
Rubiaceae	*Simira cesariana*	tree	4						1	4
Rubiaceae	*Simira cordifolia*	tree	1		2				2	3
Rubiaceae	*Simira rubescens*	tree					1		1	1
Rutaceae	*Amyris pinnata*	tree	2	7	1				3	10
Rutaceae	*Esenbeckia panamensis*	tree	1						1	1
Rutaceae	*Esenbeckia pentaphylla*	tree	1						1	1
Rutaceae	*Spathelia giraldoana*	tree					2		1	2
Rutaceae	*Swinglea glutinosa*	tree						1	1	1
Rutaceae	*Zanthoxylum caribaeum*	tree	1		12		1	2	4	16
Rutaceae	***Zanthoxylum fagara***	**shrub**		19			4	**17**[a]	3	40
Rutaceae	*Zanthoxylum gentryi*	tree		2					1	2
Rutaceae	*Zanthoxylum lenticulare*	tree		2					1	2
Rutaceae	***Zanthoxylum rhoifolium***	**tree**		17	2	1	13	5	**5**[b]	38
Rutaceae	*Zanthoxylum rigidum*	tree		1					1	1
Rutaceae	*Zanthoxylum schreberi*	tree		6				7	2	13
Rutaceae	*Zanthoxylum* sp	tree					1		1	1
Rutaceae	*Zanthoxylum* sp1	tree		2					1	2
Rutaceae	*Zanthoxylum* sp4	tree	1						1	1
Rutaceae	*Zanthoxylum verrucosum*	tree		5					1	5
Salicaceae	*Casearia aculeata*	tree		4					1	4
Salicaceae	*Casearia arborea*	tree	3						1	3
Salicaceae	*Casearia corymbosa*	tree	13	1	1				3	15

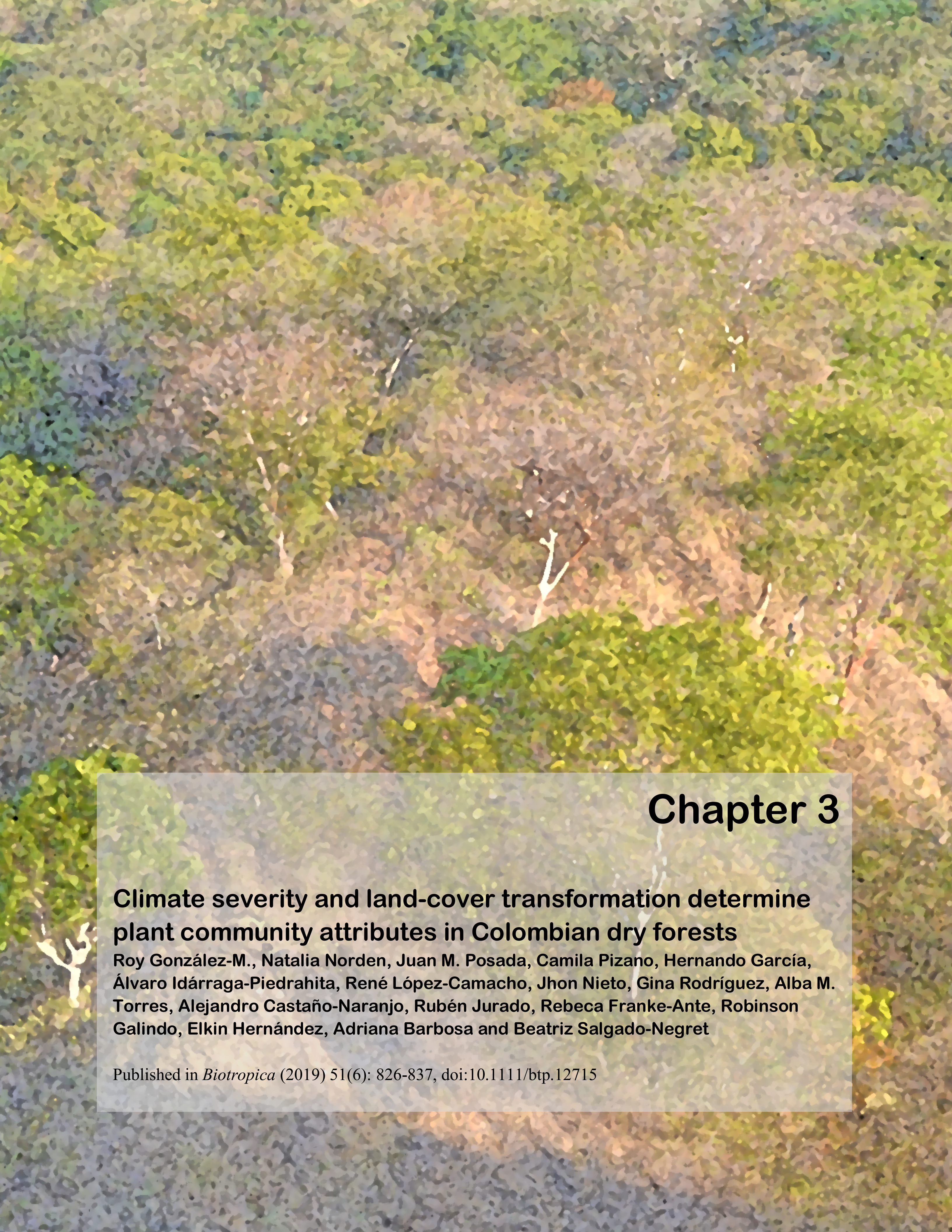
Family	Species	Growth form	Caribbean	Cauca valley	Magdalena valley	North andean	Orinoquia	Patia	All regions	All sites
Salicaceae	*Casearia guianensis*	tree					1		1	1
Salicaceae	*Casearia javitensis*	tree			2				1	2
Salicaceae	*Casearia praecox*	tree	1		3				2	4
Salicaceae	*Casearia* sp	tree			20				1	20
Salicaceae	*Casearia* sp1	tree					1		1	1
Salicaceae	*Casearia* sp3	tree	1						1	1
Salicaceae	*Casearia sylvestris*	tree		1	3		4	3	4	11
Salicaceae	*Casearia tremula*	tree	1						1	1
Salicaceae	*Casearia ulmifolia*	tree					2		1	2
Salicaceae	*Homalium guianense*	tree					2		1	2
Salicaceae	*Salix humboldtiana*	tree		1					1	1
Salicaceae	*Xylosma spiculifera*	tree	1						1	1
Sapindaceae	*Cupania americana*	tree	4	23			4	3	4	34
Sapindaceae	*Cupania cinerea*	tree	5		3				2	8
Sapindaceae	*Cupania latifolia*	tree		1					1	1
Sapindaceae	*Cupania* sp	tree			2				1	2
Sapindaceae	*Dilodendron costaricense*	tree			1				1	1
Sapindaceae	*Dilodendron elegans*	tree					2		1	2
Sapindaceae	*Dodonaea viscosa*	tree				1			1	1
Sapindaceae	*Matayba arborescens*	tree					9		1	9
Sapindaceae	*Matayba guianensis*	tree					3		1	3
Sapindaceae	*Matayba purgans*	tree					1		1	1
Sapindaceae	*Matayba* sp	tree					1		1	1
Sapindaceae	*Matayba* sp1	tree			1				1	1
Sapindaceae	*Melicoccus bijugatus*	tree	14	1		2		1	4	18
Sapindaceae	*Melicoccus oliviformis*	tree	10						1	10
Sapindaceae	*Paullinia alata*	liana		1					1	1
Sapindaceae	*Paullinia cururu*	liana	1						1	1
Sapindaceae	*Paullinia* sp2	liana	1						1	1
Sapindaceae	***Sapindus saponaria***	**tree**	4	19	1		1	3	**5**[b]	28
Sapotaceae	*Chrysophyllum cainito*	tree		1					1	1
Sapotaceae	*Chrysophyllum* sp	tree		1		1			2	2
Sapotaceae	*Elaeoluma* sp	tree					1		1	1
Sapotaceae	*Pouteria caimito*	tree					1		1	1
Sapotaceae	*Pouteria plicata*	tree					1		1	1
Sapotaceae	*Pouteria* sp	tree					13		1	13
Sapotaceae	*Pouteria* sp1	tree	1						1	1
Sapotaceae	*Pouteria* sp2	tree					1		1	1
Sapotaceae	*Pouteria* sp4	tree					1		1	1
Sapotaceae	*Pouteria* sp7	tree			3				1	3

Family	Species	Growth form	Caribbean	Cauca valley	Magdalena valley	North andean	Orinoquia	Patia	All regions	All sites
Sapotaceae	*Pouteria venosa*	tree					1		1	1
Sapotaceae	*Pradosia colombiana*	tree	19						1	19
Simaroubaceae	*Castela erecta*	shrub	1						1	1
Simaroubaceae	*Quassia amara*	tree	1						1	1
Simaroubaceae	*Simarouba amara*	tree		1			20		2	21
Siparunaceae	*Siparuna guianensis*	tree					2		1	2
Siparunaceae	*Siparuna* sp	tree			1				1	1
Smilacaceae	*Smilax* sp	liana			1				1	1
Solanaceae	*Cestrum alternifolium*	shrub	1						1	1
Solanaceae	*Cestrum mariquitense*	shrub						1	1	1
Solanaceae	*Cestrum* sp1	tree			1				1	1
Solanaceae	*Lycium tweedianum*	tree	1						1	1
Solanaceae	*Nicotiana tabacum*	shrub	1						1	1
Solanaceae	*Solanum laevigatum*	shrub		1					1	1
Solanaceae	*Solanum* sp	shrub						3	1	3
Solanaceae	*Solanum* sp1	shrub			1				1	1
Thymelaeaceae	*Daphnopsis* sp	tree		1					1	1
Ulmaceae	*Ampelocera macphersonii*	tree	5						1	5
Ulmaceae	*Ampelocera* sp1	tree			2				1	2
Ulmaceae	*Phyllostylon brasiliense*	tree	1						1	1
Ulmaceae	*Phyllostylon rhamnoides*	tree	4						1	4
Urticaceae	*Boehmeria* sp	herbaceous						2	1	2
Urticaceae	*Cecropia angustifolia*	tree		5	1		1		3	7
Urticaceae	*Cecropia engleriana*	tree					3		1	3
Urticaceae	*Cecropia longipes*	tree	2						1	2
Urticaceae	*Cecropia mutisiana*	tree		1					1	1
Urticaceae	***Cecropia peltata***	**tree**	23	5	2	**9**[a]	21		**5**[b]	60
Urticaceae	*Cecropia* sp	tree		5		1			2	6
Urticaceae	*Cecropia* sp1	tree			19				1	19
Urticaceae	*Myriocarpa longipes*	tree				1			1	1
Urticaceae	*Myriocarpa* sp	tree		1					1	1
Urticaceae	*Myriocarpa stipitata*	tree			1				1	1
Urticaceae	*Urera baccifera*	shrub	8	3			1		3	12
Urticaceae	*Urera caracasana*	tree			1			2	2	3
Urticaceae	*Urera* sp	tree				1			1	1
Velloziaceae	*Vellozia tubiflora*	shrub					1		1	1
Verbenaceae	*Citharexylum kunthianum*	shrub		10				11	2	21
Verbenaceae	*Citharexylum poeppigii*	tree					2		1	2
Verbenaceae	*Lantana camara*	shrub		2				6	2	8
Verbenaceae	*Lippia origanoides*	shrub						15	1	15

Family	Species	Growth form	Caribbean	Cauca valley	Magdalena valley	North andean	Orinoquia	Patia	All regions	All sites
Verbenaceae	*Petrea pubescens*	tree					5		1	5
Verbenaceae	*Petrea* sp	tree					1		1	1
Verbenaceae	*Verbena litoralis*	herbaceous						1	1	1
Violaceae	*Hybanthus prunifolius*	shrub	1						1	1
Violaceae	*Leonia* sp1	tree			1				1	1
Violaceae	*Rinorea pubiflora*	tree					2		1	2
Vochysiaceae	*Erisma* sp	tree					1		1	1
Vochysiaceae	*Erisma uncinatum*	tree					2		1	2
Vochysiaceae	*Qualea dinizii*	tree					4		1	4
Vochysiaceae	*Vochysia crassifolia*	tree					3		1	3
Vochysiaceae	*Vochysia lehmannii*	tree					29		1	29
Vochysiaceae	*Vochysia* sp	tree			1				1	1
Vochysiaceae	*Vochysia venezuelana*	tree					8		1	8
Zygophyllaceae	*Bulnesia arborea*	tree	49		1				2	50
Zygophyllaceae	*Bulnesia carrapo*	tree			4				1	4

Table S3. Number of tropical dry forest field sampling sites across six regions of Colombia used for different analyses

Information	Number of field sites used for the analysis (N)	Type of analysis
Environmental conditions and soils	558	Principal component analysis
Floristic composition	464	Non-metric multidimensional scaling
Environmental conditions, soils and floristic composition	456	Redundancy Analysis
Forest fragment size and shape	494	Total fragment size and shape index (perimeter/area)
Forest successional status	571	Forest successional status relative frequency
Anthropogenic pressures	571	Relative frequency of anthropogenic pressures inside forest and in the surrounding matrix
Total	571	



Chapter 3

Climate severity and land-cover transformation determine plant community attributes in Colombian dry forests

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Abstract

Tropical dry forests (TDF) are known to be resource-limited due to a marked seasonality in precipitation. However, TDF are also shaped by factors such as solar radiation, wind speed, soil fertility and land-cover transformation. Together, these factors may determine gradients of environmental harshness, that are likely to drive changes in plant community attributes. Here we evaluated the effects of environmental harshness on plant community diversity and structure of Colombian TDF based on floristic and environmental data from 15 1-ha permanent plots. We also analyzed effects on groups of legumes species only (including deciduous and non-deciduous species), deciduous species only (including legumes and non-legumes species), and the whole community excluding either legumes or deciduous separately. Drier conditions and higher land-cover transformation had the strongest negative effects on species diversity, basal area and canopy height. Soil fertility, on the contrary, did not have a significant effect on any of the evaluated variables. Interestingly, legumes maintained their diversity and basal area along the climatic gradient, while deciduous species were negatively affected by drier conditions and an increase in secondary vegetation at the landscape level. Our results suggest that although TDF are limited by water availability, land-cover transformation strongly increases environmental harshness. Yet, both legumes group and deciduous group were differentially impacted by climatic and land transformation variables. Thus, to better understand TDF plant community attributes, it is necessary to consider these gradients and to disentangle their effects on different plant functional groups.

Keywords: basal area, branching, canopy height, diversity, deciduous, forest structure, legumes, species richness

Introduction

Environmental harshness is defined as the combined effects abiotic factors filtering species and shaping forests structure (Whittaker 1965; Marks *et al.* 2016). The concept of environmental harshness, however, has been difficult to define because different factors affect plant community attributes in distinct ways (Gerstner *et al.* 2014; Stein *et al.* 2014). Although this has led many authors to reject the concept of environmental harshness, it may be useful for understanding community structuring in ecosystems experiencing multiple environmental limitations (Marks *et al.* 2016). This is the case for tropical dry forests (TDF), which experience drought conditions due to recurrent dry seasons related with low rainfall, high temperatures and high potential evapotranspiration (Murphy & Lugo 1986; Galicia *et al.* 1999; Trejo & Dirzo 2002). Water deficit, as the result of drought conditions, may induce cavitation and hydraulic failure (Markesteijn *et al.* 2011a; Méndez-Alonzo *et al.* 2012; Pineda-García *et al.* 2015), which in turn have negative consequences on plant growth, recruitment and survival (Allen *et al.* 2010). Thus, the intensity of dry seasons is likely to be one of the main drivers of plant community assembly and forest structure across TDF (Murphy & Lugo 1986, 1995; Allen *et al.* 2017a).

Climatic severity, however, may not be the only factor impacting TDF. In particular, soil fertility has been shown to influence seed germination, morphological adaptations and physiological responses of plants, with consequences for growth and survival (Murphy & Lugo 1986; Singh & Chaturvedi 2017). However, the effects of soil fertility on TDF plant communities have shown contrasting results. In Mexico, for instance, species richness increased with soil fertility (Perroni-Ventura *et al.* 2006), while species diversity declined with soil nutrient availability in Bolivia (Peña-Claros *et al.* 2012). The extent to which soil conditions determine TDF structure and species diversity therefore deserves further attention.

Changes in land-cover resulting from direct and indirect anthropogenic pressures are also important drivers plant community attributes (Gerstner *et al.* 2014; Stein *et al.* 2014). TDF are highly threatened in the Neotropics (Sánchez-Azofeifa *et al.* 2005a), and ongoing deforestation is rapidly converting the remaining natural areas into small forest fragments (Rodríguez *et al.* 2008; Portillo-Quintero & Sánchez-Azofeifa 2010). Land-cover transformation may directly impact plant diversity and forest structure through selective tree harvesting (Blackie *et al.* 2014), and indirectly through habitat loss and isolation effects (Stein *et al.* 2014). For instance, recruitment rates of vertebrate-dispersed plant species tend to be lower as fragmentation increases, as the result of a loss of dispersers in small fragments (Cordeiro & Howe 2001). Besides, deforestation may also increase climate severity, thereby reducing the likelihood of plant establishment and their persistence in forest patches. For example, higher wind exposure and lower forest area are important drivers of mortality rates in Amazonian forest patches (Laurance & Curran 2008), and of lower species richness in the Chaco forests of Argentina (Cagnolo *et al.* 2006). Land-cover change may also affect biotic interactions such as herbivory (Herrerías-Diego *et al.* 2008; Benítez-Malvido *et al.* 2018), or seed dispersal (Jacquemyn *et al.* 2001), especially of large-seeded plants, which are more dispersal limited (Cramer *et al.* 2007; Rodríguez-Cabal *et al.* 2007).

For climatic, soils and land-cover variables to constitute measures of environmental harshness in TDF, one must first evaluate whether each of these factors affect TDF diversity and structure. Only factors that effectively impact dry forests, should be considered constituents of this concept. Because TDF occur along a wide range of abiotic conditions (González-M. *et al.* 2018), evaluating the relative importance of these three key environmental factors on plant community assembly would provide critical insights into how harshness shapes TDF. For instance, at the community level, harder conditions would result in lower plant diversity and changes in forest structure moving towards characteristics that allow plants to survive under stressful environmental conditions.

How TDF respond to harsh conditions also depends on the species adaptations. As many species inhabiting TDF exhibit a wide array of strategies to overcome stressful conditions, differences among them may blur the overall community response (Singh & Chaturvedi 2017). In particular, legumes, both evergreen and deciduous, and deciduous species (including deciduous legumes), are two dominant functional groups with successful adaptations to cope with resource limitation in TDF (Houlton *et al.* 2008; Sprent 2009; Vargas *et al.* 2015; Santiago *et al.* 2016). Most legumes are associated with nitrogen-fixing bacteria, which increase their nutrient acquisition capacity and enhance their competitive ability in nutrient-poor soils (Sprent 2009). Their high levels of leaf nitrogen contents allow them to maintain high water use efficiency (Adams *et al.* 2016), which is also enhanced through the reduction of branching and leaf expansion (Li *et al.* 2009). These mechanisms alleviate carbon demands, allowing legumes to be physiologically efficient under drought conditions, and the most species-rich group across Neotropical dry forests (Gentry 1995; Lugo *et al.* 2006). Likewise, deciduous species shed their leaves during the dry season, which reduces their transpiration and respiration rates (Hulshof *et al.* 2014; Santiago *et al.* 2016). During the wet season, they produce low-cost leaves with high photosynthetic capacity (Méndez-Alonzo *et al.* 2012). Together, these mechanisms allow them to be competitive under drought conditions (Givnish 2002). Additionally, deciduous species often have small seeds and long-distance dispersal abilities, which allow them to cross dispersal barriers (Seiwa & Kikuzawa 1991, 1996; Cascante *et al.* 2002). As these two functional groups are particularly successful in TDF, one may ask whether their response to environmental harshness is similar to that of the community as a whole, or if they tend to increase in dominance as harshness increases due to their ecological adaptations.

Here, we explore the effects of climatic conditions, soil fertility and land-cover transformation on TDF plant community attributes in Colombia. Specifically, we addressed the following questions: 1) How do dry forest diversity and structure change across climatic, soil and land-cover gradients in Colombia? We expected that as climate severity increases, low soil fertility and land-cover transformation would increase environmental harshness. Thus, species richness and diversity should decrease, resulting changes in forest structure including shorter forest canopy, lower basal area and an increase of multi-stem individuals. Additionally, 2) Do legume and deciduous species show the same response to environmental harshness than the whole plant community? We predicted legume and deciduous species to respond differently to environmental harshness due to their strategies to overcome stressful conditions. For instance, they should show higher diversity and basal area under harsh conditions compared to the whole community.

Methods

Vegetation data set

Between 2013 and 2015, we established 15 1-ha permanent plots in Colombian dry forests across a wide range of environmental conditions (**Supporting Information Figure S1**; González-M *et al.* 2018) and in natural protected areas without evidence of heavy human activities or logging (> 60 years without of human disturbance). The plots were representative of the range of shape, size and land-cover uses of TDF in Colombia (**Figure S1c**). Within each plot, we tagged, measured and identified all trees, shrubs, lianas and palms ≥ 2.5 cm in diameter at breast height (DBH, measured at 1.3 m height) We measured DBH, total height, and quantified all secondary stems of each individual (van Laar & Akça 2007). We included cacti ≥ 1.5 m in height and ≥ 2.5 cm in basal diameter because of their importance in TDF (Gentry 1995). We did not register DBH for cacti nor height for lianas. Within each plot, botanical samples of all species were collected for identification (see **Appendix S1**). All plots were visited during dry and rainy seasons to determine species leaf phenology as follows. Deciduous if species dropped their leaves during the drought and had new leaves during rainy conditions, and evergreen if maintained their leaves during both periods (**Appendix S1**).

Climate, soils and land-cover data

We compiled a climatic database that included nine variables derived from two sources (**Table S1**). Annual total number of rainy days (ARD), aridity index (Aridity), isothermality (Isoth), total annual precipitation (TAP), potential evapotranspiration (PET), and total precipitation during the three driest months (TPdriest) were determined using the National Climatic Source, which is based on 2046 weather stations in Colombia, and generates monthly data of temperature, precipitation and rainy days (~90 m spatial resolution, *http://institucional.ideam.gov.co/jsp/1769*). Aridity was calculated as the TAP/PET ratio (Zomer *et al.* 2008). PET was determined as the sum of monthly potential evapotranspiration over a year using the Thornthwaite equation (Thornthwaite 1948). Isoth was estimated as the amplitude of day-to-night temperatures relative to the annual amplitude, where annual amplitude is the difference between maximum TºC of the warmest month and minimum TºC of the coldest month (O'Donnell & Ignizio 2012). Solar radiation (SRad), water vapor pressure (WVP) and wind speed (Wind) were derived from WorldClim 2.0 (Fick & Hijmans 2017).

To evaluate soil fertility, 10 soil samples were randomly taken at each plot and oven-dried at 60ºC until constant weight was reached. Soil acidity (pH) was determined as the concentration of hydrogen ions in a 1:1 soil-water mixture (Burt & Staff 2014), available phosphorus (P) was extracted with a Bray I solution and measured colourimetrically (Bray & Kurtz 1945; Menage & Pridmore 1973), extractable bases (Ca, Mg, K, Na) and cation exchange capacity (CEC) were measured using the absorption-atomic emission spectrophotometry procedure (Reeuwijk 2002), organic carbon (OC) was separated with water-soluble humic and fulvic acids at a pH of 2.0 and quantified by combustion using the Walkley–Black procedure (Walkley 1946), and textural fractions (Sand, Clay, Silt) were determined using the hydrometer method, based on the relation between sedimentary speed and particle sizes according to the Stokes law (Bouyoucos 1962; Powers *et al.* 2009) (**Table S1**). Soil analyses were performed at the Agustin Codazzi National Soil Laboratory (Colombia).

To evaluate land-cover metrics, we defined a circular area of 500 ha around each plot, based on interpretation of remote-sensing imagery from the Landsat 8 Mosaic 2014 (15x15 m resolution, cloudinness cover < 1%) and Google Earth^{Pro}© images of 2014-2015 (0.64x0.64 m resolution, 1500 m flight height) (Xu & Becker 2012; Yu & Gong 2012). Within this area, we estimated total forest cover area (Forest), forest shape index (Shape), the area covered by secondary vegetation (SecVeg), the area covered by human land-uses (ULC), the number of human land use cover types (UCL.type) and topographic roughness (Roughness) (**Table S1**). Forest, SecVeg, and ULC were quantified as percentages excluding rivers, lakes or rock outcrops (McGarigal & Marks 1995). Shape was estimated as the area/perimeter ratio, where values closer to zero indicate that fragments tend to be narrow (Moser *et al.* 2002; Berry 2007), while larger values indicate circular fragments. UCL.type included agriculture, cattle ranching and human infrastructure (see Patch Richness, McGarigal & Marks 1995). Roughness was computed as the change in elevation between adjacent cells of a DEM model (15x15 m in 500 ha) following the procedures of (Riley *et al.* 1999). All spatial analyses were performed using ArcGIS® 10.2 and remote-sensing interpretations were validated in the field.

Plant diversity and forest structure

Plant diversity was measured based on Hill numbers, also called the effective number of species. This family of diversity metrics is parameterized by the variable q, which controls the sensitivity to species relative abundance. When $q = 0$, all species are equally weighted, and ^{0}D thus corresponds to species richness. When $q = 1$, all individuals are equally weighted, and ^{1}D corresponds to the Shannon-derived diversity (Jost 2006; Chiu *et al.* 2014).

Forest structure was assessed by quantifying total basal area (BA), branching index (BI), and forest canopy height (H) in each plot (Table S2; van Laar & Akça 2007). BA was estimated as the sum of all individual basal area for trees, shrubs and lianas within each plot. BI, which is the extent to which individual trees were multi-stemmed, was calculated as:

$$\mathrm{BI} = 100 \times \left[\frac{\sum_{i=1}^{n} stems - \sum_{i=1}^{n} ind}{\sum_{i=1}^{n} stems}\right]$$

where *ind* is the total number of individuals and *stems* is the total number of branches with DBH ≥ 2.5 cm below 1.3 m height but aboveground, including trees, shrubs, palms, lianas or cactus. A BI of 0% indicates that all the individuals of the plot were single-stemmed, and BI increases as the proportion of multi-stemmed individuals increases. H, which represents the average height of the tallest individuals within a plot, was determined as the mean value of the upper quantile in height (Q_3–Q_4) of trees, shrubs, palms and cacti.

Statistical analysis

We performed a principal component analyses (PCA) for each set of environmental variables (*i.e.* 9 climate-, 11 soils- and 6 land-cover variables), and selected the first two PCA axes for describing the environmental space and as combined predictors (Wigley *et al.* 2016). To evaluate whether PCA variables were better predictors than raw environmental variables, we predicted ^{0}D, ^{1}D, BA, BI and H using, on one hand, simple and multiple linear models (SLR and MLR, respectively) with all possible combinations of the single variables, so that variance inflation factor (VIF) < 1.5 and, on the other hand, the first two PCA axes of each environmental category (for details see SI Modeling Procedures–MP). Since stem density varies considerably across plots, we ran individual-based rarefaction curves to evaluate whether the rarefied number of species differed from the observed one (**Figure S2**). In all cases, we found a strong positive correlation between plot species richness and the rarefied number of species, indicating that both metrics were valid ($\rho = 0.99 - 0.73, P < 0.001$). Thus, we kept ^{0}D and ^{1}D as response variables. Then, we selected the best-fitted model through stepwise elimination based on the corrected Akaike's Information Criterion (AICc) (Hurvich & Tsai 1993; Venables & Ripley 2002). We made sure that VIF < 5, so that the models were not affected by a correlation between predictors (Akinwande *et al.* 2015), and fulfilled all assumptions for the normal distribution of residuals (Royston 1982) and homoscedasticity (Breusch & Pagan 1979). All models showed spatial independence in their residuals (Moran's I, $P > 0.05$; **Tables S3-S5**). To compare the relative effects of the different predictors on each of our response variables, we compared the *z*-standardized β-coefficients, and performed an analysis of variance on the best-fitted model to calculate the percentage of variance explained by each predictor (Chambers & Hastie 1992).

To evaluate whether the response of legumes and deciduous species to environmental harshness was consistent with that observed for at the community level, we repeated the same set of analyses using legumes, deciduous species, and the whole community excluding either legumes or deciduous species separately. We then compared the *z*-standardized β-coefficients of the best-fitted models with those obtained for the whole plant community. All statistical analyses were performed using R version 3.4.2.

Results

Climatic, soils and land-cover gradients

As revealed by PCA analyses, the 15 1-ha plots occurred across a wide range of climatic, soil and land-cover conditions (**Figure 1**). The first axis of climatic PCA explained 56.6% of the total variance and was mostly related to climate severity (**Figure 1a**). Positive values were associated with aridity and high wind speed, solar radiation and water vapour pressure; whereas negative values were associated with high precipitation during the driest season, and more rainy days. Regarding soil variables, the first PCA axis explained 48.8% of the total variance, and was related to soil fertility. Sites with negative values of the PCA axis 1 were characterized by high CEC, high contents of extractable bases (Ca, Mg, K), high contents of clay and silt, and high pH (**Figure 1b**). Finally, the first axis of land-cover PCA explained 56.5% of the total variance, and was related to a gradient of transformation (**Figure 1c**). Sites with negative values were associated with higher forest cover, whereas sites with positive values were associated with a higher proportion of secondary vegetation, narrower forest fragments and a higher number of human land-cover types.

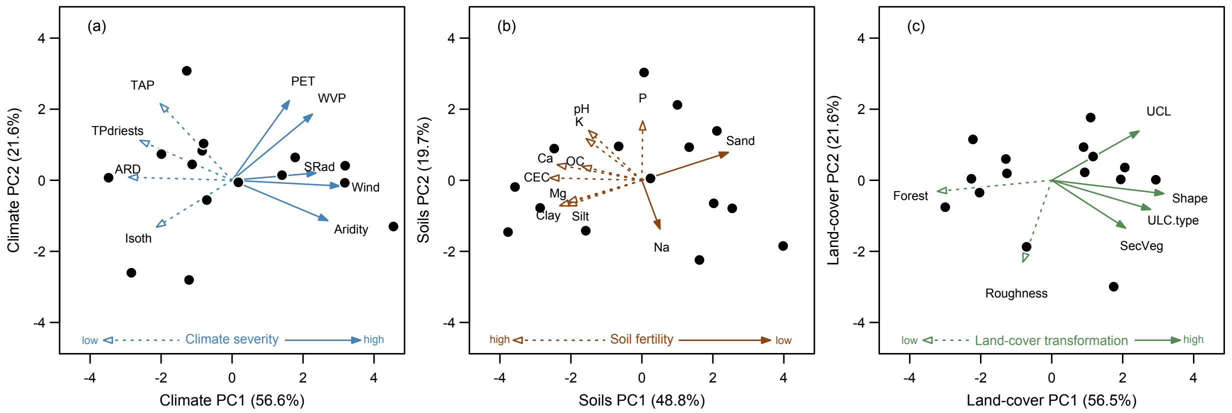

Figure 1. Principal component analysis showing climatic, soils and land-cover transformation environmental space where the 15 1-ha permanent plots are located across tropical dry forest patches (black dots) in Colombia. (a) Climatic variables include: total of annual rainy days (ARD), aridity index (Aridity), isothermality (Isoth), solar radiation (SRad), total annual precipitation (TAP), potential evapotranspiration (PET), total precipitation during the three driest months (TPdriest), water vapor pressure (WVP) and wind speed (Wind). (b) Soil variables are acidity (pH), available phosphorus (P), cation exchange capacity (CEC), extractable bases (Ca, Mg, K, Na), organic carbon (OC) and textural fractions (Sand, Clay, Silt). (c) Land-cover metrics include: forests cover (Forest), forest shape index (Shape), secondary vegetation (SecVeg), land cover used by humans (ULC), types of human land cover uses (ULC.type) and topographic roughness (Roughness).

Plant community diversity and forest structure across gradients

Overall, we tagged 31,776 individuals (40,341 stems) belonging to 536 species distributed in 79 families of trees, lianas, cacti and palms in the 15 1–ha permanent plots (**Table S2**). Species richness (^{0}D) varied between 12 and 101, and Shannon-derived diversity (^{1}D) was 3 and 49 species·ha^{-1} per plot (**Table S2**). Basal area (BA) varied from 4.82 to 30.34 m^{2}·ha^{-1}, branching index (BI) from 4.11 to 50.46%, and forest canopy height (H) from 5.62 to 18.12 m (**Table S2**). The best-fitted models predicting forest diversity and structure included the first PCA axes for both climate and land-cover ($R^2 = 0.42$–0.71, $P < 0.05$; **Figure 2**, see details in **Table S3**). Soil PCA axes did not have a significant effect on any of our response variables (**Table S3**). Overall, all models explained between 27.3 and 70.0% of the total variance (**Figure 3a**). Land-cover transformation was a strong, significant predictor of all the response variables and explained a considerable proportion of the variance (4.5-46.4%, **Figure 3a**), except for H (**Figure 2** and **3e**). Sites surrounded by a higher proportion of secondary vegetation and narrower fragments had lower ^{0}D, ^{1}D and BA, but higher BI. Climate severity was significantly associated with all response variables (**Figure 2**), and was the only significant predictor of H, explaining 27.3% of the variance (**Figure 2e**). This relationship was negative in all cases except for BI, which was positive (**Figure 2d**). In spite of a weak, although significant, correlation between climate and land-cover PCA axis 1 (see **Table S3**), the interaction between these predictors was not significant for models considering interaction effects, and in all cases VIF < 5.

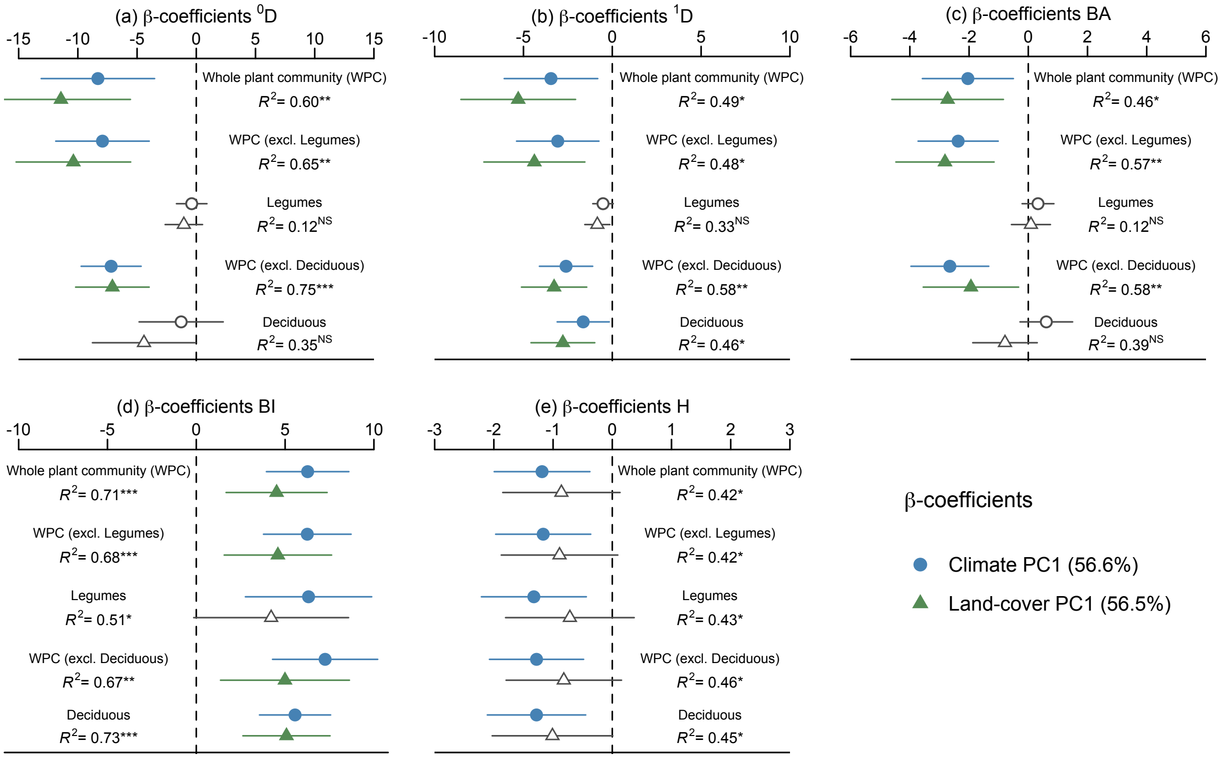

Figure 2. Best-fitted model β-coefficients showing the effects of climate severity and land-cover transformation (axis 1 of the PCAs) on (a) species richness (^{0}D), (b) species diversity (^{1}D), (c) basal area (BA), (d) branching index (BI) and (e) forest canopy height (H) for the whole plant community (WPC), for each subset of species (legumes-both evergreen and deciduous, and deciduous species-including deciduous legumes) and for the whole community without each of these groups of species. Statistical significance of the models per group are as follows: *** $P < 0.001$ ** $P < 0.01$ * $P < 0.05$ ^{NS} (not significant). β coefficients overlapping 0 represents non-significant standardized slopes of climate and land-cover transformation (axis 1 of the PCAs) for the respective model. For details on the models see Table S3.

Plant diversity and forest structure of legumes and deciduous species across gradients

Legumes, both deciduous and evergreen, had the highest number of species (102), individuals (4696) and stems (7081) in the 15 1-ha permanent plots (**Appendix S1**), representing 13.7-45.2% of the number of individuals per plot (**Table S2**). Deciduous species (including deciduous legumes) were also highly abundant, representing 54.4%-88.9% of ^{0}D across plots, and more that 50% of the number of individuals per plot (**Table S2**). We found contrasting results using the same best-fitted models predicting diversity and forest structure for the whole plant community, when compared to either legumes or deciduous species. Land-cover and climate severity did not predict ^{0}D, ^{1}D nor BA in either of these two functional groups of plants (**Figure 2a-c**, **Table S4-S5**), except for ^{1}D in deciduous species. Interestingly, as for the whole plant community, climate severity was the best predictor of BI and H for both legumes and deciduous species (**Figure 3**), with positive effects on BI ($P < 0.001$, **Figure 3d**) and negative effects on H ($P < 0.05$, **Figure 3e**).

When we ran the models with raw climatic, soils and land-cover variables for predicting forest diversity and structure for legumes and deciduous species, different predictors were found to be significant (**Figure 4**). For instance, the best-fitted model predicting ^{0}D and ^{1}D in legumes (**Table S4**) included positive effects of solar radiation and total precipitation during the three driest months. Likewise, the best-fitted model predicting BA in legumes only included the positive effect of soil available phosphorus, which had no effects at the community level (**Table S4**, **Figure 4a**). In contrast, the best-fitted models explaining ^{0}D, ^{1}D and BA for deciduous species included strong negative effects of land-cover transformation and of the proportion of secondary vegetation, similar to effects observed in the whole plant community (**Figure 4b**, **Table S5**).

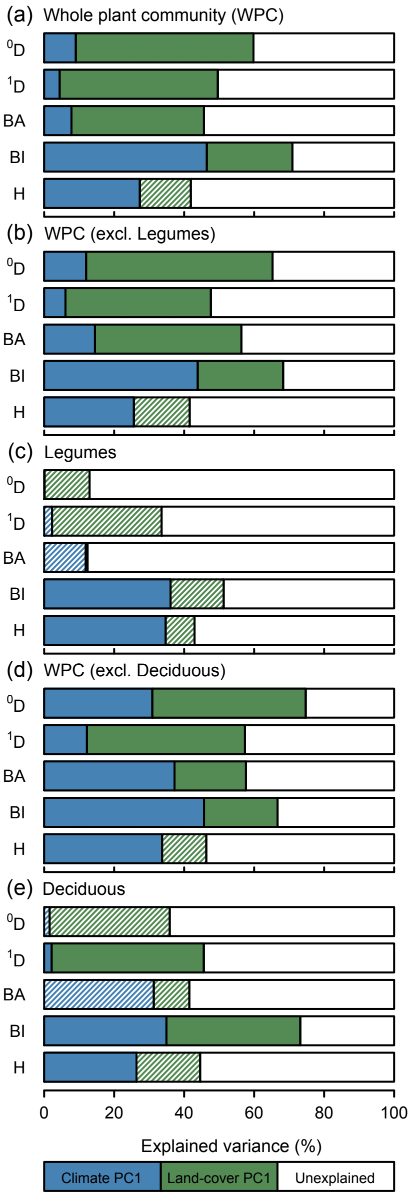

Figure 3. Explained variance of the best models obtained from a series of multiple regression analyses for communities of 15 1-ha Colombian dry forests: (a) whole plant community (WPC), (b) WPC excluding legume species (both evergreen and deciduous), (c) legume species, (d) WPC excluding deciduous species (including deciduous legumes), (e) deciduous species, and their respective plant community attributes: species richness (^{0}D), species diversity (^{1}D), basal area (BA), branching index (BI), and forest canopy height (H). Best-fitted models included as parameters the first PCA axes of climatic and land-cover transformation (56.6% and 56.5%, respectively). Achurated bars indicate non-significant effects of β-coeficientes. For details on the models see **Table S4-S5**.

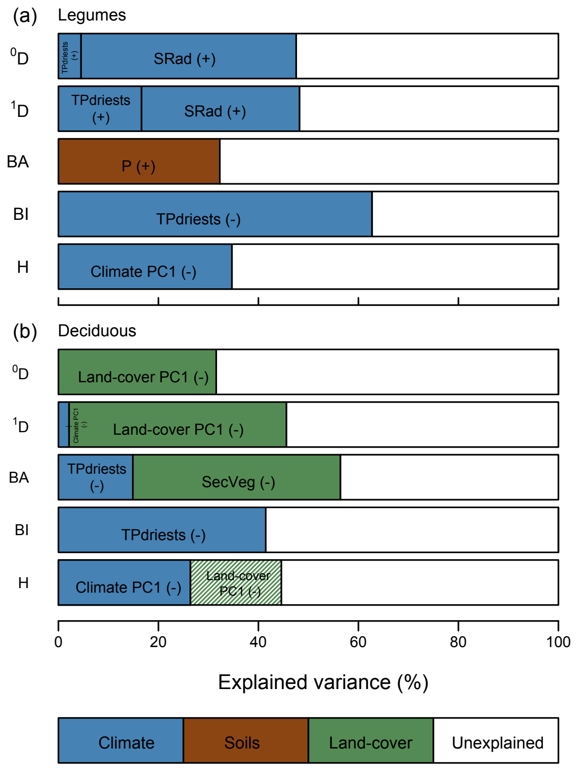

Figure 4. Explained variance for the best models obtained from a series of multiple regression analyses for species richness (^{0}D), species diversity (^{1}D), basal area (BA), branching index (BI) and forest canopy height (H) of legumes (both evergreen and deciduous) (a) and deciduous (including deciduous legumes) (b) species, estimated per hectare ($P < 0.05$). Climate: climate PC1 (56.6%, C.PC1), solar radiation (SRad) and total precipitation during the three driest months (TPdriest). Soils: available phosphorus (P). Land-cover: land-cover PC1 (56.5%, L.PC1) and secondary vegetation area (SecVeg). (+) indicates positive β-coefficients and (-) negative for the models. Achurated bars indicate non-significant effects of β-coeficientes. For details on the models see **Table S4-S5**.

Discussion

We assessed the extent to which climatic, soils and land-cover variables affected TDF diversity and structure, and compared these patterns to those obtained for different functional groups of species known to thrive in dry conditions. Our results showed that: (1) TDF are distributed along gradients of climate severity, soil fertility and land-cover transformation, although climate severity and land-cover transformation were the main determinants of TDF diversity and structure at the community level. Interestingly, (2) the responses of legumes and deciduous species to these gradients were not consistent with that of the whole plant community.

Environmental harshness of TDF cannot be defined only by rainfall seasonality

Traditionally, TDF have been associated with rainfall seasonality and relatively fertile soils (e.g., Murphy & Lugo 1986; Pennington *et al.* 2009). Our results show, however, that in Colombia, TDF are distributed across independent gradients of climate severity, soil fertility and land-cover transformation (**Figure 1**). In particular, water deficit, the main filter shaping TDF species diversity and structure (Pennington *et al.* 2009; Neves *et al.* 2015), may result from the combination of different climatic variables, and not just from rainfall regimes (González-M. *et al.* 2018). For example, at the Colorados site, water deficit was driven by high solar radiation, despite a high total annual rainfall compared to other studied sites. In contrast, at Tayrona and Macuira, we found a low rainfall and high aridity index, solar radiation and wind speed (**Table S1**). Conversely, other sites were not located under extreme climatic conditions, but were on infertile soils or embedded in heavily transformed landscapes. This was the case of Tuparro, which exhibited the highest annual precipitation, but occurred on sandy soils with low water retention, particularly during the dry season (Medina & Silva 1990; Dezzeo *et al.* 2008). Soil water deficit is critical in Tuparro, to the point that ~30% of its species are deciduous (**Table S2**). In addition, land-cover transformations may promote water deficit as they potentially increase exposure to solar radiation or wind (**Table S1**). This is the case in Taminango, Plato and La Paz, which are all surrounded by heavily transformed landscapes, and show low diversity, basal area and short forest canopy.

Dry forest plant community attributes are explained by climate severity and land-cover transformation

We hypothesized that TDF diversity and structure would be strongly affected by environmental harshness, as the result of climatic severity, low soils fertility and land-cover transformation. Our results partially support this hypothesis, as ^{0}D, ^{1}D, BA and H were lower, and BI was higher, with increasing land-cover transformation and climate severity (**Figure 2**), but the soil fertility gradient did not affect any plant community attribute.

Two mechanisms may explain these patterns. First, there is strong evidence across the Neotropics that decades of land-uses have resulted in small, isolated TDF fragments exposed to drier conditions (Lambin *et al.* 2003; Rodríguez *et al.* 2008; Portillo-Quintero & Sánchez-Azofeifa 2010). Isolation increases dispersal limitation and is likely to be accompanied by local extinctions, thereby reducing diversity (Pimm 1998; Hooke *et al.* 2012; Gerstner *et al.* 2014). In TDF plots, ^{0}D, ^{1}D and BA were strongly negatively related to land-cover transformation, suggesting that agriculture, cattle ranching and the historic exploitation of hardwood species, or large trees, for fuelwood may have affected these forest attributes (Blackie *et al.* 2014; González-M. *et al.* 2018). Second, land-cover transformation may strengthen climate severity due to edge effects, which change microclimatic conditions within forest patches (Pimm 1998). Edge effects result in a harsher environmental condition, which may affect the overall forest structure (Givnish 1995; Schindler *et al.* 2012). Indeed, the structural metrics of our plots such as canopy height and branching index, were strongly affected by climate severity, suggesting that land-cover transformation could exacerbate climatic effects. This effect was probably related to the fact that both diversity and structure are sensitive to intensified droughts, or to other environmental forces such as increased wind speed inside forests, which may produce mechanical damages (Givnish 1995; Metzger 2000; Tao *et al.* 2016).

The fact that forest canopies got shorter as climate severity increased may have three different explanations. First, short stature is advantageous because less tension is needed to move water to the canopy leaves, and the probability of cavitation is reduced in scenarios of water deficit (*hydraulic limitation hypothesis*; Ryan & Yoder 1997; Tao *et al.* 2016). Second, short trees show lower autotrophic wood respiration, thereby decreasing their allocation of photosynthates to wood, and their resistance to water flow (*the respiration hypothesis* (Sperry 1995; Ryan & Yoder 1997). Third, taller trees develop larger bending moments at their base, which may trigger damage under strong wind conditions and resulting in a counter-selected strategy (*aerodynamic drag hypothesis*, Schindler *et al.* 2012). Data on functional wood and hydraulic traits would improve our mechanistic understanding of why plant stature decreases with climate severity.

The increase in stem branching with climatic severity could also be explained as a adaptation to drought. For instance, a reduction in soil water supply coupled with high transpiration demand can cause xylem conduits to become air-filled (cavitate), stopping the flow of water and desiccating plant tissues (McDowell 2011). Inter-vessel pits connect xylem conduits, and air bubbles can travel between neighboring conduits spreading embolism if tension is high. Under this scenario, higher branching may reduce death rates as bubbles would spread across a single stem, given that each branched stem has a group of independent conduits (*compartmentalized transport system hypothesis*, Zimmermann 1983). In addition, in case of mechanical damages due to external forces such as wind, multi-stemmed individuals would reduce gravitational displacement or sway of trunks (Wilson 1995; van Bloem *et al.* 2006), and would also reduce near-surface wind speed via different architectural designs (Schindler *et al.* 2012).

Soil fertility did not have significant effects on forest diversity and structure at the community level (**Table S3**). Previous studies, however, have shown contrasting results. In particular, soil nutrient availability has been positively (Perroni-Ventura *et al.* 2006), negatively (Huston 1980; Peña-Claros *et al.* 2012) or not clearly associated (Wright 1992; Gei & Powes 2014) with species richness and biomass in Neotropical dry forests. One explanation for such inconsistencies could be related to the fact that each species or ecological functional group may have different nutrient requirements, thereby obscuring predictions at the community-level across resource gradients (Knoepp *et al.* 2000).

What drives legume and deciduous community attributes in TDF?

We hypothesized that both legumes and deciduous species, would be at an advantage under harsh conditions because they have ecological strategies to overcome stressful environments. We found support for our predictions in terms of species richness, species diversity and basal area (**Figure 3a-c**), but not for branching index nor canopy height, for which the effects of environmental gradients were similar to those observed at the community level (**Figure 3d-e, Figure 4**).

Regarding legumes, their ^{0}D and ^{1}D increased with solar radiation and total precipitation during the three driest months (**Figure 4a**), although plant community as a whole showed the opposite response with respect to solar radiation in the PCA (**Figure 2a**). An explanation for this pattern could be that legumes store nitrogen in leaves during rainy periods in TDF, when maximum symbiotic nitrogen fixation happens (Serraj *et al.* 1999). This stored nitrogen may then be allocated to the photosynthetic machinery of leaves, which, under high solar radiation, increases intercellular CO_2 consumption while maintaining low stomatal conductance and low rates of water loss under drought (Adams *et al.* 2016). Thus, assuming that most legumes are nitrogen-fixers in TDF (Hedin *et al.* 2009; Sprent 2009), this mechanism could alleviate their water consumption while maintaining their photosynthetic activity under drought conditions.

We also found that phosphorus availability had positive effects on legume BA (**Figure 4a**), which could be related to the fact that net primary productivity in TDF is limited by phosphorus (Gei & Powes 2014). Thus, we may expect an increase in plant biomass as a result of an increase in phosphorus availability. But, why is this relationship important only for legumes? One likely explanation is that N-fixers invest a fraction of their nitrogen in phosphatase enzymes production, which increases plant phosphate capture (Houlton *et al.* 2008). Thus, an increase in soil P could favour a higher basal area in legumes than in other species due to their high phosphatase activity. Although these mechanisms are plausible explanations for the patterns observed, we call for caution in their generalization as not all legumes are effective nitrogen-fixers (Sprent 2009).

On the other hand, land-cover transformation and low precipitation during the dry seasons had negative effects on ^{0}D, ^{1}D and BA of deciduous species (**Figure 4b**), suggesting that they cannot avoid the environmental harshness caused by the effects of land-cover transformation and climate severity in TDF. These findings contrast with our predictions and previous studies showing that deciduous species can break dispersal limitation barriers and maintain their diversity as land-cover transformation increases, due to their small-seed size, which facilitates long-distance dispersal and germination under high light availability (Seiwa & Kikuzawa 1991, 1996). However, deciduous species are characterized by having acquisitive resource-use strategies for high performance during the short window of rainfall pulses (Méndez-Alonzo *et al.* 2012), increasing the risks of hydraulic failure or mechanical damage under harsh environmental conditions (Markesteijn *et al.* 2011a).

Conclusions

We suggest that tropical dry forests cannot be solely defined based on rainfall seasonality. Climate and land-cover transformation are critical factors for a better understanding in how diversity and structure of TDF respond to environmental harshness. While, land-cover transformation negatively impacts species richness, diversity and basal area of TDF plant communities, probably due to forest isolation, canopy height and branching index are stronly driven climate severity. Legumes appear to be the less affected by environmental harshness. Being N-fixers and investors of phosphatase enzymes, they alleviate photosynthetic demands under harsh conditions. But, unexpectedly, deciduous species cannot avoid increases in drougth conditions and secondary vegetation, being nevativelly affected. Thus, given the highly threatened state of TDF, it is urgent to acquire a mechanistic understanding in how species respond to harsh environments, and in such provide tools for comprehensive management of this ecosystem.

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Supporting information

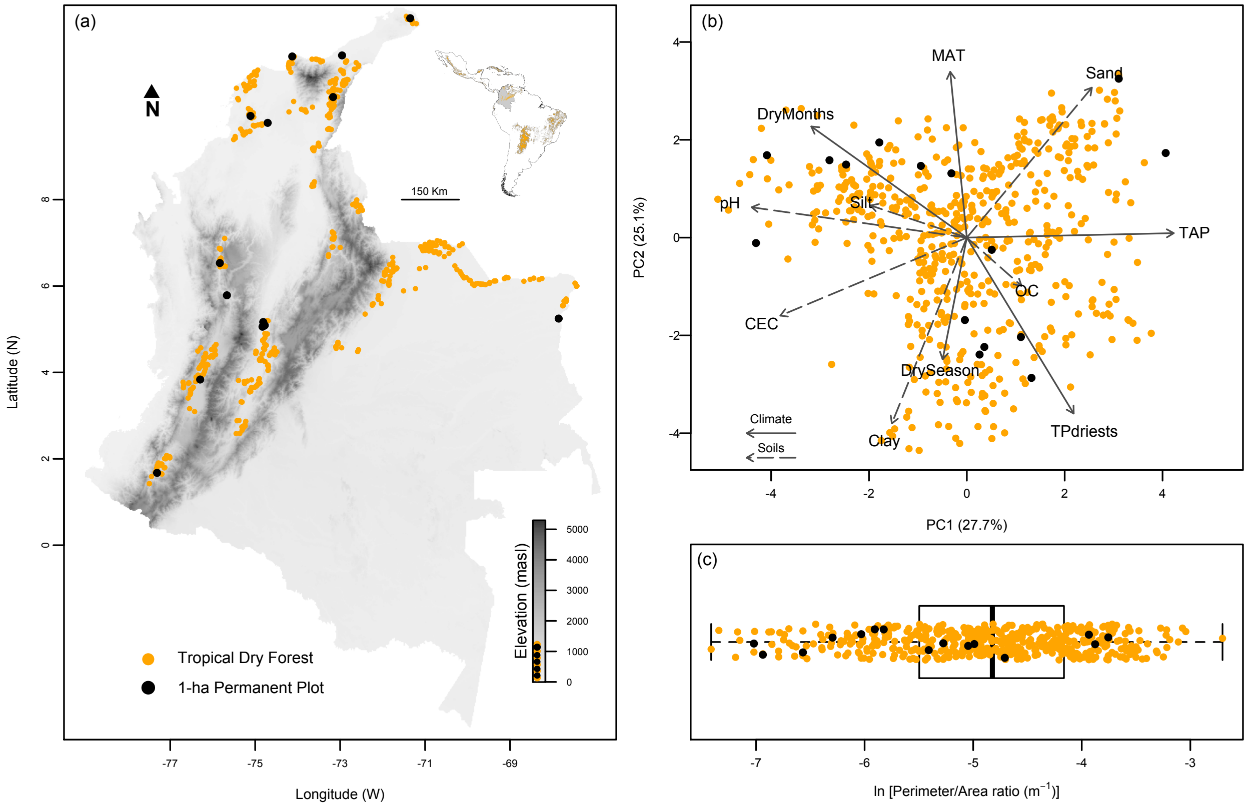


Figure S1. Distribution of 494 dry forest sampling sites in Colombia (a) orange dots (González-M. *et al.* 2018) and distribution of 15 1-ha permanent plots (black dots). (b) climatic and soils environmental conditions, and (c) forest shape. The first two axes of the PCA explained 52.8% of the variance in climate and soils conditions of TDF in Colombia. Climate included total annual of precipitation (TAP, mm), mean annual temperature (MAT, ºC), total precipitation during the three driest months (TPdriest [<100 mm·month^{-1}], mm), number of dry periods during the year with three continuous driest months (DrySeason [<100 mm·month^{-1}], no.) and total number of dry months in a year (DryMonths, no.). Climatic data from: ~90 m climatic spatial resolution model, *http://institucional.ideam.gov.co/jsp/1769*). Soils included textural fractions (Sand, Clay, Silt; %), organic carbon (OC, %), acidity (pH), and cation exchange capacity (CEC; cmol^{+}·kg^{-1}). Soils data from: (Hengl *et al.* 2014). Forests shape (m^{-1}) quantified the relation between perimeter (m) and area (m^{2}) of the forest fragment that surrounded each sampling site and 1-ha permanent plots (Moser *et al.* 2002).

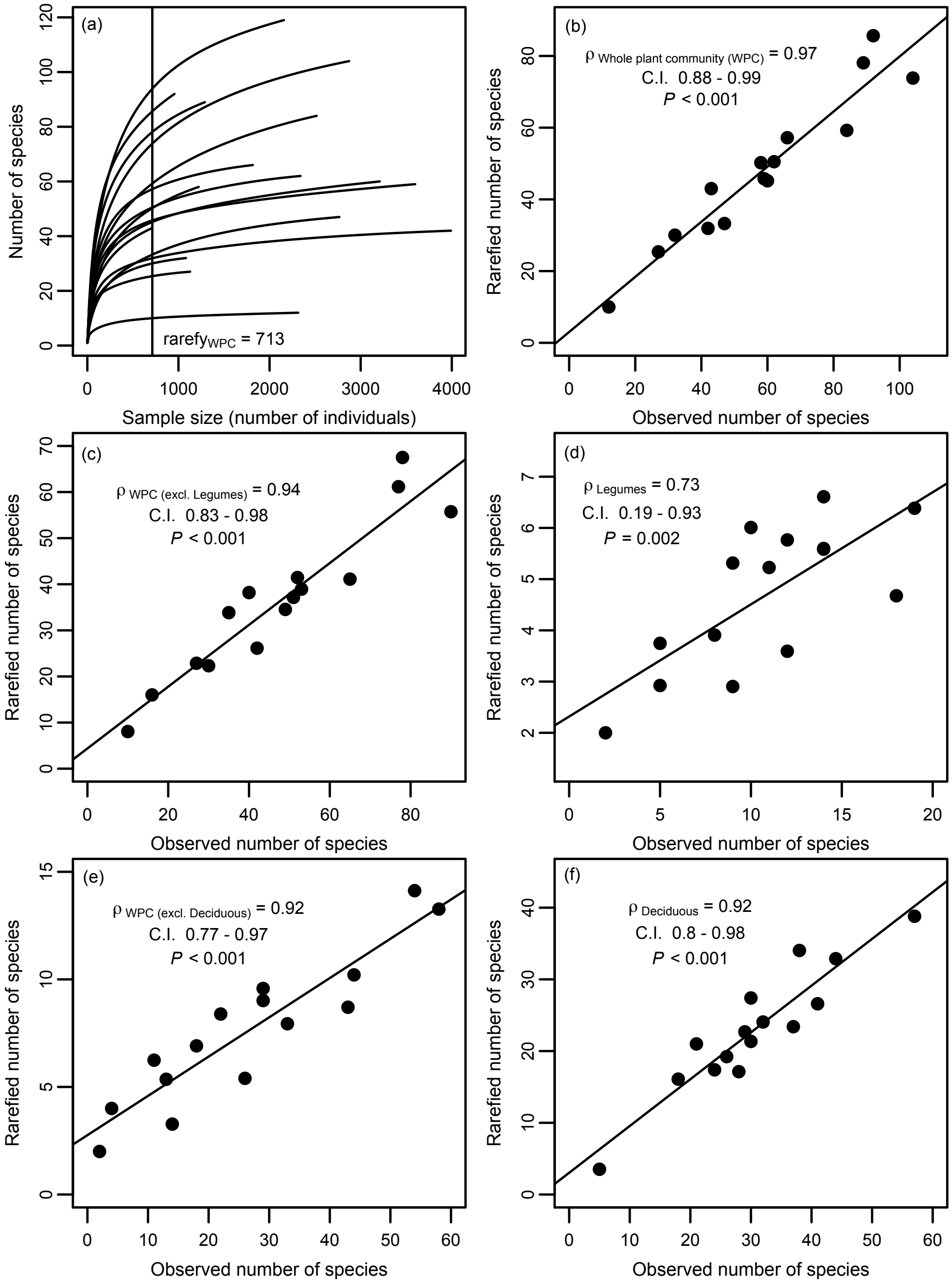


Figure S2. Pairwise Pearson (ρ) correlations between rarefy number of species and observe number of species across the plots and for each groups of plants (a-b) rarefy curve and pairwise correlation for the whole plant community, (c) pairwise correlation for the whole plant community excluding legumes, (d) pairwise correlation for legumes, (e) pairwise correlation for the whole plant community excluding deciduous species, and (f) pairwise correlation for deciduous species.

Table S1. Study sites and environmental conditions (climate, soils and land-cover) of 15 1-ha permanent plots in TDF of Colombia. Climatic variables: total annual rainy days (ARD, no.), aridity index (Aridity, [PET/TAP]), isothermality (Isoth, %), solar radiation (SRad, MJ·m^{-1} x 100), total annual precipitation (TAP, mm), potential evapotranspiration (PET, mm), total precipitation during the three driest months (TPdriest [<100 mm·month^{-1}], mm), water vapor pressure (WVP, kPa) and wind speed (Wind, m·s^{-1}). Soil variables: acidity (pH), available phosphorus (P, mg·kg^{-1}), cation exchange capacity (CEC, cmol^{+}·kg^{-1}), extractable bases (Ca [Calcium], Mg [Magnesium], K [Potassium], Na [Sodium], cmol^{+}·kg^{-1}), organic carbon (OC, %) and textural fractions (Sand, Clay, Silt, %). Land-cover metrics: forest cover area (Forest, Ha [effective area, %]), forest shape index (Shape [Perimeter/Area], m^{-1}), secondary vegetation area (SecVeg, Ha [effective area, %]), area used by humans (ULC, Ha [effective area, %]), types of human land cover uses (ULC.type, no.) and topographic roughness (Roughness, %).

Permanent Plots (1-ha)	**Caribbean**						**Magdalena river valley**				**Cauca river valley**			**Orinoquía**	**Patia**
	Macuira	**Matitas**	**Colorados**	**La Paz**	**Plato**	**Tayrona**	**Cardo.P**	**Cardo.L**	**Jabirú**	**Tambor**	**Cotové**	**Támesis**	**Vinculo**	**Tuparro**	**Tamin.**
Latitude (ºN)	12,20	11.34	9.94	10.37	9.78	11.31	5.08	5.09	5.06	5.17	6.53	5.79	3.84	5.25	1.67
Longitude (ºW)	-71.35	-72.95	-75.11	-73.17	-74.71	-74.13	-74.80	-74.77	-74.83	-74.81	-75.83	-75.67	-76.29	-67.86	-77.31
Altitude (m.a.s.l.)	113	32	301	161	21	15	260	322	302	385	509	731	1025	95	591
Climate variables															
ARD	33	56	96	109	66	95	116	113	116	126	146	180	144	152	138
Aridity	3.42	1.80	1.01	1.74	1.73	2.03	1.29	1.19	1.31	0.88	1.43	0.64	0.97	0.77	1.94
Isoth	75.43	77.62	90.25	86.46	89.59	81.35	85.97	85.91	86.03	85.83	87.29	90.27	93.30	78.07	91.78
SRad	185.69	188.21	192.08	187.33	187.83	196.79	173.36	172.78	173.28	172.87	178.49	176.36	169.95	164.10	159.45
TAP	517.0	1087.4	1528.4	1172.0	1198.3	899.4	1505.9	1541.2	1528.2	1912.5	1193.8	2183.0	1192.4	2697.2	721.4
PET	1768.6	1959.7	1546.0	2043.0	2075.5	1827.7	1946.8	1835.6	2009.1	1689.1	1712.8	1397.9	1161.3	2067.0	1400.8
TPdriest	32.1	31.9	139.3	67.9	98.7	33.4	227.8	222.5	236.8	272.7	112.7	285.8	168.5	177.1	52.4
WVP	2.67	2.77	2.75	2.69	2.92	2.87	2.63	2.53	2.65	2.50	2.55	2.38	2.14	2.80	2.36
Wind	4.84	4.17	2.35	2.74	2.20	4.45	0.93	0.92	0.93	0.90	0.83	0.79	0.87	1.37	0.96
Soils variables															
pH	6.12	6.16	7.37	5.26	6.89	7.38	6.79	6.87	6.46	6.98	6.54	6.32	6.22	4.39	7.23
P	18.14	6.07	12.17	6.07	147.09	222.59	143.24	19.36	17.08	11.33	20.08	4.09	4.70	3.32	27.89
CEC	10.01	13.65	30.89	12.14	19.43	16.43	15.61	20.08	17.01	14.73	25.71	29.54	26.68	6.69	33.10
Extractable Bases															
Ca	5.29	6.90	34.83	6.67	16.62	16.05	13.81	22.89	13.13	10.29	22.13	17.57	21.33	0.06	29.14
Mg	2.19	4.88	4.64	1.88	5.45	2.69	3.24	4.11	3.90	2.30	9.95	6.70	17.74	0.06	7.91
K	0.55	0.47	0.65	0.52	0.91	0.82	0.73	0.36	0.70	0.61	0.38	0.73	0.87	0.21	1.08
Na	0.22	0.47	0.09	0.15	0.18	0.07	0.03	0.10	0.08	0.04	0.15	0.09	0.14	0.16	0.16
OC	1.00	1.89	3.22	3.34	1.95	3.58	2.54	2.41	2.80	2.36	2.26	4.48	3.64	1.79	2.61
Textural fractions															
Sand	57.41	63.89	34.21	42.91	67.72	62.58	61.86	56.45	48.86	72.25	37.42	50.72	60.69	64.27	34.47
Clay	21.54	20.41	31.58	31.02	16.51	19.25	24.96	24.54	21.16	16.33	35.34	22.16	24.36	16.39	29.66
Silt	21.07	15.71	34.21	26.07	15.76	18.18	13.18	19.03	29.98	11.42	27.24	27.12	14.95	19.34	35.9
Land-cover metrics															
Forest	407.6 [82.4]	456.8 (91.3)	395 (79)	31.2 (6.2)	6.4 (1.3)	411.8 (100)	153.9 (30.8)	303 (60.6)	145.4 (29.1)	329.6 (65.9)	55.1 (11.5)	13.3 (2.7)	23.4 (4.7)	176.3 (51.9)	56.8 (11.5)
Shape	0.004	0.005	0.004	0.034	0.019	0.003	0.028	0.011	0.023	0.017	0.038	0.014	0.025	0.013	0.029
SecVeg	87.1 (17.6)	39.3 (7.8)	57.2 (11.4)	334.5 (66.9)	262.3 (53.8)	0 (0)	38.5 (7.7)	52.3 (10.5)	129.9 (26)	104 (20.8)	103.4 (21.6)	34.1 (6.8)	180.2 (36)	29.5 (8.7)	401.1 (81.5)
ULC	0 (0)	1.3 (0.3)	48.1 (9.6)	134.6 (26.9)	218.9 (44.9)	0 (0)	254.9 (50.9)	125.5 (25.1)	209 (41.8)	56.7 (11.3)	309.7 (64.7)	452.9 (90.5)	296.7 (59.3)	19.2 (5.6)	30.8 (6.3)

Permanent Plots (1-ha)	Caribbean						Magdalena river valley				Cauca river valley			Orinoquía	Patia
	Macuira	Matitas	Colorados	La Paz	Plato	Tayrona	Cardo.P	Cardo.L	Jabirú	Tambor	Cotové	Támesis	Vinculo	Tuparro	Tamin.
ULC.type	0	2	5	10	6	0	14	3	17	17	34	11	22	2	23
Rougdness	10.4	2.1	14.7	3.7	5.1	19.1	7.3	12.7	9.0	22.5	9.7	8.4	8.0	7.4	20.8

Table S2. Community attributes of 15 1-ha permanent plots in tropical dry forests of Colombia. Plant diversity: Species richness (^0D, number of species) and exponential of Shannon entropy (^1D, number of species). Forest structure: Basal area (BA, $m^2 \cdot ha^{-1}$), branching index (BI, %) and forest canopy height (H, m^2).

Permanent Plots (1-ha)	Caribbean						Magdalena river valley				Cauca river valley			Orinoquía	Patia
	Macuira	Matitas	Colorados	La Paz	Plato	Tayrona	Cardo.P	Cardo.L	Jabirú	Tambor	Cotové	Támesis	Vinculo	Tuparro	Tamin.
Whole plant community															
^0D	42	42	101	27	58	66	62	58	47	92	32	84	60	89	12
^1D	15	11	29	14	15	29	25	21	6	49	10	22	15	41	3
BA	18.00	13.11	20.07	8.73	6.45	24.70	19.67	25.61	20.70	30.34	19.84	22.56	19.17	17.34	4.82
BI	30.23	30.42	7.00	50.46	49.00	35.68	14.16	10.95	6.88	12.12	20.09	4.11	19.84	11.46	21.22
H	11.63	5.62	13.17	6.80	7.42	10.18	10.98	14.11	12.72	15.52	14.23	18.13	9.85	12.08	6.20
Legume species only															
^0D	7	12	14	11	18	14	9	10	5	14	5	19	9	12	2
^1D	4	3	9	6	5	7	6	7	2	7	3	9	3	7	1
BA	3.83	3.00	2.55	5.91	4.90	7.33	5.29	6.38	1.97	2.19	4.11	3.21	4.14	1.72	0.05
BI	26.34	46.56	12.00	53.12	42.58	34.34	17.75	9.92	6.90	8.39	7.81	2.46	19.43	9.21	47.83
H	11.23	5.60	15.49	6.69	7.49	9.90	12.41	13.95	14.74	15.25	16.04	19.66	10.90	11.94	7.40
Deciduous species only															
^0D	29	28	53	24	37	44	31	28	21	38	18	41	26	30	5
^1D	10	6	25	11	8	21	15	14	12	24	11	14	10	19	1
BA	16.29	9.71	8.63	8.14	5.10	17.13	9.00	11.95	3.38	5.74	8.69	9.37	8.76	5.27	4.64
BI	27.96	30.62	8.03	49.60	43.57	27.11	22.03	12.70	17.29	8.56	19.55	2.28	29.07	9.79	19.20
H	11.68	5.66	15.03	6.85	7.49	10.35	11.45	14.77	14.32	16.35	14.30	17.61	9.95	12.72	6.21

Table S3. Best models obtained from a series of multiple regression analysis for each plant community attributes (predicted variables) of the whole plant community (WPC), and climatic, soils and land-cover transformation variables (predictors) in 15 1-ha of Colombian dry forests. Squared R (R^2, significant in bold letters), Corrected Akaike's Information Criterion (AICc), variance inflation factor (VIF, is selected as lowest values, is rejected if values are higher than 5), normal distribution of residuals (Shapiro-Wilk test, is rejected if $P < 0.05$), Homoscedasticity (Breusch-Pagan test, is rejected $P < 0.05$), Moran's I Autocorrelation Index (Moran's I, is rejected if $P < 0.05$). Significant effects of β-coefficients in models are in bold letters.

Dimension	Predictor	VIF	Species richness (^0D)		Species diversity (^1D)		Basal area (BA)		Branching index (BI)		Canopy height (H)	
			β-coef.	*P*	β-coef.	*P*	β-coef.	*P*	β-coef.	*P*	β-coef.	*P*
Climate	TPdriests	1.29										
	PET	1.09										
	SRad	1.37										
	PC1 (56.6%)	1.50	**-8.31**	**0.005**	**-3.45**	**0.022**	**-2.04**	**0.021**	**6.27**	**< 0.001**	**-1.19**	**0.012**
Soil	Clay	1.12										
	pH	1.40										
	Na	1.12										
	P	1.36										
	PC1 (48.8%)	1.25										
	PC2 (19.7%)	1.22										

Dimension	Predictor	VIF	Species richness (^{0}D)		Species diversity (^{1}D)		Basal area (BA)		Branching index (BI)		Canopy height (H)	
			β-coef.	*P*	β-coef.	*P*	β-coef.	*P*	β-coef.	*P*	β-coef.	*P*
Land-cover	SecVeg	1.00										
	UCL	1.15										
	Roughness	1.15										
	PC1 (56.5%)	1.47	**-11.43**	**0.002**	**-5.3**	**0.007**	**-2.72**	**0.021**	**4.52**	**< 0.001**	-0.86	0.108
	PC2 (21.6%)	1.21										
Model	R^2		**0.60**		**0.50**		**0.46**		**0.71**		**0.42**	
	AICc		137.41		119.47		103.33		115.69		84.04	
	VIF		2.49		1.98		1.84		3.44		1.72	
	Shapiro Wilk (P)		0.95	(0.531)	0.95	(0.553)	0.98	(0.969)	0.95	(0.583)	0.97	(0.882)
	Breusch Pagan (P)		0.13	(0.937)	1.49	(0.476)	0.83	(0.660)	5.64	(0.060)	1.96	(0.376)
	Moran's I (P)		0.02	(0.384)	-0.21	(0.191)	0.04	(0.289)	-0.08	(0.922)	-0.01	(0.593)

Table S4. Best models obtained from a series of multiple regression analysis for each plant community attributes (predicted variables) of legumes species, and climatic, soils and land-cover transformation variables (predictors) in 15 1-ha of Colombian dry forests. Squared R (R^2, significant in bold letters), Corrected Akaike's Information Criterion (AICc), variance inflation factor (VIF, is selected as lowest values, is rejected if values are higher than 5), normal distribution of residuals (Shapiro-Wilk test, is rejected if $P < 0.05$), Homoscedasticity (Breusch-Pagan test, is rejected $P < 0.05$), Moran's I Autocorrelation Index (Moran's I, is rejected if $P < 0.05$). Significant effects of β-coefficients in models are in bold letters.

Dimension	Predictor	VIF	Species richness (^{0}D)		Species diversity (^{1}D)		Basal area (BA)		Branching index (BI)		Canopy height (H)	
			β-coef.	*P*	β-coef.	*P*	β-coef.	*P*	β-coef.	*P*	β-coef.	*P*
Climate	TPdriests	1.29	**2.67**	**0.035**	**1.72**	**0.011**			**-13.80**	**<0.001**		
	PET	1.09										
	SRad	1.37	**3.52**	**0.008**	**1.54**	**0.019**						
	PC1 (56.6%)	1.50									**-1.01**	**0.021**
Soil	Clay	1.12										
	pH	1.40										
	Na	1.12										
	P	1.36					**1.12**	**0.027**				
	PC1 (48.8%)	1.25										
	PC2 (19.7%)	1.22										
Land-cover	SecVeg	1.00										
	UCL	1.15										
	Roughness	1.15										
	PC1 (56.5%)	1.47										
	PC2 (21.6%)	1.21										
Model	R^2		**0.48**		**0.48**		**0.32**		**0.63**		**0.35**	
	AICc		90.43		70.18		64.12		120.64		85.01	
	VIF		1.91		1.93		1.48		2.68		1.53	
	Shapiro Wilk test (P)		0.95	(0.599)	0.97	(0.920)	0.96	(0.61)	0.99	(0.998)	0.93	(0.311)
	Breusch Pagan test (P)		1.82	(0.402)	1.79	(0.408)	0.80	(0.37)	3.43	(0.064)	0.09	(0.765)
	Moran's I (P)		-0.03	(0.669)	-0.14	(0.546)	-0.13	(0.563)	-0.15	(0.487)	-0.06	(0.913)

Table S5. Best models obtained from a series of multiple regression analysis for each plant community attributes (predicted variables) of deciduos species, and climatic, soils and land-cover transformation variables (predictors) in 15 1-ha of Colombian dry forests. Squared R (R^2, significant in bold letters), Corrected

Akaike's Information Criterion (AICc), variance inflation factor (VIF, is selected as lowest values, is rejected if values are higher than 5), normal distribution of residuals (Shapiro-Wilk test, is rejected if $P < 0.05$), Homoscedasticity (Breusch-Pagan test, is rejected $P < 0.05$), Moran's I Autocorrelation Index (Moran's I, is rejected if $P < 0.05$). Significant effects of β-coefficients in models are in bold letters.

Dimension	**Predictor**	**VIF**	**Species richness (^{0}D)**		**Species diversity (^{1}D)**		**Basal area (BA)**		**Branching index (BI)**		**Canopy height (H)**	
			β-coef.	*P*	β-coef.	*P*	β-coef.	*P*	β-coef.	*P*	β-coef.	*P*
Climate	TPdriests	1.29					**-2.41**	**0.011**	**-8.51**	**0.010**		
	PET	1.09										
	SRad	1.37										
	PC1 (56.6%)	1.50			**-1.64**	**0.045**					**-1.28**	**0.009**
Soil	Clay	1.12										
	pH	1.40										
	Na	1.12										
	P	1.36										
	PC1 (48.8%)	1.25										
	PC2 (19.7%)	1.22										
Land-cover	SecVeg	1.00					**-2.71**	**0.006**				
	UCL	1.15										
	Roughness	1.15										
	PC1 (56.5%)	1.47	**-3.58**	**0.029**	**-2.78**	**0.009**					-1.01	0.071
	PC2 (21.6%)	1.21										
Model	R^2		**0.32**		**0.46**		**0.56**		**0.42**		**0.45**	
	AIC AIC_C		118.92		101.88		82.47		119.14		84.85	
	VIF		1.46		1.84		2.29		1.71		1.80	
	Shapiro Wilk (P)		0.99	(0.993)	0.96	(0.655)	0.96	(0.692)	0.93	(0.267)	0.98	(0.965)
	Breusch Pagan (P)		0.04	(0.827)	0.45	(0.801)	4.19	(0.122)	1.34	(0.247)	2.04	(0.360)
	Moran's I (P)		0.01	(0.489)	-0.11	(0.700)	-0.15	(0.442)	-0.19	(0.264)	-0.02	(0.635)

Appendix S1. Taxonomic composition and species abundance (number of stems) of 15 1-ha permanent plots in TDF of Colombia including life forms (LF), total frequency of species across the plots ($PP_{freq.}$), total number of individuals per species across plots (N_{ind}), total number of stems per species across plots (N_{stems}) and leaf phenology. In total, 31776 individuals, 40341 stems, 536 species belonging to 79 families are reported. 272 species were categorized as deciduous and 254 as evergreen. Botanical samples for all species they were deposited in the Federico Medem Herbarium (FMB, Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Colombia).

Family	Species	LF	PPf	Nind	Nstems	Leaf Phenology
Achariaceae	no. spp=3		6	721	805	
	Lindackeria paludosa	tree	1	7	7	evergreen
	Mayna grandifolia	tree	1	2	2	evergreen
	Mayna odorata	tree	5	712	796	evergreen
Achatocarpaceae	no. spp=1		4	101	245	
	Achatocarpus nigricans	treelet	4	101	245	deciduous
Amaranthaceae	no. spp=2		2	20	21	
	Iresine sp	liana	1	11	12	evergreen
	Morf sp5	forb	1	9	9	evergreen
Anacardiaceae	no. spp=6		14	842	955	
	Anacardium excelsum	tree	2	48	49	evergreen
	Astronium graveolens	tree	13	739	850	deciduous
	Mangifera indica	tree	1	1	1	evergreen
	Spondias mombin	tree	4	27	28	deciduous
	Spondias radlkoferi	tree	2	26	26	deciduous
	Tapirira guianensis	tree	1	1	1	evergreen
Annonaceae	no. spp=9		7	1376	1423	
	Annona muricata	tree	1	3	3	evergreen
	Annona rensoniana	tree	1	2	2	evergreen
	Duguetia odorata	tree	1	5	5	evergreen
	Guatteria metensis	tree	1	2	2	evergreen
	Malmea sp	tree	1	3	3	evergreen
	Oxandra espintana	tree	3	1186	1225	evergreen
	Oxandra sp	tree	1	107	114	evergreen
	Pseudomalmea sp	tree	1	26	26	evergreen
	Rollinia mucosa	tree	2	42	43	evergreen
Apocynaceae	no. spp=18		13	1408	1707	
	Asclepias sp	forb	1	14	17	evergreen
	Aspidosperma cuspa	tree	2	727	995	evergreen
	Aspidosperma polyneuron	tree	4	360	366	evergreen
	Aspidosperma sp	tree	1	1	2	evergreen
	Aspidosperma sp1	tree	1	1	1	evergreen
	Forsteronia affinis	liana	1	19	19	deciduous
	Forsteronia sp1	liana	2	12	13	deciduous
	Forsteronia spicata	liana	1	4	4	deciduous
	Himatanthus articulatus	tree	1	15	15	deciduous
	Mandevilla sp	liana	1	87	88	deciduous
	Marsdenia sp	liana	1	8	8	deciduous
	Morf sp41	liana	1	1	1	evergreen
	Plumeria pudica	tree	1	41	45	evergreen
	Prestonia sp	liana	2	49	55	deciduous
	Prestonia trifida	liana	1	9	9	evergreen
	Tabernaemontana grandiflora	tree	2	33	40	evergreen
	Tabernaemontana markgrafiana	treelet	1	1	1	evergreen
	Tabernaemontana sp1	tree	1	26	28	deciduous
Araliaceae	no. spp=2		2	18	18	
	Aralia excelsa	treelet	1	1	1	evergreen
	Dendropanax arboreus	tree	1	17	17	evergreen
Arecaceae	no. spp=7		5	267	322	

Family	Species	LF	PPf	Nind	Nstems	Leaf Phenology
Achariaceae	no. spp=3		6	721	805	
	Aiphanes horrida	palm	1	9	9	evergreen
	Attalea butyracea	palm	1	1	1	evergreen
	Attalea microcarpa	palm	1	55	55	evergreen
	Bactris bidentula	palm	1	145	196	evergreen
	Bactris pilosa	palm	2	32	34	evergreen
	Bactris sp	palm	1	1	3	evergreen
	Syagrus sancona	palm	1	24	24	evergreen
Aristolochiaceae	no. spp=2		3	38	38	
	Aristolochia maxima	liana	1	18	18	deciduous
	Aristolochia sp	liana	2	20	20	deciduous
Asteraceae	no. spp=4		3	29	33	
	Chromolaena perglabra	shrub	2	8	10	evergreen
	Lycoseris mexicana	liana	1	18	20	deciduous
	Verbesina sp	tree	1	2	2	evergreen
	Vernonanthura patens	forb	1	1	1	evergreen
Basellaceae	no. spp=1		1	34	34	
	Anredera floribunda	liana	1	34	34	deciduous
Bignoniaceae	no. spp=23		14	2289	2800	
	Adenocalymma aspericarpum	liana	2	11	11	deciduous
	Amphilophium paniculatum	liana	1	102	108	deciduous
	Anemopaegma sp	liana	1	3	3	deciduous
	Arrabidaea sp	liana	1	17	18	deciduous
	Bignonia aequinoctialis	liana	2	18	18	deciduous
	Bignonia pterocalyx	liana	1	54	61	deciduous
	Bignonia sp	liana	1	18	18	deciduous
	Callichlamys latifolia	liana	1	2	2	deciduous
	Fridericia mollissima	liana	1	30	44	deciduous
	Fridericia pubescens	liana	1	27	29	deciduous
	Fridericia sp	liana	1	12	13	deciduous
	Handroanthus barbatus	tree	1	5	5	deciduous
	Handroanthus billbergii	tree	3	376	582	deciduous
	Handroanthus chrysanthus	tree	5	1511	1777	deciduous
	Handroanthus ochraceus	tree	2	2	2	deciduous
	Jacaranda caucana	tree	1	3	3	deciduous
	Morf sp13	tree	1	2	2	deciduous
	Morf sp36	liana	1	1	2	deciduous
	Phryganocydia sp1	liana	1	1	1	deciduous
	Roseodendron chryseum	tree	2	3	5	deciduous
	Tabebuia rosea	tree	4	33	36	deciduous
	Tanaecium tetragonolobum	liana	1	56	58	deciduous
	Xylophragma seemannianum	liana	1	2	2	deciduous
Bixaceae	no. spp=1		1	1	1	
	Cochlospermum orinocense	tree	1	1	1	deciduous
Boraginaceae	no. spp=8		9	421	696	
	Bourreria cumanensis	tree	2	306	556	evergreen
	Cordia alba	tree	2	14	29	evergreen
	Cordia alliodora	tree	2	4	7	deciduous
	Cordia bicolor	tree	1	1	1	deciduous
	Cordia gerascanthus	tree	3	43	50	deciduous
	Cordia macuirensis	tree	1	1	1	deciduous
	Cordia panamensis	tree	1	49	49	deciduous
	Cordia sp	tree	2	3	3	deciduous
Burseraceae	no. spp=5		11	269	283	
	Bursera graveolens	tree	1	13	14	deciduous
	Bursera simaruba	tree	10	149	152	deciduous
	Bursera tomentosa	tree	1	9	14	deciduous

Family	Species	LF	PPf	Nind	Nstems	Leaf Phenology
Achariaceae	no. spp=3		6	721	805	
	Protium guianense	tree	1	88	90	evergreen
	Protium tenuifolium	tree	1	10	13	evergreen
Cactaceae	no. spp=7		9	926	1126	
	Acanthocereus tetragonus	cactus	4	15	23	N/A
	Cereus hexagonus	cactus	3	166	258	N/A
	Opuntia sp	cactus	1	24	42	N/A
	Pereskia guamacho	treelet	5	28	53	deciduous
	Pilosocereus lanuginosus	cactus	2	430	468	N/A
	Stenocereus griseus	cactus	1	6	24	N/A
	Stenocereus humilis	cactus	1	257	258	N/A
Cannabaceae	no. spp=1		8	242	335	
	Celtis iguanaea	liana	8	242	335	deciduous
Capparaceae	no. spp=18		12	1255	2030	
	Belencita nemorosa	shrub	1	105	190	deciduous
	Capparidastrum frondosum	tree	1	3	3	evergreen
	Capparidastrum pachaca	tree	2	87	156	evergreen
	Capparidastrum sola	tree	1	2	3	evergreen
	Capparidastrum tenuisiliquum	tree	1	210	276	evergreen
	Capparis sp2	tree	1	3	3	evergreen
	Crateva tapia	treelet	3	5	13	deciduous
	Cynophalla amplissima	tree	2	31	38	evergreen
	Cynophalla flexuosa	tree	5	102	190	evergreen
	Cynophalla hastata	tree	1	7	8	evergreen
	Cynophalla linearis	tree	2	142	188	evergreen
	Cynophalla polyantha	tree	2	15	19	evergreen
	Cynophalla verrucosa	tree	3	363	626	evergreen
	Morf sp38	liana	1	15	23	evergreen
	Morisonia americana	tree	3	32	76	evergreen
	Morisonia sp2	treelet	1	2	3	evergreen
	Quadrella indica	tree	4	43	71	evergreen
	Quadrella odoratissima	tree	5	88	144	evergreen
Caricaceae	no. spp=1		1	2	2	
	Vasconcellea sp	treelet	1	2	2	evergreen
Celastraceae	no. spp=5		8	595	655	
	Cheiloclinium sp	liana	1	2	2	deciduous
	Hippocratea sp	liana	2	13	14	deciduous
	Hippocratea volubilis	liana	4	270	300	deciduous
	Prionostemma aspera	liana	1	288	289	deciduous
	Schaefferia frutescens	shrub	1	22	50	evergreen
Chrysobalanaceae	no. spp=7		2	66	69	
	Hirtella racemosa	tree	1	9	12	evergreen
	Licania apetala	tree	1	3	3	evergreen
	Licania micrantha	tree	1	44	44	evergreen
	Licania parvifructa	tree	1	2	2	evergreen
	Licania sp	tree	1	1	1	evergreen
	Licania sp1	tree	1	1	1	evergreen
	Licania sp2	tree	1	6	6	evergreen
Clusiaceae	no. spp=2		2	2	2	
	Clusia umbellata	tree	1	1	1	evergreen
	Garcinia intermedia	tree	1	1	1	evergreen
Combretaceae	no. spp=5		6	180	202	
	Combretum aculeatum	liana	1	93	104	deciduous
	Combretum fruticosum	liana	3	74	80	deciduous
	Combretum sp	liana	1	8	13	deciduous
	Terminalia amazonia	tree	1	4	4	evergreen
	Terminalia oblonga	tree	1	1	1	evergreen

Family	Species	LF	PPf	Nind	Nstems	Leaf Phenology
Achariaceae	no. spp=3		6	721	805	
Connaraceae	no. spp=1		1	8	8	
	Connarus ruber	treelet	1	8	8	evergreen
Convolvulaceae	no. spp=2		2	4	5	
	Ipomoea carnea	liana	1	3	3	deciduous
	Ipomoea sp	liana	1	1	2	deciduous
Ebenaceae	no. spp=2		4	6	6	
	Diospyros sp1	tree	1	1	1	evergreen
	Diospyros sp2	tree	3	5	5	evergreen
Erythroxylaceae	no. spp=4		5	30	32	
	Erythroxylum hondense	shrub	2	5	7	evergreen
	Erythroxylum jaimei	treelet	1	1	1	evergreen
	Erythroxylum macrophyllum	tree	1	15	15	evergreen
	Erythroxylum ulei	treelet	1	9	9	evergreen
Euphorbiaceae	no. spp=16		10	1813	2123	
	Acalypha diversifolia	shrub	2	137	139	evergreen
	Acalypha macrostachya	tree	1	3	3	evergreen
	Acalypha sp	shrub	1	1	1	evergreen
	Croton gossypiifolius	tree	1	11	12	deciduous
	Croton niveus	tree	1	140	188	evergreen
	Croton punctatus	shrub	1	1	1	deciduous
	Croton rhamnifolius	treelet	1	1426	1676	deciduous
	Croton schiedeanus	treelet	1	26	32	evergreen
	Croton sp	tree	1	1	1	deciduous
	Euphorbia cotinifolia	treelet	1	7	7	evergreen
	Hura crepitans	tree	2	17	17	deciduous
	Jatropha gossypiifolia	shrub	1	3	4	evergreen
	Mabea trianae	tree	1	3	4	evergreen
	Manihot carthaginensis	tree	2	3	3	deciduous
	Omphalea diandra	liana	1	6	6	evergreen
	Sapium glandulosum	tree	2	28	29	deciduous
Fabaceae	no. spp=102		15	4696	7081	
	Abarema sp	tree	1	10	14	deciduous
	Albizia carbonaria	tree	2	13	13	deciduous
	Albizia niopoides	tree	1	14	22	deciduous
	Albizia sp	treelet	1	2	2	deciduous
	Albizia sp2	tree	1	4	4	deciduous
	Bauhinia glabra	liana	3	13	16	deciduous
	Bauhinia hymenaeifolia	liana	2	50	57	deciduous
	Bauhinia petiolata	treelet	2	320	349	evergreen
	Bentamantha sp	tree	1	2	2	deciduous
	Brownea ariza	tree	1	1	1	evergreen
	Caesalpinia cassioides	shrub	1	11	21	deciduous
	Caesalpinia coriaria	treelet	3	166	279	deciduous
	Caesalpinia ebano	tree	2	5	8	deciduous
	Caesalpinia punctata	tree	1	3	3	deciduous
	Caesalpinia sp	tree	1	4	12	deciduous
	Calliandra magdalenae	tree	4	189	286	deciduous
	Cassia sp	tree	1	1	1	deciduous
	Chloroleucon mangense	tree	1	1	1	deciduous
	Clathrotropis macrocarpa	tree	1	25	25	deciduous
	Coursetia ferruginea	tree	4	98	136	deciduous
	Dioclea sp1	liana	1	4	5	deciduous
	Enterolobium cyclocarpum	tree	2	6	6	deciduous
	Enterolobium schomburgkii	tree	1	4	4	deciduous
	Enterolobium sp1	tree	2	5	12	deciduous
	Erythrina poeppigiana	tree	1	1	1	deciduous

Family	Species	LF	PPf	Nind	Nstems	Leaf Phenology
Achariaceae	no. spp=3		6	721	805	
	Erythrina velutina	tree	1	19	28	deciduous
	Gliricidia sepium	tree	1	6	23	deciduous
	Haematoxylum brasiletto	treelet	2	185	557	deciduous
	Humboldtiella arborea	tree	1	36	46	deciduous
	Inga gracilifolia	tree	1	48	52	evergreen
	Inga laurina	tree	1	1	1	evergreen
	Inga marginata	tree	1	2	3	evergreen
	Inga oerstediana	tree	1	4	4	evergreen
	Inga sp	tree	1	13	15	evergreen
	Inga sp1	tree	1	15	18	evergreen
	Inga sp4	tree	1	5	5	evergreen
	Inga sp6	tree	1	50	55	evergreen
	Inga vera	tree	1	3	3	evergreen
	Leucaena leucocephala	tree	1	38	39	deciduous
	Lonchocarpus macrophyllus	tree	1	1	1	deciduous
	Lonchocarpus pictus	tree	1	53	73	deciduous
	Lonchocarpus sanctae-marthae	tree	1	3	4	deciduous
	Lonchocarpus violaceus	tree	1	1	1	deciduous
	Luetzelburgia andina	tree	1	16	16	deciduous
	Machaerium arboreum	tree	3	747	1295	deciduous
	Machaerium biovulatum	tree	3	29	34	deciduous
	Machaerium capote	tree	6	312	345	evergreen
	Machaerium kegelii	liana	1	32	33	deciduous
	Machaerium microphyllum	liana	2	10	12	deciduous
	Machaerium mutisii	liana	1	1	1	deciduous
	Machaerium sp	liana	1	23	23	deciduous
	Machaerium sp1	tree	4	99	129	deciduous
	Machaerium sp2	liana	1	7	7	deciduous
	Machaerium sp3	liana	1	22	35	deciduous
	Machaerium sp6	tree	1	69	72	deciduous
	Morf sp7	liana	1	7	7	deciduous
	Muellera broadwayi	tree	1	7	10	deciduous
	Myrospermum frutescens	tree	4	52	73	deciduous
	Peltogyne purpurea	tree	1	3	3	deciduous
	Peltogyne sp	tree	1	41	41	deciduous
	Phanera guianensis	liana	1	22	25	deciduous
	Piptadenia flava	treelet	1	47	139	deciduous
	Piptadenia sp	tree	1	3	3	deciduous
	Pithecellobium dulce	tree	2	8	11	deciduous
	Pithecellobium lanceolatum	tree	2	163	272	deciduous
	Pithecellobium roseum	tree	1	7	16	deciduous
	Pithecellobium sp2	treelet	1	7	14	deciduous
	Platymiscium pinnatum	tree	6	85	90	deciduous
	Prosopis juliflora	treelet	4	176	322	deciduous
	Pseudosamanea guachapele	tree	2	6	7	deciduous
	Pterocarpus officinalis	tree	1	1	1	deciduous
	Pterocarpus rohrii	tree	5	308	401	deciduous
	Pterocarpus sp	tree	1	53	53	deciduous
	Pterocarpus sp4	tree	1	4	4	deciduous
	Pueraria phaseoloides	liana	1	4	4	deciduous
	Senegalia gaumeri	tree	1	1	1	deciduous
	Senegalia hayesii	shrub	1	20	27	deciduous
	Senegalia macbridei	liana	1	11	16	deciduous
	Senegalia sp	tree	1	15	18	deciduous
	Senegalia sp1	tree	3	42	54	deciduous
	Senegalia sp2	treelet	1	6	12	deciduous

Family	Species	LF	PPf	Nind	Nstems	Leaf Phenology
Achariaceae	no. spp=3		6	721	805	
	Senegalia tamarindifolia	tree	2	89	161	deciduous
	Senna atomaria	tree	2	10	13	deciduous
	Senna bacillaris	shrub	1	2	2	deciduous
	Senna pallida	treelet	1	1	1	deciduous
	Senna sp1	tree	1	7	7	deciduous
	Senna sp2	treelet	1	9	17	deciduous
	Senna spectabilis	tree	1	1	1	deciduous
	Styphnolobium sporadicum	tree	2	35	35	deciduous
	Swartzia robiniifolia	treelet	1	78	78	deciduous
	Swartzia simplex	tree	2	3	3	deciduous
	Swartzia sp1	treelet	1	7	7	deciduous
	Swartzia trianae	tree	3	150	185	deciduous
	Tachigali guianensis	tree	1	5	5	deciduous
	Vachellia collinsii	tree	1	1	4	deciduous
	Vachellia farnesiana	treelet	3	14	19	deciduous
	Vachellia macracantha	treelet	1	344	561	deciduous
	Vachellia sp	tree	2	11	45	deciduous
	Vachellia tortuosa	treelet	1	23	98	deciduous
	Vigna caracalla	liana	1	1	1	deciduous
	Zygia inaequalis	tree	1	2	2	evergreen
	Zygia sp	tree	1	2	2	evergreen
Hernandiaceae	no. spp=1		2	14	14	
	Gyrocarpus americanus	tree	2	14	14	deciduous
Lacistemataceae	no. spp=1		1	17	22	
	Lacistema aggregatum	tree	1	17	22	evergreen
Lamiaceae	no. spp=4		3	8	10	
	Aegiphila sp	shrub	1	1	1	evergreen
	Callicarpa acuminata	treelet	1	4	6	evergreen
	Vitex orinocensis	tree	1	1	1	deciduous
	Vitex sp	treelet	1	2	2	deciduous
Lauraceae	no. spp=7		7	370	407	
	Aiouea sp	tree	1	2	2	evergreen
	Endlicheria sp	tree	1	1	1	evergreen
	Licaria applanata	tree	1	108	114	evergreen
	Licaria guianensis	tree	1	1	1	evergreen
	Nectandra sp	tree	1	31	37	evergreen
	Ocotea schomburgkiana	tree	1	24	24	evergreen
	Ocotea veraguensis	tree	3	203	228	evergreen
Lecythidaceae	no. spp=8		6	422	466	
	Eschweilera sp	tree	1	8	8	evergreen
	Eschweilera tenuifolia	tree	1	94	104	evergreen
	Gustavia augusta	tree	1	67	77	evergreen
	Gustavia hexapetala	tree	1	16	17	evergreen
	Gustavia sp	tree	1	199	218	evergreen
	Gustavia superba	tree	2	20	22	evergreen
	Lecythis chartacea	tree	1	7	7	evergreen
	Lecythis minor	tree	2	11	13	evergreen
Loganiaceae	no. spp=1		1	5	5	
	Strychnos panamensis	liana	1	5	5	evergreen
Malpighiaceae	no. spp=11		12	452	746	
	Bronwenia cornifolia	liana	1	9	9	deciduous
	Bunchosia armeniaca	tree	1	6	16	evergreen
	Bunchosia diphylla	shrub	1	1	1	evergreen
	Bunchosia odorata	shrub	1	10	11	evergreen
	Bunchosia pseudonitida	tree	1	61	73	evergreen
	Bunchosia sp	shrub	1	1	2	evergreen

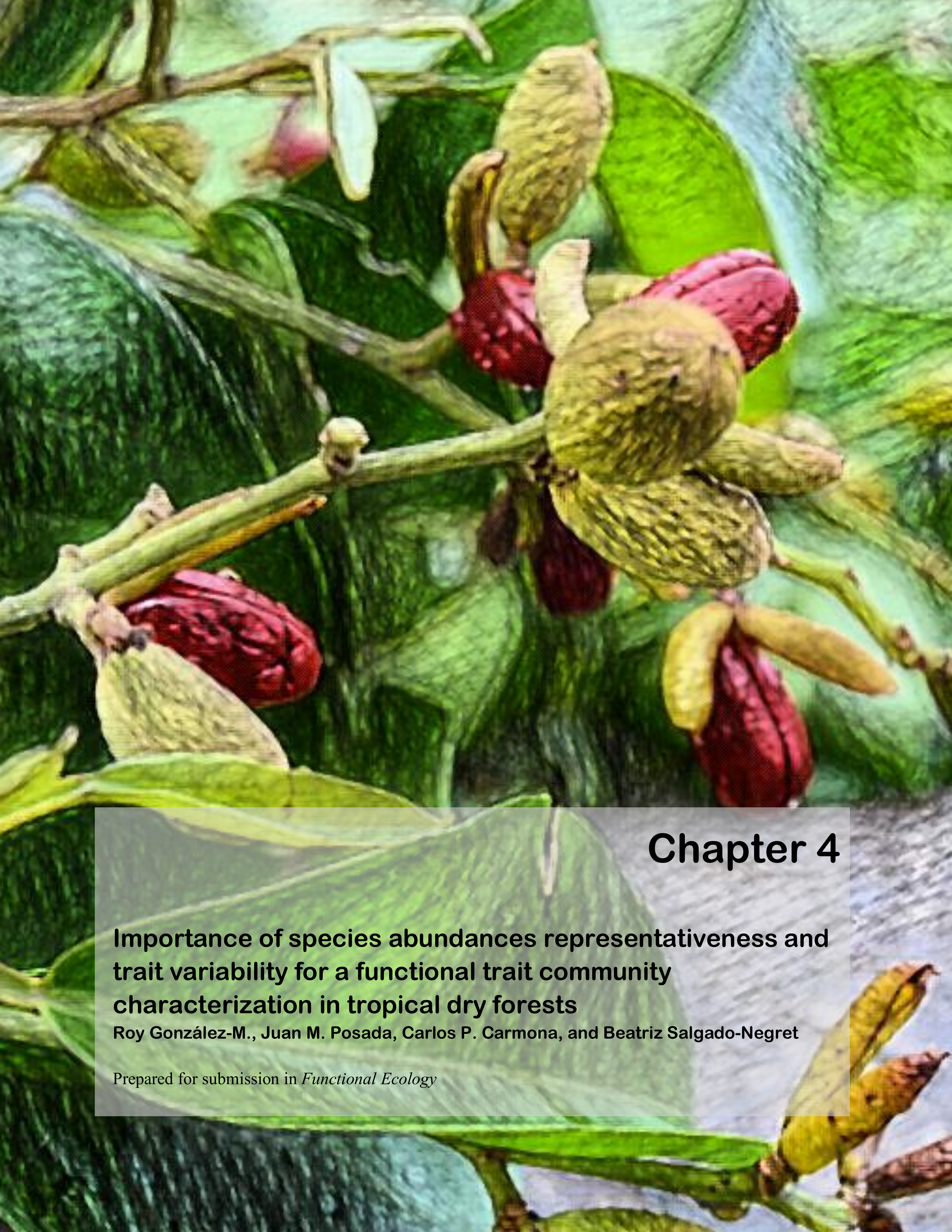
Family	Species	LF	PPf	Nind	Nstems	Leaf Phenology
Achariaceae	no. spp=3		6	721	805	
	Bunchosia sp2	liana	1	64	96	evergreen
	Hiraea reclinata	shrub	1	21	28	deciduous
	Hiraea sp	liana	3	41	77	deciduous
	Malpighia glabra	tree	8	234	429	evergreen
	Morf sp9	liana	1	4	4	evergreen
Malvaceae	no. spp=11		12	212	261	
	Apeiba tibourbou	tree	2	13	13	deciduous
	Cavanillesia platanifolia	tree	1	2	2	deciduous
	Ceiba pentandra	tree	3	10	10	deciduous
	Guazuma ulmifolia	tree	6	66	111	deciduous
	Hampea thespesioides	tree	1	9	10	evergreen
	Herrania laciniifolia	shrub	1	8	8	evergreen
	Luehea seemannii	tree	2	13	13	deciduous
	Ochroma pyramidale	tree	1	12	12	evergreen
	Pachira nukakica	tree	1	16	18	deciduous
	Pachira quinata	tree	3	25	26	deciduous
	Pseudobombax septenatum	tree	6	38	38	deciduous
Melastomataceae	no. spp=2		1	5	10	
	Graffenrieda rotundifolia	shrub	1	3	8	deciduous
	Miconia splendens	shrub	1	2	2	evergreen
Meliaceae	no. spp=11		8	3289	3440	
	Cedrela odorata	tree	1	4	4	evergreen
	Guarea glabra	tree	1	37	49	evergreen
	Guarea guidonia	tree	1	2	2	evergreen
	Guarea sp1	tree	1	2	3	evergreen
	Trichilia acuminata	tree	1	446	474	evergreen
	Trichilia carinata	tree	3	480	493	evergreen
	Trichilia elegans	tree	4	191	205	evergreen
	Trichilia hirta	tree	1	3	3	evergreen
	Trichilia martiana	tree	1	2	2	evergreen
	Trichilia oligofoliolata	tree	3	1889	1953	evergreen
	Trichilia pallida	tree	6	233	252	evergreen
Menispermaceae	no. spp=1		1	2	2	
	Morf sp8	liana	1	2	2	evergreen
Moraceae	no. spp=19		8	1216	1241	
	Brosimum alicastrum	tree	7	224	226	evergreen
	Brosimum guianense	tree	1	9	9	evergreen
	Brosimum sp	tree	1	88	92	evergreen
	Castilla elastica	tree	1	1	1	evergreen
	Clarisia biflora	tree	1	520	522	evergreen
	Clarisia racemosa	tree	1	1	1	evergreen
	Ficus americana	tree	1	13	18	evergreen
	Ficus obtusifolia	tree	1	2	2	evergreen
	Ficus sp	tree	2	3	3	evergreen
	Ficus trigona	tree	1	1	1	evergreen
	Ficus zarzalensis	tree	1	1	1	evergreen
	Helianthostylis sprucei	tree	1	30	31	evergreen
	Maclura tinctoria	tree	3	9	9	deciduous
	Pseudolmedia sp1	tree	1	19	20	evergreen
	Sorocea muriculata	tree	1	4	4	evergreen
	Sorocea sp	tree	1	10	10	evergreen
	Sorocea sprucei	tree	1	88	91	evergreen
	Sorocea trophoides	tree	1	159	166	evergreen
	Trophis racemosa	tree	1	34	34	evergreen
Myrtaceae	no. spp=20		11	1673	2076	
	Calyptranthes multiflora	tree	1	2	2	deciduous

Family	Species	LF	PPf	Nind	Nstems	Leaf Phenology
Achariaceae	no. spp=3		6	721	805	
	Calyptranthes speciosa	tree	1	1	1	deciduous
	Eugenia biflora	treelet	1	3	3	evergreen
	Eugenia florida	tree	2	8	8	evergreen
	Eugenia monticola	tree	1	141	151	evergreen
	Eugenia procera	tree	5	1348	1710	evergreen
	Eugenia sp	tree	1	1	1	evergreen
	Eugenia sp1	tree	1	1	1	evergreen
	Eugenia sp3	tree	2	22	27	evergreen
	Eugenia sp4	tree	1	13	14	evergreen
	Eugenia sp5	treelet	1	7	9	evergreen
	Eugenia venezuelensis	shrub	1	1	1	evergreen
	Morf sp1	shrub	1	1	1	evergreen
	Morf sp2	tree	1	14	16	evergreen
	Morf sp3	tree	1	1	1	evergreen
	Myrcia fallax	tree	1	22	22	deciduous
	Myrcia sp1	tree	1	8	8	deciduous
	Myrcia sp2	tree	1	3	3	deciduous
	Pseudanamomis umbellulifera	shrub	1	75	96	deciduous
	Psidium guineense	treelet	1	1	1	evergreen
Nyctaginaceae	no. spp=10		14	625	880	
	Guapira costaricana	tree	1	67	69	deciduous
	Guapira sp	tree	3	8	17	deciduous
	Guapira sp1	treelet	1	275	327	deciduous
	Guapira uberrima	tree	1	57	104	deciduous
	Neea ignicola	tree	1	2	2	deciduous
	Neea macrophylla	tree	1	14	17	deciduous
	Neea sp	tree	3	6	18	deciduous
	Neea sp1	tree	2	15	22	deciduous
	Neea sp2	tree	1	58	106	deciduous
	Pisonia aculeata	liana	9	123	198	deciduous
Ochnaceae	no. spp=1		1	4	4	
	Ouratea sp	tree	1	4	4	evergreen
Olacaceae	no. spp=1		1	23	23	
	Heisteria acuminata	tree	1	23	23	evergreen
Opiliaceae	no. spp=1		1	2	2	
	Agonandra brasiliensis	tree	1	2	2	deciduous
Petiveriaceae	no. spp=1		3	56	60	
	Seguieria americana	liana	3	56	60	evergreen
Phyllanthaceae	no. spp=3		4	113	136	
	Amanoa guianensis	tree	1	1	1	evergreen
	Margaritaria nobilis	treelet	1	1	1	deciduous
	Phyllanthus botryanthus	shrub	2	111	134	deciduous
Phytolaccaceae	no. spp=1		1	20	20	
	Trichostigma octandrum	liana	1	20	20	indet.
Piperaceae	no. spp=2		2	88	130	
	Piper amalago	shrub	1	1	1	evergreen
	Piper sp6	treelet	1	87	129	evergreen
Polygalaceae	no. spp=2		1	22	29	
	Securidaca sp	tree	1	18	25	deciduous
	Securidaca sp2	shrub	1	4	4	deciduous
Polygonaceae	no. spp=15		11	506	940	
	Coccoloba acuminata	treelet	1	1	6	evergreen
	Coccoloba caracasana	tree	1	15	30	evergreen
	Coccoloba densifrons	tree	1	1	4	evergreen
	Coccoloba obovata	tree	1	1	1	evergreen
	Coccoloba obtusifolia	tree	2	26	153	evergreen

Family	Species	LF	PPf	Nind	Nstems	Leaf Phenology
Achariaceae	no. spp=3		6	721	805	
	Coccoloba padiformis	tree	1	2	4	evergreen
	Coccoloba sp	tree	1	31	44	evergreen
	Coccoloba sp1	tree	5	128	215	evergreen
	Coccoloba sp2	tree	1	21	60	evergreen
	Coccoloba sp4	shrub	1	15	145	evergreen
	Ruprechtia ramiflora	tree	1	2	4	deciduous
	Ruprechtia sp1	tree	4	24	28	deciduous
	Triplaris americana	tree	1	2	3	deciduous
	Triplaris melaenodendron	tree	4	236	242	deciduous
	Triplaris sp	tree	1	1	1	deciduous
Primulaceae	no. spp=7		6	104	186	
	Ardisia foetida	shrub	1	4	5	deciduous
	Bonellia frutescens	shrub	1	14	20	deciduous
	Jacquinia armillaris	shrub	1	70	112	deciduous
	Jacquinia frutescens	shrub	1	10	43	deciduous
	Morf sp10	shrub	1	2	2	evergreen
	Myrsine sp1	treelet	1	1	1	evergreen
	Stylogyne turbacensis	tree	1	3	3	evergreen
Rhamnaceae	no. spp=3		4	62	101	
	Sageretia elegans	liana	1	6	6	deciduous
	Ziziphus saeri	treelet	1	3	10	deciduous
	Ziziphus strychnifolia	tree	2	53	85	deciduous
Rubiaceae	no. spp=37		14	816	1006	
	Alibertia sp	tree	1	1	1	evergreen
	Alseis blackiana	tree	1	27	33	evergreen
	Amaioua corymbosa	tree	1	5	5	evergreen
	Bertiera angustifolia	tree	1	1	1	deciduous
	Calycophyllum candidissimum	tree	1	9	13	deciduous
	Chiococca alba	shrub	1	34	36	deciduous
	Chiococca sp	shrub	2	8	14	deciduous
	Chomelia spinosa	treelet	1	8	9	deciduous
	Coffea arabica	shrub	1	2	2	evergreen
	Cordiera myrciifolia	treelet	1	2	2	evergreen
	Coussarea paniculata	treelet	1	3	3	evergreen
	Coutarea hexandra	treelet	2	7	10	deciduous
	Coutarea sp	treelet	1	5	11	deciduous
	Genipa americana	tree	2	87	88	evergreen
	Guettarda comata	tree	1	6	20	deciduous
	Guettarda roupalifolia	tree	1	42	47	deciduous
	Ixora sp	tree	1	3	4	evergreen
	Ladenbergia sp	tree	1	4	4	evergreen
	Morf sp11	liana	1	4	4	evergreen
	Morf sp17	tree	1	1	1	evergreen
	Morf sp47	tree	1	1	1	evergreen
	Morf sp49	liana	1	2	2	deciduous
	Palicourea rigida	shrub	1	9	10	evergreen
	Palicourea sp	shrub	1	1	1	evergreen
	Pittoniotis trichantha	tree	1	20	26	evergreen
	Psychotria micrantha	shrub	1	100	104	evergreen
	Psychotria sp	shrub	1	1	1	evergreen
	Randia aculeata	tree	4	11	31	deciduous
	Randia armata	tree	5	115	143	deciduous
	Randia dioica	tree	2	17	22	deciduous
	Randia obcordata	treelet	3	88	135	deciduous
	Randia pubistyla	treelet	1	3	12	deciduous
	Rudgea crassiloba	tree	1	17	18	evergreen

Family	**Species**	**LF**	**PPf**	**Nind**	**Nstems**	**Leaf Phenology**
Achariaceae	no. spp=3		6	721	805	
	Rudgea sp	shrub	1	13	14	evergreen
	Simira cordifolia	tree	4	157	173	evergreen
	Simira klugei	tree	1	1	4	deciduous
	Simira rubescens	tree	1	1	1	deciduous
Rutaceae	no. spp=13		10	830	1199	
	Amyris pinnata	tree	5	241	268	evergreen
	Esenbeckia alata	tree	2	13	14	deciduous
	Esenbeckia pentaphylla	tree	1	66	67	deciduous
	Galipea sp	tree	1	3	3	evergreen
	Spathelia sp	tree	1	3	3	deciduous
	Zanthoxylum fagara	treelet	3	111	276	deciduous
	Zanthoxylum lenticulare	tree	2	64	67	deciduous
	Zanthoxylum rhoifolium	tree	4	25	47	deciduous
	Zanthoxylum rigidum	tree	2	2	2	evergreen
	Zanthoxylum schreberi	tree	5	193	330	deciduous
	Zanthoxylum sp2	tree	2	22	25	deciduous
	Zanthoxylum sp4	tree	1	48	50	deciduous
	Zanthoxylum verrucosum	tree	1	39	47	deciduous
Salicaceae	no. spp=12		13	635	775	
	Banara ibaguensis	shrub	1	1	1	deciduous
	Casearia aculeata	tree	4	324	372	evergreen
	Casearia corymbosa	tree	4	17	21	evergreen
	Casearia praecox	tree	7	55	62	evergreen
	Casearia sp1	tree	2	5	6	evergreen
	Casearia sp2	tree	1	1	1	evergreen
	Casearia sp6	tree	1	3	3	evergreen
	Casearia sylvestris	tree	4	138	186	evergreen
	Casearia tremula	treelet	1	76	103	evergreen
	Casearia zizyphoides	treelet	1	2	3	evergreen
	Morf sp31	treelet	1	2	2	evergreen
	Xylosma intermedia	treelet	1	11	15	evergreen
Sapindaceae	no. spp=18		9	977	1173	
	Allophylus nitidulus	tree	1	1	2	deciduous
	Allophylus sp	tree	1	1	1	deciduous
	Cupania cinerea	tree	1	1	1	evergreen
	Cupania latifolia	tree	1	55	55	evergreen
	Cupania sp1	tree	1	44	52	evergreen
	Dilodendron costaricense	tree	1	11	13	deciduous
	Matayba sp	tree	1	51	60	evergreen
	Matayba sp1	tree	1	19	19	evergreen
	Melicoccus bijugatus	tree	4	507	621	evergreen
	Melicoccus oliviformis	tree	4	126	153	deciduous
	Paullinia alata	liana	1	32	32	evergreen
	Paullinia capreolata	liana	1	5	5	evergreen
	Paullinia cururu	liana	2	40	41	evergreen
	Paullinia globosa	liana	1	21	22	evergreen
	Paullinia sp	liana	1	1	1	evergreen
	Paullinia sp2	liana	1	27	60	evergreen
	Sapindus saponaria	tree	3	19	19	deciduous
	Serjania sp1	liana	1	16	16	deciduous
Sapotaceae	no. spp=11		10	443	514	
	Chrysophyllum cainito	tree	1	16	18	evergreen
	Elaeoluma sp	tree	1	1	1	evergreen
	Manilkara sp	tree	1	14	16	evergreen
	Pouteria plicata	tree	1	12	13	evergreen
	Pouteria sp1	tree	1	159	161	evergreen

Family	Species	LF	PPf	Nind	Nstems	Leaf Phenology
Achariaceae	no. spp=3		6	721	805	
	Pouteria sp3	tree	1	1	1	evergreen
	Pouteria sp4	tree	1	26	29	evergreen
	Pouteria sp7	tree	5	144	169	evergreen
	Pouteria sp8	tree	1	1	2	evergreen
	Pradosia colombiana	tree	3	51	63	deciduous
	Sideroxylon obtusifolium	treelet	1	18	41	deciduous
Siparunaceae	no. spp=1		1	21	22	
	Siparuna guianensis	tree	1	21	22	evergreen
Smilacaceae	no. spp=1		1	1	1	
	Smilax sp	liana	1	1	1	deciduous
Solanaceae	no. spp=5		2	7	9	
	Cestrum schlechtendalii	shrub	1	1	1	deciduous
	Cestrum sp1	tree	1	2	3	deciduous
	Lycianthes sp	shrub	1	1	1	evergreen
	Solanum lepidotum	shrub	1	2	3	evergreen
	Solanum sp	shrub	1	1	1	evergreen
Stemonuraceae	no. spp=1		1	13	13	
	Discophora sp	tree	1	13	13	evergreen
Thymelaeaceae	no. spp=1		1	3	3	
	Daphnopsis sp	tree	1	3	3	evergreen
Ulmaceae	no. spp=3		6	739	973	
	Ampelocera macphersonii	tree	1	448	474	evergreen
	Ampelocera sp1	tree	4	80	89	evergreen
	Phyllostylon rhamnoides	tree	1	211	410	evergreen
Urticaceae	no. spp=5		5	123	151	
	Cecropia peltata	tree	4	41	44	deciduous
	Myriocarpa stipitata	tree	1	11	15	evergreen
	Urera baccifera	shrub	1	2	2	evergreen
	Urera caracasana	tree	2	63	84	evergreen
	Urera simplex	tree	1	6	6	evergreen
Verbenaceae	no. spp=4		4	83	106	
	Citharexylum kunthianum	treelet	1	40	48	deciduous
	Lantana camara	forb	1	1	4	evergreen
	Lippia origanoides	tree	1	4	5	evergreen
	Petrea sp	tree	1	38	49	deciduous
Violaceae	no. spp=3		5	9	11	
	Leonia sp1	tree	2	2	2	evergreen
	Rinorea pubiflora	shrub	1	1	1	evergreen
	Rinorea sp1	tree	2	6	8	evergreen
Vitaceae	no. spp=2		4	19	20	
	Cissus sp	liana	1	6	6	deciduous
	Cissus verticillata	liana	3	13	14	deciduous
Vochysiaceae	no. spp=1		1	8	8	
	Vochysia vismiifolia	tree	1	8	8	evergreen
Zygophyllaceae	no. spp=1		3	18	18	
	Bulnesia arborea	tree	3	18	18	evergreen
Morf	no. fam=8, no. spp=8		6	62	71	
	Morf sp12	liana	1	4	4	deciduous
	Morf sp14	tree	1	2	2	deciduous
	Morf sp15	liana	1	1	1	indet.
	Morf sp16	liana	1	7	7	indet.
	Morf sp18	liana	1	9	9	deciduous
	Morf sp4	tree	1	33	40	evergreen
	Morf sp40	liana	1	4	6	indet.
	Morf sp6	treelet	1	2	2	deciduous



Chapter 4

Importance of species abundances representativeness and trait variability for a functional trait community characterization in tropical dry forests

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Summary

1. The community functional trait characterization in species-rich ecosystems faces sampling trade-offs on species abundances representativeness and trait variability. Overall, sampling designs for dominant species have received broad attention by using community-weighted mean (CWM) to indicate locally optimal phenotypes.

2. CWM, as a descriptor of optimal phenotypes, does not consider trait variability, failing in to explain the mechanisms behind of community trait composition. In particular, when viable co-existing strategies promote divergence, or at fine scales where ecosystems have similar filtering pulses, as is expected in Tropical Dry Forests.

3. We compared different trait sampling designs, vary the species abundance representativeness and trait variability, to evaluate differences in the level of trait community characterization and the trait-environment and trait-biomass relationships in TDF.

4. Following and abundance-weighted trait sampling design, we intensively sampled 15 functional traits in 321 species of ten 1-ha permanent plots in TDF. We sampled a least one individual per species per plot (in the case of 'rarer' species) up to 12 individuals when abundant (N=1391 tree individuals). We also monitored stem biomass growth for 19,740 trees for the sampled species, between 2013 and 2017.

5. To evaluate the abundance representativeness, we ran linear correlations between the total species abundances per community and those for the abundance-weighted trait sampling and dominant ones. To assess the main sources of trait variability, we performed a nested variance partitioning with individuals, populations, species, and communities as the ecological scales. We performed linear and linear mixed-effects models for the sampling designs to test the trait-environment and trait-biomass relationships.

6. We found that (i) sampling designs considering only dominant species did not adequately reflect the species abundance representativeness in TDF. (ii) Differences within communities explained a higher proportion of total trait variability than among them. (iii) Trait-environment and trait-biomass had consistently stronger relationships when samplings improve the species abundances representativeness and trait variability.

7. Our results indicate that abundance-weighted trait sampling designs may be useful to reconciling the trade-offs between species abundances representativeness and trait variability in samplings characterizing community trait composition, and to detect trait-environment and trait-biomass relationships in TDF.

Key-words: abundance-weighted sampling design, community weighted mean, trait variability, tropical dry forests

Introduction

Understanding the relationships between plant functional traits (traits), the environment, and forest biomass production, as well as the mechanisms behind these associations, is a recurrent goal of functional ecologists

(Bruelheide *et al.* 2018). Traits are expected to reflect the species responses to local environmental conditions, but they should also affect the plant species performance via effects on vegetative biomass growth (Poorter *et al.* 2008; Paine *et al.* 2015). Consequently, traits should determine functional species composition within communities and differences between them along environmental gradients (McGill *et al.* 2006). However, determining these relations at the community scale present critical challenges for trait sampling designs, which are associated with the species' abundance representativeness and the accuracy of the trait estimations that provide an 'adequate' description of the community trait composition (Baraloto *et al.* 2010b; Messier *et al.* 2010; Carmona *et al.* 2015; van der Plas *et al.* 2017).

Overall, studies testing the trait-environment and trait-biomass relationships usually choose sampling designs aimed to characterizing the community weighted mean trait values (CWM; Bruelheide et al., 2018; Wieczynski et al., 2019). The idea behind CWM is that being the abundances a structural parameter for species occupation within communities, it should reflect the locally optimal phenotype in response to the environment (Violle et al., 2007). Therefore, changes in CWM between communities may reflect optimal phenotypic responses to the environment (Muscarella & Uriarte 2016). Likewise, if the vegetative growth depends on species traits, the contribution of the optimal phenotype (CWM) should reflect the effects of traits on biomass within and between communities (Garnier *et al.* 2004; Finegan *et al.* 2015a). Although CWM is widely used as a descriptor of the community trait composition (Lavorel & Garnier 2002; Funk *et al.* 2017), it has some implications that need to be considered. First, it only provides information around the mean value and fails to include the variability of trait values within and among communities (Carmona *et al.* 2015). Second, the local CWM-optimal phenotype in response to the environment may be much different from the expected because there are different viable strategies co-existing as the result of alternative equally competitive functional phenotypes (Marks & Lechowicz 2006; Poorter *et al.* 2008), or because biotic interactions may change along abiotic gradients promoting community-trait divergence (Bernard-Verdier et al., 2012; Chauvet, Kunstler, Roy, & Morin, 2017; Kumordzi et al., 2019). Third, at fine spatial scale (e.g., short environmental gradients, same ecosystem abiotic conditions, small geographic extension) trait variability may be more important within communities than among them to reflect changes in community trait composition to environments with the same filtering pulses (Auger & Shipley 2013; Chalmandrier *et al.* 2017; Petruzzellis *et al.* 2017).

These implications are particularly important for tropical dry forests (TDF), a strongly drought controlled ecosystem in the Neotropics with high diversity and turnover of species (Pennington *et al.* 2009; Linares-Palomino *et al.* 2010; DRYFLOR *et al.* 2016). Under the umbrella of drought conditions, variation in species composition and functional diversity TDF are also determined by variations in temperature, winds, soil fertility, and land-cover transformation (González-M. *et al.* 2018, 2019) where tree species have different trait strategies to cope with the combinations of those environmental factors (Markesteijn *et al.* 2011a, b; Méndez-Alonzo *et al.* 2012; Pineda-García *et al.* 2015; González-M. *et al.* 2019). For instance, in response to water-constraints, resulting from arid environments (e.g., harsh climates and land-cover transformation, or high harsh climates with low soil water retention), some strategies are associated with tolerance via morphological hydraulic designs (*e.g.*, small and low density of xylem conduits, high stem wood density; Méndez-Alonzo et al., 2012), while others are associated with drought avoidance or water storage (*e.g.*, reserve water in trunks and roots, and drop the leaves, low stem wood density; Markesteijn, Poorter, Paz, et al., 2011; Sobrado, 1997). These opposing but equivalent trait strategies in response to water-constraints may produce communities highly divergent in community trait composition but similar CWM values. Thus, to adequately describe TDF community trait composition and variation of communities along environmental gradients, sampling designs are required considering community trait abundance structure but without losing the trait variability description.

There are sampling trade-offs when considering trait abundance structure and trait variability to characterize the community trait composition in highly diverse ecosystems (Baraloto *et al.* 2010b). At one extreme, an ideal functional trait characterization of a community requires measuring traits in all individuals of all species among all communities (Carmona *et al.* 2015). Although this design may reflect the entire trait community abundance structure and its variability with high accuracy, is unfeasible in most ecosystems, particularly for species-rich tropical ones where field trait samplings are time expensive (Baraloto *et al.* 2010b). To the other extreme, a more practical sampling design is to focus only on dominant species (those accounted for at least 80% of local abundance; Garnier et al., 2004) and measurement a least of one individual per species among the communities (Carmona *et al.* 2015). With the lesser effort, this design limits our understanding of the entire community trait composition and does not consider trait variability in the approach. These are why trait studies vary through the level of trait measurement and sampling effort (Baraloto *et al.* 2010b; Carmona *et al.* 2015). Thus, there is a need to find sampling designs that adequately represent the community trait composition considering both trait abundance structure and trait variability, getting close to the ideal, but generally unfeasible, sampling design when all individuals are measured.

Here, we compared the strength of different trait sampling designs to detect the trait-environment and trait-biomass production relationships in Colombian TDF, attempting to account for a high trait abundance structure representativeness and trait variability. To do that we performed an abundance-weighted trait sampling design for fieldwork, consisting in collecting traits for all tree species in all the communities in proportion to their local abundances, and simulated six alternative trait sampling designs differing in the species abundances representativeness and trait variability (**Figure 1**). We intensively sampled 15 functional traits (N=1391 trees, 321 species) in ten 1-ha permanent plots of TDF, distributed along climatic, soils, and land-cover transformation gradients (N= 29 environmental variables), and monitored tree biomass growth between 2013 and 2017 (N=19,740 trees). Our specific questions were: (i) Are the abundance-weighted trait sampling design reflect the species abundance structure of TDF tree communities? (ii) Do have sampling designs based on dominant species the abundance representativeness of TDF trees communities? (iii) What proportion of trait variation is captured among different ecological scales (i.e., individuals, populations, species and communities) in TDF? (iv) To what extent do different sampling designs detect the trait-environment and trait-biomass production relationships in TDF? Considering that Colombian TDF have a high diversity turnover but are restricted to drought regimes, where communities have species with multiple trait strategies in response to the environmental variation within this ecosystem (González-M. *et al.* 2018, 2019) we hypothesize that sampling designs incorporating the entire species abundance representativeness and a high characterization of trait variability be optimum to describe the trait composition of its communities and to detect differences of them among environmental gradients. Specifically, we expected that (i) an abundance-weighted trait sampling design be more representative of the species abundance that those designs focused in dominant species, (ii) trait variability within communities (e.g., individuals, populations and species) explained a more faction of variance than trait variability among communities, and (iii) To the extent that sampling designs choose a detailed level of trait estimation should increase the strength of trait-environment and trait-biomass production relationships.

Materials and methods

Field sampling and data sets

Field sampling was conducted in ten 1-ha permanent plots distributed across climatic, soils, and land-cover transformation gradients in TDF (González-M. et al., 2019; see details of 29 variables in **Table S1**). Between 2013 and 2015 we tagged, measured and identified all trees with a diameter at breast height ≥ 2.5 cm (DBH, measured at 1.3 m height). We measured DBH (cm) and tree height (m) and sampled wood sections of mature branches to quantify wood density (g cm^{-3}) by the volume displacement method (Pérez-Harguindeguy *et al.* 2013; Salgado-Negret *et al.* 2015). Afterward, between 2016 and 2017, we resampled all surviving trees and measured DBH increments. Overall, we measured 19,740 individuals belonging to 321 species. Based on these inventories, we estimated biomass growth rates (BGR, kg ha^{-1} yr^{-1}) of each tree as the difference in biomass between the last and the first inventory divided by the time interval of inventories (Prado-Junior *et al.* 2016; Poorter *et al.* 2017). For both inventories, biomass was calculated following the allometric formulas type I and type II suggested for TDF in Alvarez et al. (2012).

During the last inventory, we collected sun-exposed leaves for leaf traits and mature branches for wood and hydraulic traits. All species in all communities (plots) were sampled (**Figure 1a**) following an abundance-weighted trait sampling design, which consisted in measuring traits in at least one individual in species with less than two individuals per plot, all the way to 12 individuals for the most abundant species in each plot (**Figure 1a**). In total, we collected traits in 1391 individuals from 321 species. We measured nine wood traits related to water use efficiency and safety (Méndez-Alonzo, Paz, Cruz, Rosell, & Olson, 2012; Pineda-García, Paz, Meinzer, & Angeles, 2015): fiber wall thickness (FWT, μm), hydraulically weighted diameter (d_h, μm), leaf thickness (L_{th}, mm), maximum vessel area (VA_{max}, μm^2), pit area (PA, μm^2), pit diameter aperture (DA_{pit}, μm), vessel area (VA, μm^2), vessel density (VD, vessels mm^{-2}), xylem potential hydraulic conductivity (K_p, kg m^{-1} s^{-1} MPa^{-1}), anhydrous wood density (WD_0, g cm^3). We also measured six traits that are expected to be good indicators of resource-use strategies and biomass production (Poorter *et al.* 2010; Pérez-Harguindeguy *et al.* 2013; Finegan *et al.* 2015a): leaf area (LA, mm^2), leaf dry matter content (LDMC, mg g^{-1}), specific leaf area (SLA, mm^2 mg^{-1}), wood density (WD, g cm^3), and wood water content at maximal capacity (WC_{max}, kg kg^{-1}). These traits are known to be sensitive to climate, soils and land-cover transformation gradients, and they have been associated with biomass production of TDF (Prado-Junior *et al.* 2016; Poorter *et al.* 2017). For details of the sampled traits and trait descriptions see **Table S2**.

Functional trait sampling designs

We performed a sampling design in which we measured individuals of all species in proportion to the local abundance of species in each plot (**Figure 1a**; abundance-weighted trait sampling). This strategy is as close as one can get to an optimal characterisation to the "real" functional structure with a reasonable but still unfeasible for most cases, amount of trait sampling (**Figure 1b**; Baraloto et al., 2010; Carmona et al., 2015). We estimated trait values for each species within each community, simulating six different alternative designs. These simulated designs varied on the source of traits used in each community and depend on the degree to which trait variability is taken or not into account. Basically, in each site, we used either the trait values of individuals of each species from the community (**Figure 1c**; pops design), or the average trait values of all the individuals of each species across all communities (**Figure 1d**; sps design), or the average trait values of all the individuals of each species across all communities, but only considering the locally most abundant species that accounted for at least 80% of local abundance (**Figure 1e**; $sps_{80\%}$ design). Each of these strategies is placed along a trade-off between sampling effort and trait data quality, with the pops design requiring the measurement of many more individuals than the sps design, and with the sps design requiring the measurement of many more species than the sps design (see details in **Figure 1**). For each of these approaches, we also estimated the average trait value of the community using the local abundance of each species to weight their contribution towards the local mean (**Figure 1c-e**; CWM designs). CWM design did not consider trait variability within and among communities because mean traits values are weighted by the relative species abundance, providing only one trait value per community.

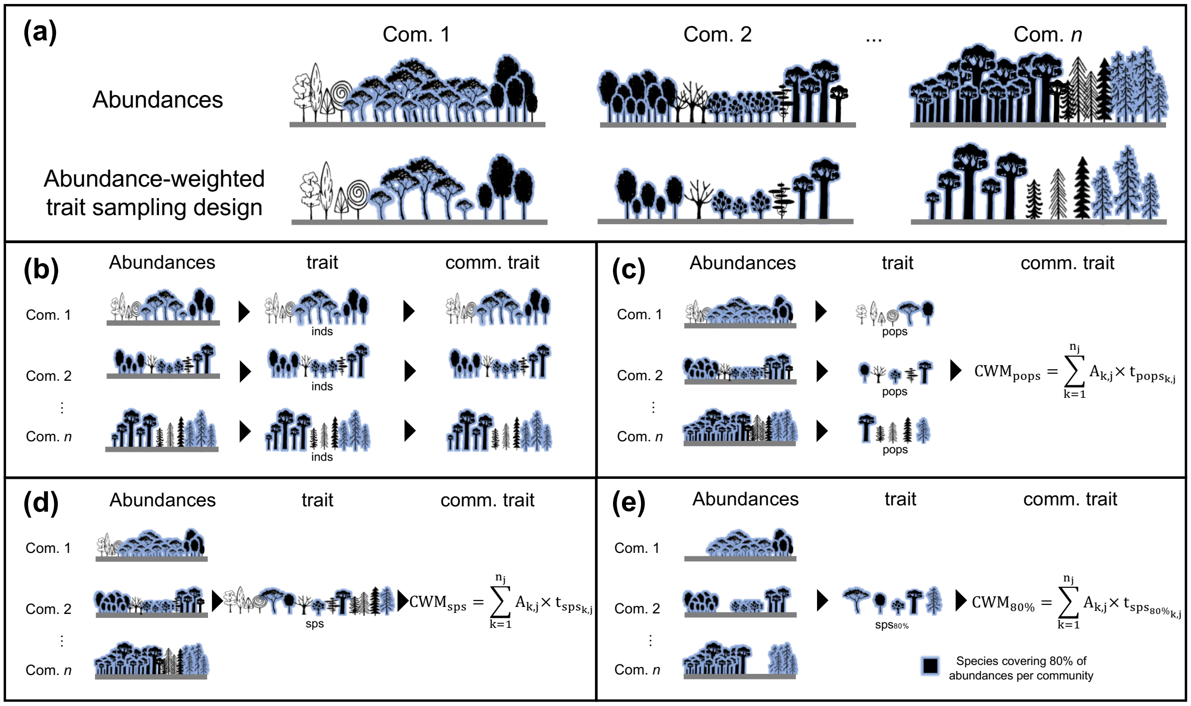

Figure 1. Illustration of the trait sampling for this study. Total species abundances on tree communities (a, upper panel) and the abundance weighted trait sampling design (b) in which all individuals of all species in proportion to the local species abundance were sampled (individuals; inds). The six simulated sampling designs varied in species abundances representativeness and trait variability. Populations (pops) is a design where we calculated average values per trait per species within a community; species (sps) corresponds to the average values per species across all communities; $sps_{80\%}$ was calculated using traits for species accounted for at least 80% of species abundance per community (1-ha permanent plot). CWM based on pops (CWM_{pops}), sps (CWM_{sps}) and $sps_{80\%}$ ($CWM_{sps80\%}$) sampling designs, where *j* is each community (*i.e.*, plot), *k* is a species collected in each community based on its abundances, *A* is the abundances of the species *k* in the community *j*, and *t* the trait value of the species *k* in the community *j* according with the trait sampling design (pops, sps and $sps_{80\%}$). Here, the inds design includes the intraspecific trait variability and the species abundance representativeness within each community. The pops design considers interspecific trait variability within and among communities, but fail to detect species abundance representation of each community. The sps design did not considers trait variability and species abundance representativeness within and among communities. The $sps_{80\%}$ design is similar to sps but only includes dominant species. CWM approaches do not consider trait variability within and among communities, but detect the abundance representativeness trait value of each community.

Statistical analyses

We ran Pearson' pairwise correlations (ρ) between the total species abundances and the sampled species abundances to evaluate if our abundance-weighted sampling design was representative of the species abundance structure of each TDF community. We log-transformed the abundances due to the differences in the magnitude of change between the plot species abundances (1-540 individuals sp^{-1} on average) and the sampled species abundances (1-8 individuals sp^{-1} on average). Significant positive ρ (P <0.001) indicates an appropriate sampling effort in each plot. Then, to evaluate if dominant species ($sps_{80\%}$) represent the species abundance structure of each community, we ran ρ again only with those species that summed at least 80% of the abundances per plot. We considered a significant $sps_{80\%}$ abundance representativeness when ρ showed significant positive associations along the complete set of species per plot (P <0.001).

Afterward, we performed a variance component analysis using individuals (inds), populations (pops), species (sps), and plots (coms) as the partitioning factors of the variance in order to account for the proportion of explained variance of the 15 functional traits across the considered scales (individuals within populations, populations within plots, species within plots and variability across plots). To do that, we used the functions *'lme'* and *'varcomp'* from R (version 3.5.3, R Core Team, 2020) following the procedures suggested in Messier et al. (2010). This analysis allowed us to how variation in a given trait changes across ecological scales (Messier *et al.* 2010; Carmona *et al.* 2015).

Finally, to evaluate the trait-environment and trait-biomass relationships, we performed linear and linear mixed-effects models based on our abundance-weighted trait sampling design and the six trait simulated sampling designs. For the inds design, we performed linear mixed-effects models with the measurement traits per individual of each species in each plot as the response variable, and the environmental variables as the predictors. Here, we used species across plots (u_{SP}) and populations within the plots (u_P) as the random effects in a nested calculation (**Table S3**). For the pops design, we performed linear mixed-effects models with the mean trait value of each species in each plot as the response variable, and the environmental variables as the predictors. For these mixed models we used species across the plots (u_{SP}) as the random effects. For the sps and $sps_{80\%}$ (mean species trait value), as well as the three CWM designs (abundance-weighted trait values), we ran simple linear models with the environmental variables as the predictors and the respective trait value as the response. The same modelling procedures were done for the trait-biomass production relationships, with BGR as the predicted variable at each organization level. For details in the modelling procedures see **Table S3**.

In both trait-environmental and trait-biomass relationships, we considered that a trait sampling design adequately detected the functional trait composition variation if β_1 was significative different from 0 (P<0.05). Models were run with all the 29 environmental variables (**Tables S4** and **S5**) using the functions *"lm"* and *"lmer"* from R. In total, we ran 3248 models for the trait-environmental relationships (464 models per design) and 105 models for the trait-biomass relationships (15 models per design). However, to facilitate the interpretation of the results we presented those based on the first axes of a principal component analysis (PCA) performed for three environmental dimensions: (i) Climate (PCA axis 1, 56.6% explained variance) in which negative values indicated low climatic severity (*i.e.*, plots with higher humidity and annual rainfall) while positive values indicated high climate severity (*i.e.*, plots with more aridity, wind speed and solar radiation). (ii) Soil nutrient limitations (PC1 48.8%) in which negative values indicated plots with low soil acidity, high cation exchange capacity and low fractions of sands, and positive values indicated plot with more infertile soils and low water retention capacity. (iii) Land-cover transformation (PC1 56.5%) where negative values were associated with plots with higher mature forest cover and positive values indicated plots with high secondary vegetation covering and high human land cover transformation. For details of the complete set of variables see **Table S1** and González-M. et al. (2019) and for the complete set of models see **Tables S4** and **S5**.

Results

All TDF tree communities accounted for significant positive correlations between the total species abundances and the sampled species abundances (ρ=0.71–0.87, *P*<0.001; **Figure 2**). Plots had between 25 and 74 total species, but the dominant species (those that summed at least 80% of the abundances per hectare) varied between 3 and 29 species per plot ($sps_{80\%}$; **Figure 2**). On each plot, dominant species represented less than 30% of the total number of species, except for one community that reached 39.2% of the species were required to reach that level of abundance (Tambor, **Figure 2**). Two communities showed significant and positive correlations by including only dominant species (Macuira and Vinculo, **Figure 2**) but with low species representativeness (26% and 20%, respectively).

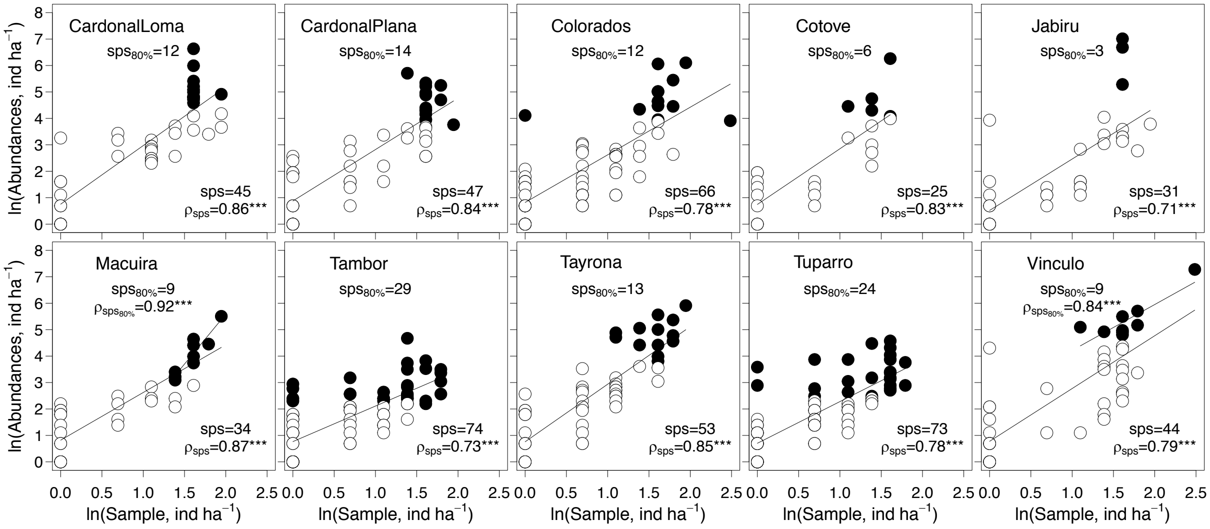

Figure 2. Pearson's pairwise correlations (ρ) between the total species abundances (Abundances, ind ha^{-1}) and the sampled species (sps) abundances (Sample, ind ha^{-1}) based on the abundance weighted trait sampling design for ten tree communities of TDF (1-ha permanent plots). Dominant species ($sps_{80\%}$; those that summed at least 80% of the abundances per hectare) are indicated in black dots. Slope lines indicate significant positive correlations (***, $P < 0.001$) for both the entire community (ρ_{sps8}) and the dominant species ($\rho_{sps80\%}$).

Differences among plots (coms) accounted for a small proportion of the variance for all the functional traits (9.6±9.2% of the explained variance; **Figure 3**), except for SLA in which they explained reached 35.7% of the total variation. Differences among populations (pops) and species (sps) accounted for the highest part of the variance in most of the traits (between 24.0 and 41.2% for each scale). Finally, differences between individuals (inds) within plots, plus the error (ε), accounted for a higher portion of the variability of the traits than differences between the plots (inds = 20.3±6.0%, **Figure 3**), with the exception of WD_0 for which the proportion of explained variance was similar (inds = coms =16.7%).

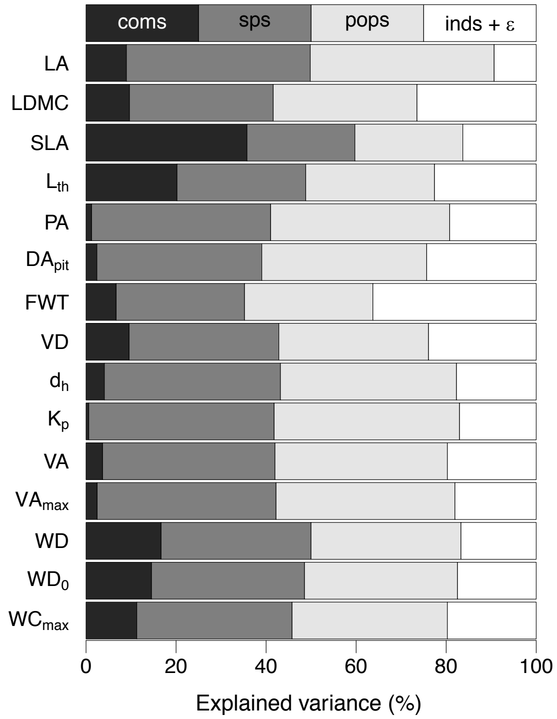

Figure 3. Partitioning of variance of the 15 studied traits across the considered ecological scales (communities or plots = coms, species within coms = sps, populations within sps within coms = pops, and individuals within pops within sps within coms). Functional traits: (a) leaf area (LA, mm^2), (b) leaf dry matter content (LDMC, mg g^{-1}), (c) specific leaf area (SLA, mm^2 mg^{-1}), (d) leaf thickness (L_{th}, mm), (e) pit area (PA, μm^2), (f) pit diameter aperture (DA_{pit}, μm), (g) fiber wall thickness (FWT, μm), (h) vessel density (VD, vessels mm^{-2}), (i) hydraulically weighted diameter (d_h, μm), (j) xylem potential hydraulic conductivity (K_s, kg m^{-1} s^{-1} MPa^{-1}), (k) vessel area (VA, μm^2), (l) maximum vessel area (VA_{max}, μm^2), (m) wood density (WD, g cm^3), (n) wood anhydrous density (WD_0, g cm^3) and (o) water content at maximum capacity (WC_{max}, kg kg^{-1}).

The proportion of significant relationships between trait-environment and trait-biomass increased with ecological scales (**Figure 4-6**). The abundance-weighted trait sampling design (inds) generated the highest number of models with significant trait-environment and trait-biomass production relationships ($P<0.05$; **Figures 4** and **6**). In total, 67.2% of the trait-environment models and 53.5% trait-biomass production models showed β_1 significantly different from 0 for inds (**Tables S4** and **S5**). Similar results were found for the three simulated trait sampling designs that considered a high trait variability (pops, sps and $sps_{80\%}$, **Figures 4** and **6**). However, the number of significant relationships was lower as designs reduced the trait values estimation (i.e., from traits estimated for inds to $sps_{80\%}$). Accordingly, pops had significant β_1 for 44.9% of the trait-environment models, while sps had 43.8% and $sps_{80\%}$ had 31.5% of models with significant β_1 (**Table S4**). Likewise, the trait-biomass production β_1 were significant 53.8% of the time for pops, 50% for sps and 46.2% for $sps_{80\%}$ (**Table S5**). The three CWM designs had a much lower number of significant relationships than the other designs for both studied relationships trait-environment (**Figure 5**) and the trait-biomass production (**Figure 6**). For the trait-environment relationships, significant β_1 were found in 1.8% models of CWM_{pops}, 3.1% for CWM_{sps} and 2.1% in $CWM_{80\%}$ (**Table S4**), while for the trait-biomass relationships significant β_1 were found in 3.8% of the models for CWM_{pops}, 23.1% for CWM_{sps} and 3.8% in $CWM_{80\%}$ (**Table S5**). CWM designs having significant β_1 did not show differential detectability with the accuracy of trait values estimation (pops, sps and sps$_{80\%}$; **Tables S4** and **S5**). Interestingly, we did not find a particular trait (e.g., hydraulic, leaf) that consistently fitted with a particular sampling design for the trait-environment relationships (**Figure 4-6**). However, the hydraulic traits showed a high number of significant models with the trait-biomass production relationships for inds, pops, sps and sps$_{80\%}$, while CWM of leaf traits were more commonly significant (**Figure 6**).

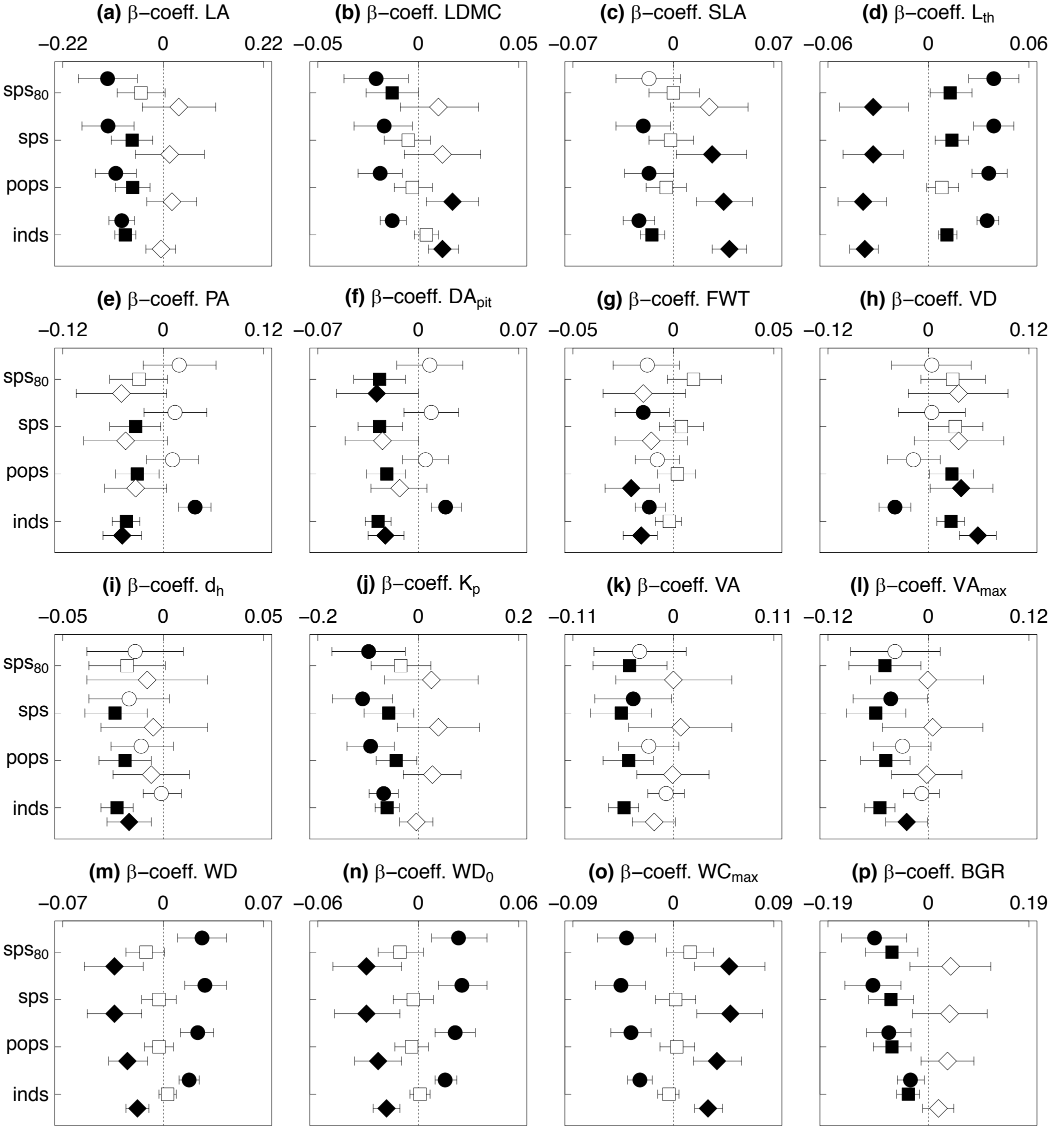

Figure 4. Fitted models and β-coefficients showing the effects of climate severity (circles), soil nutrient limitations (squares) and land-cover transformation (rhomb) on functional traits at the individuals (inds), populations (pops), species (sps) and dominant species (sps$_{80\%,}$ those that summed at least 80% of the abundances per hectare) scale. (a) Leaf area (LA, mm^2), (b) leaf dry matter content (LDMC, mg g^{-1}), (c) specific leaf area (SLA, mm^2 mg^{-1}), (d) leaf thickness (L$_{th}$, mm), (e) pit area (PA, μm^2), (f) pit diameter aperture (DA$_{pit}$, μm), (g) fiber wall thickness (FWT, μm), (h) vessel density (VD, vessels mm^{-2}), (i) hydraulically weighted diameter (d$_h$, μm), (j) xylem potential hydraulic conductivity (K$_s$, kg m^{-1} s^{-1} MPa^{-1}), (k) vessel area (VA, μm^2), (l) maximum vessel area (VA$_{max}$, μm^2), (m) wood density (WD, g cm^3), (n) wood anhydrous density (WD$_0$, g cm^3) and (o) water content at maximum capacity (WC$_{max}$,

kg kg^{-1}), and on the biomass growth rates (BGR, kg ha^{-1} yr^{-1}). Filled dots represents β_1 significantly different from 0 (P<0.05) for the trait-environment relationship with the models based on the combined (PCA axis 1) variables of climate, soil and land-cover transformation; white dots correspond to non-significant models. For details in the modelling procedures see **Table S3** and for the complete set of models see **Table S4**.

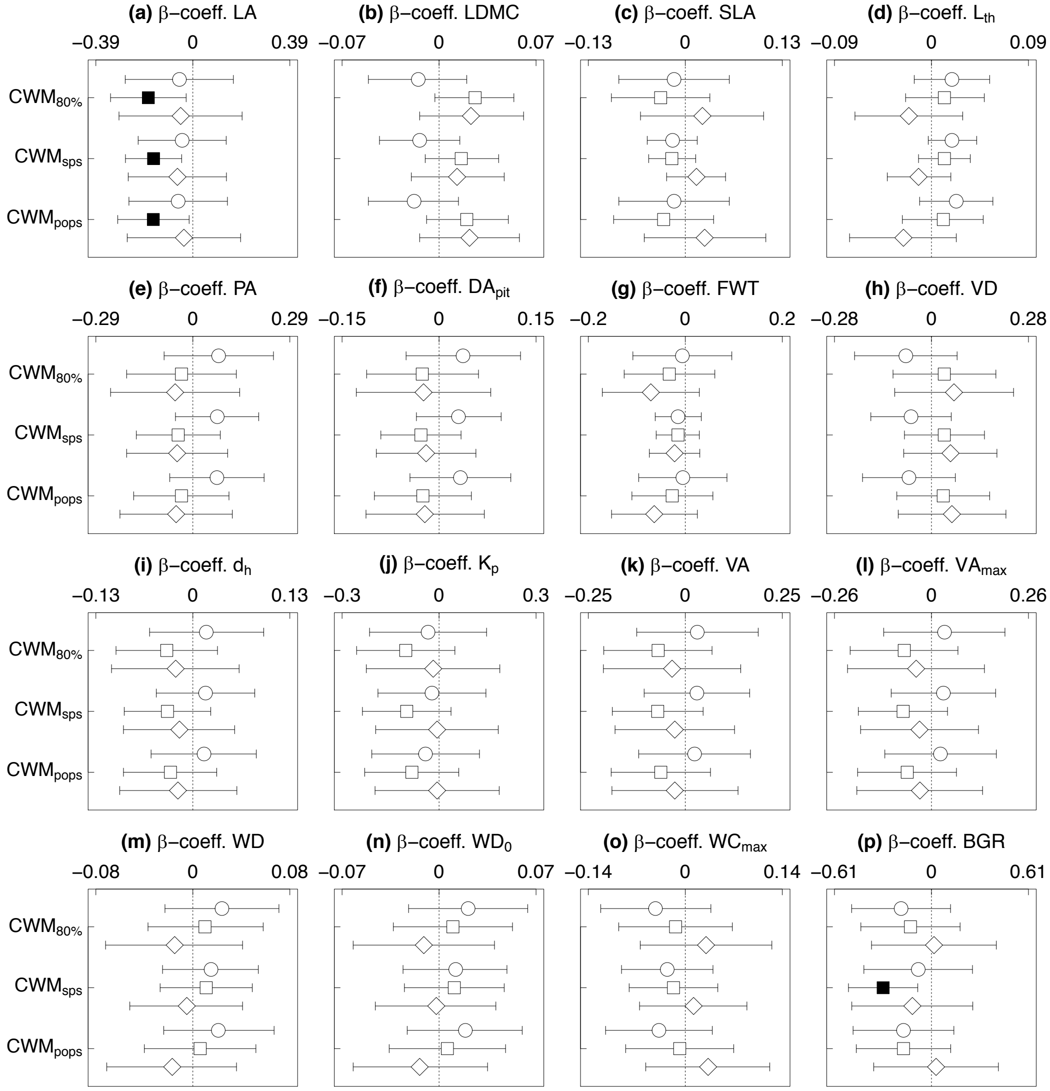

Figure 5. Fitted models and β-coefficients showing the effects of climate severity (circles), soil nutrient limitations (squares) and land-cover transformation (rhombs) on the community weighted-means (CWM) of functional traits: (a) leaf area (LA, mm^2), (b) leaf dry matter content (LDMC, mg g^{-1}), (c) specific leaf area (SLA, mm^2 mg^{-1}), (d) leaf thickness (L_{th}, mm), (e) pit area (PA, μm^2), (f) pit diameter aperture (DA_{pit}, μm), (g) fiber wall thickness (FWT, μm), (h) vessel density (VD, vessels mm^{-2}), (i) hydraulically weighted diameter (d_h, μm), (j) xylem potential hydraulic conductivity (K_s, kg m^{-1} s^{-1} MPa^{-1}), (k) vessel area (VA, μm^2), (l) maximum vessel area (VA_{max}, μm^2), (m) wood density (WD, g cm^3), (n) wood anhydrous density (WD_0, g cm^3) and (o) water content at maximum capacity (WC_{max}, kg kg^{-1}), and on the biomass growth rates (BGR, kg ha^{-1} yr^{-1}). Filled dots represent β_1 significantly different from 0 (P<0.05) for the trait-environment relationship with the models based on the combined (PCA axis 1) variables of climate, soil and land-cover transformation. For details in the modelling procedures see **Table S3** and for the complete set of models see **Table S4**.

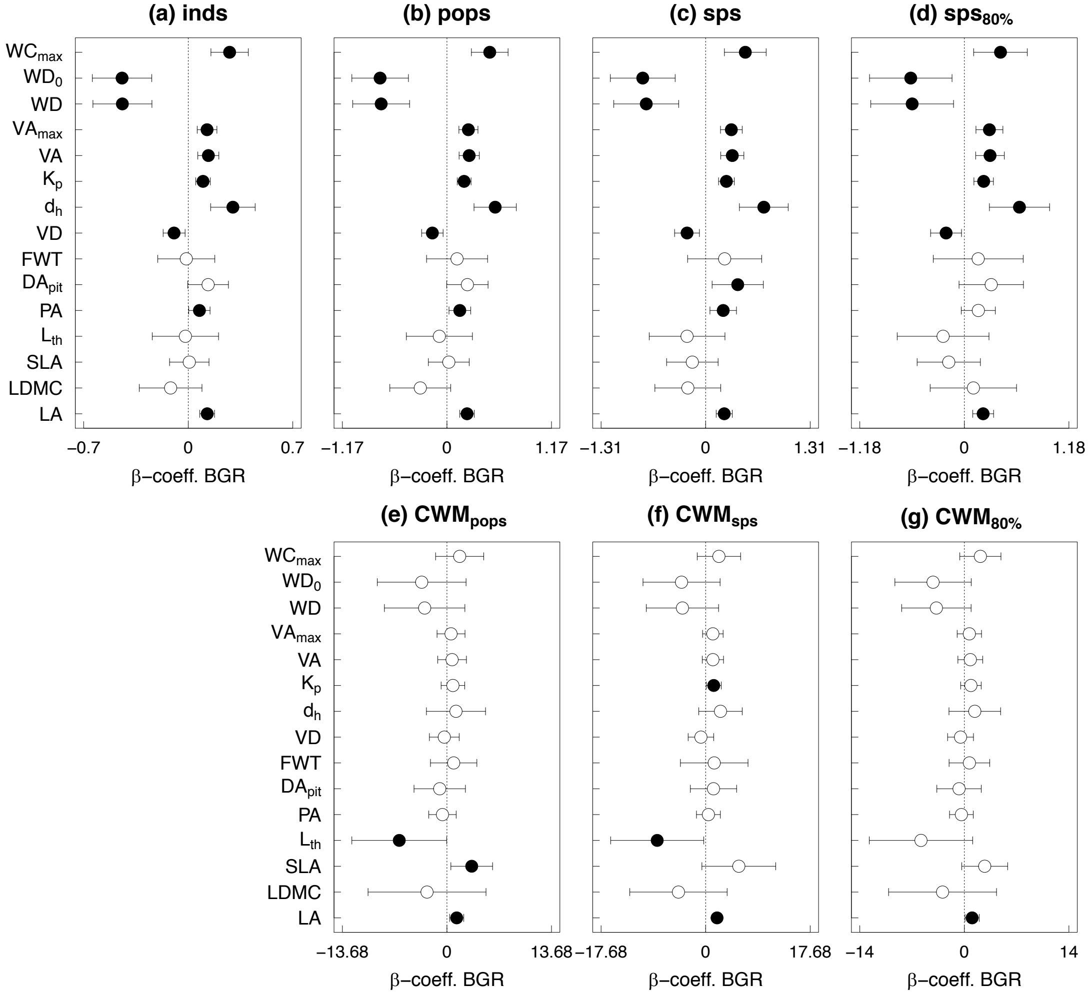

Figure 6. Fitted models and β-coefficients showing the effects of the functional traits: leaf area (LA, mm^2), leaf dry matter content (LDMC, mg g^{-1}), specific leaf area (SLA, mm^2 mg^{-1}), leaf thickness (L_{th}, mm), pit area (PA, μm^2), pit diameter aperture (DA_{pit}, μm), fiber wall thickness (FWT, μm), vessel density (VD, vessels mm^{-2}), hydraulically weighted diameter (d_h, μm), xylem potential hydraulic conductivity (K_s, kg m^{-1} s^{-1} MPa^{-1}), vessel area (VA, μm^2), maximum vessel area (VA_{max}, μm^2), wood density (WD, g cm^3), wood anhydrous density (WD_0, g cm^3) and water content at maximum capacity (WC_{max}, kg kg^{-1}) on biomass growth rates (BGR, kg ha^{-1} yr^{-1}) at the individuals (a, inds), populations (b, pops), species (c, sps) and dominant species (d, $sps_{80\%}$; those that summed at least 80% of the abundances per hectare) and community weighted means for populations (e, CWM_{pops}), species (f, CWM_{sps}), and 80% of the abundances for each community ($CWM_{80\%}$). Filled dots represent β_1 significantly different from 0 (P<0.05) for the trait-biomass production relationship with the models based on the PCA axis 1 variables of climate, soil and land-cover transformation. For details in the modelling procedures see **Table S3**.

Discussion

In this study, we compared the strength of different trait sampling designs to detect the trait-environment and trait-biomass production relationships in Colombian TDF with a high community trait characterization. An entire community trait characterization was expected for a sampling design considering both species abundances representativeness and trait variability simultaneously. Overall, we found that: (i) Our abundance-weighted trait sampling design adequately represents the species abundances structure of TDF tree communities while the sampling design based on dominant species did not. (ii) Differences within communities explained the higher proportion of total trait variation (inds, pops, and, sps) than among them (coms), highlighting the importance of considering trait variability for community trait characterization in TDF. (iii) Our abundance-weighted trait sampling design, which improves accounting both the species abundances representativeness and trait variability, was found to have the highest strength to detect the trait-environment and trait-biomass production relationships.

Bias in sampling designs based on dominant species for TDF

Community trait analyses based on dominant species assumes that they should clearly reveal directional shifts under environmental gradients or effects on ecosystem processes (Grime 1998; Díaz *et al.* 2007; Garnier *et al.* 2007). This assumption has led a broad use of sampling designs based on dominant species to test the trait-environment and trait-biomass relationships in tropical forests (Poorter *et al.* 2008; Finegan *et al.* 2015a; Prado-Junior *et al.* 2016; Poorter *et al.* 2017), but very little attention has been paid in the contributions of dominant species on the community abundance structure and the consequences for functional analyses. Our results indicate that sampling designs that focus on dominant species can be insufficient to describe the community species abundance structure in TDF adequately. We found that less than 40% of species were "dominants" in all communities (those accounted for at least 80% of local abundance; **Figure 2**) and that traits sampled for this set of species did not satisfactorily characterized the trait composition in both within and between communities (discussed below). Considering that hyper-diverse tropical communities have a wide range of functional mechanisms for species assembly, measuring traits only in dominant ones can erroneously disregard the contribution of 'rarer' species in driving community trait composition (Wright 2002); therefore, it may obscure the entire diversity-environment relationships (Keil & Chase 2019). However, measuring traits in every species for every community is not realistically possible (Pakeman & Quested 2007) in particular for hyper-diverse tropical ecosystems (Baraloto *et al.* 2010b) (discussed below). Thus, further studies evaluating trait-environment and trait-biomass in TDF need first assess the extent to which a sampling effort may affect the correct characterization of community trait composition and blur the expected relationships.

Importance of variability for community trait characterization in TDF

Studies that test trait-environment and trait-biomass production relationships based on CWM calculations are relatively common (Lavorel & Garnier 2002; Finegan *et al.* 2015a; Funk *et al.* 2017; Miller *et al.* 2019). However, CWM does not include trait variability for the analysis (Lavorel *et al.* 2008), which is important for a comprehensive understanding of functional mechanisms supporting community and ecosystem processes (Violle *et al.* 2012; Chave 2013). An important assumption behind CWM is that traits being weighted by the species abundances structure of the community reflect the 'optimal' trait phenotype in response to local environmental conditions (Muscarella & Uriarte 2016) or determining biomass within and between communities (Garnier *et al.* 2004; Finegan *et al.* 2015a). However, community trait composition may be very divergent to the extent that species have viable co-existing trait strategies, resulting in alternative equally competitive functional phenotypes (Marks & Lechowicz 2006; Poorter *et al.* 2008; Bernard-Verdier *et al.* 2012; Chauvet *et al.* 2017; Kumordzi *et al.* 2019). Thus, CWM may blur the mechanisms for a comprehensive understanding of community trait composition in TDF. In agreement with that, we found that for all traits, variance within communities reached three quarters of the portion explained with respect among communities (**Figure 3**). Where differences within and among populations/species seem to be an important variation source to understand patterns of functional diversity of TDF communities, as well as among them. For instance, within species of a community (e.g., individuals of a population) trait variability may shows the phenotypic plasticity, the presence of different genotypes and ontogenetic variations (Valladares *et al.* 2006, 2014; Benito Garzón *et al.* 2011). Additionally, for species within communities (populations) 'interspecific selective pressures' may prevent the establishment of each species in a particular location of the community determining local niche differentiation (Kraft *et al.* 2015). Finally, species between communities can experience different environmental conditions and biogeographic barriers that limit their dispersal resulting selective environmental effects (Bernard-Verdier *et al.* 2012; Anderegg *et al.* 2018). For these reasons, further studies exploring trait community composition in TDF based on CWM should consider the limitations to not include trait variability for understanding mechanisms behind of functional trait variation along gradients.

Towards a sampling design for an adequate community trait characterization in TDF

Of the different motivations to decide for trait sampling design in species-rich plant communities, such as TDF, the cost-efficiency of the sampling efforts is a common one (Baraloto *et al.* 2010b). In a perfect scenario, all of the individuals of each species in a community should be sampled for an entire community trait composition description (Carmona *et al.* 2015). However, intensive sampling designs are costly and can be unfeasible in many scenarios for highly diverse ecosystems (Pakeman & Quested 2007; Baraloto *et al.* 2010b). A common alternative practice in such scenario is to collect traits for a number of individuals in a fraction of species per community (*e.g.*, $sps_{80\%}$ in this study) at the expenses of some trait representativeness, or use CWM trait values that are estimated with the mean species trait values and their relative abundances within communities but ignore trait variability (Baraloto *et al.* 2010b; Messier *et al.* 2010; Carmona *et al.* 2015). Here we have shown that intensive trait sampling efforts increase our capacity to detect differences between communities along environmental gradients (**Figures 4** and **5**), as well as the effect of functional traits on biomass production (**Figure 6**). We found that sampling designs for accounting trait variability (i.e., from inds to $sps_{80\%}$) detected effects in 67-32% of the trait-environment models and 46-54% trait-biomass production, while those designs for CWM detected effects in less than 3.1% for trait-environment models and 23.1% for trait-biomass production models. It was because sampling designs for accounting trait variability have a higher size effect power to the extent that increasing trait observations within communities. Additionally, we also found that include all variability sources for the analysis improved consistently both studied relationships (**Figures 4** and **6**). The inds design showed the most substantial detection of trait-environment and trait-biomass production relationships (67.2 and 53.5% of models, respectively). Thus, in order to reconcile the trade-offs between costly sampling efforts for including trait variability and the underpowered of CWM where effects are missed, we recommend the use of abundance-weighted sampling designs for studies (**Figure S1**), but developing linear mixed models to control the random effects generated by the nested variability among ecological scales. If not considered, random effects may induce erroneously judge the statistical significance of the models wasting the intensive sampling efforts (Messier *et al.* 2010; Green & Macleod 2016). Finally, we would like to highlight that our results do not claim that all trait sample designs in hyper-diverse tropical ecosystems, in particular TDF, should emphasize in intensive sampling efforts or adopting our abundance-weighted sampling design, because it not only depends on the research question, but also in the financial sources and logistic requirements for fieldwork (Baraloto *et al.* 2010b; Carmona *et al.* 2015).

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Supporting information

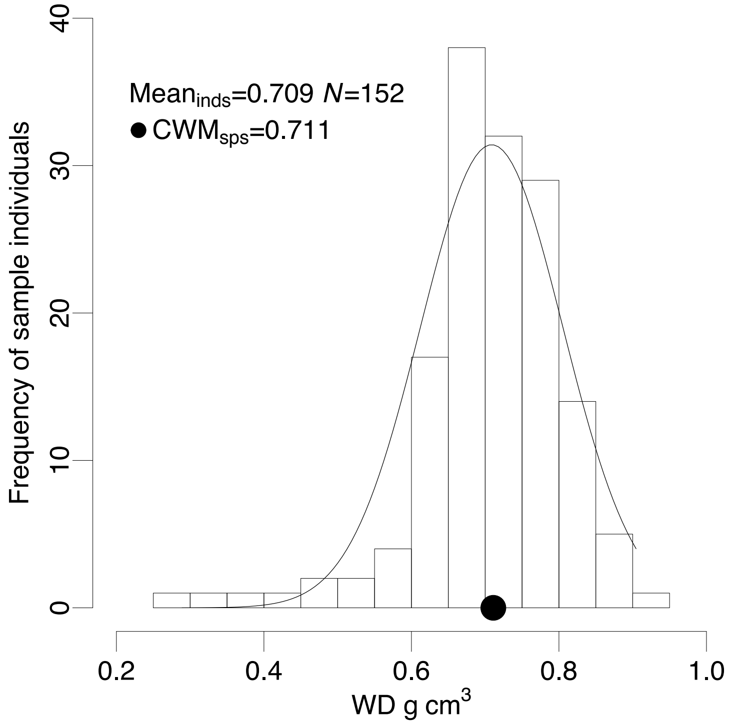


Figure S1. Example of the trait values distribution based on the abundance-weighted trait sampling design (N=sampled individuals). Mean trait value for the sampled individuals (Mean$_{inds}$) and the community weighted mean value of the sample trait using the species trait means and the species abundances (CWM$_{sps}$). Wood density (WD, g cm3).

Table S1. Environmental conditions (climate, soils and land-cover transformation) of ten 1-ha permanent plots in tropical dry forests (coms). Climate variables were determined based on 2046 weather stations in Colombia with ~90 m spatial resolution (*http://institucional.ideam.gov.co/jsp/1769*). Soils variables were obtained from 10 soil samples were randomly taken at each plot and analising at the Agustin Codazzi National Soil Laboratory. Land-cover variables were measured from a circular area of 500 ha around each plot based on interpretation of remote-sensing imagery (Landsat 8 Mosaic and Google Earth^{Pro}© images of 2014-2015, 1500 m flight height, 1:2500 in scale and 0.64x0.64 m resolution). For details of the climate, soils and land-cover transformation see PCA axes 1 in González-M. et al. (2019)

Permanent Plots (1-ha)	**CardonalLoma**	**CardonalPlana**	**Colorados**	**Cotove**	**Jabirú**	**Macuira**	**Tambor**	**Tayrona**	**Tuparro**	**Vinculo**
Climate (Climate severity, PC1 axis 1 – 56.6%*)	-0.907	-0.698	0.544	-0.536	-0.688	5.018	-1.717	3.445	-1.218	-2.362
Total annual rainy days (ARD, no.)	113	116	96	146	116	33	126	95	152	144
Aridity index (Aridity, [PET/TAP])	1.19	1.29	1.01	1.43	1.31	3.42	0.88	2.03	0.77	0.97
Isothermality (Isoth, %)	85.91	85.97	90.25	87.29	86.03	75.43	85.83	81.35	78.07	93.3
Solar radiation (SRad, MJ·m^{-1} x 100)	172.78	173.36	192.08	178.49	173.28	185.69	172.87	196.79	164.1	169.95
Total annual precipitation (TAP, mm)	1541.2	1505.9	1528.4	1193.8	1528.2	517	1912.5	899.4	2697.2	1192.4
Potential evapotranspiration (PET, mm)	1835.6	1946.8	1546	1712.8	2009.1	1768.6	1689.1	1827.7	2067	1161.3
Total precipitation during the three driest months (TPdriest [<100 mm·month^{-1}], mm)	222.5	227.8	139.3	112.7	236.8	32.1	272.7	33.4	177.1	168.5
Water vapor pressure (WVP, kPa)	2.53	2.63	2.75	2.55	2.65	2.67	2.5	2.87	2.8	2.14
Wind speed (Wind, m·s^{-1})	0.92	0.93	2.35	0.83	0.93	4.84	0.9	4.45	1.37	0.87
Soils (Soil nutrient limitations, PC1 axis 1 – 48.8%**)	-0.237	-1.094	3.481	1.550	-1.310	-2.422	-2.111	-0.066	-3.767	3.661
Acidity (pH)	6.87	6.79	7.37	6.54	6.46	6.12	6.98	7.38	4.39	6.22
Available phosphorus (P, mg·kg^{-1})	19.36	143.24	12.17	20.08	17.08	18.14	11.33	222.59	3.32	4.7
Cation exchange capacity (CEC, cmol^{+}·kg^{-1})	20.08	15.61	30.89	25.71	17.01	10.01	14.73	16.43	6.69	26.68
Extractable calcium (Ca, cmol^{+}·kg^{-1})	22.89	13.81	34.83	22.13	13.13	5.29	10.29	16.05	0.06	21.33
Extractable magnesium (Mg, cmol^{+}·kg^{-1})	4.11	3.24	4.64	9.95	3.9	2.19	2.3	2.69	0.06	17.74
Extractable potassium (K, cmol^{+}·kg^{-1})	0.36	0.73	0.65	0.38	0.7	0.55	0.61	0.82	0.21	0.87
Extractable sodium (Na, cmol^{+}·kg^{-1})	0.1	0.03	0.09	0.15	0.08	0.22	0.04	0.07	0.16	0.14
Organic carbon (OC, %)	2.41	2.54	3.22	2.26	2.8	1	2.36	3.58	1.79	3.64
Sand content (Sand %)	56.45	61.86	34.21	37.42	48.86	57.41	72.25	62.58	64.27	60.69
Clay content (Clay %)	24.54	24.96	31.58	35.34	21.16	21.54	16.33	19.25	16.39	24.36
Silt content (Silt %)	19.03	13.18	34.21	27.24	29.98	21.07	11.42	18.18	19.34	14.95
Land-cover (Land-cover transformation, PC1 axis 1 – 56.5%***)	-1.052	1.236	-1.911	3.250	1.207	-2.135	-0.691	-2.953	-1.091	2.410
Forest cover area (Forest, Ha [effective area, %])	303 [60.6]	153.9 [30.8]	395 [79]	55.1 [11.5]	145.4 [29.1]	407.6 [82.4]	329.6 [65.9]	411.8 [100]	176.3 [51.9]	23.4 [4.7]
Forest shape index (Shape [Perimeter/Area], m^{-1})	0.011	0.028	0.004	0.038	0.023	0.004	0.017	0.003	0.013	0.025
Secondary vegetation area (SecVeg, Ha [effective area, %])	52.3 [10.5]	38.5 [7.7]	57.2 [11.4]	103.4 [21.6]	129.9 [26]	87.1 [17.6]	104 [20.8]	0 [0]	29.5 [8.7]	180.2 [36]
Area used by humans (ULC, Ha [effective area, %])	125.5 [25.1]	254.9 [50.9]	48.1 [9.6]	309.7 [64.7]	209 [41.8]	0 [0]	56.7 [11.3]	0 [0]	19.2 [5.6]	296.7 [59.3]
Types of human land cover uses (ULC.type, no.)	3	14	5	34	17	0	17	0	2	22
Topographic roughness (Roughness, %)	12.7	7.3	14.7	9.7	9	10.4	22.5	19.1	7.4	8

*High values are associated to high aridity and wind speed, high solar radiation and water vapour pressure but low rainfall regimens (low values of annual precipitation, precipitation during the rainy season and number of rainy days)

**High values are associated to low cation exchange capacity, low contents of extractable bases (Ca, Mg, K), low contents of clay and silt and low pH but high contents sands. For simplicity we inverted the original PC1 axis of "soils fertility" in González-M. et al. (2019) to the same direction than climate and land-cover axes, "soil nutrient limitations"

***High values are associated to low forest cover, narrow forest shape and high proportion of secondary vegetation and high number of human land-cover types

Table S2. Description, sampling effort (*N*) and the general predictions of trait-environment and trait-biomass production relationships for tropical dry forests (TDF). Number of individuals (inds), populations (pops) and species (sps) sampled in this study in 10 1-ha permanent plots of TDF (coms, Table S1)

Trait (abbreviation, units)	Description	*N* (inds, pops, sps)	Expected relationships		References
			As gradients become harder* trait values:	High trait values determine ____ biomass production:	
Fiber wall thickness (FWT, μm)	Width wall fibers confer high hydraulic safety resistance	1294, 463, 306	Increase / Unpredicted** / Increase	Low	Madsen & Gamstedt (2013); Scholz *et al*. (2013); Sorieul *et al*. (2016)
Hydraulically weighted diameter (d_h, μm)	Large weighted diameters determine high hydraulic efficiency	1295, 463, 306	Decrease / Unpredicted** / Unpredicted**	High	Scholz *et al*. (2013); Rosell *et al*. (2017)
Leaf area (LA, mm^2)	Large leaves are correlated with low tissue investments	1335, 483, 317	Unpredicted** / Decrease / Increase	High	Pérez-Harguindeguy *et al*. (2013); Díaz *et al*. (2016)
Leaf dry matter content (LDMC, mg g^{-1})	High dry mass contents exhibit low tissue investments	1332, 485, 320	Unpredicted** / Increase / Decrease	Low	Pérez-Harguindeguy *et al*. (2013); Díaz *et al*. (2016)
Leaf thickness (L_{th}, mm)	Width leaves are correlated with high tissue investments	1252, 458, 311	Unpredicted** / Increase / Decrease	Low	Pérez-Harguindeguy *et al*. (2013); Onoda *et al*. (2011)
Maximum vessel area (VA_{max}, $μm^2$)	Large vessels diameters determine high hydraulic efficiency	1295, 463, 306	Decrease / Decrease / Decrease	High	IAWA *et al*. (2007); Scholz *et al*. (2013)
Pit area (PA, $μm^2$)	Large pit areas determine high embolism risk	1294, 463, 306	Decrease / Decrease / Decrease	High	IAWA *et al*. (2007); Scholz *et al*. (2013)
Pit diameter aperture (DA_{pit}, μm)	Small pit diameters confer high hydraulic safety	1294, 463, 306	Decrease / Decrease / Decrease	High	Scholz *et al*. (2013); Li *et al*. (2016); Helmling *et al*. (2018)
Specific leaf area (SLA, mm^2 mg^{-1})	High specific leaf mass shows low tissue investments	1324, 483, 317	Increase / Decrease / Increase	High	Wright *et al*. (2004); Pérez-Harguindeguy *et al*. (2013)
Vessel area (VA, $μm^2$)	Large conduits confer high hydraulic efficiency but low hydraulic safety	1295, 463, 306	Unpredicted** / Decrease / Increase	High	Olson & Rosell (2013); Scholz *et al*. (2013)
Vessel density (VD, vessels mm^{-2})	High conduit per square millimetres confer high hydraulic efficiency but low hydraulic safety	1295, 463, 306	Decrease / Decrease / Unpredicted**	Unpredicted**	Chave *et al*. (2009); Scholz *et al*. (2013); Jacobsen *et al*. (2005)
Wood density (WD, g cm^3)	High densities are related to high hydraulic safety and high tissue investments	1356, 485, 315	Increase / Increase / Decrease	Low	Chave *et al*. (2009); Pérez-Harguindeguy *et al*. (2013)
Wood anhydrous density (WD_0, g cm^3)	High densities are related to high tissue investments and wood mechanical stability	1348, 483, 314	Increase / Increase / Decrease	Low	Chave *et al*. (2009); Pérez-Harguindeguy *et al*. (2013)
Water content at maximal capacity (WC_{max}, kg kg^{-1})	High water contents determine low xylem mechanical resistance	1348, 483, 314	Decrease / Unpredicted** / Increase	High	Guevara (2001); Berry & Roderick (2005)
Xylem potential hydraulic conductivity (K_p, kg m^{-1} s^{-1} MPa^{-1})	High potential conductivity confers high hydraulic efficiency but low hydraulic safety	1295, 463, 306	Decrease / Unpredicted** / Increase	High	Chave *et al*. (2009); Poorter *et al*. (2010); Méndez-Alonzo *et al*. (2012)

* Increases in climate severity / soils nutrient limitations / land-cover transformation

** There are ambiguous expectations that limit providing of a specific prediction

Table S3. Modelling procedures for the abundance weighted trait sampling design (inds) and six functional trait sampling designs, 15 traits, 29 environmental variables of climate, soils, and land-cover transformation, and biomass growth rates (BGR). Functional trait sampling designs: populations (pops), species (sps), dominant species ($\text{sps}_{80\%}$, species saturating 80% of the abundances per hectare), community weighted-means based on populations (CWM_{pops}), species (CWM_{sps}) and dominant species ($\text{CWM}_{80\%}$). For the linear mixed-effects models the random effects from populations (u_{P}) and the random effects from species (u_{SP}) of each plot. For a description of the environmental variables and traits see Table S1 and S2, respectively. *Trait predictors in the models are respectively calculated based on: inds, pops, sps, $\text{sps}_{80\%}$, CWM_{pops}, CWM_{sps} and $\text{CWM}_{80\%}$

Response (Functional trait design)	Predictors		Trait-environment model	Trait-biomass production model
	Environmental variable (Envar)	Trait*		
$\text{CWM}_{80\%}$	Climate severity Isoth TAP TPdriests PET Aridity Ard SRad WVP Wind Soil nutrient limitations Sand Silt Clay pH CEC Ca Mg K Na P OC Land-cover transformation Forest Shape SecVeg UCL ULC.type Roughness	FWT d_{h} LA LDMC L_{th} VA_{max} DA_{pit} SLA VA VD WD WD_0 WC_{max} K_{p}	$\text{CWM}_{80\%} = \beta_0 + \beta_1 \times \text{Envar} + \varepsilon$	
CWM_{sps}			$\text{CWM}_{\text{sps}} = \beta_0 + \beta_1 \times \text{Envar} + \varepsilon$	
CWM_{pops}			$\text{CWM}_{\text{pops}} = \beta_0 + \beta_1 \times \text{Envar} + \varepsilon$	
BGR_{coms}			$\text{BGR}_{\text{coms}} = \beta_0 + \beta_1 \times \text{Envar} + \varepsilon$	$\text{BGR}_{\text{coms}} = \beta_0 + \beta_1 \times \text{Trait} + \varepsilon$
$\text{sps}_{80\%}$, BGR_{sps}			$\text{sps}_{80\%} = \beta_0 + \beta_1 \times \text{Envar} + \varepsilon$	$\text{BGR}_{\text{sps}_{80\%}} = \beta_0 + \beta_1 \times \text{Trait} + \varepsilon$
sps, BGR_{sps}			$\text{sps} = \beta_0 + \beta_1 \times \text{Envar} + \varepsilon$	$\text{BGR}_{\text{sps}} = \beta_0 + \beta_1 \times \text{Trait} + \varepsilon$
pops, BGR_{sps}			$\text{pops} = \beta_0 + \beta_1 \times \text{Envar} + u_{\text{SP}} + \varepsilon$	$\text{BGR}_{\text{pops}} = \beta_0 + \beta_1 \times \text{Trait} + u_{\text{SP}} + \varepsilon$
inds, BGR_{sps}			$\text{inds} = \beta_0 + \beta_1 \times \text{Envar} + u_{\text{P}} + u_{\text{SP}} + \varepsilon$	$\text{BGR}_{\text{inds}} = \beta_0 + \beta_1 \times \text{Trait} + u_{\text{P}} + u_{\text{SP}} + \varepsilon$

Table S4. Fitted models and β-coefficients showing the effects of 26 single variables of climate, soils and land-cover transformation on the functional traits for the abundance weighted trait sampling design (inds) and six functional trait sampling designs: populations (pops), species (sps), dominant species ($sps_{80\%}$, species saturating 80% of the abundances per hectare), community weighted-means based on populations (CWM_{pops}), species (CWM_{sps}) and dominant species ($CWM_{80\%}$). Confidence interval at 95% of the probability (CI). Bold letters show significant β-coefficients (*P*<0.05). For description of the environmental variables and traits see Table S1 and S2, respectively.

Trait	Environmental variable		inds		pops		sps		$sps_{80\%}$		CWM_{pops}		CWM_{sps}		$CWM_{80\%}$	
			β_0 (95% CI)	*P*	β_0 (95% CI)	*P*	β_0 (95% CI)	*P*	β_0 (95% CI)	*P*	β_0 (95% CI)	*P*	β_0 (95% CI)	*P*	β_0 (95% CI)	*P*
LA	Climate	Isoth	-0.01 (-0.022, 0.001)	0.087	0.001 (-0.018, 0.02)	0.912	0.002 (-0.021, 0.025)	0.881	0.012 (-0.013, 0.037)	0.350	-0.036 (-0.12, 0.048)	0.346	-0.043 (-0.114, 0.027)	0.195	-0.045 (-0.135, 0.045)	0.283
		TAP	0.000 (0.000, 0.001)	**0.000**	0.000 (0.000, 0.001)	**0.000**	0.000 (0.000, 0.001)	**0.000**	0.000 (0.000, 0.001)	**0.004**	0.001 (0.000, 0.001)	**0.026**	0.001 (0.000, 0.001)	**0.018**	0.001 (0.000, 0.001)	**0.026**
		TPdriests	0.003 (0.003, 0.004)	**0.000**	0.004 (0.002, 0.005)	**0.000**	0.005 (0.003, 0.006)	**0.000**	0.004 (0.003, 0.006)	**0.000**	0.003 (-0.002, 0.008)	0.152	0.003 (-0.002, 0.007)	0.195	0.003 (-0.002, 0.009)	0.189
		PET	0.000 (0.000, 0.001)	**0.000**	0.000 (0.000, 0.001)	0.207	0.000 (0.000, 0.001)	0.288	0.000 (0.000, 0.001)	0.956	0.001 (0.000, 0.003)	0.058	0.001 (0.000, 0.003)	**0.033**	0.002 (0.000, 0.003)	**0.039**
		Aridity	-0.309 (-0.398, -0.22)	**0.000**	-0.308 (-0.446, -0.169)	**0.000**	-0.345 (-0.517, -0.173)	**0.000**	-0.326 (-0.52, -0.132)	**0.001**	-0.221 (-0.802, 0.36)	0.405	-0.182 (-0.7, 0.336)	0.441	-0.223 (-0.861, 0.414)	0.443
		Ard	0.005 (0.003, 0.007)	**0.000**	0.005 (0.002, 0.008)	**0.002**	0.005 (0.002, 0.009)	**0.006**	0.005 (0.000, 0.009)	**0.038**	0.003 (-0.01, 0.017)	0.579	0.003 (-0.009, 0.015)	0.598	0.003 (-0.011, 0.018)	0.612
		SRad	0.000 (0.000, 0.000)	**0.000**	0.000 (0.000, 0.000)	**0.000**	0.000 (0.000, 0.000)	**0.001**	0.000 (0.000, 0.000)	**0.008**	0.000 (-0.001, 0.000)	0.287	0.000 (-0.001, 0.000)	0.299	0.000 (-0.001, 0.000)	0.322
		WVP	0.137 (-0.152, 0.425)	0.353	-0.193 (-0.687, 0.302)	0.444	-0.277 (-0.893, 0.34)	0.378	-0.51 (-1.153, 0.133)	0.120	1.1 (-1.07, 3.27)	0.276	1.115 (-0.756, 2.987)	0.207	1.378 (-0.921, 3.678)	0.204
		Wind	-0.127 (-0.17, -0.084)	**0.000**	-0.146 (-0.215, -0.077)	**0.000**	-0.185 (-0.275, -0.095)	**0.000**	-0.176 (-0.272, -0.079)	**0.000**	-0.101 (-0.397, 0.196)	0.456	-0.076 (-0.342, 0.189)	0.526	-0.095 (-0.421, 0.232)	0.521
	Soils	Sand	0.015 (0.011, 0.02)	**0.000**	0.014 (0.007, 0.021)	**0.000**	0.017 (0.008, 0.026)	**0.000**	0.013 (0.004, 0.023)	**0.008**	0.027 (0.000, 0.054)	**0.049**	0.026 (0.003, 0.048)	**0.031**	0.03 (0.001, 0.059)	**0.043**
		Silt	-0.049 (-0.059, -0.039)	**0.000**	-0.043 (-0.059, -0.027)	**0.000**	-0.047 (-0.067, -0.027)	**0.000**	-0.038 (-0.059, -0.016)	**0.001**	-0.072 (-0.125, -0.018)	**0.015**	-0.063 (-0.111, -0.014)	**0.017**	-0.079 (-0.137, -0.021)	**0.014**
		Clay	-0.017 (-0.023, -0.01)	**0.000**	-0.015 (-0.026, -0.003)	**0.012**	-0.02 (-0.035, -0.005)	**0.009**	-0.016 (-0.031, 0.000)	0.052	-0.034 (-0.082, 0.014)	0.145	-0.035 (-0.075, 0.006)	0.082	-0.038 (-0.09, 0.014)	0.127
		pH	-0.138 (-0.201, -0.075)	**0.000**	-0.093 (-0.193, 0.008)	0.070	-0.05 (-0.161, 0.062)	0.381	-0.003 (-0.128, 0.122)	0.963	-0.249 (-0.765, 0.268)	0.299	-0.207 (-0.669, 0.255)	0.332	-0.282 (-0.842, 0.277)	0.278
		CEC	-0.021 (-0.028, -0.013)	**0.000**	-0.015 (-0.028, -0.003)	**0.017**	-0.015 (-0.03, 0.000)	**0.046**	-0.009 (-0.025, 0.008)	0.306	-0.039 (-0.094, 0.015)	0.135	-0.041 (-0.086, 0.004)	0.070	-0.045 (-0.103, 0.013)	0.110
		Ca	-0.017 (-0.023, -0.011)	**0.000**	-0.014 (-0.023, -0.005)	**0.003**	-0.013 (-0.024, -0.002)	**0.026**	-0.008 (-0.021, 0.004)	0.178	-0.029 (-0.071, 0.013)	0.148	-0.027 (-0.064, 0.009)	0.125	-0.033 (-0.078, 0.012)	0.130
		Mg	-0.032 (-0.044, -0.021)	**0.000**	-0.025 (-0.045, -0.005)	**0.016**	-0.029 (-0.054, -0.004)	**0.025**	-0.015 (-0.041, 0.011)	0.264	-0.073 (-0.144, -0.001)	**0.047**	-0.076 (-0.13, -0.021)	**0.013**	-0.084 (-0.159, -0.009)	**0.032**
		K	-0.56 (-0.834, -0.287)	**0.000**	-0.342 (-0.797, 0.113)	0.140	-0.454 (-1.013, 0.105)	0.111	-0.151 (-0.763, 0.461)	0.627	-1.285 (-3.256, 0.686)	0.171	-1.544 (-3.07, -0.018)	**0.048**	-1.438 (-3.571, 0.694)	0.159
		Na	-1.652 (-2.745, -0.56)	**0.003**	-2.233 (-3.969, -0.498)	**0.012**	-3.425 (-5.666, -1.183)	**0.003**	-3.871 (-6.364, -1.379)	**0.002**	-1.755 (-9.592, 6.082)	0.619	-1.731 (-8.648, 5.187)	0.580	-1.829 (-10.386, 6.728)	0.635
		P	-0.003 (-0.004, -0.002)	**0.000**	-0.003 (-0.004, -0.002)	**0.000**	-0.003 (-0.005, -0.001)	**0.001**	-0.003 (-0.005, -0.001)	**0.005**	-0.003 (-0.009, 0.003)	0.336	-0.001 (-0.007, 0.004)	0.582	-0.003 (-0.009, 0.004)	0.406
		OC	-0.161 (-0.241, -0.081)	**0.000**	-0.125 (-0.255, 0.005)	0.060	-0.146 (-0.309, 0.018)	0.080	-0.094 (-0.274, 0.085)	0.301	-0.296 (-0.836, 0.243)	0.241	-0.339 (-0.784, 0.106)	0.117	-0.331 (-0.916, 0.254)	0.228
	Land-cover	Forest	0.000 (-0.002, 0.002)	0.817	-0.001 (-0.005, 0.002)	0.422	-0.001 (-0.006, 0.004)	0.716	-0.002 (-0.006, 0.003)	0.517	0.002 (-0.013, 0.017)	0.772	0.004 (-0.009, 0.017)	0.513	0.003 (-0.014, 0.019)	0.711
		Shape	1.347 (-4.461, 7.156)	0.649	5.764 (-3.853, 15.381)	0.240	8.594 (-5.156, 22.343)	0.220	9.949 (-4.036, 23.935)	0.162	-1.295 (-41.582, 38.993)	0.943	-3.831 (-39.409, 31.748)	0.810	-2.706 (-46.59, 41.177)	0.890
		SecVeg	0.009 (0.003, 0.015)	**0.003**	0.014 (0.004, 0.024)	**0.005**	0.01 (-0.003, 0.023)	0.145	0.014 (0.001, 0.028)	**0.040**	-0.004 (-0.049, 0.042)	0.851	-0.017 (-0.055, 0.021)	0.338	-0.008 (-0.057, 0.042)	0.729
		UCL	-0.004 (-0.007, -0.002)	**0.001**	-0.003 (-0.007, 0.002)	0.212	-0.003 (-0.009, 0.002)	0.247	-0.001 (-0.007, 0.005)	0.761	-0.007 (-0.025, 0.011)	0.382	-0.008 (-0.024, 0.007)	0.250	-0.009 (-0.028, 0.011)	0.340
		ULC.type	0.004 (-0.002, 0.011)	0.167	0.011 (0.001, 0.021)	**0.038**	0.012 (-0.002, 0.025)	0.090	0.015 (0.001, 0.029)	**0.033**	-0.002 (-0.045, 0.04)	0.898	-0.008 (-0.045, 0.029)	0.639	-0.005 (-0.051, 0.041)	0.813
		Roughness	0.017 (0.006, 0.028)	**0.002**	0.021 (0.003, 0.038)	**0.020**	0.03 (0.008, 0.052)	**0.009**	0.033 (0.008, 0.058)	**0.009**	0.019 (-0.071, 0.109)	0.645	0.025 (-0.054, 0.103)	0.485	0.019 (-0.08, 0.117)	0.674
LDMC	Climate	Isoth	0.004 (0.001, 0.007)	**0.006**	0.003 (-0.002, 0.007)	0.269	0.000 (-0.005, 0.006)	0.915	-0.009 (-0.034, 0.016)	0.471	0.011 (-0.002, 0.024)	0.089	0.009 (-0.003, 0.02)	0.123	0.011 (-0.002, 0.025)	0.084
		TAP	0.000 (0.000, 0.000)	0.274	0.000 (0.000, 0.000)	**0.050**	0.000 (0.000, 0.000)	**0.018**	0.000 (0.000, 0.001)	**0.002**	0.000 (0.000, 0.000)	0.873	0.000 (0.000, 0.000)	0.799	0.000 (0.000, 0.000)	0.886
		TPdriests	0.000 (0.000, 0.000)	**0.002**	0.000 (0.000, 0.001)	**0.003**	0.000 (0.000, 0.001)	**0.037**	0.002 (0.000, 0.004)	**0.012**	0.000 (-0.001, 0.001)	0.526	0.000 (-0.001, 0.001)	0.466	0.000 (-0.001, 0.001)	0.790
		PET	0.000 (0.000, 0.000)	**0.009**	0.000 (0.000, 0.000)	**0.010**	0.000 (0.000, 0.000)	**0.011**	0.001 (0.000, 0.001)	**0.000**	0.000 (0.000, 0.000)	0.843	0.000 (0.000, 0.000)	0.952	0.000 (0.000, 0.000)	0.647
		Aridity	-0.039 (-0.06, -0.018)	**0.000**	-0.052 (-0.087, -0.018)	**0.003**	-0.059 (-0.102, -0.015)	**0.008**	-0.285 (-0.48, -0.091)	**0.004**	-0.054 (-0.15, 0.042)	0.229	-0.046 (-0.132, 0.04)	0.254	-0.044 (-0.15, 0.061)	0.359
		Ard	0.001 (0.000, 0.001)	**0.000**	0.001 (0.001, 0.002)	**0.001**	0.001 (0.000, 0.002)	**0.007**	0.007 (0.003, 0.011)	**0.001**	0.001 (-0.001, 0.003)	0.239	0.001 (-0.001, 0.003)	0.405	0.001 (-0.001, 0.003)	0.346
		SRad	0.000 (0.000, 0.000)	**0.003**	0.000 (0.000, 0.000)	**0.002**	0.000 (0.000, 0.000)	**0.023**	0.000 (0.000, 0.000)	**0.005**	0.000 (0.000, 0.000)	0.591	0.000 (0.000, 0.000)	0.665	0.000 (0.000, 0.000)	0.777
		WVP	-0.024 (-0.093, 0.044)	0.486	-0.035 (-0.156, 0.087)	0.575	0.062 (-0.091, 0.216)	0.424	0.385 (-0.256, 1.026)	0.238	-0.115 (-0.512, 0.283)	0.525	-0.064 (-0.421, 0.294)	0.692	-0.128 (-0.545, 0.289)	0.499
		Wind	-0.024 (-0.034, -0.013)	**0.000**	-0.034 (-0.051, -0.017)	**0.000**	-0.031 (-0.054, -0.008)	**0.007**	-0.143 (-0.239, -0.046)	**0.004**	-0.03 (-0.078, 0.017)	0.179	-0.023 (-0.067, 0.02)	0.250	-0.026 (-0.078, 0.026)	0.283
	Soils	Sand	0.000 (-0.001, 0.001)	0.390	0.001 (-0.001, 0.003)	0.355	0.001 (-0.001, 0.003)	0.469	0.01 (0.000, 0.019)	0.054	-0.003 (-0.009, 0.002)	0.216	-0.002 (-0.007, 0.003)	0.286	-0.004 (-0.01, 0.001)	0.095
		Silt	-0.001 (-0.003, 0.002)	0.499	-0.004 (-0.008, 0.000)	**0.047**	-0.005 (-0.01, 0.000)	0.072	-0.033 (-0.055, -0.011)	**0.003**	0.004 (-0.01, 0.017)	0.547	0.002 (-0.01, 0.014)	0.697	0.007 (-0.007, 0.02)	0.292
		Clay	0.002 (0.000, 0.003)	0.066	0.000 (-0.003, 0.003)	0.918	0.000 (-0.003, 0.004)	0.902	-0.008 (-0.024, 0.008)	0.308	0.006 (-0.002, 0.014)	0.113	0.005 (-0.002, 0.013)	0.142	0.008 (0.000, 0.016)	0.051
		pH	0.000 (-0.015, 0.015)	0.984	-0.01 (-0.034, 0.015)	0.444	-0.02 (-0.047, 0.008)	0.156	-0.121 (-0.244, 0.002)	0.054	0.009 (-0.088, 0.105)	0.840	0.008 (-0.077, 0.093)	0.828	0.01 (-0.091, 0.112)	0.820

Trait	**Environmental variable**		**inds**		**pops**		**sps**		**sps$_{80\%}$**		**CWM$_{pops}$**		**CWM$_{sps}$**		**CWM$_{80\%}$**	
			β_0 (95% CI)	***P***	**β_0 (95% CI)**	***P***	**β_0 (95% CI)**	***P***	**β_0 (95% CI)**	***P***	**β_0 (95% CI)**	***P***	**β_0 (95% CI)**	***P***	**β_0 (95% CI)**	***P***
		CEC	0.001 (-0.001, 0.003)	0.199	-0.001 (-0.004, 0.002)	0.703	-0.001 (-0.005, 0.002)	0.436	-0.015 (-0.031, 0.001)	0.069	0.007 (-0.003, 0.016)	0.146	0.005 (-0.003, 0.014)	0.188	0.008 (-0.001, 0.018)	0.081
		Ca	0.002 (0.000, 0.003)	**0.021**	0.000 (-0.002, 0.002)	0.940	-0.001 (-0.003, 0.002)	0.650	-0.009 (-0.021, 0.003)	0.152	0.005 (-0.002, 0.012)	0.137	0.005 (-0.002, 0.011)	0.145	0.006 (-0.001, 0.013)	0.085
		Mg	0.002 (-0.001, 0.005)	0.162	0.001 (-0.004, 0.006)	0.821	-0.002 (-0.009, 0.004)	0.454	-0.02 (-0.046, 0.006)	0.126	0.009 (-0.006, 0.023)	0.202	0.006 (-0.008, 0.019)	0.360	0.011 (-0.004, 0.025)	0.127
		K	-0.003 (-0.068, 0.062)	0.927	-0.068 (-0.179, 0.044)	0.233	-0.109 (-0.248, 0.03)	0.123	-0.696 (-1.296, -0.095)	**0.023**	0.063 (-0.322, 0.448)	0.716	0.064 (-0.275, 0.404)	0.673	0.072 (-0.332, 0.477)	0.692
		Na	-0.447 (-0.705, -0.188)	**0.001**	-0.521 (-0.948, -0.095)	**0.017**	-0.372 (-0.936, 0.191)	0.195	-1.944 (-4.454, 0.566)	0.128	-0.363 (-1.717, 0.992)	0.554	-0.343 (-1.538, 0.851)	0.526	-0.148 (-1.602, 1.305)	0.820
		P	0.000 (0.000, 0.001)	**0.001**	0.000 (0.000, 0.001)	0.110	0.000 (0.000, 0.001)	0.435	0.001 (-0.001, 0.003)	0.362	0.000 (-0.001, 0.001)	0.841	0.000 (-0.001, 0.001)	0.949	0.000 (-0.001, 0.001)	0.947
		OC	0.033 (0.014, 0.052)	**0.001**	0.018 (-0.014, 0.05)	0.258	0.009 (-0.032, 0.05)	0.663	-0.023 (-0.202, 0.155)	0.797	0.068 (-0.018, 0.155)	0.107	0.058 (-0.02, 0.136)	0.123	0.069 (-0.023, 0.162)	0.121
	Land-cover	Forest	-0.001 (-0.001, -0.001)	**0.000**	-0.001 (-0.002, 0.000)	**0.002**	-0.001 (-0.002, 0.000)	0.058	-0.004 (-0.009, 0.001)	0.100	-0.002 (-0.004, 0.001)	0.125	-0.001 (-0.003, 0.001)	0.250	-0.002 (-0.004, 0.001)	0.128
		Shape	2.201 (0.83, 3.572)	**0.002**	3.504 (1.161, 5.847)	**0.003**	2.759 (-0.659, 6.177)	0.113	11.802 (-2.112, 25.716)	0.096	3.073 (-3.477, 9.623)	0.311	1.527 (-4.554, 7.608)	0.579	3.066 (-3.877, 10.009)	0.338
		SecVeg	-0.002 (-0.003, -0.001)	**0.004**	-0.002 (-0.004, 0.001)	0.125	-0.003 (-0.006, 0.000)	0.081	-0.015 (-0.028, -0.001)	**0.037**	0.001 (-0.007, 0.009)	0.806	0.001 (-0.006, 0.008)	0.869	0.001 (-0.007, 0.01)	0.696
		UCL	0.002 (0.001, 0.002)	**0.000**	0.002 (0.001, 0.003)	**0.001**	0.001 (0.000, 0.003)	0.114	0.004 (-0.003, 0.01)	0.255	0.002 (0.000, 0.005)	0.062	0.002 (-0.001, 0.004)	0.169	0.003 (0.000, 0.005)	0.059
		ULC.type	-0.001 (-0.002, 0.001)	0.465	0.001 (-0.002, 0.003)	0.644	-0.001 (-0.004, 0.003)	0.631	-0.004 (-0.018, 0.01)	0.578	0.002 (-0.005, 0.009)	0.563	0.000 (-0.006, 0.007)	0.865	0.002 (-0.005, 0.01)	0.531
		Roughness	-0.008 (-0.01, -0.005)	**0.000**	-0.006 (-0.01, -0.002)	**0.004**	-0.007 (-0.012, -0.001)	**0.015**	-0.028 (-0.053, -0.004)	**0.024**	-0.01 (-0.024, 0.003)	0.112	-0.009 (-0.021, 0.003)	0.137	-0.012 (-0.025, 0.002)	0.085
SLA	Climate	Isoth	0.003 (-0.001, 0.008)	0.138	0.005 (-0.002, 0.012)	0.154	0.005 (-0.002, 0.012)	0.183	0.013 (-0.012, 0.038)	0.301	-0.001 (-0.034, 0.031)	0.936	0.000 (-0.016, 0.016)	0.971	-0.002 (-0.035, 0.03)	0.875
		TAP	0.000 (0.000, 0.000)	**0.002**	0.000 (0.000, 0.000)	0.285	0.000 (0.000, 0.000)	0.463	0.000 (0.000, 0.000)	0.682	0.000 (0.000, 0.000)	0.574	0.000 (0.000, 0.000)	0.356	0.000 (0.000, 0.000)	0.535
		TPdriests	0.001 (0.001, 0.001)	**0.000**	0.001 (0.000, 0.001)	**0.010**	0.001 (0.000, 0.001)	**0.022**	0.001 (0.000, 0.003)	0.150	0.001 (-0.001, 0.003)	0.310	0.001 (0.000, 0.002)	0.078	0.001 (-0.001, 0.003)	0.275
		PET	0.000 (0.000, 0.000)	**0.024**	0.000 (0.000, 0.000)	0.328	0.000 (0.000, 0.000)	0.233	0.000 (-0.001, 0.000)	0.230	0.000 (0.000, 0.001)	0.396	0.000 (0.000, 0.000)	0.710	0.000 (0.000, 0.001)	0.341
		Aridity	-0.054 (-0.088, -0.02)	**0.002**	-0.042 (-0.094, 0.01)	0.113	-0.045 (-0.101, 0.012)	0.123	-0.089 (-0.288, 0.109)	0.375	-0.027 (-0.249, 0.194)	0.783	-0.032 (-0.138, 0.075)	0.510	-0.029 (-0.251, 0.194)	0.774
		Ard	0.002 (0.001, 0.002)	**0.000**	0.001 (0.000, 0.002)	0.061	0.001 (0.000, 0.002)	0.089	0.002 (-0.002, 0.007)	0.294	0.001 (-0.004, 0.006)	0.746	0.001 (-0.002, 0.003)	0.471	0.001 (-0.004, 0.006)	0.757
		SRad	0.000 (0.000, 0.000)	**0.000**	0.000 (0.000, 0.000)	0.255	0.000 (0.000, 0.000)	0.217	0.000 (0.000, 0.000)	0.302	0.000 (0.000, 0.000)	0.593	0.000 (0.000, 0.000)	0.206	0.000 (0.000, 0.000)	0.602
		WVP	-0.045 (-0.154, 0.065)	0.424	-0.015 (-0.198, 0.167)	0.869	-0.203 (-0.401, -0.004)	**0.046**	-0.55 (-1.192, 0.093)	0.093	0.092 (-0.766, 0.949)	0.811	-0.113 (-0.525, 0.3)	0.546	0.118 (-0.738, 0.975)	0.758
		Wind	-0.041 (-0.057, -0.024)	**0.000**	-0.029 (-0.055, -0.004)	**0.025**	-0.033 (-0.062, -0.003)	**0.031**	-0.074 (-0.173, 0.024)	0.140	-0.032 (-0.141, 0.078)	0.526	-0.029 (-0.079, 0.021)	0.213	-0.032 (-0.142, 0.078)	0.524
	Soils	Sand	0.004 (0.003, 0.006)	**0.000**	0.003 (0.000, 0.005)	0.060	0.001 (-0.002, 0.004)	0.373	0.001 (-0.009, 0.011)	0.852	0.007 (-0.004, 0.018)	0.199	0.004 (-0.001, 0.009)	0.128	0.008 (-0.003, 0.019)	0.140
		Silt	-0.013 (-0.016, -0.009)	**0.000**	-0.008 (-0.014, -0.002)	**0.009**	-0.004 (-0.01, 0.003)	0.293	-0.005 (-0.027, 0.017)	0.668	-0.017 (-0.042, 0.009)	0.173	-0.009 (-0.021, 0.004)	0.142	-0.018 (-0.043, 0.007)	0.134
		Clay	-0.005 (-0.008, -0.002)	**0.000**	-0.003 (-0.007, 0.002)	0.222	-0.002 (-0.007, 0.003)	0.492	0.000 (-0.016, 0.016)	0.998	-0.01 (-0.028, 0.009)	0.276	-0.006 (-0.015, 0.003)	0.168	-0.011 (-0.029, 0.007)	0.198
		pH	-0.022 (-0.046, 0.002)	0.068	-0.008 (-0.045, 0.029)	0.682	0.006 (-0.03, 0.042)	0.761	-0.012 (-0.137, 0.114)	0.856	-0.019 (-0.222, 0.183)	0.831	-0.003 (-0.103, 0.097)	0.945	-0.012 (-0.215, 0.192)	0.898
		CEC	-0.003 (-0.006, 0.000)	0.086	0.000 (-0.005, 0.005)	0.952	0.001 (-0.004, 0.006)	0.804	0.003 (-0.014, 0.019)	0.753	-0.006 (-0.029, 0.017)	0.565	-0.004 (-0.015, 0.007)	0.413	-0.007 (-0.029, 0.016)	0.503
		Ca	-0.005 (-0.007, -0.003)	**0.000**	-0.002 (-0.006, 0.001)	0.191	-0.001 (-0.005, 0.003)	0.617	-0.003 (-0.015, 0.01)	0.672	-0.007 (-0.024, 0.01)	0.370	-0.004 (-0.012, 0.004)	0.274	-0.007 (-0.024, 0.009)	0.342
		Mg	0.000 (-0.005, 0.004)	0.864	0.001 (-0.006, 0.009)	0.700	0.004 (-0.004, 0.012)	0.358	0.014 (-0.012, 0.04)	0.294	-0.008 (-0.042, 0.025)	0.586	-0.004 (-0.02, 0.013)	0.637	-0.011 (-0.044, 0.022)	0.478
		K	0.146 (0.042, 0.25)	**0.006**	0.201 (0.034, 0.369)	**0.018**	0.048 (-0.134, 0.229)	0.606	0.144 (-0.468, 0.756)	0.643	0.089 (-0.726, 0.905)	0.807	-0.036 (-0.437, 0.364)	0.840	0.057 (-0.761, 0.875)	0.876
		Na	-0.593 (-1.006, -0.181)	**0.005**	-0.578 (-1.22, 0.065)	0.078	-0.462 (-1.196, 0.273)	0.217	-0.135 (-2.674, 2.404)	0.917	-0.803 (-3.65, 2.044)	0.534	-0.664 (-1.992, 0.664)	0.282	-0.956 (-3.776, 1.864)	0.457
		P	-0.001 (-0.001, 0.000)	**0.000**	-0.001 (-0.001, 0.000)	**0.044**	-0.001 (-0.001, 0.000)	**0.033**	-0.002 (-0.004, 0.000)	**0.020**	-0.001 (-0.003, 0.002)	0.532	0.000 (-0.001, 0.001)	0.598	-0.001 (-0.003, 0.002)	0.575
		OC	0.006 (-0.025, 0.036)	0.718	0.034 (-0.014, 0.082)	0.163	0.003 (-0.05, 0.056)	0.900	-0.015 (-0.195, 0.164)	0.869	-0.028 (-0.244, 0.187)	0.769	-0.039 (-0.141, 0.062)	0.398	-0.037 (-0.251, 0.178)	0.705
	Land-cover	Forest	-0.002 (-0.003, -0.001)	**0.000**	-0.002 (-0.003, -0.001)	**0.003**	-0.001 (-0.003, 0.000)	0.125	-0.004 (-0.008, 0.001)	0.126	-0.001 (-0.007, 0.004)	0.575	-0.001 (-0.003, 0.002)	0.542	-0.001 (-0.007, 0.004)	0.668
		Shape	7.106 (4.946, 9.267)	**0.000**	5.89 (2.377, 9.404)	**0.001**	5.427 (1.006, 9.848)	**0.016**	12.639 (-1.313, 26.59)	0.076	5.355 (-8.764, 19.474)	0.407	3.745 (-2.834, 10.324)	0.226	5.069 (-9.141, 19.279)	0.435
		SecVeg	0.01 (0.008, 0.012)	**0.000**	0.009 (0.005, 0.013)	**0.000**	0.007 (0.003, 0.011)	**0.001**	0.022 (0.008, 0.035)	**0.002**	0.008 (-0.008, 0.023)	0.285	0.003 (-0.005, 0.01)	0.483	0.007 (-0.009, 0.022)	0.361
		UCL	0.002 (0.001, 0.003)	**0.002**	0.002 (0.000, 0.003)	**0.039**	0.001 (-0.001, 0.003)	0.296	0.003 (-0.003, 0.009)	0.337	0.001 (-0.006, 0.008)	0.783	0.001 (-0.003, 0.004)	0.699	0.001 (-0.006, 0.007)	0.866
		ULC.type	0.011 (0.008, 0.013)	**0.000**	0.009 (0.005, 0.012)	**0.000**	0.008 (0.004, 0.012)	**0.000**	0.02 (0.006, 0.034)	**0.006**	0.007 (-0.007, 0.022)	0.279	0.004 (-0.003, 0.011)	0.190	0.007 (-0.007, 0.021)	0.300
		Roughness	0.001 (-0.003, 0.006)	0.498	0.000 (-0.006, 0.006)	0.999	0.007 (0.000, 0.014)	0.058	0.009 (-0.016, 0.034)	0.467	0.003 (-0.03, 0.037)	0.822	0.006 (-0.01, 0.021)	0.434	0.006 (-0.027, 0.04)	0.672
L$_{th}$	Climate	Isoth	-0.003 (-0.006, 0.000)	**0.049**	-0.004 (-0.009, 0.000)	0.065	-0.001 (-0.006, 0.005)	0.838	-0.001 (-0.026, 0.024)	0.916	-0.002 (-0.019, 0.016)	0.839	0.000 (-0.012, 0.012)	0.946	0.000 (-0.017, 0.017)	0.993
		TAP	0.000 (0.000, 0.000)	**0.000**	0.000 (0.000, 0.000)	**0.000**	0.000 (0.000, 0.000)	**0.000**	0.000 (-0.001, 0.000)	**0.000**	0.000 (0.000, 0.000)	0.086	0.000 (0.000, 0.000)	**0.022**	0.000 (0.000, 0.000)	0.117
		TPdriests	-0.001 (-0.001, -0.001)	**0.000**	-0.001 (-0.001, -0.001)	**0.000**	-0.001 (-0.001, -0.001)	**0.000**	-0.003 (-0.005, -0.002)	**0.000**	-0.001 (-0.002, 0.000)	0.230	0.000 (-0.001, 0.000)	0.120	0.000 (-0.002, 0.001)	0.308
		PET	0.000 (0.000, 0.000)	0.413	0.000 (0.000, 0.000)	0.550	0.000 (0.000, 0.000)	0.280	0.000 (-0.001, 0.000)	0.483	0.000 (0.000, 0.000)	0.983	0.000 (0.000, 0.000)	0.729	0.000 (0.000, 0.000)	0.955
		Aridity	0.103 (0.083, 0.124)	**0.000**	0.11 (0.078, 0.141)	**0.000**	0.111 (0.074, 0.148)	**0.000**	0.464 (0.275, 0.653)	**0.000**	0.061 (-0.044, 0.166)	0.210	0.05 (-0.021, 0.121)	0.140	0.049 (-0.058, 0.156)	0.311

Trait	Environmental variable		inds		pops		sps		sps$_{80\%}$		CWM$_{pops}$		CWM$_{sps}$		CWM$_{80\%}$	
			β_0 (95% CI)	***P***	**β_0 (95% CI)**	***P***	**β_0 (95% CI)**	***P***	**β_0 (95% CI)**	***P***	**β_0 (95% CI)**	***P***	**β_0 (95% CI)**	***P***	**β_0 (95% CI)**	***P***
		Ard	-0.003 (-0.003, -0.002)	**0.000**	-0.003 (-0.004, -0.002)	**0.000**	-0.003 (-0.004, -0.002)	**0.000**	-0.012 (-0.016, -0.008)	**0.000**	-0.002 (-0.004, 0.001)	0.137	-0.001 (-0.003, 0.000)	0.088	-0.001 (-0.004, 0.001)	0.211
		SRad	0.000 (0.000, 0.000)	**0.000**	0.000 (0.000, 0.000)	**0.000**	0.000 (0.000, 0.000)	**0.000**	0.000 (0.000, 0.000)	**0.000**	0.000 (0.000, 0.000)	0.134	0.000 (0.000, 0.000)	**0.037**	0.000 (0.000, 0.000)	0.161
		WVP	0.115 (0.047, 0.183)	**0.001**	0.103 (-0.014, 0.219)	0.084	0.107 (-0.03, 0.244)	0.125	0.448 (-0.193, 1.09)	0.170	0.086 (-0.366, 0.538)	0.667	0.061 (-0.252, 0.373)	0.667	0.081 (-0.361, 0.524)	0.677
		Wind	0.049 (0.039, 0.059)	**0.000**	0.05 (0.034, 0.066)	**0.000**	0.057 (0.038, 0.077)	**0.000**	0.225 (0.13, 0.32)	**0.000**	0.031 (-0.024, 0.086)	0.230	0.027 (-0.008, 0.062)	0.109	0.025 (-0.031, 0.081)	0.329
	Soils	Sand	-0.002 (-0.003, -0.001)	**0.000**	-0.002 (-0.003, 0.000)	0.078	-0.002 (-0.004, 0.000)	**0.036**	-0.007 (-0.017, 0.003)	0.179	-0.001 (-0.008, 0.006)	0.654	-0.002 (-0.006, 0.003)	0.460	-0.002 (-0.008, 0.005)	0.609
		Silt	0.01 (0.007, 0.012)	**0.000**	0.009 (0.005, 0.013)	**0.000**	0.01 (0.005, 0.015)	**0.000**	0.036 (0.014, 0.059)	**0.002**	0.007 (-0.009, 0.023)	0.333	0.005 (-0.004, 0.015)	0.245	0.007 (-0.009, 0.022)	0.352
		Clay	0.001 (-0.001, 0.002)	0.343	0.000 (-0.003, 0.003)	0.976	0.001 (-0.003, 0.004)	0.642	0.000 (-0.016, 0.016)	0.994	0.000 (-0.011, 0.011)	0.929	0.001 (-0.006, 0.009)	0.702	0.001 (-0.01, 0.012)	0.836
		pH	0.054 (0.039, 0.068)	**0.000**	0.045 (0.022, 0.069)	**0.000**	0.048 (0.024, 0.072)	**0.000**	0.233 (0.112, 0.353)	**0.000**	0.056 (-0.039, 0.152)	0.204	0.046 (-0.019, 0.111)	0.140	0.056 (-0.037, 0.149)	0.196
		CEC	0.004 (0.002, 0.006)	**0.000**	0.002 (-0.001, 0.006)	0.110	0.004 (0.001, 0.008)	**0.016**	0.017 (0.000, 0.033)	**0.048**	0.004 (-0.009, 0.016)	0.508	0.003 (-0.005, 0.011)	0.357	0.004 (-0.008, 0.017)	0.417
		Ca	0.005 (0.003, 0.006)	**0.000**	0.003 (0.001, 0.006)	**0.002**	0.004 (0.002, 0.007)	**0.001**	0.018 (0.006, 0.03)	**0.004**	0.005 (-0.004, 0.013)	0.254	0.004 (-0.002, 0.009)	0.196	0.005 (-0.003, 0.013)	0.198
		Mg	-0.002 (-0.005, 0.001)	0.199	-0.002 (-0.007, 0.003)	0.359	0.000 (-0.005, 0.006)	0.886	-0.002 (-0.029, 0.025)	0.882	0.000 (-0.02, 0.019)	0.965	0.002 (-0.011, 0.014)	0.755	0.000 (-0.018, 0.019)	0.970
		K	0.003 (-0.064, 0.07)	0.938	0.005 (-0.105, 0.114)	0.936	0.177 (0.053, 0.3)	**0.005**	0.767 (0.159, 1.376)	**0.014**	0.016 (-0.447, 0.479)	0.937	0.138 (-0.141, 0.418)	0.286	0.032 (-0.42, 0.484)	0.873
		Na	0.411 (0.147, 0.676)	**0.002**	0.533 (0.116, 0.951)	**0.012**	0.233 (-0.274, 0.741)	0.367	0.053 (-2.503, 2.608)	0.967	0.296 (-1.279, 1.871)	0.670	0.181 (-0.884, 1.245)	0.706	0.18 (-1.373, 1.733)	0.792
		P	0.000 (0.000, 0.001)	**0.000**	0.000 (0.000, 0.001)	**0.015**	0.001 (0.000, 0.001)	**0.001**	0.003 (0.001, 0.005)	**0.001**	0.000 (-0.001, 0.002)	0.504	0.000 (0.000, 0.001)	0.364	0.000 (-0.001, 0.002)	0.505
		OC	0.000 (-0.019, 0.02)	0.966	-0.018 (-0.049, 0.013)	0.255	0.02 (-0.016, 0.056)	0.281	0.114 (-0.064, 0.293)	0.208	0.014 (-0.101, 0.129)	0.783	0.032 (-0.043, 0.107)	0.356	0.024 (-0.087, 0.135)	0.628
	Land-cover	Forest	0.002 (0.002, 0.003)	**0.000**	0.002 (0.002, 0.003)	**0.000**	0.002 (0.001, 0.003)	**0.000**	0.009 (0.004, 0.014)	**0.000**	0.002 (-0.001, 0.005)	0.246	0.001 (-0.001, 0.003)	0.339	0.001 (-0.002, 0.004)	0.342
		Shape	-7.965 (-9.525, -6.404)	**0.000**	-7.974 (-10.587, -5.362)	**0.000**	-7.83 (-11.207, -4.453)	**0.000**	-29.684 (-45.243, -14.126)	**0.000**	-5.899 (-14.688, 2.891)	0.157	-2.722 (-7.685, 2.242)	0.242	-5.02 (-13.977, 3.937)	0.227
		SecVeg	-0.005 (-0.006, -0.004)	**0.000**	-0.004 (-0.007, -0.002)	**0.000**	-0.003 (-0.006, 0.000)	**0.030**	-0.015 (-0.029, -0.002)	**0.028**	-0.003 (-0.012, 0.006)	0.439	-0.001 (-0.007, 0.005)	0.712	-0.003 (-0.011, 0.006)	0.482
		UCL	-0.002 (-0.002, -0.001)	**0.000**	-0.002 (-0.003, -0.001)	**0.003**	-0.001 (-0.002, 0.000)	0.178	-0.004 (-0.011, 0.002)	0.202	-0.001 (-0.005, 0.003)	0.626	0.000 (-0.003, 0.002)	0.739	-0.001 (-0.005, 0.004)	0.777
		ULC.type	-0.009 (-0.011, -0.007)	**0.000**	-0.009 (-0.012, -0.006)	**0.000**	-0.006 (-0.009, -0.002)	**0.001**	-0.024 (-0.04, -0.008)	**0.004**	-0.007 (-0.017, 0.003)	0.151	-0.002 (-0.008, 0.003)	0.346	-0.006 (-0.016, 0.004)	0.212
		Roughness	0.003 (0.001, 0.006)	**0.013**	0.003 (-0.002, 0.007)	0.217	0.002 (-0.003, 0.007)	0.405	0.017 (-0.007, 0.042)	0.171	0.003 (-0.015, 0.02)	0.740	0.001 (-0.011, 0.013)	0.861	0.002 (-0.016, 0.019)	0.827
PA	Climate	Isoth	-0.029 (-0.037, -0.021)	**0.000**	-0.019 (-0.032, -0.007)	**0.003**	-0.021 (-0.036, -0.006)	**0.006**	-0.028 (-0.054, -0.003)	**0.029**	-0.041 (-0.099, 0.017)	0.140	-0.042 (-0.092, 0.007)	0.082	-0.045 (-0.112, 0.023)	0.166
		TAP	0.000 (0.000, 0.000)	0.393	0.000 (0.000, 0.000)	0.150	0.000 (0.000, 0.000)	0.170	0.000 (0.000, 0.000)	0.325	0.000 (-0.001, 0.001)	0.722	0.000 (-0.001, 0.000)	0.732	0.000 (-0.001, 0.001)	0.747
		TPdriests	-0.001 (-0.001, 0.000)	**0.001**	-0.001 (-0.001, 0.000)	0.213	-0.001 (-0.002, 0.000)	0.256	-0.001 (-0.003, 0.001)	0.296	-0.003 (-0.006, 0.001)	0.129	-0.003 (-0.006, 0.001)	0.117	-0.003 (-0.007, 0.001)	0.139
		PET	0.000 (0.000, 0.000)	**0.001**	0.000 (0.000, 0.000)	0.275	0.000 (0.000, 0.001)	0.168	0.000 (0.000, 0.001)	0.292	0.000 (-0.002, 0.001)	0.763	0.000 (-0.001, 0.001)	0.877	0.000 (-0.002, 0.001)	0.708
		Aridity	0.118 (0.056, 0.18)	**0.000**	0.023 (-0.071, 0.118)	0.628	0.026 (-0.086, 0.139)	0.645	0.043 (-0.157, 0.242)	0.675	0.242 (-0.17, 0.654)	0.212	0.244 (-0.116, 0.604)	0.157	0.263 (-0.213, 0.74)	0.238
		Ard	-0.001 (-0.003, 0.000)	0.076	0.001 (-0.002, 0.003)	0.602	0.000 (-0.002, 0.003)	0.772	0.000 (-0.004, 0.004)	0.960	-0.003 (-0.013, 0.007)	0.466	-0.003 (-0.012, 0.005)	0.397	-0.004 (-0.015, 0.008)	0.495
		SRad	0.000 (0.000, 0.000)	0.811	0.000 (0.000, 0.000)	0.367	0.000 (0.000, 0.000)	0.431	0.000 (0.000, 0.000)	0.933	0.000 (0.000, 0.000)	0.814	0.000 (0.000, 0.000)	0.810	0.000 (0.000, 0.000)	0.836
		WVP	0.326 (0.121, 0.531)	**0.002**	0.192 (-0.149, 0.534)	0.268	0.304 (-0.104, 0.712)	0.144	0.495 (-0.178, 1.168)	0.149	0.136 (-1.623, 1.895)	0.863	0.219 (-1.359, 1.798)	0.757	0.104 (-1.911, 2.119)	0.908
		Wind	0.06 (0.03, 0.09)	**0.000**	0.029 (-0.018, 0.076)	0.223	0.036 (-0.024, 0.095)	0.236	0.064 (-0.036, 0.163)	0.210	0.113 (-0.098, 0.325)	0.252	0.112 (-0.075, 0.299)	0.203	0.123 (-0.122, 0.368)	0.279
	Soils	Sand	0.006 (0.002, 0.009)	**0.000**	0.003 (-0.002, 0.008)	0.205	0.004 (-0.002, 0.01)	0.221	0.006 (-0.005, 0.016)	0.272	-0.003 (-0.029, 0.023)	0.777	-0.001 (-0.024, 0.023)	0.930	-0.005 (-0.034, 0.025)	0.711
		Silt	-0.009 (-0.016, -0.002)	**0.012**	-0.007 (-0.019, 0.004)	0.208	-0.009 (-0.023, 0.005)	0.194	-0.011 (-0.034, 0.012)	0.335	0.02 (-0.037, 0.077)	0.439	0.014 (-0.038, 0.066)	0.553	0.025 (-0.04, 0.09)	0.406
		Clay	-0.01 (-0.015, -0.005)	**0.000**	-0.005 (-0.012, 0.003)	0.249	-0.005 (-0.015, 0.005)	0.297	-0.009 (-0.026, 0.007)	0.277	-0.001 (-0.043, 0.04)	0.938	-0.005 (-0.042, 0.033)	0.786	0.000 (-0.047, 0.048)	0.984
		pH	-0.085 (-0.13, -0.041)	**0.000**	-0.089 (-0.156, -0.022)	**0.009**	-0.085 (-0.156, -0.014)	**0.019**	-0.089 (-0.215, 0.036)	0.163	-0.177 (-0.568, 0.214)	0.327	-0.185 (-0.529, 0.159)	0.251	-0.206 (-0.652, 0.239)	0.317
		CEC	-0.016 (-0.021, -0.01)	**0.000**	-0.012 (-0.02, -0.003)	**0.006**	-0.012 (-0.022, -0.002)	**0.015**	-0.016 (-0.033, 0.001)	0.067	-0.015 (-0.061, 0.03)	0.461	-0.018 (-0.058, 0.023)	0.343	-0.016 (-0.068, 0.037)	0.513
		Ca	-0.011 (-0.015, -0.007)	**0.000**	-0.009 (-0.015, -0.002)	**0.007**	-0.009 (-0.016, -0.002)	**0.014**	-0.011 (-0.024, 0.001)	0.079	-0.013 (-0.047, 0.022)	0.426	-0.015 (-0.045, 0.015)	0.288	-0.013 (-0.053, 0.027)	0.464
		Mg	-0.017 (-0.026, -0.009)	**0.000**	-0.01 (-0.025, 0.004)	0.151	-0.014 (-0.031, 0.003)	0.108	-0.021 (-0.049, 0.006)	0.129	-0.008 (-0.077, 0.062)	0.807	-0.011 (-0.073, 0.051)	0.693	-0.006 (-0.086, 0.073)	0.858
		K	-0.457 (-0.65, -0.264)	**0.000**	-0.355 (-0.661, -0.049)	**0.023**	-0.395 (-0.756, -0.034)	**0.032**	-0.462 (-1.083, 0.158)	0.143	-0.993 (-2.461, 0.474)	0.157	-0.903 (-2.222, 0.415)	0.153	-1.152 (-2.824, 0.519)	0.151
		Na	1.809 (1.043, 2.574)	**0.000**	1.322 (0.144, 2.501)	**0.028**	1.713 (0.252, 3.174)	**0.022**	1.731 (-0.844, 4.305)	0.187	4.967 (0.564, 9.37)	**0.032**	4.781 (1.058, 8.504)	**0.018**	5.784 (0.824, 10.743)	**0.028**
		P	0.000 (-0.001, 0.001)	0.886	0.000 (-0.001, 0.001)	0.864	0.000 (-0.002, 0.001)	0.494	0.000 (-0.002, 0.002)	0.973	-0.001 (-0.006, 0.004)	0.637	-0.001 (-0.005, 0.003)	0.537	-0.001 (-0.007, 0.004)	0.559
		OC	-0.155 (-0.21, -0.099)	**0.000**	-0.091 (-0.178, -0.004)	**0.041**	-0.112 (-0.217, -0.006)	**0.038**	-0.127 (-0.31, 0.055)	0.170	-0.345 (-0.688, -0.002)	**0.049**	-0.341 (-0.628, -0.054)	**0.025**	-0.391 (-0.786, 0.005)	0.052
	Land-cover	Forest	0.003 (0.001, 0.004)	**0.000**	0.002 (-0.001, 0.004)	0.207	0.002 (-0.001, 0.005)	0.237	0.004 (-0.001, 0.009)	0.125	0.003 (-0.008, 0.014)	0.491	0.003 (-0.007, 0.013)	0.465	0.004 (-0.009, 0.016)	0.526
		Shape	-7.158 (-11.265, -3.051)	**0.001**	-4.662 (-11.247, 1.922)	0.165	-7.258 (-16.38, 1.865)	0.119	-11.394 (-26.034, 3.246)	0.127	-7.308 (-36.977, 22.362)	0.586	-7.017 (-33.678, 19.644)	0.561	-7.954 (-41.961, 26.053)	0.604
		SecVeg	-0.006 (-0.01, -0.002)	**0.003**	-0.004 (-0.011, 0.003)	0.218	-0.004 (-0.013, 0.004)	0.326	-0.009 (-0.024, 0.005)	0.215	-0.007 (-0.04, 0.027)	0.669	-0.004 (-0.035, 0.027)	0.780	-0.006 (-0.045, 0.033)	0.733

Trait	Environmental variable		inds		pops		sps		$sps_{80\%}$		CWM_{pops}		CWM_{sps}		$CWM_{80\%}$	
			β_0 (95% CI)	*P*	β_0 (95% CI)	*P*	β_0 (95% CI)	*P*	β_0 (95% CI)	*P*	β_0 (95% CI)	*P*	β_0 (95% CI)	*P*	β_0 (95% CI)	*P*
		UCL	-0.005 (-0.007, -0.003)	**0.000**	-0.004 (-0.007, -0.001)	**0.018**	-0.005 (-0.009, -0.001)	**0.013**	-0.007 (-0.014, -0.001)	**0.022**	-0.006 (-0.019, 0.008)	0.361	-0.006 (-0.018, 0.006)	0.294	-0.006 (-0.022, 0.009)	0.381
		ULC.type	-0.01 (-0.014, -0.005)	**0.000**	-0.007 (-0.014, 0.000)	0.062	-0.009 (-0.018, 0.000)	0.059	-0.012 (-0.027, 0.003)	0.114	-0.007 (-0.038, 0.024)	0.611	-0.006 (-0.034, 0.022)	0.624	-0.007 (-0.043, 0.028)	0.651
		Roughness	0.003 (-0.005, 0.011)	0.400	0.000 (-0.012, 0.013)	0.942	-0.002 (-0.017, 0.012)	0.751	0.007 (-0.018, 0.033)	0.578	0.000 (-0.069, 0.068)	0.990	0.000 (-0.062, 0.062)	0.998	-0.001 (-0.08, 0.077)	0.975
DA_{pit}	Climate	Isoth	-0.017 (-0.022, -0.013)	**0.000**	-0.013 (-0.019, -0.006)	**0.000**	-0.015 (-0.023, -0.008)	**0.000**	-0.043 (-0.068, -0.018)	**0.001**	-0.022 (-0.053, 0.009)	0.134	-0.022 (-0.047, 0.003)	0.075	-0.024 (-0.06, 0.011)	0.153
		TAP	0.000 (0.000, 0.000)	0.175	0.000 (0.000, 0.000)	0.067	0.000 (0.000, 0.000)	0.081	0.000 (0.000, 0.000)	0.074	0.000 (0.000, 0.000)	0.849	0.000 (0.000, 0.000)	0.902	0.000 (0.000, 0.000)	0.830
		TPdriests	0.000 (-0.001, 0.000)	**0.001**	0.000 (-0.001, 0.000)	0.184	0.000 (-0.001, 0.000)	0.202	-0.001 (-0.003, 0.001)	0.319	-0.001 (-0.003, 0.001)	0.199	-0.001 (-0.003, 0.001)	0.184	-0.001 (-0.004, 0.001)	0.202
		PET	0.000 (0.000, 0.000)	**0.000**	0.000 (0.000, 0.000)	0.126	0.000 (0.000, 0.000)	**0.027**	0.001 (0.000, 0.001)	0.052	0.000 (-0.001, 0.001)	0.879	0.000 (-0.001, 0.001)	0.996	0.000 (-0.001, 0.001)	0.817
		Aridity	0.064 (0.031, 0.097)	**0.000**	0.013 (-0.037, 0.062)	0.613	0.024 (-0.035, 0.082)	0.427	0.031 (-0.169, 0.23)	0.761	0.115 (-0.112, 0.342)	0.276	0.106 (-0.084, 0.296)	0.236	0.131 (-0.127, 0.39)	0.276
		Ard	0.000 (-0.001, 0.000)	0.220	0.001 (0.000, 0.002)	0.261	0.000 (-0.001, 0.002)	0.609	0.002 (-0.003, 0.006)	0.491	-0.001 (-0.007, 0.004)	0.591	-0.001 (-0.006, 0.003)	0.584	-0.002 (-0.008, 0.005)	0.570
		SRad	0.000 (0.000, 0.000)	0.360	0.000 (0.000, 0.000)	0.151	0.000 (0.000, 0.000)	0.156	0.000 (0.000, 0.000)	0.372	0.000 (0.000, 0.000)	0.942	0.000 (0.000, 0.000)	0.980	0.000 (0.000, 0.000)	0.935
		WVP	0.185 (0.077, 0.293)	**0.001**	0.113 (-0.067, 0.292)	0.218	0.189 (-0.022, 0.4)	0.079	0.627 (-0.044, 1.298)	0.067	0.08 (-0.866, 1.025)	0.851	0.107 (-0.694, 0.908)	0.766	0.064 (-1.014, 1.142)	0.894
		Wind	0.032 (0.016, 0.047)	**0.000**	0.016 (-0.009, 0.04)	0.210	0.022 (-0.009, 0.053)	0.158	0.063 (-0.037, 0.162)	0.218	0.053 (-0.064, 0.169)	0.328	0.048 (-0.051, 0.146)	0.295	0.059 (-0.074, 0.192)	0.336
	Soils	Sand	0.004 (0.002, 0.005)	**0.000**	0.003 (0.000, 0.005)	**0.039**	0.004 (0.001, 0.007)	**0.021**	0.011 (0.001, 0.021)	**0.033**	0.000 (-0.014, 0.014)	0.964	0.001 (-0.011, 0.013)	0.878	-0.001 (-0.017, 0.015)	0.903
		Silt	-0.006 (-0.01, -0.003)	**0.001**	-0.006 (-0.012, 0.000)	**0.049**	-0.008 (-0.015, -0.001)	**0.021**	-0.024 (-0.047, -0.002)	**0.037**	0.008 (-0.024, 0.039)	0.595	0.004 (-0.023, 0.031)	0.738	0.01 (-0.026, 0.045)	0.548
		Clay	-0.006 (-0.009, -0.004)	**0.000**	-0.004 (-0.008, 0.000)	0.053	-0.005 (-0.011, 0.000)	**0.038**	-0.016 (-0.033, 0.000)	0.051	-0.003 (-0.025, 0.019)	0.766	-0.004 (-0.023, 0.015)	0.630	-0.002 (-0.028, 0.023)	0.826
		pH	-0.057 (-0.08, -0.034)	**0.000**	-0.061 (-0.096, -0.026)	**0.001**	-0.06 (-0.097, -0.024)	**0.001**	-0.16 (-0.285, -0.036)	**0.012**	-0.098 (-0.307, 0.111)	0.310	-0.1 (-0.272, 0.072)	0.217	-0.11 (-0.349, 0.129)	0.320
		CEC	-0.01 (-0.013, -0.007)	**0.000**	-0.009 (-0.013, -0.004)	**0.000**	-0.01 (-0.015, -0.005)	**0.000**	-0.027 (-0.044, -0.011)	**0.001**	-0.01 (-0.034, 0.014)	0.346	-0.011 (-0.031, 0.009)	0.247	-0.011 (-0.038, 0.017)	0.390
		Ca	-0.007 (-0.009, -0.005)	**0.000**	-0.007 (-0.01, -0.003)	**0.000**	-0.007 (-0.011, -0.004)	**0.000**	-0.02 (-0.032, -0.008)	**0.001**	-0.009 (-0.027, 0.01)	0.306	-0.009 (-0.024, 0.006)	0.194	-0.009 (-0.03, 0.012)	0.343
		Mg	-0.01 (-0.014, -0.005)	**0.000**	-0.006 (-0.014, 0.001)	0.104	-0.01 (-0.018, -0.001)	**0.029**	-0.03 (-0.058, -0.002)	**0.033**	-0.006 (-0.043, 0.032)	0.735	-0.007 (-0.038, 0.025)	0.640	-0.005 (-0.048, 0.037)	0.774
		K	-0.238 (-0.34, -0.136)	**0.000**	-0.176 (-0.337, -0.015)	**0.032**	-0.259 (-0.445, -0.073)	**0.007**	-0.703 (-1.32, -0.086)	**0.026**	-0.499 (-1.303, 0.305)	0.190	-0.479 (-1.138, 0.181)	0.133	-0.565 (-1.482, 0.352)	0.193
		Na	0.948 (0.544, 1.351)	**0.000**	0.676 (0.056, 1.296)	**0.033**	1.092 (0.339, 1.846)	**0.005**	2.345 (-0.222, 4.912)	0.073	2.252 (-0.388, 4.892)	0.085	2.142 (0.037, 4.247)	**0.047**	2.633 (-0.334, 5.601)	0.075
		P	0.000 (0.000, 0.000)	0.404	0.000 (0.000, 0.001)	0.621	0.000 (-0.001, 0.000)	0.628	0.000 (-0.002, 0.002)	0.928	0.000 (-0.003, 0.002)	0.819	0.000 (-0.003, 0.002)	0.661	0.000 (-0.003, 0.002)	0.740
		OC	-0.092 (-0.121, -0.062)	**0.000**	-0.055 (-0.101, -0.009)	**0.018**	-0.081 (-0.136, -0.027)	**0.003**	-0.196 (-0.377, -0.015)	**0.034**	-0.184 (-0.369, 0.002)	0.052	-0.172 (-0.319, -0.025)	**0.027**	-0.211 (-0.421, 0.000)	0.050
	Land-cover	Forest	0.001 (0.000, 0.002)	**0.001**	0.001 (-0.001, 0.002)	0.389	0.001 (-0.001, 0.003)	0.229	0.004 (-0.001, 0.009)	0.137	0.002 (-0.004, 0.007)	0.566	0.001 (-0.004, 0.006)	0.534	0.002 (-0.005, 0.008)	0.579
		Shape	-2.793 (-4.963, -0.623)	**0.012**	-1.258 (-4.724, 2.209)	0.476	-3.636 (-8.366, 1.094)	0.131	-10.957 (-25.603, 3.688)	0.142	-2.405 (-18.555, 13.745)	0.740	-2.295 (-16.003, 11.414)	0.710	-2.78 (-21.171, 15.61)	0.736
		SecVeg	-0.004 (-0.006, -0.001)	**0.001**	-0.002 (-0.006, 0.001)	0.178	-0.003 (-0.007, 0.002)	0.227	-0.011 (-0.026, 0.003)	0.126	-0.004 (-0.022, 0.014)	0.592	-0.003 (-0.018, 0.013)	0.705	-0.004 (-0.025, 0.016)	0.650
		UCL	-0.002 (-0.003, -0.001)	**0.000**	-0.002 (-0.003, 0.000)	**0.025**	-0.003 (-0.005, -0.001)	**0.003**	-0.009 (-0.015, -0.003)	**0.005**	-0.003 (-0.01, 0.005)	0.425	-0.003 (-0.009, 0.003)	0.341	-0.003 (-0.011, 0.005)	0.434
		ULC.type	-0.005 (-0.007, -0.002)	**0.000**	-0.003 (-0.006, 0.001)	0.135	-0.005 (-0.01, -0.001)	**0.025**	-0.015 (-0.029, 0.000)	0.053	-0.003 (-0.02, 0.014)	0.700	-0.002 (-0.017, 0.012)	0.720	-0.003 (-0.022, 0.016)	0.720
		Roughness	0.000 (-0.004, 0.005)	0.846	-0.001 (-0.007, 0.006)	0.872	-0.002 (-0.01, 0.005)	0.574	0.004 (-0.022, 0.029)	0.783	0.000 (-0.037, 0.037)	0.999	0.001 (-0.03, 0.032)	0.943	0.000 (-0.042, 0.042)	0.990
FWT	Climate	Isoth	0.001 (-0.002, 0.004)	0.672	0.002 (-0.003, 0.006)	0.502	0.003 (-0.002, 0.009)	0.206	0.025 (0.000, 0.051)	0.053	-0.006 (-0.046, 0.033)	0.715	-0.002 (-0.023, 0.02)	0.865	-0.008 (-0.052, 0.036)	0.688
		TAP	0.000 (0.000, 0.000)	**0.000**	0.000 (0.000, 0.000)	**0.008**	0.000 (0.000, 0.000)	**0.015**	0.000 (0.000, 0.000)	0.151	0.000 (0.000, 0.000)	0.441	0.000 (0.000, 0.000)	0.210	0.000 (0.000, 0.001)	0.421
		TPdriests	0.000 (0.000, 0.001)	**0.001**	0.000 (0.000, 0.001)	0.134	0.000 (0.000, 0.001)	**0.044**	0.001 (0.000, 0.003)	0.120	0.001 (-0.002, 0.003)	0.464	0.001 (-0.001, 0.002)	0.229	0.001 (-0.002, 0.004)	0.450
		PET	0.000 (0.000, 0.000)	0.053	0.000 (0.000, 0.000)	0.131	0.000 (0.000, 0.000)	0.212	-0.001 (-0.001, 0.000)	**0.035**	0.000 (-0.001, 0.001)	0.909	0.000 (0.000, 0.000)	0.873	0.000 (-0.001, 0.001)	0.961
		Aridity	-0.049 (-0.072, -0.025)	**0.000**	-0.043 (-0.077, -0.01)	**0.012**	-0.059 (-0.1, -0.019)	**0.004**	-0.24 (-0.438, -0.043)	**0.017**	-0.033 (-0.304, 0.237)	0.783	-0.044 (-0.185, 0.096)	0.488	-0.039 (-0.343, 0.265)	0.775
		Ard	0.000 (0.000, 0.001)	0.593	0.000 (-0.001, 0.001)	0.868	0.000 (0.000, 0.001)	0.280	0.000 (-0.004, 0.005)	0.834	-0.001 (-0.008, 0.005)	0.589	0.000 (-0.003, 0.003)	0.964	-0.002 (-0.008, 0.005)	0.614
		SRad	0.000 (0.000, 0.000)	**0.001**	0.000 (0.000, 0.000)	0.456	0.000 (0.000, 0.000)	0.199	0.000 (0.000, 0.000)	0.889	0.000 (0.000, 0.000)	0.595	0.000 (0.000, 0.000)	0.239	0.000 (0.000, 0.000)	0.563
		WVP	-0.056 (-0.134, 0.021)	0.155	-0.013 (-0.135, 0.11)	0.839	-0.045 (-0.193, 0.103)	0.551	-0.283 (-0.958, 0.393)	0.410	-0.054 (-1.101, 0.993)	0.908	-0.115 (-0.667, 0.437)	0.644	-0.051 (-1.228, 1.126)	0.923
		Wind	-0.007 (-0.018, 0.005)	0.255	-0.002 (-0.019, 0.014)	0.779	-0.016 (-0.038, 0.005)	0.134	-0.043 (-0.143, 0.057)	0.399	0.019 (-0.117, 0.156)	0.754	-0.008 (-0.082, 0.065)	0.797	0.02 (-0.133, 0.174)	0.771
	Soils	Sand	0.000 (-0.002, 0.001)	0.562	-0.001 (-0.003, 0.001)	0.311	-0.001 (-0.004, 0.001)	0.187	-0.009 (-0.02, 0.001)	0.069	0.005 (-0.01, 0.02)	0.478	0.002 (-0.006, 0.01)	0.509	0.006 (-0.011, 0.023)	0.438
		Silt	-0.003 (-0.006, 0.000)	**0.034**	-0.001 (-0.005, 0.003)	0.733	0.000 (-0.005, 0.004)	0.857	0.008 (-0.015, 0.031)	0.491	-0.018 (-0.05, 0.014)	0.239	-0.011 (-0.027, 0.006)	0.188	-0.021 (-0.057, 0.015)	0.211
		Clay	0.002 (0.000, 0.004)	**0.018**	0.003 (0.000, 0.005)	0.062	0.004 (0.001, 0.008)	**0.023**	0.021 (0.004, 0.037)	**0.014**	-0.004 (-0.028, 0.021)	0.745	-0.001 (-0.014, 0.012)	0.867	-0.005 (-0.032, 0.023)	0.702
		pH	-0.028 (-0.045, -0.011)	**0.001**	-0.01 (-0.034, 0.014)	0.425	-0.012 (-0.038, 0.014)	0.350	0.019 (-0.107, 0.145)	0.768	-0.049 (-0.294, 0.195)	0.655	-0.05 (-0.176, 0.076)	0.391	-0.06 (-0.334, 0.214)	0.629
		CEC	-0.002 (-0.004, 0.000)	0.115	0.000 (-0.003, 0.003)	0.931	0.001 (-0.002, 0.005)	0.551	0.013 (-0.004, 0.03)	0.127	-0.012 (-0.039, 0.014)	0.317	-0.007 (-0.021, 0.008)	0.317	-0.015 (-0.044, 0.015)	0.285
		Ca	-0.001 (-0.002, 0.001)	0.254	0.001 (-0.002, 0.003)	0.598	0.001 (-0.002, 0.004)	0.513	0.01 (-0.002, 0.023)	0.101	-0.007 (-0.028, 0.014)	0.471	-0.004 (-0.015, 0.007)	0.391	-0.008 (-0.032, 0.015)	0.434

Trait	**Environmental variable**		**inds**		**pops**		**sps**		**sps$_{80\%}$**		**CWM$_{pops}$**		**CWM$_{sps}$**		**CWM$_{80\%}$**	
			β_0 (95% CI)	***P***	**β_0 (95% CI)**	***P***	**β_0 (95% CI)**	***P***	**β_0 (95% CI)**	***P***	**β_0 (95% CI)**	***P***	**β_0 (95% CI)**	***P***	**β_0 (95% CI)**	***P***
		Mg	-0.001 (-0.005, 0.002)	0.381	-0.002 (-0.007, 0.003)	0.422	0.000 (-0.006, 0.006)	0.977	0.005 (-0.023, 0.033)	0.708	-0.013 (-0.053, 0.028)	0.489	-0.005 (-0.027, 0.017)	0.622	-0.015 (-0.06, 0.03)	0.470
		K	-0.002 (-0.075, 0.071)	0.963	-0.013 (-0.123, 0.097)	0.819	-0.031 (-0.163, 0.1)	0.641	0.172 (-0.451, 0.796)	0.586	0.244 (-0.733, 1.22)	0.581	0.055 (-0.476, 0.586)	0.818	0.261 (-0.838, 1.361)	0.598
		Na	-0.025 (-0.316, 0.266)	0.866	-0.107 (-0.532, 0.317)	0.620	-0.092 (-0.624, 0.441)	0.735	-1.114 (-3.694, 1.466)	0.396	-0.664 (-4.18, 2.851)	0.675	-0.315 (-2.199, 1.568)	0.709	-0.789 (-4.734, 3.155)	0.657
		P	0.000 (-0.001, 0.000)	**0.006**	0.000 (-0.001, 0.000)	0.157	-0.001 (-0.001, 0.000)	**0.013**	-0.002 (-0.004, 0.000)	**0.049**	0.000 (-0.003, 0.003)	0.989	0.000 (-0.002, 0.001)	0.644	0.000 (-0.003, 0.003)	0.953
		OC	0.000 (-0.021, 0.021)	0.981	0.01 (-0.022, 0.041)	0.548	0.011 (-0.028, 0.049)	0.589	0.119 (-0.063, 0.301)	0.200	0.01 (-0.253, 0.274)	0.931	-0.007 (-0.148, 0.134)	0.910	0.009 (-0.287, 0.306)	0.943
	Land-cover	Forest	0.000 (0.000, 0.001)	0.143	0.001 (0.000, 0.002)	**0.049**	0.000 (-0.001, 0.001)	0.826	0.002 (-0.003, 0.007)	0.405	0.003 (-0.003, 0.009)	0.326	0.001 (-0.003, 0.004)	0.669	0.003 (-0.004, 0.01)	0.336
		Shape	-3.825 (-5.362, -2.288)	**0.000**	-4.323 (-6.655, -1.992)	**0.000**	-3.105 (-6.398, 0.189)	0.065	-16.154 (-30.721, -1.588)	**0.030**	-12.55 (-27.35, 2.251)	0.086	-4.607 (-13.462, 4.248)	0.265	-13.821 (-30.61, 2.968)	0.094
		SecVeg	0.000 (-0.002, 0.001)	0.664	-0.001 (-0.004, 0.001)	0.290	0.000 (-0.003, 0.004)	0.788	0.003 (-0.011, 0.018)	0.674	-0.004 (-0.024, 0.016)	0.680	0.000 (-0.011, 0.011)	0.965	-0.005 (-0.027, 0.018)	0.654
		UCL	-0.001 (-0.002, -0.001)	**0.000**	-0.002 (-0.003, -0.001)	**0.003**	-0.001 (-0.002, 0.000)	0.191	-0.004 (-0.011, 0.002)	0.190	-0.005 (-0.012, 0.002)	0.161	-0.002 (-0.006, 0.002)	0.331	-0.006 (-0.014, 0.003)	0.166
		ULC.type	-0.005 (-0.007, -0.003)	**0.000**	-0.005 (-0.007, -0.002)	**0.000**	-0.003 (-0.006, 0.001)	0.099	-0.011 (-0.025, 0.004)	0.162	-0.015 (-0.029, -0.001)	**0.041**	-0.006 (-0.015, 0.003)	0.148	-0.017 (-0.033, -0.001)	**0.041**
		Roughness	-0.002 (-0.005, 0.001)	0.268	0.001 (-0.003, 0.006)	0.512	-0.001 (-0.006, 0.005)	0.797	0.01 (-0.016, 0.036)	0.450	0.005 (-0.036, 0.045)	0.798	0.000 (-0.022, 0.021)	0.961	0.005 (-0.041, 0.051)	0.814
VD	Climate	Isoth	0.023 (0.015, 0.031)	**0.000**	0.02 (0.007, 0.033)	**0.003**	0.016 (0.000, 0.032)	**0.048**	0.022 (-0.004, 0.047)	0.097	0.035 (-0.022, 0.091)	0.193	0.033 (-0.015, 0.081)	0.147	0.039 (-0.023, 0.101)	0.187
		TAP	0.000 (0.000, 0.000)	0.355	0.000 (0.000, 0.000)	0.106	0.000 (0.000, 0.000)	0.054	0.000 (0.000, 0.000)	0.062	0.000 (-0.001, 0.001)	0.865	0.000 (0.000, 0.001)	0.924	0.000 (-0.001, 0.001)	0.855
		TPdriests	0.002 (0.001, 0.002)	**0.000**	0.001 (0.000, 0.002)	**0.022**	0.000 (-0.001, 0.001)	0.610	0.001 (-0.001, 0.003)	0.432	0.003 (-0.001, 0.006)	0.131	0.002 (-0.001, 0.005)	0.141	0.003 (-0.001, 0.007)	0.124
		PET	0.000 (0.000, 0.000)	0.210	0.000 (0.000, 0.000)	0.503	0.000 (0.000, 0.000)	0.713	0.000 (-0.001, 0.000)	0.830	0.000 (-0.001, 0.002)	0.664	0.000 (-0.001, 0.001)	0.850	0.000 (-0.001, 0.002)	0.682
		Aridity	-0.086 (-0.146, -0.025)	**0.006**	-0.023 (-0.118, 0.073)	0.638	0.042 (-0.078, 0.162)	0.487	0.091 (-0.109, 0.29)	0.371	-0.166 (-0.575, 0.243)	0.376	-0.146 (-0.502, 0.21)	0.371	-0.189 (-0.639, 0.262)	0.363
		Ard	0.001 (-0.001, 0.002)	0.418	-0.001 (-0.003, 0.001)	0.489	-0.002 (-0.005, 0.001)	0.152	-0.004 (-0.008, 0.001)	0.100	0.002 (-0.008, 0.011)	0.693	0.002 (-0.007, 0.01)	0.686	0.002 (-0.009, 0.013)	0.683
		SRad	0.000 (0.000, 0.000)	**0.031**	0.000 (0.000, 0.000)	0.941	0.000 (0.000, 0.000)	0.386	0.000 (0.000, 0.000)	0.677	0.000 (0.000, 0.000)	0.505	0.000 (0.000, 0.000)	0.493	0.000 (0.000, 0.000)	0.491
		WVP	-0.259 (-0.459, -0.06)	**0.011**	-0.205 (-0.549, 0.139)	0.243	-0.19 (-0.625, 0.245)	0.390	-0.36 (-1.034, 0.315)	0.294	-0.332 (-1.972, 1.308)	0.653	-0.417 (-1.825, 0.991)	0.514	-0.39 (-2.199, 1.42)	0.633
		Wind	-0.091 (-0.12, -0.062)	**0.000**	-0.056 (-0.103, -0.009)	**0.020**	-0.022 (-0.085, 0.041)	0.498	-0.037 (-0.137, 0.063)	0.462	-0.125 (-0.318, 0.068)	0.173	-0.108 (-0.276, 0.061)	0.179	-0.139 (-0.351, 0.073)	0.170
	Soils	Sand	-0.002 (-0.005, 0.001)	0.119	-0.002 (-0.007, 0.003)	0.435	-0.005 (-0.011, 0.002)	0.167	-0.005 (-0.015, 0.005)	0.343	-0.001 (-0.025, 0.024)	0.947	-0.002 (-0.023, 0.019)	0.838	-0.001 (-0.028, 0.026)	0.954
		Silt	0.001 (-0.006, 0.008)	0.783	0.003 (-0.009, 0.014)	0.654	0.011 (-0.003, 0.026)	0.123	0.012 (-0.011, 0.035)	0.290	-0.011 (-0.066, 0.045)	0.671	-0.007 (-0.056, 0.041)	0.742	-0.012 (-0.073, 0.049)	0.663
		Clay	0.006 (0.001, 0.01)	**0.022**	0.004 (-0.004, 0.012)	0.347	0.006 (-0.005, 0.017)	0.262	0.007 (-0.01, 0.023)	0.437	0.007 (-0.032, 0.046)	0.686	0.008 (-0.025, 0.042)	0.575	0.008 (-0.035, 0.051)	0.691
		pH	0.072 (0.029, 0.115)	**0.001**	0.094 (0.027, 0.161)	**0.006**	0.08 (0.004, 0.155)	**0.039**	0.114 (-0.011, 0.239)	0.073	0.11 (-0.273, 0.492)	0.527	0.092 (-0.241, 0.426)	0.541	0.123 (-0.3, 0.545)	0.522
		CEC	0.012 (0.007, 0.017)	**0.000**	0.012 (0.003, 0.02)	**0.007**	0.012 (0.002, 0.023)	**0.022**	0.016 (-0.001, 0.033)	0.066	0.015 (-0.027, 0.058)	0.432	0.015 (-0.022, 0.052)	0.377	0.017 (-0.031, 0.064)	0.445
		Ca	0.011 (0.007, 0.014)	**0.000**	0.011 (0.004, 0.017)	**0.001**	0.011 (0.003, 0.018)	**0.007**	0.014 (0.002, 0.027)	**0.025**	0.015 (-0.017, 0.047)	0.306	0.014 (-0.014, 0.041)	0.287	0.016 (-0.019, 0.052)	0.315
		Mg	0.009 (0.001, 0.017)	**0.035**	0.008 (-0.006, 0.022)	0.275	0.01 (-0.008, 0.028)	0.264	0.013 (-0.015, 0.041)	0.360	0.01 (-0.056, 0.075)	0.743	0.014 (-0.042, 0.07)	0.585	0.011 (-0.061, 0.083)	0.737
		K	0.108 (-0.081, 0.297)	0.261	0.178 (-0.132, 0.488)	0.261	0.214 (-0.172, 0.6)	0.276	0.276 (-0.346, 0.899)	0.383	0.375 (-1.176, 1.926)	0.592	0.436 (-0.895, 1.766)	0.472	0.457 (-1.25, 2.163)	0.554
		Na	-1.691 (-2.435, -0.947)	**0.000**	-1.484 (-2.672, -0.297)	**0.014**	-0.822 (-2.387, 0.743)	0.302	-0.985 (-3.566, 1.596)	0.453	-3.037 (-8.105, 2.032)	0.204	-2.486 (-6.965, 1.992)	0.236	-3.516 (-9.052, 2.02)	0.181
		P	0.000 (-0.001, 0.000)	0.663	0.000 (-0.001, 0.001)	0.696	0.000 (-0.001, 0.002)	0.712	0.000 (-0.002, 0.002)	0.917	0.000 (-0.004, 0.005)	0.959	0.000 (-0.004, 0.004)	0.978	0.000 (-0.005, 0.005)	0.903
		OC	0.071 (0.017, 0.126)	**0.010**	0.083 (-0.005, 0.171)	0.065	0.058 (-0.055, 0.171)	0.311	0.045 (-0.138, 0.228)	0.625	0.178 (-0.214, 0.571)	0.325	0.178 (-0.157, 0.512)	0.256	0.203 (-0.229, 0.635)	0.310
	Land-cover	Forest	-0.004 (-0.005, -0.002)	**0.000**	-0.002 (-0.005, 0.000)	0.053	-0.002 (-0.005, 0.002)	0.308	-0.003 (-0.008, 0.002)	0.310	-0.005 (-0.015, 0.005)	0.311	-0.004 (-0.013, 0.004)	0.275	-0.005 (-0.016, 0.006)	0.309
		Shape	9.245 (5.269, 13.221)	**0.000**	5.308 (-1.331, 11.947)	0.117	4.527 (-5.203, 14.258)	0.361	5.497 (-9.198, 20.192)	0.462	8.109 (-19.649, 35.868)	0.520	6.893 (-17.333, 31.118)	0.530	9.017 (-21.651, 39.684)	0.517
		SecVeg	0.002 (-0.002, 0.006)	0.251	0.001 (-0.006, 0.008)	0.778	0.001 (-0.008, 0.011)	0.788	0.004 (-0.01, 0.019)	0.580	0.003 (-0.029, 0.036)	0.815	0.006 (-0.022, 0.033)	0.654	0.003 (-0.032, 0.039)	0.845
		UCL	0.007 (0.005, 0.008)	**0.000**	0.005 (0.002, 0.008)	**0.000**	0.005 (0.001, 0.009)	**0.012**	0.007 (0.001, 0.013)	**0.027**	0.007 (-0.004, 0.019)	0.187	0.007 (-0.004, 0.017)	0.171	0.008 (-0.005, 0.021)	0.184
		ULC.type	0.006 (0.001, 0.01)	**0.011**	0.003 (-0.005, 0.01)	0.484	0.003 (-0.007, 0.012)	0.561	0.002 (-0.012, 0.017)	0.742	0.003 (-0.027, 0.033)	0.834	0.003 (-0.023, 0.029)	0.805	0.003 (-0.03, 0.036)	0.849
		Roughness	-0.019 (-0.027, -0.012)	**0.000**	-0.011 (-0.023, 0.001)	0.070	-0.009 (-0.024, 0.007)	0.272	-0.017 (-0.043, 0.008)	0.188	-0.029 (-0.09, 0.031)	0.292	-0.026 (-0.078, 0.026)	0.282	-0.033 (-0.099, 0.034)	0.291
d$_h$	Climate	Isoth	-0.012 (-0.016, -0.008)	**0.000**	-0.009 (-0.015, -0.002)	**0.009**	-0.009 (-0.017, -0.001)	**0.023**	-0.021 (-0.046, 0.005)	0.115	-0.018 (-0.046, 0.009)	0.160	-0.02 (-0.044, 0.005)	0.106	-0.021 (-0.051, 0.008)	0.137
		TAP	0.000 (0.000, 0.000)	**0.000**	0.000 (0.000, 0.000)	**0.000**	0.000 (0.000, 0.000)	**0.001**	0.000 (0.000, 0.000)	**0.007**	0.000 (0.000, 0.000)	0.615	0.000 (0.000, 0.000)	0.611	0.000 (0.000, 0.000)	0.622
		TPdriests	0.000 (-0.001, 0.000)	0.068	0.000 (0.000, 0.000)	0.854	0.000 (0.000, 0.001)	0.505	0.000 (-0.002, 0.002)	0.975	-0.001 (-0.003, 0.001)	0.416	-0.001 (-0.002, 0.001)	0.411	-0.001 (-0.003, 0.001)	0.402
		PET	0.000 (0.000, 0.000)	0.675	0.000 (0.000, 0.000)	0.758	0.000 (0.000, 0.000)	0.268	0.000 (0.000, 0.001)	0.622	0.000 (-0.001, 0.001)	0.952	0.000 (-0.001, 0.001)	0.828	0.000 (-0.001, 0.001)	0.991
		Aridity	-0.011 (-0.041, 0.019)	0.487	-0.044 (-0.091, 0.004)	0.074	-0.059 (-0.118, 0.001)	0.054	-0.172 (-0.371, 0.026)	0.089	0.041 (-0.169, 0.251)	0.667	0.048 (-0.15, 0.245)	0.593	0.051 (-0.178, 0.28)	0.619
		Ard	0.001 (0.000, 0.002)	**0.001**	0.002 (0.001, 0.003)	**0.002**	0.002 (0.001, 0.003)	**0.003**	0.006 (0.001, 0.01)	**0.011**	0.000 (-0.005, 0.005)	0.946	0.000 (-0.005, 0.005)	0.993	0.000 (-0.005, 0.005)	0.982
		SRad	0.000 (0.000, 0.000)	**0.007**	0.000 (0.000, 0.000)	**0.025**	0.000 (0.000, 0.000)	**0.008**	0.000 (0.000, 0.000)	0.157	0.000 (0.000, 0.000)	0.907	0.000 (0.000, 0.000)	0.922	0.000 (0.000, 0.000)	0.931

Trait	Environmental variable		inds		pops		sps		$sps_{80\%}$		CWM_{pops}		CWM_{sps}		$CWM_{80\%}$	
			β_0 (95% CI)	*P*	β_0 (95% CI)	*P*	β_0 (95% CI)	*P*	β_0 (95% CI)	*P*	β_0 (95% CI)	*P*	β_0 (95% CI)	*P*	β_0 (95% CI)	*P*
K_p		WVP	0.057 (-0.042, 0.156)	0.261	0.056 (-0.117, 0.229)	0.527	0.061 (-0.156, 0.278)	0.579	0.246 (-0.43, 0.921)	0.474	0.122 (-0.693, 0.936)	0.740	0.185 (-0.578, 0.948)	0.592	0.159 (-0.73, 1.048)	0.690
		Wind	0.013 (-0.001, 0.028)	0.070	-0.002 (-0.026, 0.021)	0.841	-0.014 (-0.046, 0.017)	0.380	-0.015 (-0.115, 0.085)	0.766	0.033 (-0.071, 0.137)	0.487	0.032 (-0.066, 0.131)	0.474	0.039 (-0.074, 0.152)	0.451
	Soils	Sand	0.003 (0.001, 0.004)	**0.001**	0.002 (-0.001, 0.004)	0.173	0.003 (0.000, 0.006)	0.058	0.006 (-0.005, 0.016)	0.277	0.002 (-0.01, 0.014)	0.692	0.003 (-0.008, 0.014)	0.558	0.003 (-0.011, 0.016)	0.669
		Silt	-0.006 (-0.009, -0.003)	**0.001**	-0.006 (-0.011, 0.000)	0.056	-0.01 (-0.017, -0.002)	**0.009**	-0.018 (-0.041, 0.005)	0.125	-0.001 (-0.029, 0.027)	0.932	-0.003 (-0.029, 0.024)	0.827	-0.001 (-0.032, 0.029)	0.913
		Clay	-0.004 (-0.006, -0.001)	**0.003**	-0.002 (-0.006, 0.002)	0.393	-0.003 (-0.008, 0.002)	0.236	-0.006 (-0.022, 0.011)	0.512	-0.005 (-0.024, 0.014)	0.564	-0.006 (-0.024, 0.011)	0.431	-0.006 (-0.026, 0.015)	0.542
		pH	-0.071 (-0.092, -0.05)	**0.000**	-0.071 (-0.105, -0.038)	**0.000**	-0.066 (-0.103, -0.029)	**0.001**	-0.155 (-0.28, -0.031)	**0.015**	-0.1 (-0.276, 0.077)	0.229	-0.097 (-0.263, 0.069)	0.213	-0.112 (-0.304, 0.08)	0.216
		CEC	-0.009 (-0.011, -0.006)	**0.000**	-0.007 (-0.011, -0.003)	**0.001**	-0.008 (-0.013, -0.003)	**0.002**	-0.018 (-0.034, -0.001)	**0.040**	-0.011 (-0.031, 0.009)	0.233	-0.012 (-0.03, 0.007)	0.181	-0.013 (-0.034, 0.009)	0.218
		Ca	-0.007 (-0.009, -0.006)	**0.000**	-0.006 (-0.009, -0.003)	**0.000**	-0.007 (-0.011, -0.003)	**0.000**	-0.016 (-0.028, -0.004)	**0.011**	-0.01 (-0.025, 0.004)	0.142	-0.011 (-0.024, 0.003)	0.108	-0.012 (-0.027, 0.004)	0.132
		Mg	-0.005 (-0.009, -0.001)	**0.014**	-0.004 (-0.011, 0.003)	0.253	-0.006 (-0.015, 0.003)	0.198	-0.012 (-0.04, 0.016)	0.385	-0.008 (-0.04, 0.024)	0.594	-0.01 (-0.04, 0.02)	0.463	-0.01 (-0.044, 0.025)	0.546
		K	-0.221 (-0.314, -0.129)	**0.000**	-0.213 (-0.367, -0.058)	**0.007**	-0.254 (-0.445, -0.063)	**0.009**	-0.526 (-1.146, 0.094)	0.096	-0.376 (-1.093, 0.341)	0.261	-0.407 (-1.068, 0.254)	0.193	-0.424 (-1.205, 0.358)	0.246
		Na	0.833 (0.465, 1.2)	**0.000**	0.609 (0.011, 1.207)	**0.046**	0.573 (-0.207, 1.352)	0.149	1.153 (-1.427, 3.733)	0.380	1.378 (-1.169, 3.925)	0.247	1.343 (-1.058, 3.745)	0.233	1.598 (-1.159, 4.355)	0.218
		P	0.000 (-0.001, 0.000)	0.052	0.000 (-0.001, 0.000)	0.109	-0.001 (-0.001, 0.000)	0.099	-0.001 (-0.003, 0.001)	0.474	0.000 (-0.003, 0.002)	0.713	0.000 (-0.002, 0.002)	0.696	0.000 (-0.003, 0.002)	0.655
		OC	-0.064 (-0.091, -0.038)	**0.000**	-0.049 (-0.094, -0.005)	**0.029**	-0.056 (-0.112, 0.000)	**0.050**	-0.085 (-0.268, 0.097)	0.358	-0.126 (-0.305, 0.053)	0.144	-0.135 (-0.297, 0.028)	0.092	-0.146 (-0.338, 0.047)	0.119
	Land-cover	Forest	0.001 (0.000, 0.002)	**0.015**	0.000 (-0.001, 0.001)	0.833	0.000 (-0.002, 0.001)	0.803	0.001 (-0.004, 0.006)	0.821	0.001 (-0.004, 0.007)	0.533	0.001 (-0.003, 0.006)	0.518	0.002 (-0.004, 0.007)	0.500
		Shape	-1.849 (-3.825, 0.127)	0.067	-0.002 (-3.346, 3.341)	0.999	0.638 (-4.222, 5.498)	0.796	-0.208 (-14.92, 14.504)	0.978	-1.819 (-15.823, 12.186)	0.772	-1.443 (-14.744, 11.857)	0.809	-2.419 (-17.716, 12.879)	0.725
		SecVeg	0.000 (-0.002, 0.002)	0.737	0.000 (-0.003, 0.004)	0.819	0.000 (-0.004, 0.005)	0.893	-0.001 (-0.016, 0.013)	0.840	-0.002 (-0.018, 0.014)	0.806	-0.002 (-0.017, 0.013)	0.769	-0.002 (-0.019, 0.016)	0.823
		UCL	-0.003 (-0.003, -0.002)	**0.000**	-0.002 (-0.003, 0.000)	**0.014**	-0.002 (-0.004, 0.000)	**0.048**	-0.006 (-0.012, 0.001)	0.082	-0.003 (-0.009, 0.003)	0.272	-0.003 (-0.009, 0.003)	0.262	-0.004 (-0.01, 0.003)	0.240
		ULC.type	-0.001 (-0.003, 0.001)	0.264	0.000 (-0.003, 0.004)	0.784	0.000 (-0.005, 0.005)	0.994	0.001 (-0.014, 0.016)	0.919	-0.001 (-0.015, 0.014)	0.922	0.000 (-0.014, 0.014)	0.947	-0.001 (-0.017, 0.015)	0.887
		Roughness	0.006 (0.002, 0.01)	**0.001**	0.003 (-0.003, 0.009)	0.397	0.001 (-0.007, 0.009)	0.854	0.01 (-0.016, 0.036)	0.441	0.01 (-0.021, 0.041)	0.499	0.009 (-0.021, 0.038)	0.514	0.01 (-0.024, 0.044)	0.507
	Climate	Isoth	-0.02 (-0.031, -0.008)	**0.001**	-0.007 (-0.027, 0.013)	0.475	-0.013 (-0.037, 0.012)	0.310	-0.004 (-0.03, 0.022)	0.775	-0.03 (-0.1, 0.04)	0.348	-0.039 (-0.105, 0.027)	0.209	-0.039 (-0.112, 0.035)	0.257
		TAP	0.000 (0.000, 0.001)	**0.000**	0.000 (0.000, 0.001)	**0.000**	0.000 (0.000, 0.001)	**0.000**	0.000 (0.000, 0.001)	**0.001**	0.000 (0.000, 0.001)	0.125	0.000 (0.000, 0.001)	0.174	0.000 (0.000, 0.001)	0.127
		TPdriests	0.001 (0.000, 0.002)	**0.017**	0.001 (0.000, 0.003)	**0.041**	0.002 (0.000, 0.004)	**0.036**	0.001 (-0.001, 0.003)	0.209	0.000 (-0.004, 0.005)	0.852	0.000 (-0.005, 0.005)	0.981	0.000 (-0.005, 0.005)	0.877
		PET	0.000 (0.000, 0.000)	0.182	0.000 (0.000, 0.001)	0.416	0.000 (0.000, 0.001)	0.224	0.000 (0.000, 0.001)	0.754	0.000 (-0.001, 0.002)	0.800	0.000 (-0.001, 0.002)	0.601	0.000 (-0.001, 0.002)	0.726
		Aridity	-0.247 (-0.336, -0.157)	**0.000**	-0.34 (-0.482, -0.198)	**0.000**	-0.365 (-0.545, -0.186)	**0.000**	-0.332 (-0.527, -0.137)	**0.001**	-0.128 (-0.624, 0.369)	0.570	-0.059 (-0.558, 0.441)	0.793	-0.102 (-0.642, 0.438)	0.675
		Ard	0.008 (0.006, 0.01)	**0.000**	0.009 (0.006, 0.013)	**0.000**	0.01 (0.006, 0.014)	**0.000**	0.009 (0.004, 0.013)	**0.000**	0.005 (-0.006, 0.016)	0.300	0.004 (-0.007, 0.015)	0.417	0.004 (-0.007, 0.016)	0.407
		SRad	0.000 (0.000, 0.000)	**0.000**	0.000 (0.000, 0.000)	**0.000**	0.000 (0.000, 0.000)	**0.000**	0.000 (0.000, 0.000)	**0.039**	0.000 (-0.001, 0.000)	0.304	0.000 (-0.001, 0.000)	0.365	0.000 (-0.001, 0.000)	0.309
		WVP	-0.003 (-0.302, 0.295)	0.983	0.042 (-0.484, 0.567)	0.875	0.043 (-0.624, 0.71)	0.899	0.044 (-0.632, 0.72)	0.897	0.087 (-1.87, 2.044)	0.921	0.284 (-1.638, 2.207)	0.742	0.187 (-1.917, 2.29)	0.843
		Wind	-0.067 (-0.111, -0.024)	**0.002**	-0.108 (-0.18, -0.037)	**0.003**	-0.139 (-0.235, -0.044)	**0.004**	-0.096 (-0.195, 0.004)	0.059	-0.039 (-0.293, 0.216)	0.736	-0.018 (-0.272, 0.235)	0.871	-0.026 (-0.302, 0.25)	0.834
	Soils	Sand	0.007 (0.003, 0.012)	**0.001**	0.004 (-0.004, 0.011)	0.331	0.007 (-0.003, 0.017)	0.157	0.003 (-0.007, 0.013)	0.590	0.008 (-0.02, 0.036)	0.531	0.011 (-0.017, 0.038)	0.399	0.01 (-0.02, 0.04)	0.452
		Silt	-0.025 (-0.036, -0.015)	**0.000**	-0.022 (-0.039, -0.004)	**0.015**	-0.031 (-0.053, -0.009)	**0.006**	-0.017 (-0.04, 0.006)	0.139	-0.019 (-0.083, 0.045)	0.509	-0.022 (-0.085, 0.041)	0.445	-0.024 (-0.092, 0.044)	0.441
		Clay	-0.007 (-0.014, 0.000)	0.062	0.001 (-0.011, 0.013)	0.894	-0.002 (-0.019, 0.014)	0.769	0.002 (-0.015, 0.018)	0.849	-0.011 (-0.056, 0.034)	0.591	-0.016 (-0.06, 0.028)	0.419	-0.014 (-0.063, 0.034)	0.511
		pH	-0.215 (-0.278, -0.151)	**0.000**	-0.21 (-0.311, -0.108)	**0.000**	-0.207 (-0.322, -0.093)	**0.000**	-0.142 (-0.267, -0.018)	**0.026**	-0.295 (-0.69, 0.101)	0.124	-0.306 (-0.69, 0.077)	0.103	-0.339 (-0.754, 0.076)	0.096
		CEC	-0.021 (-0.029, -0.013)	**0.000**	-0.014 (-0.027, -0.001)	**0.036**	-0.019 (-0.035, -0.003)	**0.019**	-0.01 (-0.027, 0.007)	0.235	-0.028 (-0.075, 0.02)	0.216	-0.031 (-0.077, 0.014)	0.149	-0.034 (-0.083, 0.016)	0.153
		Ca	-0.018 (-0.024, -0.013)	**0.000**	-0.014 (-0.023, -0.004)	**0.005**	-0.018 (-0.029, -0.006)	**0.003**	-0.011 (-0.023, 0.002)	0.089	-0.025 (-0.06, 0.009)	0.128	-0.029 (-0.061, 0.004)	0.076	-0.03 (-0.066, 0.006)	0.087
		Mg	-0.012 (-0.024, 0.001)	0.066	-0.007 (-0.029, 0.015)	0.528	-0.011 (-0.038, 0.017)	0.444	-0.004 (-0.031, 0.024)	0.800	-0.019 (-0.095, 0.057)	0.582	-0.025 (-0.099, 0.049)	0.453	-0.026 (-0.107, 0.055)	0.477
		K	-0.807 (-1.086, -0.529)	**0.000**	-0.754 (-1.223, -0.286)	**0.002**	-0.889 (-1.473, -0.305)	**0.003**	-0.541 (-1.16, 0.079)	0.087	-1.187 (-2.777, 0.404)	0.124	-1.279 (-2.797, 0.238)	0.088	-1.305 (-3.005, 0.395)	0.115
		Na	0.793 (-0.324, 1.91)	0.164	0.187 (-1.636, 2.009)	0.840	0.439 (-1.962, 2.841)	0.719	-0.156 (-2.74, 2.428)	0.905	1.428 (-5.114, 7.97)	0.628	2.03 (-4.329, 8.39)	0.483	1.888 (-5.102, 8.877)	0.551
		P	-0.001 (-0.002, 0.000)	**0.008**	-0.001 (-0.003, 0.000)	0.059	-0.002 (-0.004, 0.000)	0.054	-0.001 (-0.003, 0.001)	0.309	-0.001 (-0.007, 0.004)	0.592	-0.001 (-0.007, 0.004)	0.522	-0.002 (-0.007, 0.004)	0.531
		OC	-0.129 (-0.21, -0.048)	**0.002**	-0.052 (-0.187, 0.083)	0.454	-0.089 (-0.262, 0.084)	0.314	0.000 (-0.184, 0.183)	0.996	-0.262 (-0.706, 0.182)	0.210	-0.32 (-0.732, 0.092)	0.111	-0.325 (-0.785, 0.136)	0.142
	Land-cover	Forest	-0.001 (-0.003, 0.002)	0.639	-0.003 (-0.006, 0.001)	0.141	-0.004 (-0.009, 0.001)	0.107	-0.002 (-0.007, 0.003)	0.387	0.000 (-0.012, 0.013)	0.961	0.001 (-0.012, 0.013)	0.919	0.001 (-0.013, 0.014)	0.876
		Shape	3.14 (-2.831, 9.112)	0.302	8.121 (-2.003, 18.244)	0.116	12.403 (-2.462, 27.268)	0.102	7.723 (-6.956, 22.402)	0.301	3.96 (-29.5, 37.421)	0.792	4.137 (-28.934, 37.208)	0.780	1.954 (-34.216, 38.125)	0.904
		SecVeg	0.000 (-0.006, 0.006)	0.907	0.001 (-0.009, 0.012)	0.793	0.002 (-0.013, 0.016)	0.825	0.001 (-0.014, 0.015)	0.924	-0.004 (-0.042, 0.034)	0.805	-0.003 (-0.04, 0.035)	0.865	-0.004 (-0.045, 0.036)	0.807
		UCL	-0.004 (-0.007, -0.001)	**0.005**	-0.002 (-0.006, 0.003)	0.501	-0.002 (-0.008, 0.004)	0.539	-0.002 (-0.008, 0.005)	0.592	-0.004 (-0.02, 0.011)	0.546	-0.005 (-0.02, 0.01)	0.498	-0.006 (-0.022, 0.011)	0.443
		ULC.type	0.003 (-0.004, 0.009)	0.403	0.008 (-0.003, 0.018)	0.164	0.007 (-0.007, 0.022)	0.324	0.008 (-0.007, 0.022)	0.322	0.004 (-0.031, 0.039)	0.820	0.004 (-0.03, 0.039)	0.777	0.001 (-0.037, 0.039)	0.937

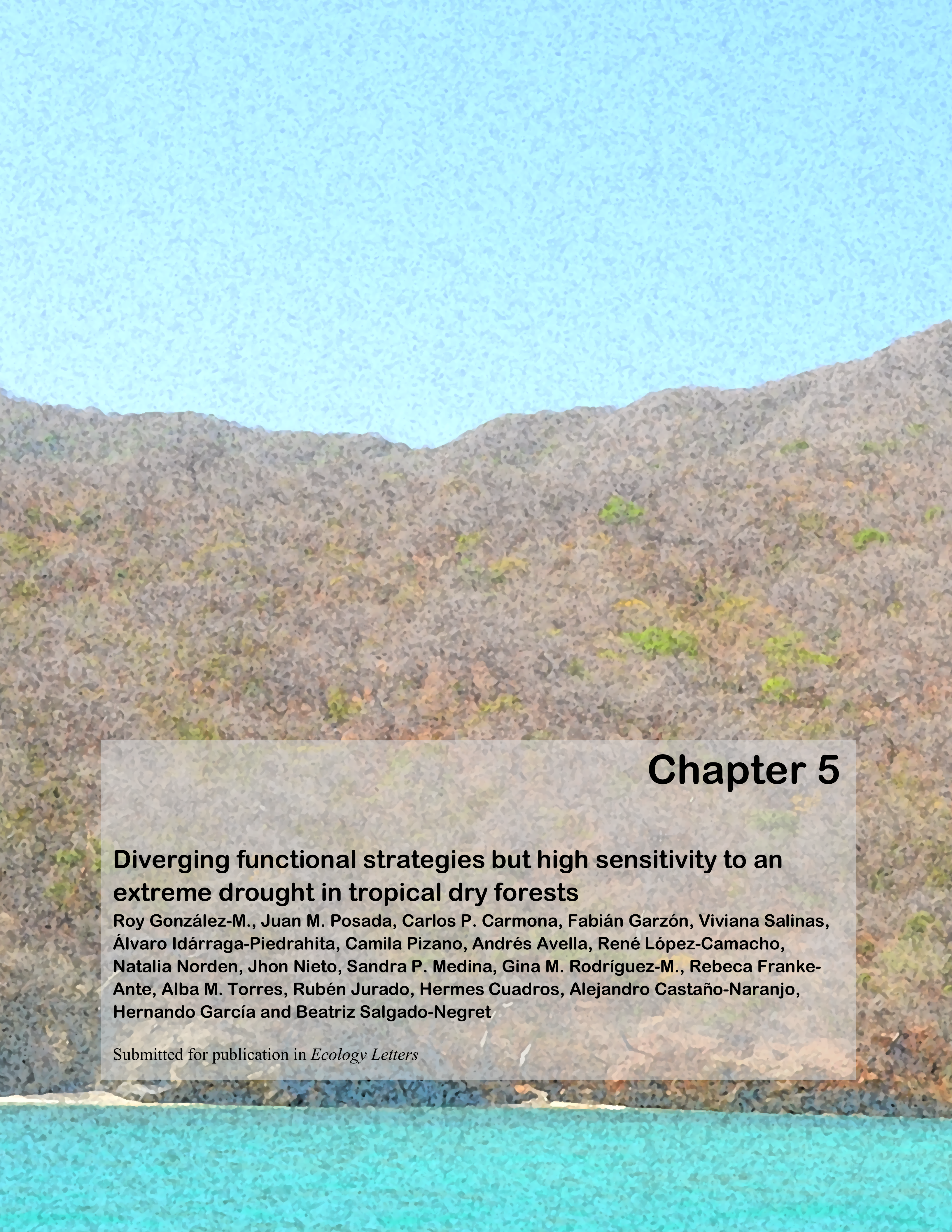
Trait	Environmental variable		inds		pops		sps		$sps_{80\%}$		CWM_{pops}		CWM_{sps}		$CWM_{80\%}$	
			β_0 (95% CI)	*P*	β_0 (95% CI)	*P*	β_0 (95% CI)	*P*	β_0 (95% CI)	*P*	β_0 (95% CI)	*P*	β_0 (95% CI)	*P*	β_0 (95% CI)	*P*
		Roughness	0.011 (-0.001, 0.022)	0.062	0.002 (-0.017, 0.02)	0.869	-0.004 (-0.028, 0.02)	0.764	0.006 (-0.02, 0.031)	0.667	0.015 (-0.06, 0.09)	0.658	0.014 (-0.061, 0.089)	0.676	0.015 (-0.067, 0.096)	0.688
VA	Climate	Isoth	-0.027 (-0.035, -0.019)	**0.000**	-0.021 (-0.035, -0.008)	**0.002**	-0.022 (-0.038, -0.005)	**0.012**	-0.025 (-0.05, 0.001)	0.058	-0.037 (-0.093, 0.019)	0.171	-0.039 (-0.09, 0.012)	0.114	-0.042 (-0.102, 0.019)	0.153
		TAP	0.000 (0.000, 0.000)	**0.000**	0.000 (0.000, 0.000)	**0.000**	0.000 (0.000, 0.000)	**0.000**	0.000 (0.000, 0.000)	**0.005**	0.000 (0.000, 0.001)	0.635	0.000 (0.000, 0.001)	0.620	0.000 (0.000, 0.001)	0.646
		TPdriests	0.000 (-0.001, 0.000)	0.105	0.000 (-0.001, 0.001)	0.899	0.001 (-0.001, 0.002)	0.406	0.000 (-0.002, 0.002)	0.875	-0.001 (-0.005, 0.002)	0.427	-0.001 (-0.005, 0.002)	0.428	-0.002 (-0.006, 0.003)	0.404
		PET	0.000 (0.000, 0.000)	0.437	0.000 (0.000, 0.000)	0.522	0.000 (0.000, 0.001)	0.169	0.000 (0.000, 0.001)	0.429	0.000 (-0.001, 0.001)	0.983	0.000 (-0.001, 0.001)	0.784	0.000 (-0.001, 0.001)	0.999
		Aridity	-0.023 (-0.087, 0.04)	0.471	-0.085 (-0.185, 0.015)	0.095	-0.128 (-0.254, -0.002)	**0.046**	-0.172 (-0.37, 0.026)	0.089	0.075 (-0.354, 0.504)	0.697	0.09 (-0.315, 0.496)	0.621	0.095 (-0.373, 0.563)	0.652
		Ard	0.003 (0.002, 0.005)	**0.000**	0.004 (0.002, 0.007)	**0.000**	0.005 (0.002, 0.008)	**0.000**	0.007 (0.003, 0.011)	**0.002**	0.001 (-0.009, 0.011)	0.792	0.001 (-0.009, 0.01)	0.877	0.001 (-0.01, 0.012)	0.868
		SRad	0.000 (0.000, 0.000)	**0.000**	0.000 (0.000, 0.000)	**0.002**	0.000 (0.000, 0.000)	**0.001**	0.000 (0.000, 0.000)	**0.036**	0.000 (0.000, 0.000)	0.831	0.000 (0.000, 0.000)	0.876	0.000 (0.000, 0.000)	0.882
		WVP	0.028 (-0.181, 0.238)	0.792	0.022 (-0.34, 0.385)	0.904	0.04 (-0.419, 0.5)	0.863	0.128 (-0.548, 0.804)	0.710	0.173 (-1.494, 1.84)	0.817	0.347 (-1.217, 1.911)	0.623	0.25 (-1.569, 2.068)	0.760
		Wind	0.018 (-0.013, 0.048)	0.260	-0.013 (-0.063, 0.037)	0.615	-0.042 (-0.108, 0.024)	0.215	-0.031 (-0.131, 0.069)	0.540	0.056 (-0.159, 0.271)	0.564	0.057 (-0.146, 0.26)	0.534	0.069 (-0.165, 0.302)	0.516
	Soils	Sand	0.007 (0.003, 0.01)	**0.000**	0.005 (0.000, 0.01)	**0.046**	0.008 (0.002, 0.015)	**0.017**	0.008 (-0.002, 0.018)	0.119	0.005 (-0.019, 0.03)	0.642	0.007 (-0.016, 0.03)	0.512	0.006 (-0.021, 0.032)	0.638
		Silt	-0.016 (-0.023, -0.008)	**0.000**	-0.015 (-0.027, -0.003)	**0.012**	-0.024 (-0.039, -0.009)	**0.002**	-0.024 (-0.047, -0.001)	**0.041**	-0.004 (-0.06, 0.053)	0.884	-0.007 (-0.06, 0.047)	0.783	-0.004 (-0.066, 0.058)	0.885
		Clay	-0.009 (-0.014, -0.004)	**0.000**	-0.006 (-0.014, 0.002)	0.147	-0.009 (-0.02, 0.002)	0.108	-0.009 (-0.026, 0.008)	0.291	-0.011 (-0.05, 0.027)	0.520	-0.014 (-0.05, 0.022)	0.389	-0.012 (-0.054, 0.03)	0.514
		pH	-0.166 (-0.21, -0.121)	**0.000**	-0.17 (-0.24, -0.1)	**0.000**	-0.157 (-0.236, -0.079)	**0.000**	-0.188 (-0.311, -0.064)	**0.003**	-0.206 (-0.564, 0.151)	0.220	-0.197 (-0.537, 0.142)	0.217	-0.227 (-0.618, 0.164)	0.218
		CEC	-0.021 (-0.026, -0.015)	**0.000**	-0.018 (-0.027, -0.009)	**0.000**	-0.02 (-0.031, -0.009)	**0.000**	-0.023 (-0.039, -0.006)	**0.008**	-0.023 (-0.064, 0.018)	0.231	-0.024 (-0.062, 0.014)	0.177	-0.025 (-0.07, 0.019)	0.229
		Ca	-0.018 (-0.022, -0.014)	**0.000**	-0.016 (-0.023, -0.01)	**0.000**	-0.018 (-0.026, -0.01)	**0.000**	-0.02 (-0.033, -0.008)	**0.001**	-0.022 (-0.051, 0.008)	0.125	-0.022 (-0.049, 0.005)	0.097	-0.024 (-0.056, 0.008)	0.125
		Mg	-0.008 (-0.016, 0.001)	0.076	-0.007 (-0.022, 0.009)	0.395	-0.01 (-0.029, 0.009)	0.297	-0.009 (-0.037, 0.018)	0.505	-0.012 (-0.077, 0.054)	0.687	-0.018 (-0.08, 0.043)	0.508	-0.015 (-0.087, 0.056)	0.639
		K	-0.506 (-0.702, -0.31)	**0.000**	-0.509 (-0.832, -0.185)	**0.002**	-0.575 (-0.978, -0.172)	**0.005**	-0.602 (-1.221, 0.017)	0.057	-0.8 (-2.251, 0.652)	0.240	-0.832 (-2.183, 0.518)	0.193	-0.886 (-2.469, 0.696)	0.233
		Na	1.866 (1.088, 2.644)	**0.000**	1.467 (0.216, 2.717)	**0.022**	1.302 (-0.345, 2.949)	0.121	1.449 (-1.129, 4.026)	0.269	2.815 (-2.379, 8.009)	0.247	2.613 (-2.343, 7.569)	0.259	3.255 (-2.359, 8.868)	0.218
		P	0.000 (-0.001, 0.000)	0.113	-0.001 (-0.002, 0.000)	0.183	-0.001 (-0.002, 0.000)	0.165	-0.001 (-0.003, 0.001)	0.596	-0.001 (-0.005, 0.004)	0.733	-0.001 (-0.005, 0.004)	0.751	-0.001 (-0.006, 0.004)	0.667
		OC	-0.138 (-0.195, -0.081)	**0.000**	-0.118 (-0.211, -0.026)	**0.012**	-0.125 (-0.243, -0.007)	**0.039**	-0.106 (-0.288, 0.077)	0.256	-0.243 (-0.615, 0.129)	0.170	-0.263 (-0.601, 0.074)	0.110	-0.277 (-0.678, 0.124)	0.150
	Land-cover	Forest	0.001 (0.000, 0.002)	0.190	-0.001 (-0.003, 0.002)	0.689	-0.002 (-0.005, 0.002)	0.374	-0.001 (-0.006, 0.004)	0.705	0.002 (-0.008, 0.013)	0.645	0.002 (-0.008, 0.012)	0.604	0.003 (-0.009, 0.014)	0.595
		Shape	-1.09 (-5.282, 3.103)	0.610	2.567 (-4.434, 9.568)	0.472	5.192 (-5.067, 15.452)	0.320	4.625 (-10.075, 19.326)	0.536	-1.095 (-29.808, 27.617)	0.932	-0.809 (-28.092, 26.474)	0.947	-2.349 (-33.702, 29.004)	0.867
		SecVeg	0.000 (-0.004, 0.005)	0.843	0.001 (-0.006, 0.009)	0.688	0.002 (-0.008, 0.012)	0.747	0.000 (-0.015, 0.014)	0.978	-0.002 (-0.034, 0.031)	0.901	-0.003 (-0.034, 0.027)	0.813	-0.001 (-0.037, 0.034)	0.925
		UCL	-0.005 (-0.006, -0.003)	**0.000**	-0.003 (-0.006, 0.000)	0.052	-0.003 (-0.008, 0.001)	0.146	-0.004 (-0.01, 0.002)	0.203	-0.005 (-0.018, 0.007)	0.362	-0.005 (-0.017, 0.007)	0.336	-0.006 (-0.02, 0.007)	0.315
		ULC.type	0.000 (-0.005, 0.004)	0.854	0.002 (-0.005, 0.01)	0.531	0.002 (-0.008, 0.012)	0.726	0.003 (-0.012, 0.018)	0.714	0.001 (-0.029, 0.032)	0.912	0.001 (-0.027, 0.03)	0.920	0.001 (-0.032, 0.034)	0.947
		Roughness	0.011 (0.003, 0.019)	**0.005**	0.004 (-0.009, 0.016)	0.592	-0.001 (-0.018, 0.015)	0.887	0.004 (-0.022, 0.03)	0.748	0.02 (-0.043, 0.083)	0.485	0.018 (-0.042, 0.078)	0.509	0.023 (-0.046, 0.091)	0.472
VA_{max}	Climate	Isoth	-0.028 (-0.037, -0.02)	**0.000**	-0.022 (-0.036, -0.007)	**0.004**	-0.024 (-0.041, -0.006)	**0.009**	-0.025 (-0.051, 0.001)	0.055	-0.038 (-0.096, 0.02)	0.166	-0.042 (-0.094, 0.01)	0.098	-0.044 (-0.107, 0.018)	0.141
		TAP	0.000 (0.000, 0.000)	**0.000**	0.000 (0.000, 0.000)	**0.000**	0.000 (0.000, 0.000)	**0.000**	0.000 (0.000, 0.001)	**0.004**	0.000 (0.000, 0.001)	0.599	0.000 (0.000, 0.001)	0.588	0.000 (-0.001, 0.001)	0.625
		TPdriests	0.000 (-0.001, 0.000)	0.151	0.000 (-0.001, 0.001)	0.946	0.001 (-0.001, 0.002)	0.405	0.000 (-0.002, 0.002)	0.802	-0.001 (-0.006, 0.003)	0.420	-0.001 (-0.005, 0.002)	0.418	-0.002 (-0.006, 0.003)	0.382
		PET	0.000 (0.000, 0.000)	0.206	0.000 (0.000, 0.000)	0.347	0.000 (0.000, 0.001)	0.094	0.000 (0.000, 0.001)	0.287	0.000 (-0.001, 0.001)	0.967	0.000 (-0.001, 0.001)	0.723	0.000 (-0.001, 0.002)	0.948
		Aridity	-0.03 (-0.098, 0.038)	0.389	-0.106 (-0.213, 0.000)	0.051	-0.136 (-0.27, -0.003)	**0.045**	-0.182 (-0.38, 0.016)	0.072	0.067 (-0.38, 0.515)	0.737	0.09 (-0.328, 0.507)	0.634	0.095 (-0.392, 0.582)	0.666
		Ard	0.004 (0.002, 0.005)	**0.000**	0.005 (0.003, 0.007)	**0.000**	0.005 (0.003, 0.008)	**0.000**	0.007 (0.003, 0.011)	**0.002**	0.001 (-0.009, 0.012)	0.757	0.001 (-0.009, 0.01)	0.862	0.001 (-0.01, 0.012)	0.861
		SRad	0.000 (0.000, 0.000)	**0.000**	0.000 (0.000, 0.000)	**0.003**	0.000 (0.000, 0.000)	**0.001**	0.000 (0.000, 0.000)	**0.036**	0.000 (0.000, 0.000)	0.850	0.000 (0.000, 0.000)	0.885	0.000 (0.000, 0.000)	0.917
		WVP	0.068 (-0.156, 0.291)	0.553	0.062 (-0.324, 0.448)	0.752	0.098 (-0.39, 0.585)	0.694	0.191 (-0.485, 0.867)	0.578	0.243 (-1.485, 1.971)	0.754	0.42 (-1.179, 2.02)	0.562	0.341 (-1.541, 2.223)	0.687
		Wind	0.018 (-0.015, 0.05)	0.291	-0.019 (-0.072, 0.035)	0.494	-0.044 (-0.114, 0.027)	0.223	-0.035 (-0.135, 0.065)	0.491	0.058 (-0.165, 0.281)	0.566	0.062 (-0.147, 0.27)	0.515	0.074 (-0.167, 0.316)	0.498
	Soils	Sand	0.007 (0.004, 0.011)	**0.000**	0.006 (0.000, 0.011)	**0.038**	0.009 (0.002, 0.017)	**0.011**	0.009 (-0.001, 0.019)	0.093	0.005 (-0.02, 0.031)	0.645	0.008 (-0.016, 0.031)	0.478	0.006 (-0.022, 0.034)	0.643
		Silt	-0.018 (-0.025, -0.01)	**0.000**	-0.017 (-0.03, -0.005)	**0.008**	-0.027 (-0.043, -0.011)	**0.001**	-0.025 (-0.048, -0.003)	**0.030**	-0.004 (-0.062, 0.055)	0.891	-0.008 (-0.063, 0.047)	0.743	-0.004 (-0.068, 0.061)	0.903
		Clay	-0.01 (-0.016, -0.005)	**0.000**	-0.007 (-0.016, 0.002)	0.138	-0.01 (-0.022, 0.001)	0.080	-0.01 (-0.026, 0.007)	0.248	-0.012 (-0.051, 0.028)	0.521	-0.015 (-0.052, 0.021)	0.364	-0.013 (-0.057, 0.031)	0.510
		pH	-0.165 (-0.213, -0.118)	**0.000**	-0.172 (-0.247, -0.098)	**0.000**	-0.165 (-0.249, -0.082)	**0.000**	-0.184 (-0.307, -0.06)	**0.004**	-0.21 (-0.583, 0.164)	0.232	-0.207 (-0.554, 0.141)	0.208	-0.231 (-0.639, 0.178)	0.229
		CEC	-0.022 (-0.028, -0.016)	**0.000**	-0.019 (-0.028, -0.009)	**0.000**	-0.022 (-0.034, -0.011)	**0.000**	-0.023 (-0.04, -0.006)	**0.007**	-0.024 (-0.066, 0.018)	0.227	-0.026 (-0.065, 0.012)	0.154	-0.027 (-0.073, 0.02)	0.221
		Ca	-0.018 (-0.023, -0.014)	**0.000**	-0.016 (-0.023, -0.01)	**0.000**	-0.019 (-0.027, -0.01)	**0.000**	-0.02 (-0.032, -0.008)	**0.001**	-0.022 (-0.053, 0.009)	0.136	-0.023 (-0.051, 0.004)	0.087	-0.024 (-0.058, 0.009)	0.133
		Mg	-0.01 (-0.019, 0.000)	**0.040**	-0.008 (-0.024, 0.008)	0.328	-0.013 (-0.033, 0.008)	0.220	-0.012 (-0.039, 0.016)	0.407	-0.014 (-0.082, 0.054)	0.646	-0.021 (-0.083, 0.042)	0.462	-0.018 (-0.092, 0.056)	0.590
		K	-0.52 (-0.73, -0.311)	**0.000**	-0.528 (-0.873, -0.183)	**0.003**	-0.615 (-1.043, -0.188)	**0.005**	-0.615 (-1.234, 0.003)	0.051	-0.855 (-2.354, 0.645)	0.225	-0.866 (-2.252, 0.52)	0.187	-0.951 (-2.585, 0.683)	0.216

Trait	Environmental variable		inds		pops		sps		$\text{sps}_{80\%}$		CWM_{pops}		CWM_{sps}		$\text{CWM}_{80\%}$	
			β_0 (95% CI)	*P*	β_0 (95% CI)	*P*	β_0 (95% CI)	*P*	β_0 (95% CI)	*P*	β_0 (95% CI)	*P*	β_0 (95% CI)	*P*	β_0 (95% CI)	*P*
		Na	1.658 (0.826, 2.491)	**0.000**	1.213 (-0.122, 2.548)	0.075	1.219 (-0.531, 2.969)	0.171	1.114 (-1.466, 3.694)	0.396	2.697 (-2.779, 8.174)	0.289	2.587 (-2.548, 7.722)	0.279	3.207 (-2.696, 9.11)	0.246
		P	0.000 (-0.001, 0.000)	0.481	0.000 (-0.001, 0.001)	0.395	-0.001 (-0.002, 0.001)	0.308	0.000 (-0.002, 0.002)	0.816	0.000 (-0.005, 0.004)	0.857	0.000 (-0.005, 0.004)	0.829	-0.001 (-0.006, 0.005)	0.785
		OC	-0.132 (-0.193, -0.072)	**0.000**	-0.105 (-0.204, -0.006)	**0.037**	-0.128 (-0.254, -0.002)	**0.046**	-0.096 (-0.279, 0.087)	0.302	-0.244 (-0.634, 0.146)	0.188	-0.266 (-0.616, 0.084)	0.117	-0.285 (-0.704, 0.134)	0.155
	Land-cover	Forest	0.001 (0.000, 0.003)	0.132	0.000 (-0.003, 0.002)	0.714	-0.002 (-0.005, 0.002)	0.418	-0.001 (-0.006, 0.004)	0.734	0.003 (-0.008, 0.013)	0.612	0.003 (-0.008, 0.013)	0.567	0.003 (-0.009, 0.015)	0.551
		Shape	-1.447 (-5.922, 3.028)	0.526	2.733 (-4.726, 10.191)	0.472	5.271 (-5.624, 16.166)	0.342	4.66 (-10.04, 19.36)	0.533	-1.39 (-31.222, 28.443)	0.917	-1.406 (-29.463, 26.652)	0.911	-2.971 (-35.541, 29.599)	0.839
		SecVeg	-0.001 (-0.006, 0.003)	0.518	0.000 (-0.008, 0.007)	0.940	0.000 (-0.011, 0.01)	0.955	-0.003 (-0.017, 0.012)	0.715	-0.005 (-0.038, 0.029)	0.747	-0.005 (-0.037, 0.026)	0.722	-0.005 (-0.042, 0.032)	0.764
		UCL	-0.005 (-0.007, -0.003)	**0.000**	-0.003 (-0.006, 0.000)	0.070	-0.003 (-0.008, 0.001)	0.147	-0.004 (-0.01, 0.002)	0.220	-0.006 (-0.019, 0.008)	0.355	-0.006 (-0.018, 0.007)	0.308	-0.007 (-0.021, 0.007)	0.299
		ULC.type	-0.002 (-0.006, 0.003)	0.496	0.002 (-0.006, 0.01)	0.670	0.001 (-0.01, 0.012)	0.896	0.002 (-0.013, 0.017)	0.830	0.000 (-0.031, 0.032)	0.972	0.000 (-0.029, 0.03)	0.983	0.000 (-0.035, 0.034)	0.981
		Roughness	0.012 (0.003, 0.02)	**0.006**	0.004 (-0.01, 0.017)	0.607	-0.002 (-0.019, 0.015)	0.820	0.003 (-0.022, 0.029)	0.796	0.021 (-0.045, 0.086)	0.487	0.019 (-0.043, 0.081)	0.505	0.023 (-0.048, 0.095)	0.477
WD	Climate	Isoth	-0.002 (-0.005, 0.000)	0.099	-0.006 (-0.011, -0.001)	**0.012**	-0.007 (-0.013, -0.002)	**0.013**	-0.037 (-0.061, -0.012)	**0.004**	-0.002 (-0.023, 0.02)	0.845	0.001 (-0.017, 0.019)	0.895	-0.001 (-0.023, 0.021)	0.905
		TAP	0.000 (0.000, 0.000)	**0.021**	0.000 (0.000, 0.000)	0.087	0.000 (0.000, 0.000)	0.230	0.000 (0.000, 0.000)	0.690	0.000 (0.000, 0.000)	0.395	0.000 (0.000, 0.000)	0.353	0.000 (0.000, 0.000)	0.298
		TPdriests	0.000 (0.000, 0.000)	**0.032**	0.000 (-0.001, 0.000)	**0.039**	-0.001 (-0.001, 0.000)	**0.005**	-0.001 (-0.003, 0.000)	0.144	0.000 (-0.002, 0.001)	0.649	0.000 (-0.001, 0.001)	0.627	0.000 (-0.002, 0.001)	0.529
		PET	0.000 (0.000, 0.000)	**0.000**	0.000 (0.000, 0.000)	**0.000**	0.000 (0.000, 0.000)	**0.001**	0.001 (0.000, 0.001)	**0.000**	0.000 (0.000, 0.001)	0.648	0.000 (0.000, 0.000)	0.734	0.000 (0.000, 0.001)	0.769
		Aridity	0.04 (0.018, 0.062)	**0.000**	0.062 (0.026, 0.097)	**0.001**	0.066 (0.023, 0.11)	**0.003**	0.242 (0.046, 0.438)	**0.016**	0.058 (-0.081, 0.197)	0.362	0.04 (-0.078, 0.159)	0.457	0.067 (-0.075, 0.209)	0.309
		Ard	-0.002 (-0.002, -0.001)	**0.000**	-0.002 (-0.003, -0.001)	**0.000**	-0.002 (-0.003, -0.001)	**0.000**	-0.007 (-0.011, -0.002)	**0.002**	-0.002 (-0.005, 0.001)	0.119	-0.001 (-0.004, 0.001)	0.230	-0.002 (-0.005, 0.001)	0.107
		SRad	0.000 (0.000, 0.000)	**0.000**	0.000 (0.000, 0.000)	**0.023**	0.000 (0.000, 0.000)	**0.013**	0.000 (0.000, 0.000)	0.123	0.000 (0.000, 0.000)	0.494	0.000 (0.000, 0.000)	0.487	0.000 (0.000, 0.000)	0.418
		WVP	0.211 (0.141, 0.281)	**0.000**	0.259 (0.134, 0.383)	**0.000**	0.338 (0.187, 0.488)	**0.000**	1.268 (0.643, 1.893)	**0.000**	0.159 (-0.391, 0.71)	0.523	0.108 (-0.358, 0.574)	0.608	0.148 (-0.427, 0.723)	0.570
		Wind	0.018 (0.007, 0.028)	**0.001**	0.026 (0.009, 0.044)	**0.004**	0.039 (0.016, 0.062)	**0.001**	0.123 (0.025, 0.22)	**0.014**	0.026 (-0.045, 0.097)	0.420	0.015 (-0.046, 0.076)	0.577	0.029 (-0.044, 0.103)	0.382
	Soils	Sand	-0.001 (-0.002, 0.000)	0.151	0.000 (-0.002, 0.002)	0.903	0.000 (-0.002, 0.002)	0.961	0.008 (-0.002, 0.018)	0.112	-0.001 (-0.009, 0.007)	0.759	-0.002 (-0.009, 0.005)	0.525	-0.002 (-0.011, 0.007)	0.606
		Silt	0.002 (0.000, 0.005)	0.098	0.001 (-0.003, 0.005)	0.625	0.002 (-0.003, 0.007)	0.491	-0.011 (-0.033, 0.012)	0.339	0.002 (-0.017, 0.021)	0.786	0.004 (-0.012, 0.02)	0.570	0.005 (-0.015, 0.024)	0.600
		Clay	0.001 (-0.001, 0.003)	0.245	-0.001 (-0.004, 0.002)	0.594	-0.001 (-0.005, 0.003)	0.674	-0.015 (-0.031, 0.001)	0.059	0.002 (-0.011, 0.015)	0.765	0.003 (-0.008, 0.014)	0.538	0.003 (-0.011, 0.016)	0.649
		pH	0.016 (0.000, 0.031)	0.052	0.009 (-0.016, 0.035)	0.477	0.003 (-0.025, 0.031)	0.826	0.005 (-0.119, 0.129)	0.939	0.018 (-0.115, 0.151)	0.761	0.018 (-0.093, 0.129)	0.711	0.022 (-0.116, 0.16)	0.721
		CEC	0.001 (-0.001, 0.003)	0.260	-0.001 (-0.004, 0.002)	0.600	-0.001 (-0.005, 0.003)	0.595	-0.013 (-0.03, 0.003)	0.115	0.001 (-0.014, 0.016)	0.846	0.003 (-0.009, 0.016)	0.559	0.003 (-0.013, 0.018)	0.718
		Ca	0.003 (0.002, 0.004)	**0.000**	0.001 (-0.001, 0.004)	0.217	0.001 (-0.002, 0.004)	0.470	-0.002 (-0.014, 0.01)	0.740	0.003 (-0.008, 0.014)	0.539	0.004 (-0.005, 0.013)	0.356	0.004 (-0.008, 0.016)	0.456
		Mg	-0.006 (-0.009, -0.003)	**0.000**	-0.009 (-0.014, -0.004)	**0.001**	-0.01 (-0.016, -0.003)	**0.002**	-0.048 (-0.074, -0.022)	**0.000**	-0.004 (-0.026, 0.019)	0.721	0.000 (-0.019, 0.019)	0.997	-0.002 (-0.025, 0.021)	0.854
		K	-0.034 (-0.102, 0.035)	0.335	-0.081 (-0.198, 0.035)	0.171	-0.081 (-0.221, 0.06)	0.259	-0.468 (-1.073, 0.137)	0.129	0.114 (-0.416, 0.644)	0.633	0.101 (-0.342, 0.544)	0.613	0.133 (-0.416, 0.681)	0.592
		Na	0.002 (-0.268, 0.272)	0.990	0.219 (-0.232, 0.67)	0.339	0.381 (-0.193, 0.956)	0.193	0.495 (-2.059, 3.05)	0.703	0.253 (-1.657, 2.162)	0.768	0.223 (-1.376, 1.822)	0.756	0.381 (-1.59, 2.351)	0.668
		P	0.000 (0.000, 0.001)	**0.001**	0.000 (0.000, 0.001)	**0.042**	0.001 (0.000, 0.001)	**0.028**	0.002 (0.000, 0.004)	**0.049**	0.000 (-0.001, 0.002)	0.766	0.000 (-0.001, 0.001)	0.824	0.000 (-0.001, 0.002)	0.787
		OC	-0.005 (-0.025, 0.014)	0.587	-0.028 (-0.061, 0.005)	0.099	-0.026 (-0.067, 0.015)	0.210	-0.164 (-0.342, 0.014)	0.070	0.006 (-0.137, 0.148)	0.929	0.017 (-0.101, 0.136)	0.745	0.008 (-0.14, 0.156)	0.907
	Land-cover	Forest	0.001 (0.000, 0.001)	**0.001**	0.001 (0.000, 0.002)	**0.004**	0.002 (0.001, 0.003)	**0.003**	0.007 (0.002, 0.012)	**0.003**	0.001 (-0.003, 0.004)	0.636	0.000 (-0.003, 0.003)	0.938	0.001 (-0.003, 0.004)	0.691
		Shape	-3.858 (-5.28, -2.437)	**0.000**	-4.577 (-7.023, -2.131)	**0.000**	-6.522 (-9.966, -3.078)	**0.000**	-22.149 (-36.12, -8.177)	**0.002**	-4.388 (-13.421, 4.646)	0.295	-2.154 (-10.102, 5.793)	0.549	-4.197 (-13.692, 5.298)	0.338
		SecVeg	-0.005 (-0.007, -0.004)	**0.000**	-0.006 (-0.009, -0.004)	**0.000**	-0.008 (-0.011, -0.004)	**0.000**	-0.029 (-0.043, -0.016)	**0.000**	-0.003 (-0.013, 0.008)	0.581	-0.001 (-0.01, 0.008)	0.768	-0.002 (-0.014, 0.009)	0.656
		UCL	0.000 (-0.001, 0.000)	0.160	-0.001 (-0.002, 0.000)	0.077	-0.002 (-0.003, 0.000)	**0.032**	-0.007 (-0.014, -0.001)	**0.016**	0.000 (-0.005, 0.004)	0.810	0.000 (-0.003, 0.004)	0.839	0.000 (-0.005, 0.004)	0.893
		ULC.type	-0.007 (-0.008, -0.005)	**0.000**	-0.008 (-0.01, -0.005)	**0.000**	-0.009 (-0.012, -0.005)	**0.000**	-0.032 (-0.045, -0.018)	**0.000**	-0.006 (-0.015, 0.003)	0.142	-0.003 (-0.011, 0.005)	0.354	-0.006 (-0.015, 0.004)	0.190
		Roughness	-0.008 (-0.01, -0.005)	**0.000**	-0.006 (-0.01, -0.001)	**0.009**	-0.006 (-0.011, 0.000)	**0.043**	-0.013 (-0.038, 0.012)	0.314	-0.011 (-0.031, 0.009)	0.234	-0.011 (-0.027, 0.005)	0.156	-0.012 (-0.033, 0.008)	0.210
WD_0	Climate	Isoth	-0.003 (-0.006, 0.000)	**0.026**	-0.006 (-0.011, -0.002)	**0.010**	-0.007 (-0.013, -0.001)	**0.015**	-0.034 (-0.059, -0.009)	**0.008**	-0.002 (-0.021, 0.018)	0.845	0.001 (-0.016, 0.018)	0.853	-0.001 (-0.021, 0.019)	0.918
		TAP	0.000 (0.000, 0.000)	0.171	0.000 (0.000, 0.000)	0.179	0.000 (0.000, 0.000)	0.368	0.000 (0.000, 0.000)	0.720	0.000 (0.000, 0.000)	0.421	0.000 (0.000, 0.000)	0.412	0.000 (0.000, 0.000)	0.313
		TPdriests	0.000 (0.000, 0.000)	**0.025**	0.000 (-0.001, 0.000)	**0.042**	-0.001 (-0.001, 0.000)	**0.007**	-0.001 (-0.003, 0.000)	0.142	0.000 (-0.001, 0.001)	0.626	0.000 (-0.001, 0.001)	0.658	0.000 (-0.002, 0.001)	0.500
		PET	0.000 (0.000, 0.000)	**0.000**	0.000 (0.000, 0.000)	**0.000**	0.000 (0.000, 0.000)	**0.002**	0.001 (0.000, 0.001)	**0.001**	0.000 (0.000, 0.000)	0.584	0.000 (0.000, 0.000)	0.703	0.000 (0.000, 0.000)	0.712
		Aridity	0.034 (0.012, 0.056)	**0.003**	0.056 (0.019, 0.092)	**0.003**	0.058 (0.014, 0.102)	**0.009**	0.22 (0.024, 0.416)	**0.028**	0.05 (-0.076, 0.176)	0.389	0.032 (-0.081, 0.145)	0.536	0.058 (-0.072, 0.187)	0.334
		Ard	-0.001 (-0.002, -0.001)	**0.000**	-0.002 (-0.003, -0.001)	**0.000**	-0.002 (-0.002, -0.001)	**0.002**	-0.006 (-0.01, -0.002)	**0.008**	-0.002 (-0.004, 0.001)	0.157	-0.001 (-0.004, 0.001)	0.315	-0.002 (-0.005, 0.001)	0.148
		SRad	0.000 (0.000, 0.000)	**0.002**	0.000 (0.000, 0.000)	0.053	0.000 (0.000, 0.000)	**0.043**	0.000 (0.000, 0.000)	0.210	0.000 (0.000, 0.000)	0.510	0.000 (0.000, 0.000)	0.555	0.000 (0.000, 0.000)	0.431
		WVP	0.229 (0.158, 0.299)	**0.000**	0.252 (0.126, 0.378)	**0.000**	0.32 (0.167, 0.473)	**0.000**	1.151 (0.514, 1.788)	**0.000**	0.157 (-0.338, 0.652)	0.485	0.099 (-0.341, 0.538)	0.619	0.144 (-0.374, 0.663)	0.539
		Wind	0.016 (0.006, 0.027)	**0.002**	0.025 (0.007, 0.042)	**0.007**	0.035 (0.012, 0.058)	**0.003**	0.111 (0.013, 0.209)	**0.026**	0.022 (-0.043, 0.086)	0.464	0.011 (-0.047, 0.069)	0.676	0.024 (-0.043, 0.091)	0.430

Trait	Environmental variable		inds		pops		sps		$sps_{80\%}$		CWM_{pops}		CWM_{sps}		$CWM_{80\%}$	
			β_0 (95% CI)	***P***	**β_0 (95% CI)**	***P***	**β_0 (95% CI)**	***P***	**β_0 (95% CI)**	***P***	**β_0 (95% CI)**	***P***	**β_0 (95% CI)**	***P***	**β_0 (95% CI)**	***P***
WC_{max}	Soils	Sand	-0.001 (-0.002, 0.000)	0.232	0.000 (-0.002, 0.002)	0.892	0.000 (-0.003, 0.002)	0.846	0.007 (-0.003, 0.017)	0.198	-0.001 (-0.009, 0.006)	0.721	-0.002 (-0.008, 0.004)	0.487	-0.002 (-0.01, 0.006)	0.552
		Silt	0.002 (-0.001, 0.004)	0.211	0.001 (-0.003, 0.005)	0.710	0.002 (-0.004, 0.007)	0.524	-0.009 (-0.032, 0.014)	0.430	0.002 (-0.015, 0.02)	0.754	0.004 (-0.011, 0.019)	0.560	0.005 (-0.013, 0.022)	0.550
		Clay	0.001 (-0.001, 0.003)	0.292	-0.001 (-0.004, 0.002)	0.634	0.000 (-0.004, 0.004)	0.882	-0.012 (-0.029, 0.004)	0.129	0.002 (-0.01, 0.014)	0.727	0.003 (-0.007, 0.013)	0.485	0.003 (-0.009, 0.015)	0.597
		pH	0.008 (-0.008, 0.024)	0.317	0.004 (-0.022, 0.03)	0.745	-0.003 (-0.031, 0.025)	0.832	-0.01 (-0.134, 0.114)	0.874	0.013 (-0.107, 0.134)	0.804	0.013 (-0.092, 0.118)	0.779	0.017 (-0.108, 0.142)	0.763
		CEC	0.001 (-0.001, 0.002)	0.584	-0.001 (-0.004, 0.002)	0.493	-0.001 (-0.005, 0.003)	0.534	-0.012 (-0.029, 0.004)	0.143	0.001 (-0.012, 0.015)	0.809	0.003 (-0.008, 0.015)	0.527	0.003 (-0.011, 0.017)	0.666
		Ca	0.003 (0.001, 0.004)	**0.001**	0.001 (-0.001, 0.004)	0.335	0.001 (-0.002, 0.004)	0.604	-0.002 (-0.015, 0.01)	0.730	0.003 (-0.007, 0.013)	0.509	0.004 (-0.005, 0.012)	0.341	0.004 (-0.007, 0.014)	0.420
		Mg	-0.007 (-0.01, -0.004)	**0.000**	-0.009 (-0.014, -0.004)	**0.001**	-0.009 (-0.015, -0.002)	**0.007**	-0.042 (-0.069, -0.016)	**0.002**	-0.003 (-0.023, 0.017)	0.735	0.000 (-0.017, 0.018)	0.956	-0.001 (-0.022, 0.02)	0.890
		K	-0.07 (-0.138, -0.001)	**0.046**	-0.101 (-0.219, 0.016)	0.090	-0.095 (-0.236, 0.046)	0.187	-0.453 (-1.061, 0.155)	0.144	0.069 (-0.413, 0.552)	0.749	0.072 (-0.348, 0.493)	0.702	0.085 (-0.416, 0.586)	0.707
		Na	0.065 (-0.206, 0.336)	0.638	0.27 (-0.184, 0.725)	0.243	0.459 (-0.115, 1.033)	0.116	0.813 (-1.742, 3.368)	0.532	0.274 (-1.446, 1.993)	0.723	0.224 (-1.282, 1.73)	0.740	0.402 (-1.374, 2.177)	0.616
		P	0.000 (0.000, 0.000)	**0.003**	0.000 (0.000, 0.001)	0.065	0.000 (0.000, 0.001)	**0.050**	0.002 (0.000, 0.004)	0.070	0.000 (-0.001, 0.002)	0.785	0.000 (-0.001, 0.001)	0.864	0.000 (-0.001, 0.002)	0.809
		OC	-0.009 (-0.029, 0.011)	0.377	-0.029 (-0.062, 0.005)	0.095	-0.025 (-0.067, 0.016)	0.230	-0.145 (-0.324, 0.033)	0.111	0.005 (-0.124, 0.133)	0.936	0.017 (-0.094, 0.129)	0.731	0.007 (-0.127, 0.14)	0.912
	Land-cover	Forest	0.001 (0.000, 0.001)	**0.001**	0.001 (0.000, 0.002)	**0.006**	0.002 (0.000, 0.003)	**0.011**	0.006 (0.001, 0.011)	**0.013**	0.001 (-0.003, 0.004)	0.697	0.000 (-0.003, 0.003)	0.954	0.000 (-0.003, 0.004)	0.775
		Shape	-3.753 (-5.178, -2.328)	**0.000**	-4.391 (-6.858, -1.924)	**0.001**	-5.965 (-9.432, -2.498)	**0.001**	-19.948 (-34.017, -5.878)	**0.006**	-3.563 (-11.84, 4.714)	0.350	-1.569 (-9.135, 5.998)	0.645	-3.25 (-11.989, 5.489)	0.416
		SecVeg	-0.006 (-0.007, -0.004)	**0.000**	-0.006 (-0.009, -0.004)	**0.000**	-0.007 (-0.011, -0.004)	**0.000**	-0.027 (-0.041, -0.014)	**0.000**	-0.003 (-0.012, 0.007)	0.563	-0.001 (-0.01, 0.008)	0.786	-0.002 (-0.012, 0.008)	0.650
		UCL	-0.001 (-0.001, 0.000)	0.090	-0.001 (-0.002, 0.000)	0.073	-0.001 (-0.003, 0.000)	0.059	-0.006 (-0.013, 0.000)	**0.041**	0.000 (-0.004, 0.004)	0.879	0.001 (-0.003, 0.004)	0.745	0.000 (-0.004, 0.004)	0.989
		ULC.type	-0.007 (-0.008, -0.005)	**0.000**	-0.007 (-0.01, -0.005)	**0.000**	-0.008 (-0.012, -0.005)	**0.000**	-0.03 (-0.044, -0.016)	**0.000**	-0.005 (-0.013, 0.003)	0.171	-0.003 (-0.011, 0.005)	0.418	-0.005 (-0.014, 0.004)	0.241
		Roughness	-0.008 (-0.01, -0.005)	**0.000**	-0.006 (-0.01, -0.001)	**0.012**	-0.007 (-0.012, -0.001)	**0.018**	-0.017 (-0.042, 0.009)	0.196	-0.011 (-0.029, 0.007)	0.198	-0.011 (-0.026, 0.004)	0.122	-0.012 (-0.03, 0.006)	0.169
	Climate	Isoth	0.004 (-0.001, 0.009)	0.081	0.009 (0.002, 0.017)	**0.018**	0.011 (0.002, 0.02)	**0.020**	0.034 (0.009, 0.059)	**0.007**	0.004 (-0.032, 0.04)	0.794	-0.001 (-0.031, 0.029)	0.937	0.003 (-0.035, 0.041)	0.842
		TAP	0.000 (0.000, 0.000)	**0.013**	0.000 (0.000, 0.000)	0.059	0.000 (0.000, 0.000)	0.135	0.000 (0.000, 0.000)	0.510	0.000 (0.000, 0.000)	0.395	0.000 (0.000, 0.000)	0.349	0.000 (0.000, 0.000)	0.305
		TPdriests	0.000 (0.000, 0.001)	**0.030**	0.001 (0.000, 0.001)	**0.039**	0.001 (0.000, 0.002)	**0.003**	0.001 (0.000, 0.003)	0.106	0.000 (-0.002, 0.003)	0.660	0.000 (-0.002, 0.002)	0.640	0.001 (-0.002, 0.003)	0.548
		PET	0.000 (0.000, 0.000)	**0.000**	0.000 (0.000, 0.000)	**0.001**	0.000 (0.000, 0.000)	**0.003**	-0.001 (-0.001, 0.000)	**0.001**	0.000 (-0.001, 0.001)	0.651	0.000 (-0.001, 0.001)	0.749	0.000 (-0.001, 0.001)	0.760
		Aridity	-0.07 (-0.105, -0.035)	**0.000**	-0.1 (-0.156, -0.044)	**0.000**	-0.111 (-0.179, -0.043)	**0.001**	-0.257 (-0.452, -0.061)	**0.010**	-0.105 (-0.337, 0.127)	0.327	-0.073 (-0.271, 0.125)	0.419	-0.121 (-0.361, 0.119)	0.278
		Ard	0.003 (0.002, 0.004)	**0.000**	0.003 (0.002, 0.004)	**0.000**	0.003 (0.002, 0.004)	**0.000**	0.007 (0.003, 0.011)	**0.001**	0.004 (-0.001, 0.009)	0.090	0.003 (-0.002, 0.007)	0.184	0.004 (-0.001, 0.009)	0.080
		SRad	0.000 (0.000, 0.000)	**0.000**	0.000 (0.000, 0.000)	**0.022**	0.000 (0.000, 0.000)	**0.010**	0.000 (0.000, 0.000)	0.124	0.000 (0.000, 0.000)	0.489	0.000 (0.000, 0.000)	0.490	0.000 (0.000, 0.000)	0.424
		WVP	-0.348 (-0.46, -0.236)	**0.000**	-0.381 (-0.577, -0.186)	**0.000**	-0.501 (-0.739, -0.263)	**0.000**	-1.183 (-1.819, -0.547)	**0.000**	-0.272 (-1.199, 0.656)	0.518	-0.177 (-0.961, 0.608)	0.618	-0.257 (-1.237, 0.722)	0.561
		Wind	-0.03 (-0.046, -0.013)	**0.000**	-0.042 (-0.07, -0.014)	**0.003**	-0.063 (-0.098, -0.027)	**0.001**	-0.125 (-0.222, -0.028)	**0.012**	-0.047 (-0.166, 0.072)	0.389	-0.028 (-0.13, 0.074)	0.544	-0.053 (-0.177, 0.071)	0.354
	Soils	Sand	0.001 (0.000, 0.003)	0.125	0.000 (-0.003, 0.003)	0.930	0.001 (-0.003, 0.005)	0.654	-0.006 (-0.016, 0.004)	0.231	0.002 (-0.012, 0.016)	0.804	0.003 (-0.008, 0.015)	0.555	0.003 (-0.012, 0.017)	0.663
		Silt	-0.004 (-0.008, 0.000)	0.071	-0.002 (-0.009, 0.004)	0.490	-0.004 (-0.013, 0.004)	0.282	0.007 (-0.016, 0.03)	0.545	-0.003 (-0.035, 0.029)	0.819	-0.006 (-0.033, 0.02)	0.598	-0.007 (-0.04, 0.027)	0.649
		Clay	-0.002 (-0.004, 0.001)	0.225	0.001 (-0.004, 0.005)	0.736	0.000 (-0.006, 0.006)	0.959	0.012 (-0.004, 0.029)	0.132	-0.002 (-0.025, 0.02)	0.813	-0.005 (-0.023, 0.014)	0.568	-0.004 (-0.027, 0.019)	0.707
		pH	-0.026 (-0.051, -0.001)	**0.038**	-0.016 (-0.056, 0.024)	0.427	-0.005 (-0.049, 0.038)	0.807	-0.004 (-0.129, 0.12)	0.946	-0.03 (-0.254, 0.194)	0.767	-0.03 (-0.216, 0.157)	0.725	-0.035 (-0.27, 0.2)	0.739
		CEC	-0.002 (-0.005, 0.001)	0.233	0.001 (-0.004, 0.006)	0.716	0.001 (-0.005, 0.007)	0.772	0.011 (-0.005, 0.028)	0.181	-0.002 (-0.027, 0.024)	0.893	-0.005 (-0.026, 0.016)	0.596	-0.003 (-0.03, 0.023)	0.783
		Ca	-0.005 (-0.007, -0.003)	**0.000**	-0.003 (-0.006, 0.001)	0.162	-0.002 (-0.007, 0.002)	0.351	0.001 (-0.011, 0.013)	0.882	-0.005 (-0.024, 0.014)	0.576	-0.006 (-0.022, 0.009)	0.385	-0.006 (-0.026, 0.014)	0.506
		Mg	0.011 (0.006, 0.015)	**0.000**	0.014 (0.005, 0.022)	**0.001**	0.014 (0.004, 0.024)	**0.007**	0.044 (0.017, 0.07)	**0.001**	0.007 (-0.03, 0.045)	0.664	0.001 (-0.031, 0.032)	0.953	0.005 (-0.035, 0.044)	0.782
		K	0.056 (-0.052, 0.165)	0.309	0.118 (-0.063, 0.3)	0.201	0.106 (-0.114, 0.325)	0.345	0.405 (-0.204, 1.013)	0.191	-0.183 (-1.078, 0.711)	0.649	-0.168 (-0.914, 0.578)	0.617	-0.214 (-1.15, 0.722)	0.613
		Na	-0.037 (-0.466, 0.393)	0.866	-0.398 (-1.102, 0.305)	0.266	-0.731 (-1.623, 0.161)	0.108	-0.864 (-3.419, 1.691)	0.506	-0.481 (-3.694, 2.731)	0.739	-0.434 (-3.117, 2.25)	0.719	-0.704 (-4.054, 2.646)	0.641
		P	0.000 (-0.001, 0.000)	**0.003**	0.000 (-0.001, 0.000)	0.071	-0.001 (-0.002, 0.000)	**0.040**	-0.002 (-0.004, 0.000)	0.067	0.000 (-0.003, 0.002)	0.835	0.000 (-0.002, 0.002)	0.901	0.000 (-0.003, 0.003)	0.857
		OC	0.015 (-0.016, 0.046)	0.353	0.045 (-0.007, 0.097)	0.087	0.039 (-0.025, 0.104)	0.228	0.153 (-0.025, 0.332)	0.092	0.002 (-0.238, 0.242)	0.982	-0.02 (-0.22, 0.18)	0.820	0.001 (-0.251, 0.253)	0.994
	Land-cover	Forest	-0.002 (-0.002, -0.001)	**0.000**	-0.002 (-0.003, -0.001)	**0.003**	-0.003 (-0.004, -0.001)	**0.004**	-0.007 (-0.011, -0.002)	**0.007**	-0.002 (-0.007, 0.004)	0.578	0.000 (-0.005, 0.005)	0.885	-0.001 (-0.008, 0.005)	0.629
		Shape	6.584 (4.329, 8.84)	**0.000**	7.468 (3.66, 11.276)	**0.000**	10.251 (4.884, 15.618)	**0.000**	21.861 (7.837, 35.886)	**0.002**	8.013 (-6.998, 23.024)	0.253	4.157 (-9.109, 17.422)	0.491	7.853 (-8.105, 23.811)	0.289
		SecVeg	0.009 (0.006, 0.011)	**0.000**	0.01 (0.006, 0.013)	**0.000**	0.012 (0.006, 0.017)	**0.000**	0.028 (0.014, 0.041)	**0.000**	0.004 (-0.014, 0.023)	0.598	0.002 (-0.014, 0.017)	0.803	0.004 (-0.016, 0.023)	0.670
		UCL	0.001 (0.000, 0.002)	0.096	0.002 (0.000, 0.003)	0.072	0.002 (0.000, 0.005)	0.053	0.007 (0.001, 0.013)	**0.032**	0.001 (-0.006, 0.009)	0.730	0.000 (-0.007, 0.006)	0.912	0.001 (-0.007, 0.009)	0.804
		ULC.type	0.011 (0.009, 0.014)	**0.000**	0.012 (0.008, 0.016)	**0.000**	0.013 (0.008, 0.019)	**0.000**	0.031 (0.018, 0.045)	**0.000**	0.011 (-0.004, 0.026)	0.123	0.006 (-0.007, 0.02)	0.319	0.011 (-0.005, 0.026)	0.162
		Roughness	0.012 (0.008, 0.016)	**0.000**	0.009 (0.002, 0.017)	**0.009**	0.01 (0.002, 0.019)	**0.020**	0.017 (-0.008, 0.042)	0.187	0.018 (-0.016, 0.052)	0.263	0.018 (-0.009, 0.045)	0.169	0.02 (-0.016, 0.055)	0.234
Models with significant β_0 (P<0.05, %)				**67.2**		**44.9**		**43.8**		**31.5**		**1.8**		**3.1**		**2.1**

Table S5. Fitted models and β-coefficients showing the effects of 26 single variables of climate, soils and land-cover transformation on biomass grow rates (BGR) for the abundance weighted trait sampling design (inds) and six functional trait sampling designs: populations (pops), species (sps), dominant species (sps$_{80\%}$, species saturating 80% of the abundances per hectare), community weighted-means based on populations (CWM$_{pops}$), species (CWM$_{sps}$) and dominant species (CWM$_{80\%}$). Confidence interval at 95% of the probability (CI). Bold letters show significant β-coefficients (*P*<0.05). For description of the environmental variables see Table S1.

Trait	**Environmental variable**		**inds**		**pops**		**sps**		**sps$_{80\%}$**		**CWM$_{pops}$**		**CWM$_{sps}$**		**CWM$_{80\%}$**	
			β_0 (95% CI)	**P**	**β_0 (95% CI)**	**P**	**β_0 (95% CI)**	**P**	**β_0 (95% CI)**	**P**	**β_0 (95% CI)**	**P**	**β_0 (95% CI)**	**P**	**β_0 (95% CI)**	**P**
BGR	Climate	Isoth	-0.008 (-0.018, 0.003)	0.139	-0.009 (-0.026, 0.009)	0.326	-0.007 (-0.029, 0.014)	0.501	-0.005 (-0.03, 0.02)	0.682	-0.018 (-0.17, 0.133)	0.790	-0.083 (-0.22, 0.053)	0.195	-0.006 (-0.158, 0.146)	0.932
		TAP	0.000 (0.000, 0.000)	**0.000**	0.000 (0.000, 0.000)	**0.000**	0.000 (0.000, 0.001)	**0.000**	0.000 (0.000, 0.001)	**0.001**	0.001 (0.000, 0.002)	0.054	0.001 (0.000, 0.002)	**0.018**	0.001 (0.000, 0.002)	**0.040**
		TPdriests	0.001 (0.000, 0.002)	**0.005**	0.002 (0.001, 0.004)	**0.000**	0.003 (0.002, 0.005)	**0.000**	0.003 (0.002, 0.005)	**0.000**	0.005 (-0.003, 0.014)	0.185	0.005 (-0.003, 0.014)	0.195	0.005 (-0.004, 0.014)	0.254
		PET	0.000 (0.000, 0.000)	0.156	0.000 (0.000, 0.001)	0.068	0.000 (0.000, 0.001)	0.072	0.000 (0.000, 0.001)	0.185	0.001 (-0.002, 0.004)	0.623	0.003 (0.000, 0.005)	**0.033**	0.000 (-0.003, 0.003)	0.813
		Aridity	-0.084 (-0.164, -0.004)	**0.040**	-0.193 (-0.323, -0.063)	**0.004**	-0.293 (-0.454, -0.132)	**0.000**	-0.291 (-0.485, -0.096)	**0.004**	-0.513 (-1.465, 0.438)	0.249	-0.351 (-1.35, 0.648)	0.441	-0.622 (-1.529, 0.286)	0.153
		Ard	0.003 (0.001, 0.004)	**0.006**	0.005 (0.002, 0.008)	**0.001**	0.006 (0.003, 0.01)	**0.001**	0.006 (0.002, 0.01)	**0.005**	0.012 (-0.01, 0.033)	0.242	0.006 (-0.018, 0.029)	0.598	0.015 (-0.006, 0.035)	0.139
		SRad	0.000 (0.000, 0.000)	**0.000**	0.000 (0.000, 0.000)	**0.000**	0.000 (0.000, 0.000)	**0.000**	0.000 (0.000, 0.000)	**0.001**	-0.001 (-0.001, 0.000)	0.122	0.000 (-0.001, 0.000)	0.299	0.000 (-0.001, 0.000)	0.175
		WVP	-0.069 (-0.329, 0.192)	0.605	-0.181 (-0.638, 0.275)	0.436	-0.151 (-0.725, 0.424)	0.606	-0.221 (-0.864, 0.421)	0.498	-0.218 (-4.225, 3.789)	0.903	2.15 (-1.457, 5.758)	0.207	-0.241 (-4.247, 3.765)	0.893
		Wind	-0.042 (-0.08, -0.003)	**0.033**	-0.103 (-0.167, -0.04)	**0.002**	-0.157 (-0.241, -0.073)	**0.000**	-0.151 (-0.247, -0.054)	**0.002**	-0.201 (-0.7, 0.299)	0.382	-0.147 (-0.659, 0.365)	0.526	-0.2 (-0.7, 0.3)	0.383
	Soils	Sand	0.006 (0.002, 0.01)	**0.002**	0.013 (0.006, 0.019)	**0.000**	0.015 (0.006, 0.023)	**0.001**	0.015 (0.005, 0.025)	**0.002**	0.031 (-0.023, 0.085)	0.221	0.049 (0.006, 0.093)	**0.031**	0.022 (-0.034, 0.079)	0.386
		Silt	-0.02 (-0.029, -0.011)	**0.000**	-0.038 (-0.053, -0.024)	**0.000**	-0.042 (-0.061, -0.024)	**0.000**	-0.042 (-0.064, -0.02)	**0.000**	-0.106 (-0.21, -0.002)	**0.047**	-0.121 (-0.214, -0.028)	**0.017**	-0.089 (-0.203, 0.025)	0.111
		Clay	-0.007 (-0.013, -0.001)	**0.033**	-0.015 (-0.025, -0.004)	**0.006**	-0.016 (-0.03, -0.002)	**0.023**	-0.018 (-0.034, -0.002)	**0.026**	-0.027 (-0.119, 0.065)	0.519	-0.067 (-0.144, 0.011)	0.082	-0.014 (-0.108, 0.08)	0.745
		pH	-0.108 (-0.165, -0.051)	**0.000**	-0.135 (-0.227, -0.043)	**0.004**	-0.117 (-0.22, -0.014)	**0.026**	-0.1 (-0.223, 0.024)	0.114	-0.587 (-1.405, 0.232)	0.137	-0.398 (-1.289, 0.492)	0.332	-0.551 (-1.386, 0.284)	0.166
		CEC	-0.013 (-0.02, -0.005)	**0.001**	-0.02 (-0.032, -0.009)	**0.001**	-0.02 (-0.034, -0.006)	**0.004**	-0.02 (-0.036, -0.004)	**0.016**	-0.054 (-0.152, 0.045)	0.245	-0.078 (-0.165, 0.008)	0.070	-0.041 (-0.143, 0.062)	0.388
		Ca	-0.012 (-0.017, -0.006)	**0.000**	-0.018 (-0.026, -0.009)	**0.000**	-0.017 (-0.027, -0.006)	**0.002**	-0.017 (-0.029, -0.005)	**0.006**	-0.054 (-0.123, 0.016)	0.114	-0.052 (-0.123, 0.018)	0.125	-0.044 (-0.118, 0.03)	0.210
		Mg	-0.006 (-0.017, 0.005)	0.288	-0.015 (-0.034, 0.003)	0.109	-0.021 (-0.045, 0.002)	0.076	-0.018 (-0.044, 0.008)	0.170	-0.03 (-0.187, 0.126)	0.666	-0.146 (-0.251, -0.041)	**0.013**	-0.017 (-0.176, 0.141)	0.808
		K	-0.129 (-0.378, 0.12)	0.309	-0.254 (-0.674, 0.167)	0.236	-0.474 (-0.993, 0.044)	0.073	-0.31 (-0.916, 0.295)	0.314	-0.482 (-4.276, 3.311)	0.777	-2.976 (-5.918, -0.034)	**0.048**	-0.567 (-4.353, 3.218)	0.738
		Na	0.058 (-0.926, 1.043)	0.908	-1.13 (-2.748, 0.487)	0.170	-2.057 (-4.158, 0.044)	0.055	-2.737 (-5.236, -0.238)	**0.032**	-1.439 (-14.999, 12.121)	0.813	-3.337 (-16.673, 9.999)	0.580	-1.471 (-15.028, 12.087)	0.809
		P	-0.001 (-0.002, 0.000)	**0.018**	-0.001 (-0.003, 0.000)	**0.032**	-0.002 (-0.003, 0.000)	0.083	-0.001 (-0.003, 0.001)	0.258	-0.005 (-0.015, 0.005)	0.281	-0.003 (-0.013, 0.008)	0.582	-0.005 (-0.015, 0.006)	0.324
		OC	-0.069 (-0.141, 0.003)	0.060	-0.11 (-0.23, 0.01)	0.072	-0.132 (-0.284, 0.02)	0.088	-0.125 (-0.303, 0.052)	0.166	-0.068 (-1.076, 0.94)	0.880	-0.653 (-1.511, 0.205)	0.117	0.072 (-0.935, 1.08)	0.872
	Land-cover	Forest	-0.002 (-0.003, 0.000)	0.091	-0.003 (-0.006, 0.000)	0.084	-0.003 (-0.008, 0.001)	0.134	-0.003 (-0.008, 0.002)	0.211	-0.004 (-0.03, 0.021)	0.694	0.007 (-0.018, 0.032)	0.513	-0.003 (-0.029, 0.022)	0.762
		Shape	4.061 (-1.185, 9.308)	0.129	8.858 (-0.024, 17.741)	0.051	13.251 (0.471, 26.032)	**0.042**	13.231 (-0.704, 27.167)	0.063	5.303 (-63.414, 74.021)	0.863	-7.385 (-75.974, 61.205)	0.810	3.014 (-65.795, 71.824)	0.922
		SecVeg	0.006 (0.001, 0.012)	**0.017**	0.009 (0.000, 0.019)	**0.042**	0.004 (-0.009, 0.016)	0.564	0.005 (-0.009, 0.018)	0.517	0.033 (-0.04, 0.106)	0.328	-0.032 (-0.106, 0.041)	0.338	0.029 (-0.045, 0.103)	0.397
		UCL	0.000 (-0.003, 0.002)	0.701	0.000 (-0.004, 0.004)	0.874	-0.001 (-0.006, 0.005)	0.838	0.000 (-0.006, 0.006)	0.969	-0.006 (-0.038, 0.026)	0.698	-0.016 (-0.046, 0.014)	0.250	-0.006 (-0.038, 0.025)	0.653
		ULC.type	0.004 (-0.002, 0.01)	0.165	0.008 (-0.001, 0.017)	0.092	0.008 (-0.005, 0.02)	0.230	0.009 (-0.005, 0.023)	0.201	0.009 (-0.063, 0.08)	0.786	-0.015 (-0.086, 0.056)	0.639	0.009 (-0.062, 0.081)	0.773
		Roughness	-0.002 (-0.012, 0.008)	0.701	0.003 (-0.013, 0.019)	0.727	0.004 (-0.017, 0.025)	0.705	0.007 (-0.017, 0.032)	0.556	0.016 (-0.14, 0.171)	0.822	0.048 (-0.103, 0.199)	0.485	0.032 (-0.122, 0.186)	0.641
Models with significant β_0 (P<0.05, %)				**53.8**		**53.8**		**50.0**		**46.2**		**3.8**		**23.1**		**3.8**



Chapter 5

Diverging functional strategies but high sensitivity to an extreme drought in tropical dry forests

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Abstract

Extreme drought events have negative effects on forest diversity and functioning. At the species level, however, these effects are still unclear, as species vary in their response to drought through specific functional traits combinations. We used long-term demographic records of 21,821 trees and extensive databases of traits to understand the responses of 338 tropical dry forests tree species to ENSO_{2015}, the driest event in decades in Northern South America. Functional differences between species were related to hydraulic safety-efficiency trade-offs, but unexpectedly, dominant species were characterized by high investment in leaf and wood tissues regardless of their leaf phenology habit. Despite strong species functional differences, tree mortality covered a higher space of trait combinations than tree growth. Our results indicate that irrespective of the drought adaptations, most trees will be negatively affected under drier scenarios predicted for tropical dry forests.

Introduction

Tropical forest diversity and functioning are continuously threatened by a global increase in drought events (Allen *et al.* 2010, 2015; Nunes Garcia *et al.* 2018). Extreme droughts can increase tree mortality and significantly reduce ecosystem biomass gain due to low tree growth and recruitment (Condit *et al.* 1996; Slik 2004; Allen *et al.* 2010; Maza-Villalobos *et al.* 2013), even in forests considered to be historically water-limited such as tropical dry forests (TDF; Allen *et al.* 2015; Powers *et al.* 2020). However, it is still not entirely clear how extreme drought events affect ecosystem processes, nor are the mechanisms mediating species' drought responses (Allen *et al.* 2010). Trait-based ecology provides a framework to understand how species respond to environmental filters, how they vary their demography, and, ultimately, what their fitness is (Pistón *et al.* 2019). Thus, studying the functional responses of species to extreme drought events, and how these translate into changes in biomass, can improve our ability to predict forests changes to future climatic drier scenarios (Aubry-Kientz *et al.* 2013; McDowell *et al.* 2018).

There is a general expectation that TDF tree species are adapted to cope with water limitation and should be more resistant to drought than species from mesic ecosystems (Dodd & Ryan 2016). Studies have shown changes in traits in response to both more extended and more frequent dry periods, such as an increase in shorter stature, and denser wood species (Esquivel-Muelbert *et al.* 2019), or more deciduous species (Fauset *et al.* 2012), highlighting that some traits should provide an advantage under water constraints (Dodd & Ryan 2016). Nevertheless, critical knowledge gaps remain regarding the ecological viability of multiple trait combinations (Méndez-Alonzo *et al.* 2012), trait relationships with demographic rates under droughts (Mendivelso *et al.* 2013; Allen *et al.* 2017b), or the role of traits in explaining species' dominance (Prado-Junior *et al.* 2016; Aguirre-Gutiérrez *et al.* 2019). This lack of knowledge is especially acute given the difficulty of having simultaneous trait and demographic data for a large number of tree species during extreme droughts, information which will ultimately be essential to help us forecast how TDF may respond to future drier scenarios (Allen *et al.* 2010; Aguirre-Gutiérrez *et al.* 2019).

Previous studies examining traits in TDF suggest that tree species are distributed along a continuum of functional traits related to a hydraulic safety-efficiency trade-off, which in turn should be associated with the degree of investment in tissues (from 'costly' to 'cheap' tissues) (**Figure 1**; Markesteijn *et al.* 2011a, b; Méndez-Alonzo *et al.* 2012; Pineda-García *et al.* 2015). On one side of this continuum, species have a high density of narrow xylem conduits, high carbon investment in thicker fibre cell walls, denser wood and leaves, and high leaf retention time (Méndez-Alonzo *et al.* 2012). These species with costly, but hydraulically-safe tissues, are expected to be drought-tolerant, have the low photosynthetic capacity and low growth rates because of their slow water transport, and a low mortality risk since their narrow and reinforced conduits support negative water potentials and enhance mechanical stability (Poorter *et al.* 2008; Markesteijn *et al.* 2011a; Beeckman 2016). On the other side of this continuum, species have soft woods with larger xylem conduits and thin leaves with short retention time (Méndez-Alonzo *et al.* 2012). These species are expected to have fast growth rates during the rainy seasons due to their high water transport capacity and photosynthetic rates (Santiago *et al.* 2004a; Markesteijn *et al.* 2011a). However, they also have low hydraulic safety margins and may suffer higher mortality when water becomes limited (Méndez-Alonzo *et al.* 2012; Pineda-García *et al.* 2015).

Based on the above, we can expect drought-tolerant species to be more dominant and less vulnerable to extreme droughts in TDF than species with 'cheap' but hydraulically-efficient tissues (**Figure 1b**) (Méndez-Alonzo *et al.* 2012; Pineda-García *et al.* 2015). Yet, the predominance of deciduous species in TDF (Pennington *et al.* 2009; Linares-Palomino *et al.* 2011) suggests that lower leaf retention time in species that are hydraulically-efficient, but with low investment in tissues, may also be a successful strategy to survive under high water constraints (**Figure 1c**; Markesteijn *et al.* 2011a, b). By dropping their leaves, these drought-avoidance species reduce hydraulic cavitation risks via lower transpiration rates and prevent drought-induced mortality (McDowell *et al.* 2018). Accordingly, both drought-tolerant and drought-avoidance functional strategies could be successful in TDF (Sterck *et al.* 2011). The pervasive existence of these functional strategies in TDF (Méndez-Alonzo *et al.* 2012) carries the idea that other trait combinations are unlikely to occur or, when present, they will not favour the performance of species under strong water constraints (**Figure 1a-c**; Ziemińska *et al.* 2015; Gleason *et al.* 2016). For instance, it has been demonstrated that high hydraulic conductivity and high wood density do not simultaneously occur in stems (Gleason *et al.* 2016), or that species cannot simultaneously grow stems that have high wood density, high fibre wall fractions, and large fibre lumens (Ziemińska *et al.* 2015). Likewise, large-leaves species with dense wood would have higher risks of cavitation in low rainfall ecosystems, as the result of major transpiration demands (Baraloto *et al.* 2010a). However, the prevalence of trade-offs in hydraulic safety-efficiency and tissues investment in determining species dominance in TDF or demographic responses to extreme droughts is still untested. Similarly, little is known about the existence of other trait combinations and their consequences on species performance in TDF.

Here, we use a network of 11 1-ha permanent plots in TDF with a comprehensive dataset of standing biomass and demography for 21,821 individual trees belonging to 338 species, and measurements of 15 leaf and hydraulic functional traits, to construct the functional traits space and relate functional trait combinations to species dominance and responses to the extreme "El Niño" drought of 2015 in Northern South America ($ENSO_{2015}$). We assessed three main questions: (1) Does functional trait space reflect trade-offs in hydraulic safety-efficiency and investment in tissues for TDF tree species? (2) What are the dominant functional trait combinations of tree species in TDF? (3) How is functional space to demographic changes in biomass and net biomass balances after an extreme drought in TDF? Overall, we expected that the dominant (high biomass) species in the functional space would be associated with traits shaping the trade-offs in hydraulic safety-efficiency and investment in tissues (**Figure 1**), but we also expected to find species with trait combinations outside these trade-offs, with low dominance and poor performance after $ENSO_{2015}$. Specifically, species with either high safety and expensive tissues, or high efficiency and cheap tissues should both experience low mortality and have high growth rates under $ENSO_{2015}$, because they are adapted to cope with water constraints via drought-tolerance or drought-avoidance strategies (**Figure 1b**, **c**). These species would, in turn, have high positive net biomass balances after $ENSO_{2015}$ (**Figure 1b-c**). In contrast, species with other functional trait combinations should be less adapted to cope with water limitations, showing negative net biomass balances due to high mortality and low growth rates after $ENSO_{2015}$ (**Figure 1d**).

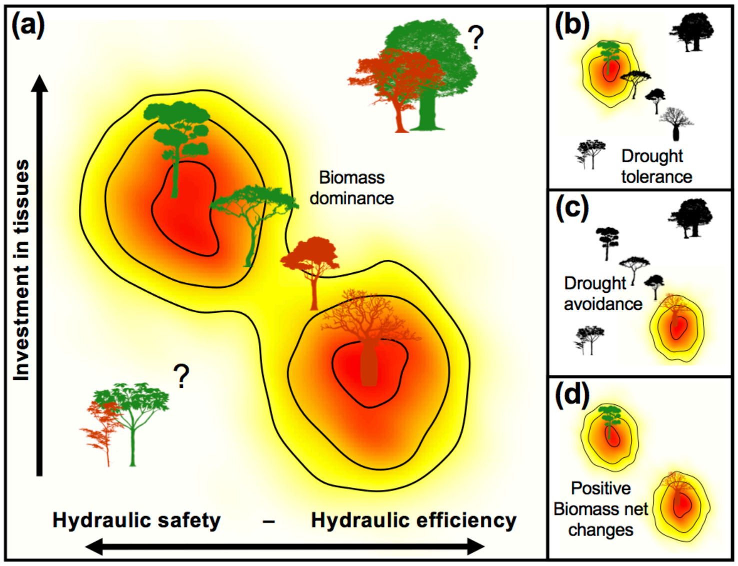

Figure 1. Schematic diagram representing hypotheses about the distribution of functional trait combinations across the continuum of hydraulic safety-efficiency and investment in tissues trade-offs (a, adapted from Méndez-Alonzo *et al.* 2012). Within this trait space, dominant species (higher biomass) are expected to be bounded by trade-offs in trait combinations that favour drought tolerance (b) or drought avoidance (c). Therefore, positive biomass net changes (red areas in the continuum) can be expected for both strategies under an extreme drought (d). Here, both drought tolerance and drought avoidance are alternative optimal strategies for species in response to water-constraints in TDF. Because species with other trait combinations are not expected to cope with drought conditions, they should not be present or be associated to lower performance under extreme drought conditions.

Material and methods

Study area and censuses data

Between 2013 and 2014, we established 11 1-ha permanent plots in mature TDF of Colombia, Northern South America (**Figure 2a**). Plots were located in areas of floristic representativeness of the three main dry formations among the region (*i.e.*, Caribbean lowlands, Inter Andean region, and dry Savannas, **Table S1**; Portillo-Quintero & Sánchez-Azofeifa 2010; DRYFLOR *et al.* 2016; González-M *et al.* 2018) and without evidence of logging. Mean annual temperature varied between 23.4 and 28.3 ºC, mean annual precipitation between 517.0-2697.2 mm, and mean annual potential evapotranspiration between 1161-2067 mm. All sites experienced between one and two dry seasons (4-9 dry months) and soils had high proportions of sand (34.2-72.3%) and high aridity (0.8-3.4; see **Table S1** for more details). Within each plot, all individual trees with a diameter at breast height ≥ 2.5 cm (DBH, censused at 1.3 m height) were tagged, and their DBH and height (m) were recorded (van Laar & Akça 2007). Subsequently, between 2016 and 2017, all plots were resampled, and DBH of all surviving trees (which allowed to estimate growth as an increment in DBH) and recruits (new individuals with DBH ≥2.5 cm) were measured. In total, 21,821 individual trees (26,132 stems) were measured. Between censuses, all sites experienced one of the strongest drought events of the last 36 years, “El Niño” Southern Oscillation 2015-2016 (**Figure 2b**, ENSO$_{2015}$, Kogan & Guo 2017). During this event, mean annual temperatures were almost 3ºC above, normal and cumulative rainfall anomalies reached -250 mm (Anyamba *et al.* 2019), inducing intense water deficits in several areas of Neotropical dry forests (**Figure 2b**, **Table S1**). ENSO$_{2015}$ started in October 2014 with dry peaks between May 2015 and January 2016 and lasted until June 2016 (L’Heureux *et al.* 2017). It was considered catastrophic for trees with low hydraulic safety margins and resulted in high tree mortality rates in TDF of Central America (Powers *et al.* 2020).

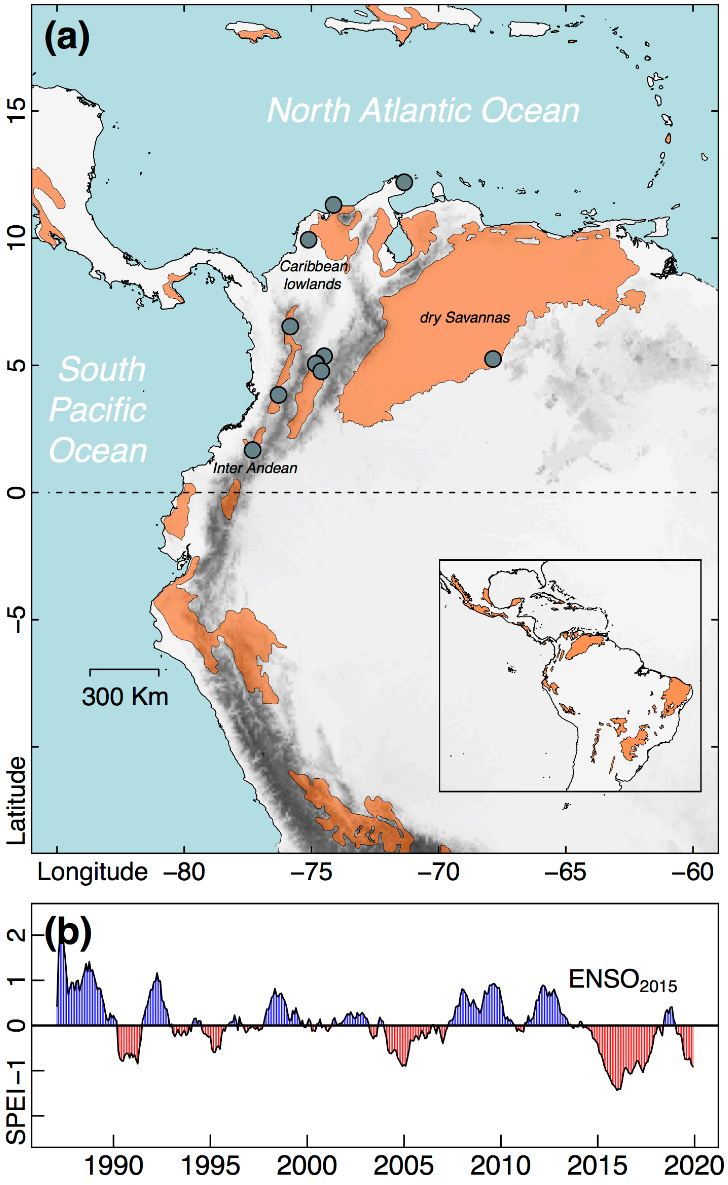

Figure 2. Geographic distribution and average inter-annual drought regimes of the study sites. (a) Distribution of dry ecosystems in Northern South America (orange area, adapted from Portillo-Quintero & Sánchez-Azofeifa 2010; DRYFLOR *et al.* 2016). Blue circles indicate the location of the 11 1-ha permanent plots installed for monitoring mature forests across the region. (b) The Standardised Precipitation-Evapotranspiration Index (SPEI; Vicente-Serrano *et al.* 2012) was calculated based on long-term data from weather stations near the plots (1980 to 2019). SPEI

determines the magnitude and strength of drought conditions during the period of analysis, where negative values indicate the SPEI mean for drought periods (red colour) and positive values correspond to wet periods (blue colour). All plots experienced the extreme $ENSO_{2015}$ (red area between 2015 and 2016). For extended details see **Table S1** in supporting information.

Functional traits

We measured 15 functional traits in 1553 individual trees, in 524 populations belonging to 338 species. Here, a population refers to all sampled individuals of the same species within a plot; we considered individual populations separately to account for local trait and biomass variations of species among plots. We measured four leaf traits and eleven wood traits, which characterizes the hydraulic safety-efficiency trade-off as well as investment in tissues across a broad range of values (**Table 1**, Scholz *et al.* 2013; Salgado-Negret *et al.* 2015). We collected traits for all tree species in each plot following an abundance-weighted trait sampling scheme (Carmona *et al.* 2015). Accordingly, within each plot, we measured traits in 5-8 individuals for the most abundant species, 1-3 individuals for species with less than five individuals per plot, and one individual for species with only one individual per plot. For individual trees for which some traits had missing values (only 4% of sampled individuals, for a total of 0.98%), we imputed trait values using the R package "*missForest*" (missing value imputation for mixed-type, Stekhoven & Bühlmann, 2012). We accounted for differences in the imputation process by including plots and species as predictors. Species with imputed individual-trait values were strongly linearly correlated with their not-imputed trait values ($P<0.001$, **Figure S1**).

Standing biomass and biomass changes

To estimate biomass (tons, t) of each individual stem, we used the allometric formulas Type I and Type II for TDF from Alvarez *et al.* (2012), which consider DBH (cm), tree height (m) and stem wood density (g cm^{-3}). Stem wood density was measured using the water displacement method and calculated as dry mass divided by fresh volume for 1-8 samples individual trees per species in each plot (Pérez-Harguindeguy *et al.* 2013). Standing biomass of each species (t ha^{-1}) was estimated as the sum of biomass of all its trees in each plot for the first census (t_0). Biomass growth of survivors for each species (BG_S, t ha^{-1} yr^{-1}) was estimated as the annual biomass increment produced by the growth of all trees surviving from t_0 to the final census (t_{fin}) in a plot. Biomass growth of recruits for each species (BG_R, t ha^{-1} yr^{-1}) was estimated as the annual biomass increment obtained from all trees that attaining at least 2.5 cm DBH in t_{fin} and that were not sampled in t_0 in a plot. Here, we considered that each new tree was recruited immediately after t_0 and assumed that had an initial DBH of 0 to avoid biomass overestimation (Talbot *et al.* 2014). Biomass mortality for each species (BM, t ha^{-1} yr^{-1}) was estimated as the biomass loss obtained from dead trees between t_0 and t_{fin}. To correctly compare BM with BG_S and BG_R, we calculated the biomass mortality of each tree as the biomass in t_0 minus the biomass of the same tree calculated with a DBH of 2.5 cm (Talbot *et al.* 2014). Finally, we estimated the net biomass change for each species (NBC, t ha^{-1} yr^{-1}) as the net annual change in biomass during the time interval between t_0 and t_{fin} (Prado-Junior *et al.* 2016; Poorter *et al.* 2017), so that: $NBC = BG_S + BG_R - BM$.

Table 1. Description of the selected functional traits, trait function dimensions, mean–ranges and global reference ranges.

Trait (abbreviation)	Units	Description	Trait function (dimension)	Trait mean ±SD $(\bar{Q}_{>0.1}-\bar{Q}_{<0.9})$	Reference range	References
Fibre wall thickness (FWT)	µm	[a] Double wall between adjacent fibres [b] Resistance of internal and external stresses [c] Greater walls, higher hydraulic safety	Water exploitative safety (wood)	5.54 ±1.52 (3.24–8.55)	4–12	Madsen & Gamstedt (2013); Scholz *et al.* (2013); Sorieul *et al.* (2016)
Hydraulically weighted diameter (d_h)	µm	[a] Sum of circle conduits diameters *d* divided by the number of conduits *N* in a surface area $\left(\sum \frac{d^4}{N}\right)^{0.25}$ [b] Conductance of conduits [c] Larger weighted diameters, higher hydraulic efficiency	Water exploitative efficiency (wood)	58.64 ±22.39 (31.23–105.74)	1–300	Scholz *et al.* (2013); Rosell *et al.* (2017)
Leaf area (LA)	mm^2	[a] Projected area of a leaf [b] Light interception, energy and water balance [c] Larger LA, cheaper tissues and high water demands	Investment in tissues Water exploitative efficiency (leaves)	1.25×10^4 ±2.15×10^4 (1.05×10^3–5.77×10^4)	1–>20×10^6	Pérez-Harguindeguy *et al.* (2013); Díaz *et al.* (2016)
Leaf dry matter content (LDMC)	mg g^{-1}	[a] Dry mass per unit of lamina surface area [b] Tissue investments and carbon-gain strategies [c] Higher LDMC, robust tissues	Investment in tissues (leaves)	379.38 ±91.31 (209.46–533.64)	50–700	Pérez-Harguindeguy *et al.* (2013); Díaz *et al.* (2016)
Leaf thickness (L_{th})	mm	[a] Leaf mesophilic density (or thickness) [b] Physical strength and leaf longevity [c] Thicker leaves, higher tissue investments	Investment in tissues (leaves)	0.21 ±0.06 (0.13–0.33)	0.11–0.74	Pérez-Harguindeguy *et al.* (2013); Onoda *et al.* (2011)
Maximum vessel area (VA_{max})	$µm^2$	[a] Average conduit surface area of the last VA percentile (>75, Q_3–Q_4) [b] Hydraulically efficiency [c] Greater conduits, higher water flows but higher conduits embolism risk	Water exploitative efficiency (wood)	2942.59 ±2623.32 (589.12–8904.27)	7853–31415	IAWA *et al.* (2007); Scholz *et al.* (2013)
Pit area (PA)	$µm^2$	[a] Pit aperture surface area [b] Air-water interfaces for conduits [c] Larger pits, higher water flows but higher conduits embolism risk	Water exploitative efficiency (wood)	19.68 ±16.30 (4.37–55.15)	12–78	IAWA *et al.* (2007); Scholz *et al.* (2013)
Pit diameter aperture (DA_{pit})	µm	[a] Horizontal pit membrane diameter [b] Embolism resistance inter-conduits [c] Smaller and denser pits, higher hydraulic safety	Water exploitative safety (wood)	2.90 ±1.19 (1.38–5.38)	0.5–7	Scholz *et al.* (2013); Li *et al.* (2016); Helmling *et al.* (2018)
Specific leaf area (SLA)	mm^2 mg^{-1}	[a] Area of a fresh leaf divided by its oven-dry mass [b] Carbon capture and leaf longevity	Water exploitative efficiency (leaves)	15.39 ±7.33 (7.24–32.22)	<1–300	Wright *et al.* (2004); Pérez-Harguindeguy *et al.* (2013)

Trait (abbreviation)	Units	Description	Trait function (dimension)	Trait mean ±SD ($\bar{Q}_{>0.1}$– $\bar{Q}_{<0.9}$)	Reference range	References
		[c] Higher SLA, lower tissue investments				
Vessel area (VA)	μm^2	[a] Average conduit surface area [b] Hydraulic conductivity [c] Greater conduits, higher hydraulic efficiency but lower hydraulic safety	Water exploitative efficiency and safety (wood)	1676.93 ±1484.11 (391.73–5094.72)	196–37600	Olson & Rosell (2013); Scholz *et al.* (2013)
Vessel density (VD)	vessels mm^{-2}	[a] Number of conduits per cross-sectional area [b] Resistance to strength and vessel implosion [c] Higher density, higher hydraulic safety	Water exploitative safety (wood)	71.71 ±50.54 (15.22–181.83)	1–1000	Chave *et al.* (2009); Scholz *et al.* (2013); Jacobsen *et al.* (2005)
Wood density (WD)	g cm^3	[a] Oven-dry mass divided by saturated volume of the wood section [b] Wood stability, aboveground biomass construction and carbon-gain strategies [c] Harder woods, lower water demands and higher tissue investments	Investment in tissues Water exploitative safety (wood)	0.63 ±0.15 (0.32–0.84)	0.1–1.2	Chave *et al.* (2009); Pérez-Harguindeguy *et al.* (2013)
Wood anhydrous density (WD_0)	g cm^3	[a] Oven-dry mass divided by anhydrous volume of the wood section [b] Wood stability [c] Greater wood anhydrous densities, higher tissue investments	Investment in tissues (wood)	0.72 ±0.17 (0.38–0.96)	0.1–1.5	Chave *et al.* (2009); Pérez-Harguindeguy *et al.* (2013)
Water content at maximal capacity (WC_{max})	kg kg^{-1}	[a] Free and fixed water capacity in cells. $[(1.5 - WD_0) \times 1.5WD_0] + WC_{fsp}$ (Water content at fibre saturation point); $WC_{fsp} = \frac{1}{WD} - \frac{1}{WD_0}$ [b] Shrinkage and swelling of xylem cells [c] Higher water content, lower xylem mechanical resistance	Water exploitative efficiency (wood)	1.05 ±0.61 (0.53–2.54)	0.2–5.0	Guevara (2001); Berry & Roderick (2005)
Xylem potential hydraulic conductivity (K_p)	kg m^{-1} s^{-1} MPa^{-1}	[a] Theoretical specific xylem hydraulic conductivity per cross-sectional area. $\frac{\pi \rho_{\omega}}{128\,\eta} \times \sum {d_h}^4 \times VD$; ρ_{ω}=998.2 kg m^{-3}; η=1.002x10^{-9} MPa s^{-1}; d_h and VD by m units [b] Water exploitation abilities [c] Higher potential conductivity, higher hydraulic efficiency	Water exploitative efficiency (wood)	25.09 ± 43.78 (2.25–113.72)	0.3–200	Chave *et al.* (2009); Poorter *et al.* (2010); Méndez-Alonzo *et al.* (2012)

[a] Trait-based ecology definition and method of calculation

[b] Trait association to functions and mechanisms of a tree

[c] Trait association to hydraulic safety-efficiency trade off of a tree

Statistical analyses

To characterize the functional trait space in TDF, we performed a Principal Component Analysis (PCA) with trait values at the individual level (*i.e.*, each score in the PCA refers to an individual tree). We selected the two first PCA axes, which explained 61.32% of the variance, and performed a *varimax* rotation to improve the interpretability of the resulting 2-dimensional functional trait space. The rotation did not change the coordinate system of the initial PCA (ρ=0.9, P<0.001). Both axes of the functional space were defined as multidimensional traits for evaluating the trait probability density (TPD) of species, and their respective biomass dimensions (*i.e.*, standing biomass, biomass demographic changes, and biomass net changes), following the procedures in Carmona *et al.* (2016, 2019).

The TPD approach is based on the estimation of Gaussian kernel density functions (bivariate in this case) around each observation. Here, the TPD function of a given species represented the probabilities of observing different trait values (or combinations of them in the case of our 2-dimensional space) in those species, considering all sampled individuals (Carmona *et al.* 2016). For species with at least three individuals, the standard deviation (bandwidth) around each observation was selected using the unconstrained bandwidth estimation implemented in the R package *ks* (Chacón & Duong 2018), as implemented in the *TPDs* function of the R package "*TPD*" (Carmona *et al.* 2019). For species with less than or equal to two individuals within a plot, the standard deviation for each PCA axis and plot were predicted by regressing standard deviations against the mean value of species (considering all species within the plot). For extended details see **Figure S2**.

To calculate the trait probability densities for each biomass dimension (TPD_C), we combined all TPD of the individual species based on the sum of the probability functions, rescaled by the relative biomass dimension of each species (see **Figure S2**). Then, to evaluate the amount of functional space occupied by each TPD_C, we estimated the *Functional Richness* (F_{Ric}) index suggested by Carmona *et al.* (2016, 2019). F_{Ric} refers to the sum of each biomass dimensions' hypervolumes, considering their probability distributions for values above 0. We estimated differences in F_{Ric} between biomass dimensions (*e.g.*, BG_S vs. BM) by calculating F_{Ric} 999 times, with half the species randomly selected each time. To evaluated dissimilarities on the occupancy of the functional space between biomass dimensions, we ran an *Overlap-based functional dissimilarity* (β_O) index, where values vary from 0 to 1 and indicate maximum dissimilarity between hypervolumes when β_O amounts to 1 (Carmona *et al.* 2019). We estimated if β_O was higher than expected by chance with a null model, in which TPDs scores were randomized and β_O was calculated 999 times (Traba *et al.* 2019). All statistical analyses were performed using R (v3.5.3; *www.r-project.org*).

Results

Functional trait space and biomass dominance in TDF

The functional trait space of 524 populations belonging 338 TDF tree species is summarized in the first two-dimensions of the PCA (**Figure 3a**). The first PCA axis (36.75% of explained variance) reflected the hydraulic safety-efficiency trade-off. The high safety side was characterized by a high density of narrow vessels with high fibre wall thickness, whereas the hydraulic-efficiency side had wide vessels and pits with high xylem potential hydraulic conductivity. The second PCA axis (24.57% of explained variance) reflected differences of investment in tissues, where negative values were related to large leaves with high SLA, and high content of water at maximal capacity ('cheap' tissues), while positive values corresponded to high LDMC and high wood density ('costly' tissues). The 50% probability threshold in the TPD ($TPD_{<50\%}$; **Figure 3a**) showed that more than half of the populations (288) occurred along the hydraulic safety-efficiency trade-off but were restricted to the side of high investment in tissues. Surprisingly, many populations had combinations of traits outside of these trade-offs ($TPD_{50\text{-}99\%}$ = 236; **Figure 3a**). When TPD was rescaled by standing biomass, the $TPD_{<50\%}$ was narrower and included 220 populations, which accounted for 61% of total biomass (592.8 t, **Figure 3b**). Populations with costly and hydraulically-safe tissues and costly and hydraulically-efficient tissues accounted for 37.4% of total biomass ($TPD_{<20\%}$= 76 populations with 362.9 t, **Figure 3b**), while populations with other trait combinations were widespread but with low biomass across the functional space (**Figure 3b**). For instance, species with the dominant trait combinations such as *Trichilia oligofoliolata* (a costly and hydraulically-safe evergreen species) or *Astronium graveolens* (a costly and hydraulically-efficient deciduous species) reached to 53.6 and 21.5 t ha^{-1}, respectively. In contrast, species with different trait combinations and low investment in tissues such as *Urera simplex* (an evergreen species with intermediate hydraulically-efficiency) or *Pseudobombax septenatum* (the typical deciduous and hydraulically-efficient species) only reached 0.02 and 4.7 t ha^{-1}, respectively (**Figure 3b**). For extended details of functional trait combinations and biomass scores of species see **Table S2**.

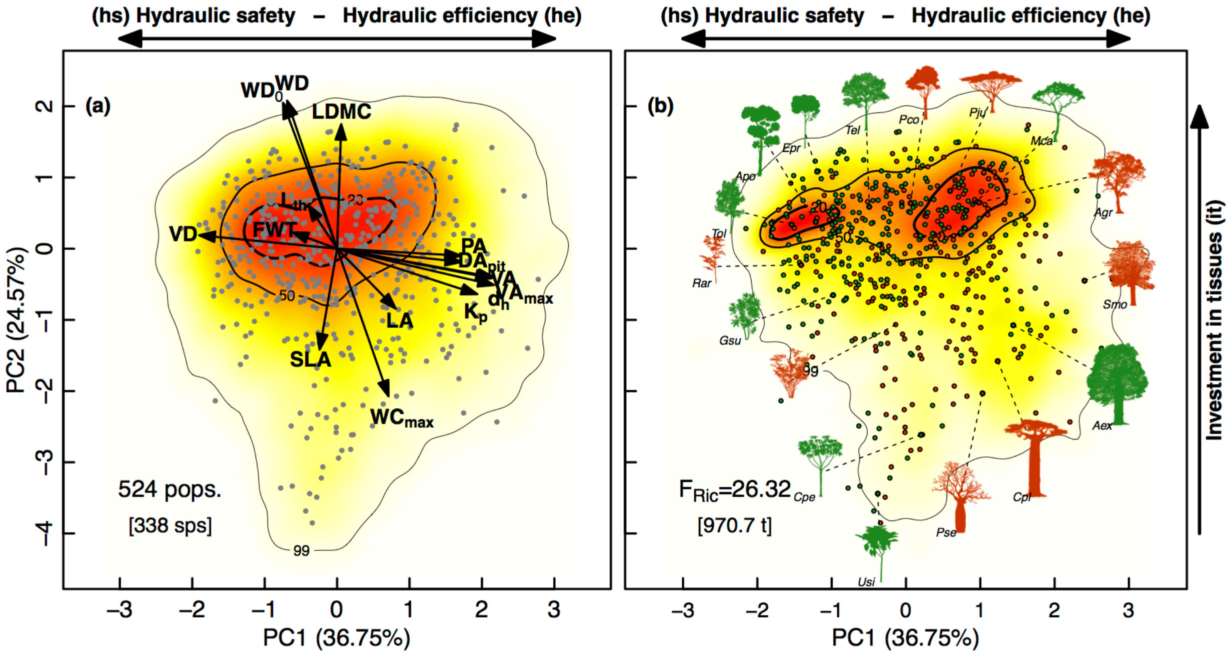

Figure 3. Trait probability densities (TPD) showing the functional trait combinations of species populations along an axis hydraulic safety-efficiency trade-off (hs-he, PC1 36.75% explained variance) and an axis of investment in tissues (it, PC2 24.57% explained variance). (a) TPD where each species at each plot has an equivalent weight (grey points). (b) TPD where each species population is rescaled by its equivalent biomass at each plot (green points represent evergreen species and orange points deciduous species). Functional traits: Fibre wall thickness (FWT, µm), hydraulically weighted diameter (d_h, µm), leaf area (LA, mm^2), leaf dry matter content (LDMC, mg g^{-1}), leaf thickness (L_{th}, mm), maximum vessel area (VA_{max}, µm^2), pit area (PA, µm^2), pit diameter aperture (DA_{pit}, µm), specific leaf area (SLA, mm^2 mg^{-1}), vessel area (VA, µm^2), vessel density (VD, vessels mm^{-2}), wood density (WD, g cm^3), wood anhydrous density (WD_0, g cm^3), water content at maximum capacity (WC_{max}, kg kg^{-1}), and xylem potential hydraulic conductivity (K_s, kg m^{-1} s^{-1} MPa^{-1}). The whole pool (TWP) of populations in the TPD. Functional Richness (F_{Ric}). Examples of species with different functional trait combinations in TDF*: Anacardium excelsum (Aex), Aspidosperma polyneuron (Apo), Astronium graveolens (Agr), Cavanillesia platanifolia (Cpl), Cecropia peltate (Cpe), Eugenia procera (Epr), Gustavia superba (Gsu), Machaerium capote (Mca), Pradosia colombiana (Pco), Prosopis juliflora*

(Pju), Pseudobombax septenatum (Pse), Randia armata (Rar), Spondias mombin (Smo), Trichilia oligofoliolata (Tol), Trichilia elegans (Tel), Urera simplex (Usi), Zanthoxylum rhoifolium (Zrh). Functional Richness (F_{Ric}).

TDF functional and biomass changes after $ENSO_{2015}$

Total biomass growth of surviving trees was 24.5 t yr^{-1} (2.23 t ha^{-1} yr^{-1} ± 0.67), biomass growth of recruiting trees was 1.10 t yr^{-1} (0.10 t ha^{-1} yr^{-1} ± 0.11) and biomass mortality was 7.2 t yr^{-1} (0.65 t ha^{-1} yr^{-1} ± 0.35; **Table S1**). We found high dissimilarity between functional trait spaces of all demographic dimensions, at all probability thresholds (P<0.001, **Figure 1b**, **c**, **f**, **Figure S3**), but resulting in contrasting responses to $ENSO_{2015}$. The two dominant functional trait combinations, hydraulically safe with high investment and hydraulically efficient with high investment, showed the largest biomass growth of surviving trees ($TPD_{20\%}$= 50 populations, 10.4 t yr^{-1} [42% total biomass] and $TPD_{50\%}$= 167 populations, 14.3 t yr^{-1} [58%]; **Figure 4a**). In contrast, the largest biomass for recruited trees was restricted to species with combinations of costly and hydraulically-safe traits or 'cheap' and hydraulically-efficient traits ($TPD_{50\%}$= 27 species, 0.64 t yr^{-1} [57%]; **Figure 4e**). Species with low investment in tissues and high hydraulic efficiency were mainly deciduous (71%, *e.g. Zanthoxylum lenticulare* = 0.17 t ha^{-1} yr^{-1}). The highest loss of biomass by mortality was mainly ascribed to species with costly but hydraulically-safe tissues ($TPD_{20\%}$= 142 populations, 4.61 t yr^{-1} [64%]; **Figure 4i**), and a second group of functional trait combinations was related to species with costly and hydraulically-efficient tissues ($TPD_{20-50\%}$= 97 populations, 2.88 t yr^{-1} [40%]; **Figure 4i**). Here, it is important to highlight that biomass loss by mortality accounted for a higher functional space of trait combinations with respect to the other demographic dimensions (F_{Ric}=27.67, P<0.001, **Figure 1d**, **g**, **h**). These results were consistent across all tested probability thresholds (**Figure S4**).

Net biomass change was 18.4 t yr^{-1} (1.68 t ha^{-1} yr^{-1} ± 0.56), varying between 0.82 and 2.50 t ha^{-1} yr^{-1} per plot (**Table S1**). Positive changes in net biomass reached 20.3 t yr^{-1} (1.84 t ha^{-1} yr^{-1} ± 0.61) but were restricted to the dominant functional trait combinations (**Figure 5a**, $TPD_{<50\%}$). Negative changes in net biomass attained 1.9 t yr^{-1} (0.17 t ha^{-1} yr^{-1} ± 0.11) and included species with costly hydraulically-safe tissues, but also 'intermediate' species with traits between both ends of the hydraulic safety and efficiency trade-offs and with intermediate investment in tissues (**Figure 5b**, $TPD_{<50\%}$). Functional dissimilarities between positive and negative biomass dimensions (β_O) were significant at all probability thresholds (P<0.001; **Figure 5c**). Negative biomass changes occupied a higher fraction of the functional space when compared to positive biomass changes for all probability thresholds (Diff. F_{Ric}=4.93, P<0.001; **Figure 5c**). Notably, total biomass in all plots after $ENSO_{2015}$ was 989.1 t, but the 50% threshold probability showed a clear divergence of both dominant functional trait combinations that were not detected for the initial biomass (see **Figures 3b** and **5c**).

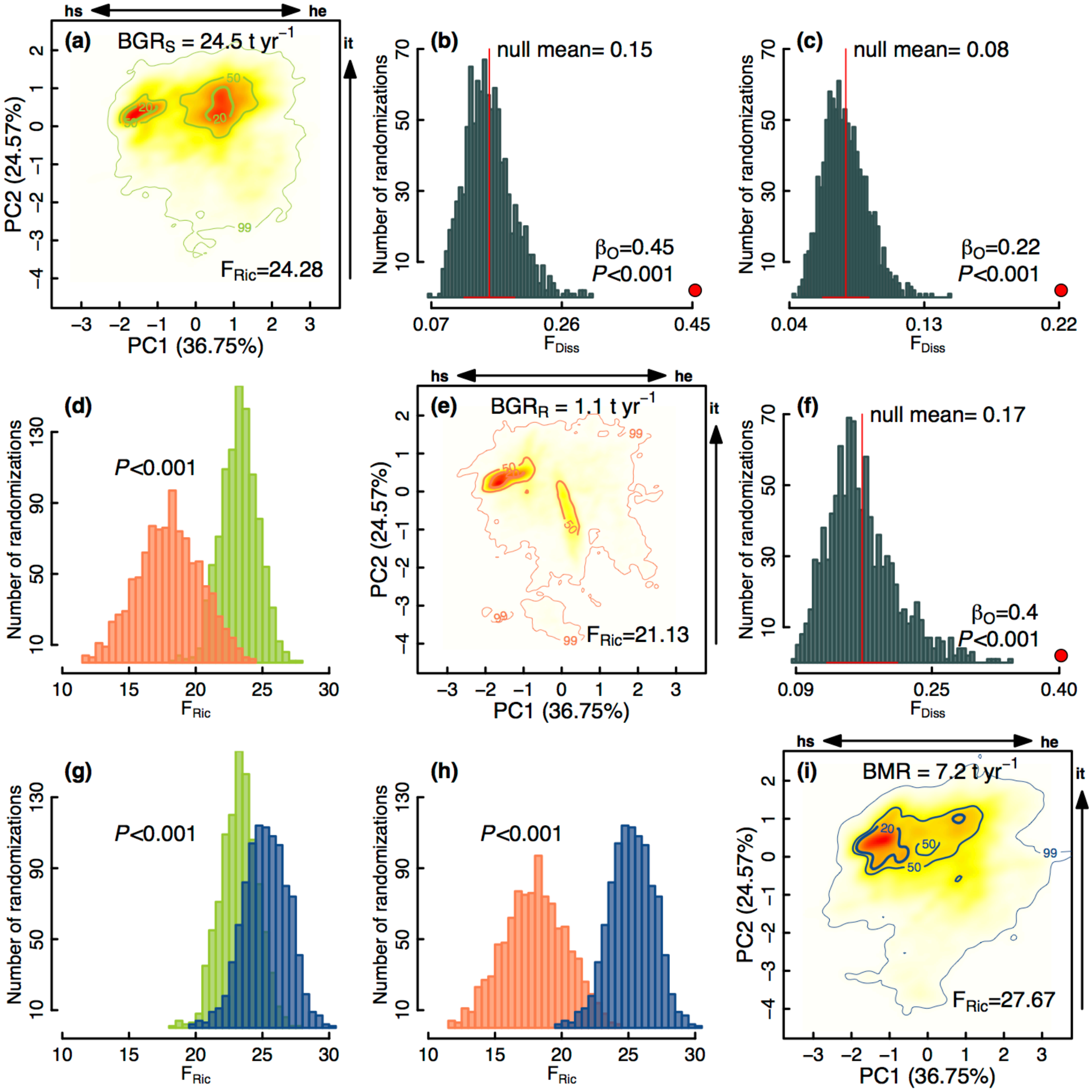

Figure 4. Trait probability densities (TPD) showing the functional trait combinations of species populations rescaled by biomass growth of survivors (a, BG_S in green colour), biomass growth of recruits (e, BG_R in orange colours) and biomass mortality (i, BM in blue colour). Null models for Functional Dissimilarity (F_{Diss}, b, c, f) between biomass growth and mortality TPD's. Significant β_O ($P<0.001$) indicates that dissimilarity between paired TPD demographic dimensions is greater than the expected by chance (999 randomizations). Functional Richness (F_{Ric}, d, g, h) between biomass growth and mortality TPD's (b, c, f). Significative differences between the paired frequency distributions indicate different F_{Ric} of the contrasted TPD's demographic dimensions ($P<0.001$, 999 randomizations). Hydraulic safety (hs), hydraulic efficiency (he), investments in tissues (ti).

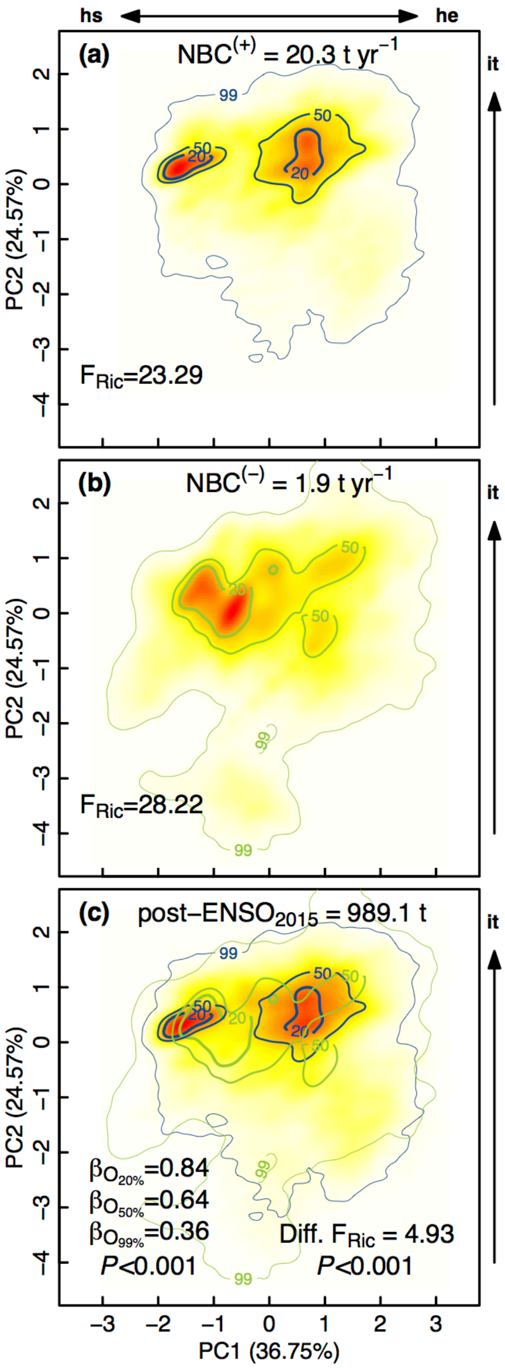

Figure 5. Trait probability densities (TPD) showing the functional space of trait combinations for species populations rescaled by positive net biomass changes (a, $NBC^{(+)}$ in blue colours), by negative net biomass changes (b, $NBC^{(-)}$ in green colours) and by standing biomass after $ENSO_{2015}$ (c). F_{Ric} refers to functional richness and F_{Diss} to functional dissimilarity. Significant □$_{O}$ (*P*<0.001) indicate that functional dissimilarity between positive and negative net biomass change TPD's is greater than expected by chance (999 randomizations). Differences in functional richness (Diff. F_{Ric}, *P*<0.001) indicate that negative net biomass changes TPD's had a higher F_{Ric} than positive net biomass changes TPD's (999 randomizations). Hydraulic safety (hs), hydraulic efficiency (he), investments in tissues (ti).

Discussion

Tropical dry forests (TDF) experience frequent water limitations as the result of annual rainfall seasonality (Linares-Palomino *et al.* 2011) and inter-annual extreme droughts (Allen *et al.* 2010). In response to these conditions, species have developed a particular suite of functional traits (Pennington *et al.* 2009; Aguirre-Gutiérrez *et al.* 2019), with important consequences for ecosystem functioning. To understand the functional responses of TDF tree species to extreme drought events, we assessed the functional trait space of a large number of tree species and evaluated if particular suites of trait combinations determined differences in species standing biomass and demographic biomass changes to one of the driest events in decades ($ENSO_{2015}$). Our results showed that: (1) TDF tree species are distributed across a broad functional trait space associated with trade-offs in hydraulic safety-efficiency and investment in tissues. (2) Biomass-dominant species were located along the hydraulic safety-efficient trade-off but only at the high investment in tissues side. Yet, almost half of the species had other trait combinations but with lower biomass dominance. (3) Biomass loss by mortality covered a broader functional trait space than biomass growth, but net biomass losses were mostly experienced by species with intermediated hydraulically safety-efficiency and lower investment in tissues.

The hydraulic safety-efficiency trade-off and costly tissues govern species dominance in TDF

As expected, most TDF tree species were distributed along the hydraulic safety-efficiency trade-off (**Figure 3**). Yet, another important fraction of species was found to occupy the functional space with alternative trait combinations. We found a first numerous group of species with high standing biomass in the functional space combining hydraulically-safe traits (**Figure 3b**) such as narrow vessels and pit areas and high vessel density (Markesteijn *et al.* 2011b; Onoda *et al.* 2011; Méndez-Alonzo *et al.* 2012). A second group of dominant species was associated with traits of high water transport efficiency (**Figure 2a**) such as wide vessels, large pit areas and high xylem potential hydraulic conductivity (Sobrado 1997; Pineda-García *et al.* 2015). However, and contrary to our expectations, this trade-off was not related to a parallel trade-off in tissue investments since both groups of dominant species were found to have dense leaves and stems (**Figure 2**). This unexpected result disagrees with previous studies that have suggested that species with high hydraulic-efficiency, traditionally associated with deciduousness for avoiding cavitation risks under water-constraints, have low investment in tissues but high nutrient concentration which would enable them to maximize growth rates in their reduced growing season (Brodribb *et al.* 2010; Markesteijn *et al.* 2011a, b; Méndez-Alonzo *et al.* 2012). In contrast, our results suggest that not investing in expensive tissues has negative consequences on biomass dominance, irrespective of leaf habit (**Figure 5c**). Despite this result being novel, it is consistent with the physiological mechanisms of species to deal with drought. For instance, high wood density, which may result from a different combination of tissue and cell distributions such as high investments in fibre wall thickness (Ziemińska *et al.* 2015) or an increasing abundance of fibre (Jacobsen *et al.* 2007), can protect vessels from implosion when water shortage creates strong negative xylem potentials (Hacke *et al.* 2001b; Pratt *et al.* 2007). Likewise, thick and dense leaves may be more resistant to drought because living cells have rigid walls preventing cell collapse caused by negative turgor pressures developing in them under substantial water loss (Salleo & Nakdini 2000). Additionally, dense and rigid leaves have smaller transpiring surfaces, hence reducing wilting and water requirements (Niinemets 2001; Poorter *et al.* 2009). However, it is important to acknowledge that investment in costly tissues may also respond to other factors that favour species dominance. Tough tissues may provide protection against herbivores and against other physical hazards (Turner 1994; Cunningham *et al.* 1999). For instance, *Aspidosperma polyneuron*, a dominant species with dense leaves, showed lower leaf area removed by herbivory than *Sapium glandulosum*, which have low dominance and thin tissues (Silva *et al.* 2015; **Table S2**). Moreover, dense tissues in deciduous species may retard leaf loss during the dry seasons increasing the carbon gain window, or reduce cavitation risk on instantaneous dry conditions during the rainy seasons (Powers & Tiffin 2010; Lopezaraiza-Mikel *et al.* 2013).

The fact that investment in expensive tissues relates to high standing biomass in TDF opens new questions about the mechanisms that may mediate the dominance patterns of species under future climatic scenarios. For example, if extreme droughts become more frequent and intense in the tropics (Allen *et al.* 2010, 2015), and building dense tissues is energetically expensive and time-consuming (Chave *et al.* 2009; Osnas *et al.* 2013), how will the functional space be modified in tropical forests in the future? Answering this question requires models that integrate not only species losses but also changes in the functional patterns at community scales (Lawlor & Tezara 2009; McDowell *et al.* 2018).

Biomass demographic changes in TDF following the ENSO_{2015}

After ENSO_{2015} the functional space of biomass loss by mortality was significantly broader than the space of growth and recruitment (**Figure 4**), and negative net biomass change showed a higher covering of this functional space respect to positive net biomass change (**Figure 5**). These findings support the idea that under extreme droughts, tree mortality may be more widespread than forest recovery via the growth of trees (Allen *et al.* 2010), and that is an important driver of functional trait composition and forests functioning (Fauset *et al.* 2012; Aguirre-Gutiérrez *et al.* 2019; Esquivel-Muelbert *et al.* 2019). Growth, recruitment, and mortality of trees were mostly shaped by differences in the hydraulic safety-efficiency and investments in tissue (**Figure 4**). However, we did not find support for a coordinated demographic response of both dominant strategies along the hydraulic safety-efficiency trade-off and "costly-to-cheaper" tissue investments (Méndez-Alonzo *et al.* 2012). The higher biomass gained by survivors' growth was restricted to species with costly, but hydraulically-safe tissues or costly and hydraulically-efficient tissues, which is consistent with the prediction that species having dominant functional trait combinations would perform better under water constraints. Our results also demonstrate that irrespective of the hydraulic designs or leaf habits, as long as species invest in expensive leaf and wood tissues, they would effectively respond to extreme drought conditions. This result may be related to the fact that building expensive tissues implies more biomass per volume fraction, where despite the expected low growth rates for the costly and hydraulically-safety tissue species, they can pack high carbon stocks at constant growth rates during long periods (Poorter *et al.* 2017). Likewise, costly and hydraulically-efficient tissue species have important carbon gains during the reduced growing season when they not only invest in performance but also protect their structures from coping with water-constraints (Somavilla *et al.* 2014).

Interestingly, biomass of recruited trees was the only demographic dimension following the expected coordination between the hydraulic safety-efficiency trade-off with the "costly" to "cheap" investment in tissues axis. Markesteijn *et al.* (2011a) found that pioneer and deciduous tree species generally combine high hydraulic conductivity with low stem densities, which favours short-term gain in biomass at the expense of long-term survival. This strategy favours high volumetric and height gain, to rapidly ascend in the canopy and gain a photosynthetic edge. This same explanation may apply in our study if we take into account that the high recruitment of hydraulically-efficient species, also correspond to species mainly deciduous with high values of specific leaf area and water content at maximum capacity, which are traits associated with fast growth (Wright *et al.* 2004; Poorter *et al.* 2008).

The broader functional space associated with tree mortality, in comparison to biomass gain by growth, suggests that most TDF species are sensitive to extreme droughts. Additionally, we observed that high mortality was concentrated in species with costly and hydraulically-safe tissues, followed, to a lesser extent, by species with costly and hydraulically-efficient tissues (**Figure 4c**). This unexpected result contrasts with previous studies suggesting that 'conservative' traits associated with high hydraulic-safety should be positively related to survival rates in TDF (Prado-Junior *et al.* 2016; Powers *et al.* 2020), where biomechanical resistance or narrow hydraulic conduits are enough to counteract water-constraints (Pineda-García *et al.* 2015; Beeckman 2016). Likewise, it supports the idea that drought-induced mortality can be countered by avoidance strategies such as leaf dropping (Sobrado 1997). However, it is important to note that although biomass losses by mortality and functional space reduction were evident in this study as the result of one extreme drought episode ($ENSO_{2015}$), long time monitoring is necessary to determine if under normal climatic conditions, TDF recover the loss of biomass and functionality that follow extreme droughts; or if on the contrary, these species have widespread mortality risks across the whole hydraulic safety-efficiency functional space under these particular strong droughts (Powers *et al.* 2020).

The sensitivity of TDF to future drier scenarios

Future drier scenarios are expected to change the functional space and functioning of TDF (Allen *et al.* 2010, 2015). However, the strength and direction of these changes are still unclear because of the absence of studies on the functional sensitivity of species to extreme droughts, and the absence of long monitoring trait-demographic data to evaluate the consequences of extreme droughts on forest functioning. Recently, it was demonstrated that $ENSO_{2015}$ caused high mortality of TDF species with low hydraulic safety margins (Powers *et al.* 2020). Our results suggest that, irrespective of their hydraulic designs, species with low investment in tissues were strongly sensitive to $ENSO_{2015}$, resulting in important negative net biomass balances. In a broader context, biomass net balance after $ENSO_{2015}$ was over two times lower than balances for a rainy period. For instance, between 2009 and 2011 (wet period for TDF in Northern South America, SPEI > 1; **Figure 2b**), El Vinculo, one of our study sites, had a net biomass gain of 3.4 t ha^{-1} yr^{-1} (tress with DBH > 5cm; Torres *et al.* 2012), while after $ENSO_{2015}$ it only reached 1.73 t ha^{-1} yr^{-1} (trees with DBH > 2.5cm). This result, together with the narrower functional space of positive biomass gain than of negative biomass gains (**Figure 5c**), suggests that both functional diversity and biomass productivity should decrease in future drier scenarios. Further studies should model how future scenarios of changes in rainfall regimes may impact forest biomass dynamics (Allen *et al.* 2017a) but also if the functional trait space will become narrower due to these events.

Acknowledgements

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Supporting information

Table S1. Extended information of the 11 1-ha permanent Tropical Dry Forests (TDF) plots. *Biomass:* Standing biomass (t ha^{-1}) estimated as the sum of biomass of all trees for the first census (t_0). Biomass growth of survivors (BG_S, t ha^{-1} yr^{-1}) was estimated as annual biomass increments resulting from the growth of all trees that survived from t_0 to the final census (t_{fin}). Biomass growth of recruits (BG_R, t ha^{-1} yr^{-1}) was estimated as annual biomass increment obtained from all trees that attained at least 2.5 cm DBH in t_{fin} and were not sampled in t_0. To avoid biomass overestimation, we consider that each new tree was recruited immediately after t_0 and assumed that they had an initial DBH of 0 (Talbot *et al.* 2014). Biomass mortality (BM, t ha^{-1} yr^{-1}) was estimated as biomass loss from all trees that died between t_0 and t_{fin}; biomass for a DBH of 2.5 cm was subtracted to each dead tree (Talbot *et al.* 2014). Net biomass change (NBC, t ha^{-1} yr^{-1}) corresponded to the net annual change in biomass per plot between t_0 and t_{fin} (Prado-Junior *et al.* 2016; Poorter *et al.* 2017); it was estimated as: $NBC = BG_S + BG_R - BM$. The *Standardised Precipitation-Evapotranspiration Index* (SPEI; Vicente-Serrano *et al.* 2012) shows the mean for wet periods (wet), dry periods (dry), and $ENSO_{2015}$. SPEI was calculated based on long-term data from weather stations near the plots (1980 to 2019), and shows the magnitude and strength of drought conditions during the period of analysis, where negative values indicate the SPEI mean for drought periods (red colour) and positive values correspond to wet periods (blue colour). *Climatic conditions*: Total annual rainy days (ARD, no.), aridity index (Aridity, [PET/TAP]), isothermality (Isoth, %), solar radiation (SRad, MJ·m^{-1} x 100), total annual precipitation (TAP, mm), potential evapotranspiration (PET, mm), number of periods with three consecutive dry months ($Dry_{Periods}$, # [three month with <100 mm·month^{-1}]), mean annual temperature (MAT, ºC), total precipitation during the three driest months (TP_{Driest} [<100 mm·month^{-1}], mm), number of dry months (D_{Months}, months with <100 mm·month^{-1}), water vapor pressure (WVP, kPa) and wind speed (Wind, m·s^{-1}). *Soil conditions*: Acidity (pH), available phosphorus (P, mg·kg^{-1}), cation exchange capacity (CEC, cmol^{+}·kg^{-1}), extractable bases (Ca [Calcium], Mg [Magnesium], K [Potassium], Na [Sodium], cmol^{+}·kg^{-1}), organic carbon (OC, %) and textural fractions (Sand, Clay, Silt, %). *Land-cover and terrain characteristics*: Surrounding forest area (ha) and topographic roughness (Roughness, %).

Study sites	**TDF in the Caribbean lowlands' region**			**TDF in the Inter Andean region**							**TDF in the dry Savannas**
Site name	Macuira National Park	Sanctuary of Flora and Fauna Colorados	Tayrona National Park	Cardonal Plana Forests	Cardonal Loma Forests	Jabirú Private Natural Reserve	Tambor Private Natural Reserve	Cotove Research Station	El Vinculo Regional Park	Taminango Research Station	Tuparro National Park
Latitude (ºN)	12.20	9.94	11.31	5.08	5.09	5.06	5.17	6.53	3.84	1.67	5.25
Longitude (ºW)	-71.35	-75.11	-74.13	-74.80	-74.77	-74.83	-74.81	-75.83	-76.29	-77.31	-67.86
Altitude (masl)	113	301	15	260	322	302	385	509	1025	591	95
Number of species	34	66	53	49	47	35	77	28	45	9	76
Deciduous/Evergreen	24/10	30/36	34/19	21/28	22/25	15/20	27/50	15/13	19/26	5/4	22/54
Standing biomass	80.9	103.8	110.7	87.6	132.9	106.1	116.1	76.9	62.0	19.9	73.8
BG_S	1.45	2.68	1.85	1.65	2.63	3.59	2.58	2.44	2.22	1.18	2.25
BG_R	0.002	0.007	0.048	0.212	0.027	0.360	0.166	0.178	0.087	0.020	0.007
BM	0.63	0.63	0.40	0.87	1.01	1.45	0.66	0.41	0.59	0.25	0.30
BNC	0.82	2.06	1.49	0.99	1.64	2.50	2.09	2.21	1.73	0.95	1.96
Weather stations (Δt=1980-2019)	2			4							1
SPEI wet	0.82			0.81							0.74
SPEI dry	-0.77			-0.80							-0.80

Study sites	TDF in the Caribbean lowlands' region			TDF in the Inter Andean region							TDF in the dry Savannas
SPEI ENSO$_{2015}$ (□t=May/2015-Jan/2016)	-1.42			-1.21							-1.87
Climate											
Ard	33	96	95	116	113	116	126	146	144	138	152
Aridity	3.42	1.01	2.03	1.29	1.19	1.31	0.88	1.43	0.97	1.94	0.77
Dry$_{Periods}$	1	1	1	2	2	2	2	1	2	2	1
D$_{Months}$	10	5	9	5	5	5	4	6	5	9	4
Isoth	75.43	90.25	81.35	85.97	85.91	86.03	85.83	87.29	93.30	91.78	78.07
MAT	27.11	26.1	27.38	27.86	27.44	27.86	26.81	26.92	23.38	25.25	28.25
SRad	185.69	192.08	196.79	173.36	172.78	173.28	172.87	178.49	169.95	159.45	164.10
TAP	517.0	1528.4	899.4	1505.9	1541.2	1528.2	1912.5	1193.8	1192.4	721.4	2697.2
PET	1768.6	1546.0	1827.7	1946.8	1835.6	2009.1	1689.1	1712.8	1161.3	1400.8	2067.0
TP$_{Driest}$	32.1	139.3	33.4	227.8	222.5	236.8	272.7	112.7	168.5	52.4	177.1
WVP	2.67	2.75	2.87	2.63	2.53	2.65	2.50	2.55	2.14	2.36	2.80
Wind	4.84	2.35	4.45	0.93	0.92	0.93	0.90	0.83	0.87	0.96	1.37
Soils											
pH	6.12	7.37	7.38	6.79	6.87	6.46	6.98	6.54	6.22	7.23	4.39
P	18.14	12.17	222.59	143.24	19.36	17.08	11.33	20.08	4.70	27.89	3.32
CEC	10.01	30.89	16.43	15.61	20.08	17.01	14.73	25.71	26.68	33.10	6.69
Extractable Bases											
Ca	5.29	34.83	16.05	13.81	22.89	13.13	10.29	22.13	21.33	29.14	0.06
Mg	2.19	4.64	2.69	3.24	4.11	3.90	2.30	9.95	17.74	7.91	0.06
K	0.55	0.65	0.82	0.73	0.36	0.70	0.61	0.38	0.87	1.08	0.21
Na	0.22	0.09	0.07	0.03	0.10	0.08	0.04	0.15	0.14	0.16	0.16
OC	1.00	3.22	3.58	2.54	2.41	2.80	2.36	2.26	3.64	2.61	1.79
Textural fractions											
Sand	57.41	34.21	62.58	61.86	56.45	48.86	72.25	37.42	60.69	34.47	64.27
Clay	21.54	31.58	19.25	24.96	24.54	21.16	16.33	35.34	24.36	29.66	16.39
Silt	21.07	34.21	18.18	13.18	19.03	29.98	11.42	27.24	14.95	35.9	19.34
Forest area	407.6	395.0	411.8	153.9	303.0	145.4	329.6	55.1	23.4	56.8	176.3
Roughness	10.4	14.7	19.1	7.3	12.7	9.0	22.5	9.7	8.0	20.8	7.4

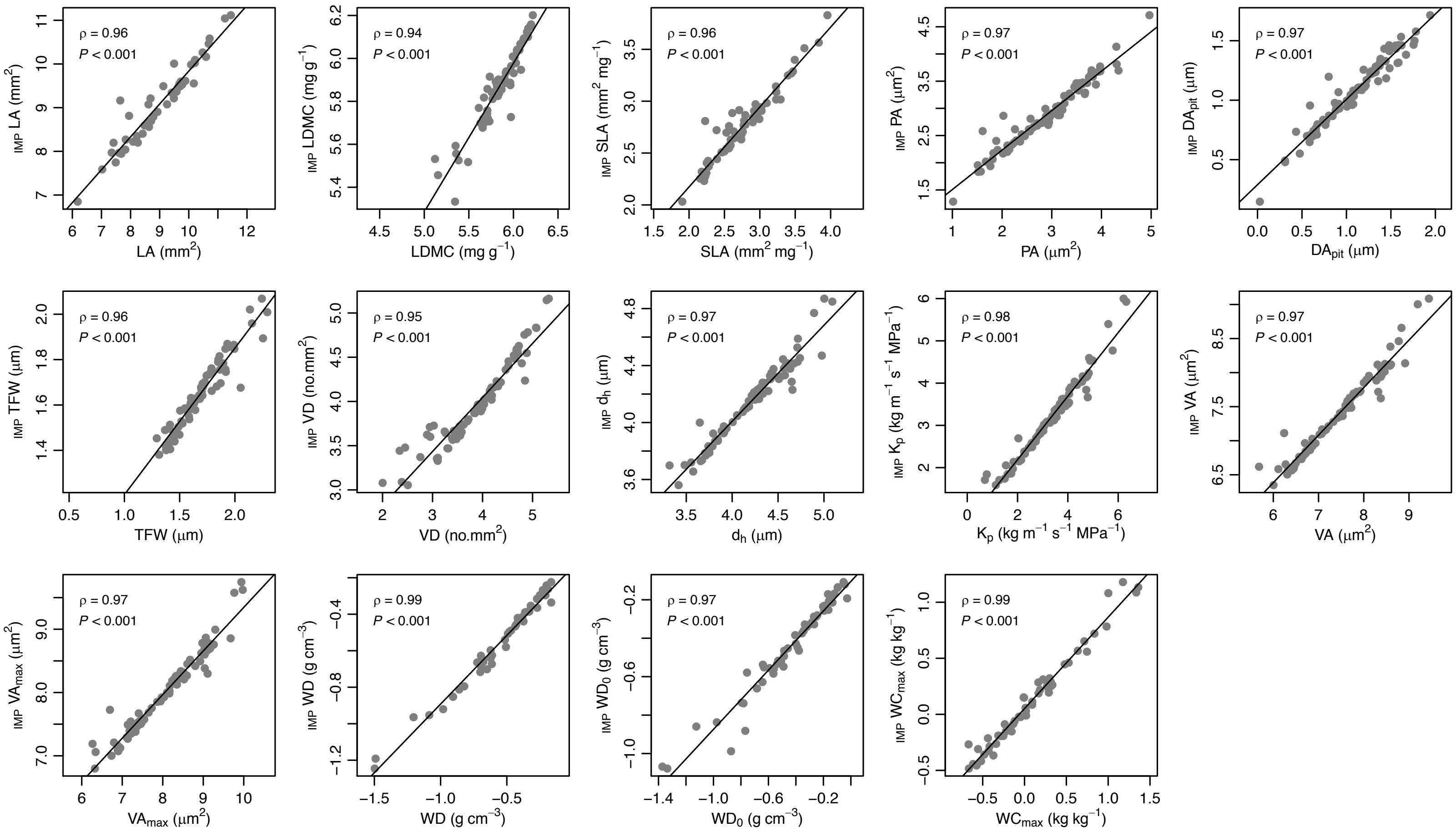
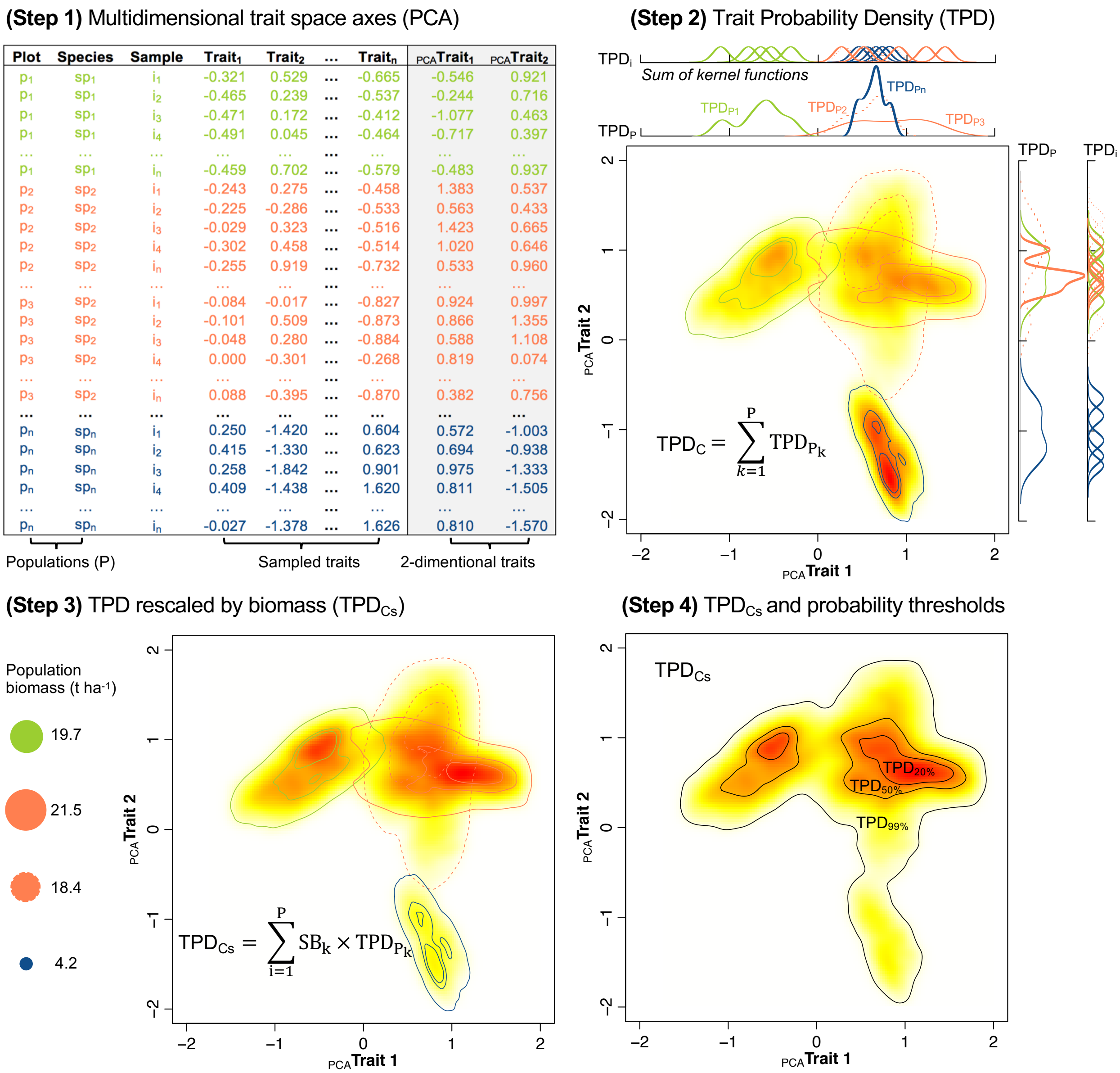


Figure S1. Pairwise correlations between imputed individual-trait values (IMP) and not-imputed individual-trait values. *Functional traits:* Fibre wall thickness (FWT, µm), hydraulically weighted diameter (d_h, µm), leaf area (LA, mm^2), leaf dry matter content (LDMC, mg g^{-1}), leaf thickness (L_{th}, mm), maximum vessel area (VA_{max}, µm^2), pit area (PA, µm^2), pit diameter aperture (DA_{pit}, µm), specific leaf area (SLA, mm^2 mg^{-1}), vessel area (VA, µm^2), vessel density (VD, vessels mm^{-2}), wood density (WD, g cm^3), anhydrous wood density (WD_0, g cm^3), water content at maximum capacity (WC_{max}, kg kg^{-1}), and xylem potential hydraulic conductivity (K_s, kg m^{-1} s^{-1} MPa^{-1}).



(Step 1) Multidimensional trait space axes (PCA)

Plot	Species	Sample	Trait$_1$	Trait$_2$	...	Trait$_n$	$_{PCA}$Trait$_1$	$_{PCA}$Trait$_2$
p_1	sp_1	i_1	-0.321	0.529	...	-0.665	-0.546	0.921
p_1	sp_1	i_2	-0.465	0.239	...	-0.537	-0.244	0.716
p_1	sp_1	i_3	-0.471	0.172	...	-0.412	-1.077	0.463
p_1	sp_1	i_4	-0.491	0.045	...	-0.464	-0.717	0.397
...	...	...	...	...	...	...	...	...
p_1	sp_1	i_n	-0.459	0.702	...	-0.579	-0.483	0.937
p_2	sp_2	i_1	-0.243	0.275	...	-0.458	1.383	0.537
p_2	sp_2	i_2	-0.225	-0.286	...	-0.533	0.563	0.433
p_2	sp_2	i_3	-0.029	0.323	...	-0.516	1.423	0.665
p_2	sp_2	i_4	-0.302	0.458	...	-0.514	1.020	0.646
p_2	sp_2	i_n	-0.255	0.919	...	-0.732	0.533	0.960
...	...	...	...	...	...	...	...	...
p_3	sp_2	i_1	-0.084	-0.017	...	-0.827	0.924	0.997
p_3	sp_2	i_2	-0.101	0.509	...	-0.873	0.866	1.355
p_3	sp_2	i_3	-0.048	0.280	...	-0.884	0.588	1.108
p_3	sp_2	i_4	0.000	-0.301	...	-0.268	0.819	0.074
...	...	...	...	...	...	...	...	...
p_3	sp_2	i_n	0.088	-0.395	...	-0.870	0.382	0.756
...	...	...	...	...	...	...	...	...
p_n	sp_n	i_1	0.250	-1.420	...	0.604	0.572	-1.003
p_n	sp_n	i_2	0.415	-1.330	...	0.623	0.694	-0.938
p_n	sp_n	i_3	0.258	-1.842	...	0.901	0.975	-1.333
p_n	sp_n	i_4	0.409	-1.438	...	1.620	0.811	-1.505
...	...	...	...	...	...	...	...	...
p_n	sp_n	i_n	-0.027	-1.378	...	1.626	0.810	-1.570

(Step 2) Trait Probability Density (TPD)

(Step 3) TPD rescaled by biomass (TPD$_{Cs}$)

(Step 4) TPD$_{Cs}$ and probability thresholds

Figure S2. Conceptual framework showing the steps to calculate Trait Probability Densities (TPD) in this study. In the example, we used four populations (P; in total we had 524 populations) belonging to three species (sp; in total we had 338 species) sampled in four plots (p; in total we had 11 plots). Here, a population refers to all sampled individuals (i) of the same species within a plot, for both traits and biomass. *Step 1*. To describe each individual's functional characterization in a 2-dimensional trait space, we performed a PCA analysis that reduces the matrix of sampled traits (in total 15 functional traits) to the principal axes of variation. The PCA analysis provides the uncorrelated and compressed first components as the new trait values ($_{PCA}$trait$_1$ and $_{PCA}$trait$_2$). In this study, the first PCA axis (36.75% of explained variance) reflected the hydraulic safety-efficiency trade-off. Negative values in PC1, high safety, describe species having a high density of narrow vessels with high fibre wall thickness, whereas positive values, hydraulic efficiency, characterized species having large vessels and pits with high xylem potential hydraulic conductivity. The second PCA axis (24.57% of explained variance) reflected differences of investment in tissues, where negative values were related to large leaves with high SLA, and high content of water at maximal capacity (‘cheap’ tissues), while positive values corresponded to high LDMC and high wood density (‘costly’ tissues). *Step 2*. TPD was calculated following the procedures suggested by Carmona *et al.* (2016) based on the bivariate gaussian kernel density functions. In the example, we first calculated the TPD of each population (TPD$_P$) as the sum of all individual trait density probabilities (TPD_i). We then summed all bivariate density functions for populations (TPD_P) to obtain the trait probability density for all species in TDF (TPD_C). *Step 3*. To calculated the TPD_C rescaled by biomass (TPD_{Cs}) each TPD_P was multiplying by the relative biomass of each population. As the relative biomass sum to 1 across all TDF populations, the sum of all the rescaled TPDP functions' integrals was 1. We made this procedure for all biomass dimensions used in this study (e.g., standing biomass–SB, biomass growth of survivors, biomass growth of recruits, and net biomass change). *Step 4*. At last, we calculated the functional trait space occupied by the TPD_C and TPD_{Cs} at three probability thresholds (20%, 50%, and 99%) using the *Functional Richness* (F_{Ric}) index suggested by Carmona *et al.* (2016, 2019).

Table S2. Functional trait space scores and biomass values for 524 populations belonging to 338 species in TDF. *Functional trait space*: The first PCA axis (PC1, 36.75% of explained variance) reflected the hydraulic safety-efficiency trade-off; negative values in PC1 corresponded to high safety for species having a high density of narrow vessels with high fibre wall thickness, whereas positive values corresponded to high hydraulic efficiency, characterized by species having large vessels and pits, with high xylem potential hydraulic conductivity. The second PCA axis (PC2, 24.57% of explained variance) reflected differences in tissue investment, where negative values were related to large leaves with high SLA, and high content of water at maximal capacity ('cheap' tissues), while positive values refereed to high LDMC and high wood density ('costly' tissues). *Biomass*: Standing biomass (kg ha^{-1}) refers to the sum of biomass for all trees of each species in each plot for the first census (t_0). Biomass growth of survivors (BG_S, kg ha^{-1} yr^{-1}) refers to the annual biomass increment produced by the growth of all trees of each species that survived from t_0 to the final census (t_{fin}) in a plot. Biomass growth of recruits (BG_R, kg ha^{-1} yr^{-1}) refers to the annual biomass increment obtained from all trees of each species that attained at least 2.5 cm DBH in t_{fin} and that were not sampled in t_0 in a plot. Biomass mortality (BM, kg ha^{-1} yr^{-1}) refers to the biomass loss obtained from all trees of each species between t_0 and t_{fin}. Net biomass change (NBC, kg ha^{-1} yr^{-1}) refers to the net annual change in biomass during the time interval between t_0 and t_{fin} (Prado-Junior *et al.* 2016; Poorter *et al.* 2017). Values were rounded to two decimals. Voucher code (v) and individual tagged number (tag) are provided when a species was not fully identified.

Study sites	Family	Species	PC1	PC2	Standing Biomass	BG_S	BG_R	BM	NBC
Caribbean lowlands' region									
Macuira National Park									
	Anacardiaceae	*Astronium graveolens*	0.72	0.86	18409.31	343.19	0.00	124.88	218.31
	Bignoniaceae	*Handroanthus billbergii*	0.77	0.89	27936.60	632.26	0.00	24.00	608.26
	Bignoniaceae	*Handroanthus chrysanthus*	0.20	-0.17	90.30	3.63	0.00	0.00	3.63
	Boraginaceae	*Cordia alba*	0.85	-0.85	83.04	0.57	0.00	0.00	0.57
	Boraginaceae	*Cordia macuirensis*	-0.74	0.24	1.11	0.00	0.00	0.00	0.00
	Burseraceae	*Bursera graveolens*	0.84	-1.26	3455.96	45.83	0.00	19.35	26.48
	Burseraceae	*Bursera simaruba*	0.77	-1.27	4258.10	103.30	0.00	14.87	88.43
	Capparaceae	*Capparidastrum pachaca*	-1.18	1.09	312.30	0.00	0.00	29.44	-29.44
	Capparaceae	*Capparis* sp2 [v. HC-6659, tag. 129]	-0.91	0.24	44.91	0.31	0.00	4.99	-4.68
	Capparaceae	*Cynophalla linearis*	-0.80	1.26	2715.36	30.16	0.00	30.49	-0.34
	Capparaceae	*Cynophalla verrucosa*	-0.93	0.66	17.67	0.31	0.00	3.24	-2.92
	Euphorbiaceae	*Croton punctatus*	-1.21	-0.33	3.27	0.14	0.00	0.00	0.14
	Fabaceae	*Erythrina velutina*	1.46	-1.42	4361.96	18.78	0.00	29.57	-10.79
	Fabaceae	*Lonchocarpus pictus*	1.21	1.00	4629.47	45.76	1.40	149.13	-101.97
	Fabaceae	*Lonchocarpus violaceus*	2.14	1.42	177.17	1.57	0.00	0.00	1.57
	Fabaceae	*Machaerium arboreum*	0.95	0.66	4397.31	24.01	0.00	112.22	-88.21
	Fabaceae	*Myrospermum frutescens*	0.89	1.05	214.38	5.19	0.00	0.00	5.19
	Fabaceae	*Myrospermum* sp [tag. 578]	0.51	1.29	60.49	0.41	0.00	0.00	0.41
	Fabaceae	*Pithecellobium dulce*	0.77	0.44	14.03	0.57	0.00	0.00	0.57
	Fabaceae	*Prosopis juliflora*	0.59	0.81	628.57	49.89	0.00	8.54	41.35
	Hernandiaceae	*Gyrocarpus americanus*	0.82	-2.07	878.74	11.22	0.00	13.42	-2.21

Study sites	Family	Species	PC1	PC2	Standing Biomass	BG_S	BG_R	BM	NBC
	Malpighiaceae	*Bunchosia odorata*	-0.90	0.27	31.31	1.82	0.12	5.48	-3.54
	Malvaceae	*Pachira quinata*	1.54	-0.60	2490.44	35.96	0.00	0.00	35.96
	Nyctaginaceae	*Neea* sp [tag. 707]	-0.23	0.04	113.45	1.38	0.00	0.00	1.38
	Polygonaceae	*Coccoloba caracasana*	-0.84	0.59	811.09	24.73	0.00	0.00	24.73
	Polygonaceae	*Coccoloba* sp [tag. 218]	-0.24	0.55	1715.88	21.97	0.00	18.11	3.86
	Rubiaceae	*Chiococca* sp [v. HC-6652, tag. 461]	-1.92	-0.04	120.51	1.75	0.00	7.83	-6.07
	Rubiaceae	*Coutarea* sp [v. HC-6641, tag. 35]	-1.81	0.37	62.18	1.89	0.00	2.70	-0.81
	Rubiaceae	*Randia aculeata*	-1.72	0.54	230.77	4.58	0.00	19.10	-14.51
	Rutaceae	*Zanthoxylum schreberi*	-1.57	0.65	280.67	3.10	0.00	7.19	-4.09
	Salicaceae	*Casearia* sp6 [v. HC-6635, tag. 262]	-1.64	-0.19	133.73	0.79	0.00	8.48	-7.69
	Sapindaceae	*Melicoccus bijugatus*	0.26	0.34	717.19	2.06	0.00	0.00	2.06
	Sapindaceae	*Melicoccus oliviformis*	1.05	1.07	958.62	13.98	0.00	0.00	13.98
	Sapotaceae	*Pradosia colombiana*	-0.13	1.23	560.42	22.72	0.00	0.00	22.72
Sanctuary of Flora and Fauna Colorados									
	Achariaceae	*Mayna grandifolia*	-0.60	0.22	3.45	0.53	0.00	0.00	0.53
	Achatocarpaceae	*Achatocarpus nigricans*	-0.68	-1.27	477.08	15.90	0.00	0.85	15.06
	Anacardiaceae	*Astronium graveolens*	0.64	0.18	25.21	0.93	0.00	0.00	0.93
	Anacardiaceae	*Spondias radlkoferi*	-0.02	-1.27	2035.18	38.86	0.00	9.52	29.34
	Annonaceae	*Oxandra* sp [v. HC-6491, tag. 13]	-0.86	0.75	2041.64	39.03	1.06	34.36	5.73
	Apocynaceae	*Aspidosperma polyneuron*	-1.21	0.37	2565.56	92.31	0.00	1.77	90.54
	Apocynaceae	*Aspidosperma* sp [tag. 2991]	0.94	0.35	0.00	0.00	0.00	0.00	0.00
	Apocynaceae	*Tabernaemontana cymosa*	-1.19	-1.18	20.21	0.07	0.00	0.00	0.07
	Apocynaceae	*Tabernaemontana* sp1 [v. HC-6532, tag. 202]	-0.28	-3.49	365.03	7.03	0.02	4.84	2.21
	Asteraceae	*Chromolaena perglabra*	-1.34	-0.11	305.73	0.94	0.00	12.05	-11.11
	Burseraceae	*Bursera simaruba*	-0.20	-3.06	2274.64	15.26	0.00	63.36	-48.09
	Capparaceae	*Cynophalla verrucosa*	-1.01	0.48	2158.41	40.76	0.03	14.89	25.89
	Capparaceae	*Quadrella indica*	-0.33	-0.81	136.08	0.33	0.00	0.00	0.33
	Capparaceae	*Quadrella odoratissima*	-0.30	0.44	1002.69	9.76	0.00	5.15	4.61
	Euphorbiaceae	*Hura crepitans*	1.33	-0.29	4.45	0.07	0.00	0.00	0.07
	Fabaceae	*Albizia* sp2 [v. HC-6494, tag. 81]	0.78	0.29	336.48	20.87	0.00	0.00	20.87
	Fabaceae	*Coursetia ferruginea*	1.16	0.16	13037.52	32.53	0.00	6.43	26.10
	Fabaceae	*Inga vera*	0.80	-0.20	19.81	5.07	0.00	0.00	5.07
	Fabaceae	*Peltogyne purpurea*	0.29	1.15	13.26	0.00	0.00	0.00	0.00
	Fabaceae	*Peltogyne* sp [v. HC-6497, tag. 31]	0.05	0.73	2291.65	22.04	0.00	69.46	-47.42
	Fabaceae	*Platymiscium pinnatum*	0.78	0.48	1096.60	77.17	0.00	0.00	77.17
	Fabaceae	*Pterocarpus rohrii*	0.19	0.13	196.01	1.59	0.23	0.60	1.22
	Fabaceae	*Senegalia* sp [v. HC-6506, tag. 44]	0.80	-0.62	1753.04	32.52	0.00	57.33	-24.81

Study sites	Family	Species	PC1	PC2	Standing Biomass	BG_S	BG_R	BM	NBC
	Fabaceae	*Swartzia simplex*	-0.06	0.65	2.24	0.00	0.04	0.00	0.04
	Fabaceae	*Zygia* sp [tag. 836]	0.67	1.49	95.74	0.00	0.00	0.00	0.00
	Lamiaceae	*Aegiphila* sp [v. HC-6531, tag. 221]	1.34	-0.57	14.18	1.33	0.00	0.00	1.33
	Lamiaceae	*Vitex* sp [tag. 307]	-0.46	0.01	2.52	0.00	0.00	0.00	0.00
	Lecythidaceae	*Gustavia superba*	-0.98	-0.65	154.51	5.70	0.07	0.73	5.04
	Lecythidaceae	*Lecythis minor*	0.05	0.12	0.00	0.00	0.00	0.00	0.00
	Malpighiaceae	*Malpighia glabra*	-0.97	-0.25	26.00	2.11	0.00	0.00	2.11
	Malvaceae	*Cavanillesia platanifolia*	1.23	-1.58	5827.36	1.58	0.00	0.00	1.58
	Malvaceae	*Ceiba pentandra*	1.89	-0.77	5318.54	0.00	0.00	0.00	0.00
	Malvaceae	*Guazuma ulmifolia*	0.78	-1.07	246.46	10.04	0.00	0.00	10.04
	Malvaceae	*Pachira quinata*	-0.34	-3.85	66.58	2.03	0.00	1.25	0.78
	Meliaceae	*Trichilia acuminata*	-1.01	1.09	6437.26	116.53	2.00	122.73	-4.20
	Meliaceae	*Trichilia elegans*	-0.86	-0.19	186.96	3.71	0.00	0.00	3.71
	Moraceae	*Brosimum alicastrum*	0.71	0.61	2335.12	680.01	1.10	7.69	673.42
	Moraceae	*Brosimum* sp [v. HC-6558, tag. 1613]	0.48	0.54	7426.03	121.18	0.00	25.31	95.87
	Moraceae	*Sorocea sprucei*	0.54	0.53	1333.92	61.54	0.00	2.17	59.37
	Myrtaceae	*Eugenia procera*	-1.14	0.98	599.88	10.68	0.12	5.88	4.92
	Nyctaginaceae	*Guapira* sp [v. HC-6578, tag. 974]	-0.01	-0.73	142.22	1.49	0.00	0.00	1.49
	Phyllanthaceae	*Margaritaria nobilis*	-0.01	-0.07	17.73	0.00	0.00	0.00	0.00
	Polygonaceae	*Coccoloba padiformis*	-0.05	0.59	3.02	0.18	0.08	0.00	0.27
	Polygonaceae	*Coccoloba* sp1 [v. HC-6507, tag. 52]	0.33	0.86	3111.72	167.95	0.00	1.51	166.44
	Primulaceae	*Ardisia foetida*	-0.26	-0.49	48.89	0.50	0.09	1.31	-0.71
	Rubiaceae	*Alibertia* sp [v. HC-6536, tag. 236]	-0.55	0.40	15.30	0.00	0.00	0.00	0.00
	Rubiaceae	*Chiococca* sp [v. HC-6595, tag. 270]	-1.50	0.29	40.93	0.06	0.00	0.00	0.06
	Rubiaceae	*Coutarea hexandra*	-0.97	-0.92	15.42	2.17	0.00	0.00	2.17
	Rubiaceae	*Morf* sp17 [tag. 1001]	-0.63	-2.49	35.07	0.00	0.00	0.00	0.00
	Rubiaceae	*Pittoniotis* sp [tag. 1190]	0.17	-0.38	131.74	0.00	0.00	0.00	0.00
	Rubiaceae	*Pittoniotis trichantha*	-0.64	0.09	2279.77	18.46	0.00	25.37	-6.90
	Rubiaceae	*Rudgea* sp [v. HC-6599, tag. 1065]	-1.01	0.16	55.10	2.42	0.13	0.00	2.55
	Rutaceae	*Amyris pinnata*	-1.11	0.07	1291.98	50.45	0.04	0.00	50.49
	Rutaceae	*Esenbeckia pentaphylla*	-0.89	-0.04	5109.60	267.80	0.00	2.96	264.83
	Rutaceae	*Galipea* sp [tag. 1236]	-0.63	0.51	144.94	9.17	0.03	0.00	9.20
	Rutaceae	*Zanthoxylum* sp4 [v. HC-6494, tag. 17]	-1.10	0.75	1078.15	32.41	0.00	13.09	19.32
	Salicaceae	*Casearia sylvestris*	-1.15	-0.39	8.72	0.65	0.00	0.00	0.65
	Sapindaceae	*Allophylus* sp [v. HC-6619, tag. 159]	-0.76	-0.14	0.00	0.00	0.00	0.00	0.00
	Sapindaceae	*Melicoccus bijugatus*	0.71	1.50	29.25	1.29	0.00	0.00	1.29
	Sapindaceae	*Melicoccus oliviformis*	1.05	1.06	74.68	4.13	0.00	0.00	4.13

Study sites	Family	Species	PC1	PC2	Standing Biomass	BG_S	BG_R	BM	NBC
	Sapotaceae	*Manilkara* sp [tag. 318]	0.05	1.27	211.63	10.99	0.00	0.00	10.99
	Sapotaceae	*Pouteria* sp1 [v. HC-6508, tag. 739]	-0.41	0.87	5949.59	95.35	0.28	39.00	56.62
	Sapotaceae	*Pouteria* sp2 [tag. 955]	0.13	0.19	0.00	0.00	0.00	0.00	0.00
	Sapotaceae	*Pouteria* sp3 [tag. 163]	-0.40	0.93	79.45	2.24	0.00	0.00	2.24
	Sapotaceae	*Pouteria* sp7 [v. HC-6480, tag. 124]	-0.53	0.91	351.82	9.93	0.04	14.39	-4.41
	Sapotaceae	*Pradosia colombiana*	0.06	0.64	3054.36	53.25	0.00	0.00	53.25
	Stemonuraceae	*Discophora* sp [v. HC-6557, tag. 581]	-0.85	0.42	118.59	3.66	0.00	0.00	3.66
	Ulmaceae	*Ampelocera macphersonii*	0.12	0.61	16791.18	435.47	2.07	82.40	355.14
	Zygophyllaceae	*Bulnesia arborea*	0.03	1.09	1394.12	38.86	0.00	0.00	38.86
Tayrona National Park									
	Anacardiaceae	*Astronium graveolens*	0.71	0.72	15716.00	388.46	0.07	0.00	388.53
	Anacardiaceae	*Spondias mombin*	-0.28	-1.68	5446.50	58.83	0.00	6.18	52.64
	Asteraceae	*Chromolaena perglabra*	-1.39	-1.06	26.77	0.15	0.00	1.46	-1.31
	Boraginaceae	*Cordia alba*	0.20	-1.18	335.60	6.29	11.15	6.16	11.28
	Boraginaceae	*Cordia* sp [v. HC-6723, tag. 355]	0.15	-0.55	4.37	0.32	0.11	0.00	0.43
	Burseraceae	*Bursera simaruba*	0.65	-1.93	2812.19	82.75	0.00	14.64	68.11
	Capparaceae	*Capparidastrum pachaca*	-0.28	0.90	3562.54	59.14	2.98	5.38	56.73
	Capparaceae	*Capparidastrum tenuisiliquum*	-1.21	-0.18	1072.35	12.74	7.69	10.22	10.20
	Capparaceae	*Crateva tapia*	-0.01	-0.79	130.66	1.32	0.00	0.00	1.32
	Capparaceae	*Cynophalla flexuosa*	-0.19	0.82	273.64	3.65	0.00	3.70	-0.05
	Capparaceae	*Cynophalla verrucosa*	-0.98	0.59	2666.03	39.82	4.67	12.16	32.33
	Capparaceae	*Quadrella indica*	-0.54	0.12	278.74	5.71	0.05	0.00	5.76
	Capparaceae	*Quadrella odoratissima*	-0.13	0.78	14742.47	81.11	1.45	15.39	67.17
	Erythroxylaceae	*Erythroxylum hondense*	-1.61	0.49	54.78	0.66	0.00	0.00	0.66
	Euphorbiaceae	*Croton niveus*	-0.74	0.11	970.89	6.56	1.76	37.91	-29.59
	Euphorbiaceae	*Hura crepitans*	1.58	-1.37	2791.77	13.54	0.00	0.00	13.54
	Euphorbiaceae	*Manihot carthaginensis*	2.78	-0.43	45.26	2.72	0.00	0.00	2.72
	Fabaceae	*Albizia niopoides*	1.06	0.62	809.64	22.77	5.29	2.80	25.26
	Fabaceae	*Caesalpinia punctata*	1.65	1.74	4546.64	39.54	0.00	0.00	39.54
	Fabaceae	*Coursetia ferruginea*	1.14	-0.21	203.30	11.40	0.71	2.24	9.87
	Fabaceae	*Machaerium capote*	1.40	0.48	938.48	170.91	0.00	0.64	170.27
	Fabaceae	*Machaerium* sp1 [v. HC-6729, tag. 144]	1.32	0.41	961.96	11.58	0.00	2.64	8.94
	Fabaceae	*Muellera broadwayi*	1.61	0.42	2510.94	26.68	0.00	0.00	26.68
	Fabaceae	*Pithecellobium roseum*	0.41	1.40	148.99	0.70	0.00	2.84	-2.14
	Fabaceae	*Platymiscium pinnatum*	1.28	1.11	1925.33	16.85	0.00	0.45	16.40
	Fabaceae	*Prosopis juliflora*	0.58	0.30	1391.18	29.63	0.00	0.00	29.63
	Fabaceae	*Pterocarpus rohrii*	0.77	0.24	19481.61	323.73	0.60	145.43	178.90

Study sites	Family	Species	PC1	PC2	Standing Biomass	BG_S	BG_R	BM	NBC
	Fabaceae	*Senegalia tamarindifolia*	0.44	0.18	1261.20	30.78	2.28	34.57	-1.50
	Fabaceae	*Senna atomaria*	1.10	0.56	167.96	5.72	0.00	0.00	5.72
	Fabaceae	*Senna* sp [tag. 272]	1.18	-0.10	116.60	3.69	0.00	0.00	3.69
	Fabaceae	*Senna* sp1 [v. HC-6714, tag. 1179]	0.43	0.39	247.13	3.63	0.00	3.48	0.15
	Fabaceae	*Vachellia farnesiana*	0.76	0.99	588.53	18.60	0.46	11.23	7.84
	Hernandiaceae	*Gyrocarpus americanus*	-0.25	-1.33	894.85	8.84	0.00	0.00	8.84
	Indet	Morf sp14 [tag. 746]	-0.58	0.43	11.76	0.97	0.00	0.00	0.97
	Lecythidaceae	*Eschweilera* sp [v. HC-6681, tag. 109]	-1.90	0.34	81.97	0.58	0.09	0.00	0.67
	Malvaceae	*Guazuma ulmifolia*	-0.28	-0.84	273.76	4.78	0.00	2.70	2.08
	Malvaceae	*Pseudobombax septenatum*	1.03	-2.03	738.37	77.31	0.05	0.00	77.37
	Moraceae	*Brosimum alicastrum*	0.20	0.16	7.89	0.08	0.00	0.61	-0.53
	Myrtaceae	*Eugenia* sp1 [v. HC-6699, tag. 731]	-0.88	1.39	3.21	0.06	0.00	0.00	0.06
	Nyctaginaceae	*Guapira* sp [tag. 335]	-0.51	-0.75	67.03	1.22	2.77	0.54	3.44
	Nyctaginaceae	*Guapira uberrima*	-0.67	-0.55	1418.54	10.24	0.27	36.49	-25.98
	Polygonaceae	*Coccoloba obtusifolia*	-0.24	-0.03	528.40	13.33	0.61	8.45	5.49
	Polygonaceae	*Triplaris americana*	-0.03	-0.60	201.87	1.25	0.00	0.00	1.25
	Primulaceae	*Bonellia frutescens*	-1.18	-0.02	197.15	1.02	0.00	0.54	0.48
	Rubiaceae	*Calycophyllum candidissimum*	-0.32	0.00	227.01	3.62	0.46	2.00	2.08
	Rubiaceae	*Psychotria* sp [v. HC-6751, tag. 1375]	-1.26	-1.23	2.57	0.15	0.00	0.00	0.15
	Rubiaceae	*Randia aculeata*	-1.20	0.43	18.45	0.12	0.00	0.00	0.12
	Rubiaceae	*Simira cordifolia*	-1.46	-0.50	8.78	0.10	0.00	0.00	0.10
	Salicaceae	*Casearia praecox*	-1.65	-0.37	141.08	3.21	0.00	0.80	2.41
	Sapindaceae	*Melicoccus bijugatus*	1.23	0.84	7216.29	104.82	4.17	0.00	108.99
	Sapindaceae	*Melicoccus oliviformis*	0.66	0.96	4161.97	93.63	0.22	0.00	93.85
	Sapindaceae	*Sapindus saponaria*	0.77	0.77	109.50	10.52	0.00	0.00	10.52
	Sapotaceae	*Pradosia colombiana*	-0.21	0.63	8115.70	31.90	0.00	30.86	1.04
Inter Andean region									
Cardonal Loma Forests									
	Achariaceae	*Mayna odorata*	-1.17	0.65	2284.78	50.21	2.84	70.86	-17.81
	Anacardiaceae	*Astronium graveolens*	0.98	0.65	21467.34	409.48	0.00	55.33	354.15
	Apocynaceae	*Aspidosperma polyneuron*	-0.61	0.69	19754.58	413.49	0.15	48.91	364.73
	Bignoniaceae	*Tabebuia rosea*	1.13	1.15	3876.59	113.01	0.00	0.00	113.01
	Boraginaceae	*Cordia gerascanthus*	0.44	0.54	1314.39	17.22	4.81	22.97	-0.94
	Burseraceae	*Bursera simaruba*	1.37	-0.73	4669.39	64.98	0.00	47.15	17.83
	Capparaceae	*Cynophalla polyantha*	0.34	1.26	496.55	8.59	0.00	0.00	8.59
	Capparaceae	*Quadrella odoratissima*	0.22	1.17	658.24	11.19	0.00	0.00	11.19
	Ebenaceae	*Diospyros* sp2 [v. RG-1910, tag. 2731]	0.27	0.70	3.62	0.15	0.00	0.00	0.15

Study sites	Family	Species	PC1	PC2	Standing Biomass	BG_S	BG_R	BM	NBC
	Euphorbiaceae	*Croton schiedeanus*	-0.36	0.06	159.04	3.04	0.04	2.18	0.90
	Euphorbiaceae	*Croton* sp [v. RG-1874, tag. 245]	0.03	1.11	19.60	0.00	0.00	0.00	0.00
	Fabaceae	*Bauhinia petiolata*	-0.57	1.25	1626.90	48.15	6.01	46.87	7.29
	Fabaceae	*Calliandra magdalenae*	-0.01	1.39	880.81	11.15	0.00	46.40	-35.25
	Fabaceae	*Machaerium capote*	0.81	0.54	9203.82	137.01	1.61	63.81	74.82
	Fabaceae	*Machaerium* sp1 [v. RG-1891, tag. 368]	1.19	1.08	711.25	9.26	0.00	7.06	2.21
	Fabaceae	*Machaerium* sp6 [v. RG-1850, tag. 2917]	1.02	0.80	3414.98	28.98	0.39	93.39	-64.02
	Fabaceae	*Platymiscium pinnatum*	1.34	0.96	3485.97	59.63	0.00	27.60	32.03
	Fabaceae	*Pterocarpus rohrii*	0.92	0.69	10523.74	185.76	0.00	91.40	94.35
	Fabaceae	*Senegalia* sp1 [v. RG-1895, tag. 996]	1.75	0.21	902.60	15.07	1.28	36.85	-20.50
	Fabaceae	*Swartzia trianae*	-0.26	0.80	3054.22	49.11	0.02	21.91	27.22
	Malpighiaceae	*Bunchosia* sp [v. RG-1894, tag. 981]	-1.57	0.58	4.93	0.11	0.00	0.00	0.11
	Malpighiaceae	*Malpighia glabra*	-0.99	0.34	142.82	1.71	0.05	12.60	-10.84
	Malvaceae	*Pseudobombax septenatum*	1.89	-1.11	4245.40	14.96	0.00	0.00	14.96
	Meliaceae	*Trichilia carinata*	-0.95	0.47	1076.77	31.80	0.59	0.00	32.39
	Meliaceae	*Trichilia elegans*	-0.49	0.59	3937.68	79.62	0.77	37.35	43.04
	Meliaceae	*Trichilia oligofoliolata*	-1.38	0.85	12045.54	442.70	4.53	25.55	421.69
	Meliaceae	*Trichilia pallida*	-0.97	0.22	4405.16	74.92	0.02	25.26	49.69
	Myrtaceae	*Eugenia procera*	-1.51	1.03	1545.02	46.44	2.40	8.16	40.68
	Myrtaceae	Morf sp1 [v. RG-1881, tag. 376]	-1.22	1.23	1.75	0.00	0.00	0.00	0.00
	Nyctaginaceae	*Neea* sp1 [v. RG-1871, tag. 161]	-0.12	0.24	208.16	1.81	0.00	11.87	-10.06
	Polygonaceae	*Coccoloba* sp1 [v. RG-1843, tag. 2103]	-0.09	1.64	3112.52	62.82	0.84	2.86	60.80
	Polygonaceae	*Ruprechtia* sp1 [v. RG-1914, tag. 3445]	-0.31	-0.53	1.84	0.20	0.00	0.00	0.20
	Polygonaceae	*Triplaris melaenodendron*	0.73	0.20	1378.28	11.83	0.37	34.78	-22.58
	Rhamnaceae	*Ziziphus strychnifolia*	0.42	0.88	1189.79	11.16	0.00	13.78	-2.62
	Rubiaceae	*Guettarda comata*	-0.92	0.05	393.97	3.37	0.00	1.98	1.40
	Rubiaceae	*Randia aculeata*	-1.48	-0.12	3.79	0.00	0.00	0.82	-0.82
	Rubiaceae	*Randia armata*	-1.03	0.41	630.48	10.75	0.00	34.21	-23.46
	Rutaceae	*Amyris pinnata*	-0.91	0.64	1032.39	23.31	0.00	21.35	1.96
	Rutaceae	*Esenbeckia alata*	-1.55	0.92	3.62	0.05	0.00	0.00	0.05
	Rutaceae	*Zanthoxylum* sp2 [v. RG-1848, tag. 2890]	-0.40	-0.09	781.82	30.46	0.00	6.73	23.73
	Salicaceae	*Casearia corymbosa*	-1.39	0.68	784.87	6.10	0.00	6.54	-0.44
	Salicaceae	*Casearia praecox*	-1.79	0.28	1182.97	11.29	0.03	0.29	11.03
	Salicaceae	*Casearia* sp1 [v. RG-1897, tag. 1086]	-1.81	0.35	39.69	0.18	0.00	0.00	0.18
	Salicaceae	*Casearia sylvestris*	-1.60	0.45	4714.76	96.70	0.00	74.45	22.25
	Sapotaceae	*Pouteria* sp7 [v. RG-1865, tag. 111]	-0.27	0.73	1254.55	21.70	0.11	12.97	8.84
	Ulmaceae	*Ampelocera* sp1 [v. RG-1870, tag. 166]	0.16	1.23	141.07	8.85	0.00	0.00	8.85

Study sites	Family	Species	PC1	PC2	Standing Biomass	BG_S	BG_R	BM	NBC
	Violaceae	*Rinorea* sp1 [tag. 788]	-0.91	1.34	114.25	2.17	0.00	0.00	2.17
Cardonal Plana Forests									
	Achariaceae	*Mayna odorata*	-1.25	0.54	2754.22	46.62	0.00	126.23	-79.61
	Achatocarpaceae	*Achatocarpus nigricans*	-0.70	-0.35	2796.34	66.47	15.62	36.78	45.31
	Anacardiaceae	*Astronium graveolens*	1.10	0.48	7433.11	99.65	0.22	43.32	56.54
	Anacardiaceae	*Spondias mombin*	2.40	-0.45	111.97	0.61	0.00	0.00	0.61
	Annonaceae	*Oxandra espintana*	-0.45	0.37	4184.72	66.75	45.21	47.11	64.84
	Apocynaceae	*Aspidosperma polyneuron*	-0.99	0.57	117.44	1.37	0.00	0.00	1.37
	Bignoniaceae	*Handroanthus chrysanthus*	0.73	-0.06	357.53	0.68	0.00	0.00	0.68
	Bignoniaceae	*Tabebuia rosea*	0.39	0.06	397.18	15.92	0.00	0.00	15.92
	Boraginaceae	*Cordia gerascanthus*	0.18	-0.06	872.97	13.91	0.00	28.09	-14.18
	Boraginaceae	*Cordia* sp [v. RG-1938, tag. 248]	-0.64	-0.64	60.73	0.74	0.00	5.42	-4.69
	Capparaceae	*Capparidastrum frondosum*	0.04	0.52	0.00	0.00	0.00	0.00	0.00
	Capparaceae	*Morisonia americana*	0.37	0.69	43.91	0.00	0.00	0.00	0.00
	Ebenaceae	*Diospyros* sp2 [v. RG-1957, tag. 472]	0.32	-0.16	130.60	0.89	0.00	0.00	0.89
	Fabaceae	*Bauhinia petiolata*	-0.94	1.06	1041.69	18.28	0.00	20.00	-1.71
	Fabaceae	*Calliandra magdalenae*	0.19	1.14	2016.74	55.83	2.24	24.74	33.34
	Fabaceae	*Machaerium capote*	0.99	0.43	7619.72	179.43	11.26	17.83	172.86
	Fabaceae	*Machaerium* sp1 [tag. 1525]	1.11	0.98	1.19	0.07	0.00	0.00	0.07
	Fabaceae	*Pterocarpus rohrii*	1.61	0.20	1046.32	9.66	0.02	0.00	9.68
	Fabaceae	*Senegalia* sp1 [tag. 458]	0.48	-0.66	8141.87	171.32	0.65	122.91	49.07
	Fabaceae	*Swartzia trianae*	0.54	0.15	7312.02	170.46	0.00	5.93	164.52
	Lamiaceae	*Aegiphila* sp1 [tag. 832]	0.63	-1.01	458.57	8.03	0.00	0.00	8.03
	Lauraceae	*Ocotea veraguensis*	0.64	0.57	5356.22	27.54	0.16	37.93	-10.23
	Lecythidaceae	*Gustavia* sp [v. RG-1917, tag. 7]	-0.89	0.67	803.96	12.26	37.94	26.13	24.08
	Malpighiaceae	*Malpighia glabra*	-1.46	0.19	57.34	1.68	0.07	1.97	-0.21
	Malvaceae	*Guazuma ulmifolia*	0.68	-1.41	47.85	2.86	0.12	0.00	2.98
	Meliaceae	*Trichilia carinata*	-1.05	0.52	4816.82	87.28	7.54	54.14	40.69
	Meliaceae	*Trichilia elegans*	-0.89	0.41	515.18	11.54	0.03	6.68	4.90
	Meliaceae	*Trichilia oligofoliolata*	-1.39	0.98	79.21	3.49	0.00	0.00	3.49
	Meliaceae	*Trichilia pallida*	-0.80	-0.47	3059.99	32.61	0.05	35.52	-2.85
	Moraceae	*Brosimum alicastrum*	0.94	-0.03	30.71	0.00	0.00	0.00	0.00
	Myrtaceae	*Eugenia procera*	-1.20	1.08	743.38	16.29	0.12	13.44	2.97
	Myrtaceae	*Eugenia* sp5 [v. RG-1928, tag. 1901]	-0.84	1.36	259.65	0.78	10.27	21.40	-10.35
	Nyctaginaceae	*Neea* sp1 [tag. 1414]	0.25	0.46	10.70	0.08	0.00	1.23	-1.15
	Polygonaceae	*Coccoloba acuminata*	0.06	0.51	19.50	0.11	0.00	0.00	0.11
	Polygonaceae	*Coccoloba* sp1 [tag. 30]	-0.94	1.21	3298.38	45.58	11.87	21.13	36.32

Study sites	Family	Species	PC1	PC2	Standing Biomass	BG_S	BG_R	BM	NBC
	Polygonaceae	*Ruprechtia* sp1 [v. RG-1941, tag. 47]	-0.01	-0.70	1422.93	33.43	0.09	0.00	33.52
	Polygonaceae	*Triplaris melaenodendron*	0.64	0.12	4160.65	66.97	11.88	53.36	25.49
	Rhamnaceae	*Ziziphus strychnifolia*	1.33	0.64	2835.82	40.88	0.92	4.42	37.38
	Rubiaceae	*Randia armata*	-0.94	0.47	798.70	37.34	49.60	25.19	61.75
	Rubiaceae	*Simira cordifolia*	-0.95	0.37	3744.38	69.36	0.85	57.17	13.04
	Rutaceae	*Esenbeckia alata*	-0.99	1.01	1455.53	9.88	0.00	0.00	9.88
	Rutaceae	*Zanthoxylum rhoifolium*	-0.41	-0.54	462.96	22.03	0.00	9.98	12.05
	Rutaceae	*Zanthoxylum rigidum*	-0.77	-0.13	1.13	0.29	0.00	0.00	0.29
	Salicaceae	*Casearia corymbosa*	-1.57	-0.16	33.32	1.60	0.00	0.00	1.60
	Salicaceae	*Casearia praecox*	-1.81	0.17	133.88	2.18	0.00	0.00	2.18
	Salicaceae	*Casearia sylvestris*	-1.03	0.50	1592.36	22.26	0.00	14.56	7.70
	Sapotaceae	*Pouteria* sp7 [tag. 10]	-0.24	1.02	2867.13	51.62	0.17	4.45	47.33
	Sapotaceae	*Pouteria* sp8 [v. RG-1925, tag. 1629]	0.29	0.95	70.93	72.65	0.00	0.00	72.65
	Ulmaceae	*Ampelocera* sp1 [v. RG-1918, tag. 6]	0.70	1.49	2061.80	53.54	5.29	5.53	53.31
Cotove Research Station									
	Achatocarpaceae	*Achatocarpus nigricans*	-1.26	-1.52	267.39	9.68	0.00	1.72	7.95
	Anacardiaceae	*Astronium graveolens*	1.04	-0.34	3618.92	30.89	0.08	51.48	-20.52
	Apocynaceae	*Tabernaemontana grandiflora*	-1.68	-2.14	18.04	0.00	0.00	3.78	-3.78
	Araliaceae	*Aralia excelsa*	-0.36	-2.53	0.00	0.00	0.00	0.00	0.00
	Burseraceae	*Bursera simaruba*	0.64	-2.18	3768.94	26.65	0.11	28.94	-2.18
	Capparaceae	*Quadrella indica*	-0.23	-0.21	218.43	10.02	0.19	5.43	4.78
	Erythroxylaceae	*Erythroxylum hondense*	-1.12	0.28	1.20	0.10	0.00	0.00	0.10
	Fabaceae	*Enterolobium cyclocarpum*	0.93	-1.48	6953.70	4.02	0.00	60.81	-56.79
	Fabaceae	*Leucaena leucocephala*	1.04	-0.68	2162.75	7.03	0.00	71.77	-64.75
	Fabaceae	*Platymiscium pinnatum*	0.28	-0.25	139.58	1.49	0.00	0.00	1.49
	Fabaceae	*Pseudosamanea guachapele*	0.95	-0.67	3250.49	16.61	0.00	60.55	-43.94
	Indet.	Morf sp6 [tag. 461]	-1.05	-0.18	3.33	0.05	0.00	0.00	0.05
	Malpighiaceae	*Bunchosia armeniaca*	0.10	0.58	388.21	2.67	0.00	7.73	-5.06
	Malpighiaceae	*Malpighia glabra*	-0.60	-0.22	1208.35	15.56	2.39	3.00	14.94
	Malvaceae	*Ceiba pentandra*	2.27	-1.15	1077.99	52.46	0.00	0.85	51.61
	Moraceae	*Brosimum alicastrum*	0.71	0.90	70.42	0.58	0.00	0.00	0.58
	Moraceae	*Castilla elastica*	0.49	-2.49	0.95	0.00	0.00	0.46	-0.46
	Myrtaceae	*Eugenia venezuelensis*	-0.08	1.02	2.92	0.10	0.00	0.00	0.10
	Phyllanthaceae	*Phyllanthus botryanthus*	-0.75	-0.50	568.43	13.02	2.79	17.77	-1.96
	Rubiaceae	*Chomelia spinosa*	-1.18	-0.81	93.40	0.40	0.00	2.07	-1.67
	Rutaceae	*Amyris pinnata*	-0.20	0.49	372.87	4.06	0.00	8.64	-4.58
	Rutaceae	*Zanthoxylum fagara*	-0.04	-0.20	1169.75	23.07	0.40	37.14	-13.68

Study sites	Family	Species	PC1	PC2	Standing Biomass	BG$_S$	BG$_R$	BM	NBC
	Rutaceae	*Zanthoxylum lenticulare*	0.20	-0.65	1119.22	31.23	170.26	6.38	195.11
	Rutaceae	*Zanthoxylum schreberi*	-0.46	-0.73	1466.26	21.07	1.31	9.11	13.27
	Salicaceae	*Casearia corymbosa*	-2.15	0.28	39.57	0.30	0.00	2.80	-2.51
	Salicaceae	*Casearia praecox*	-0.32	-0.06	104.51	0.71	0.05	8.82	-8.06
	Sapindaceae	*Melicoccus bijugatus*	0.80	0.45	48647.07	2165.66	0.61	16.57	2149.70
	Sapindaceae	*Sapindus saponaria*	1.80	-0.17	120.06	2.96	0.00	0.00	2.96
Jabirú Private Natural Reserve									
	Achariaceae	*Mayna odorata*	-1.21	-0.58	78.59	9.41	0.00	0.00	9.41
	Anacardiaceae	*Astronium graveolens*	0.24	-0.56	5465.49	72.52	0.00	12.98	59.54
	Annonaceae	*Oxandra espintana*	-1.42	-0.21	8387.17	427.89	2.32	195.58	234.63
	Apocynaceae	*Aspidosperma polyneuron*	-1.34	-0.15	183.57	7.77	0.00	0.00	7.77
	Bignoniaceae	*Handroanthus chrysanthus*	0.09	-0.21	1263.06	29.48	0.00	43.38	-13.90
	Boraginaceae	*Cordia gerascanthus*	-0.25	-0.67	206.10	9.33	0.00	0.00	9.33
	Burseraceae	*Bursera simaruba*	0.22	-2.61	635.96	11.06	0.00	0.00	11.06
	Capparaceae	*Cynophalla flexuosa*	-0.25	-0.44	45.38	1.05	0.00	0.00	1.05
	Capparaceae	*Cynophalla polyantha*	-0.64	-0.51	389.28	6.57	0.00	0.00	6.57
	Ebenaceae	*Diospyros* sp2 [v. JAC-2202, tag. 1830]	0.11	0.65	399.30	4.89	0.00	0.00	4.89
	Fabaceae	*Machaerium capote*	-0.09	-0.70	8017.24	114.57	0.00	37.15	77.42
	Fabaceae	*Piptadenia* sp [v. JAC-2187, tag. 1196]	0.25	-0.62	1166.38	0.14	0.00	90.05	-89.91
	Fabaceae	*Platymiscium pinnatum*	1.06	0.20	219.90	9.82	0.00	0.00	9.82
	Fabaceae	*Swartzia trianae*	-0.25	0.28	255.91	11.52	0.00	0.00	11.52
	Lauraceae	*Ocotea veraguensis*	-0.07	-0.21	863.26	9.31	0.00	0.00	9.31
	Malvaceae	*Pseudobombax septenatum*	-0.01	-2.51	1285.20	15.41	0.00	0.00	15.41
	Meliaceae	*Trichilia carinata*	-1.06	0.07	3734.54	153.10	0.00	216.59	-63.49
	Meliaceae	*Trichilia oligofoliolata*	-1.54	0.34	53642.81	2172.34	357.75	265.73	2264.36
	Meliaceae	*Trichilia pallida*	-1.38	-0.73	3215.02	82.06	0.00	46.27	35.79
	Myrtaceae	*Eugenia procera*	-1.40	0.45	2261.94	119.08	0.28	121.55	-2.19
	Nyctaginaceae	*Guapira* sp [v. JAC-2204, tag. 2498]	-0.15	-1.84	78.79	1.91	0.00	7.04	-5.13
	Polygonaceae	*Coccoloba* sp1 [tag. 1275]	-0.38	0.68	4.65	0.38	0.00	0.00	0.38
	Polygonaceae	*Coccoloba* sp2 [v. JAC-2171, tag. 618]	-0.71	0.51	5832.28	115.60	0.00	174.90	-59.30
	Polygonaceae	*Ruprechtia* sp1 [v. JAC-2189, tag. 1093]	-0.41	-1.37	547.98	6.98	0.00	0.00	6.98
	Polygonaceae	*Triplaris melaenodendron*	0.64	-0.82	1775.49	51.12	0.00	38.85	12.26
	Rubiaceae	*Randia armata*	-1.41	-0.23	832.59	23.45	0.00	24.14	-0.69
	Rubiaceae	*Randia dioica*	-0.33	0.06	7.39	1.10	0.00	0.00	1.10
	Rutaceae	*Amyris pinnata*	-1.70	-0.67	0.00	0.00	0.00	0.00	0.00
	Rutaceae	*Zanthoxylum rhoifolium*	-0.27	-2.33	416.47	11.06	0.00	35.83	-24.77
	Rutaceae	*Zanthoxylum rigidum*	-0.34	-0.44	25.32	0.87	0.00	0.00	0.87

Study sites	Family	Species	PC1	PC2	Standing Biomass	BG$_S$	BG$_R$	BM	NBC
	Rutaceae	*Zanthoxylum schreberi*	-0.48	-0.44	146.79	0.00	0.00	2.74	-2.74
	Salicaceae	*Casearia praecox*	-1.59	-0.60	1023.44	12.53	0.00	121.45	-108.92
	Salicaceae	*Casearia* sp1 [tag. 157]	-1.70	-0.58	538.81	19.35	0.00	0.00	19.35
	Sapotaceae	*Pouteria* sp7 [v. JAC-2152, tag. 120]	-0.97	-0.14	1750.20	42.08	0.00	6.23	35.86
	Ulmaceae	*Ampelocera* sp1 [v. JAC-2154, tag. 79]	-0.23	0.20	1057.49	32.49	0.00	6.29	26.21
	Violaceae	*Leonia* sp1 [v. JAC-2207, tag. 2494]	-0.51	-2.31	374.12	1.72	0.00	0.00	1.72
Tambor Private Natural Reserve									
	Achariaceae	*Mayna odorata*	-0.68	-0.47	87.78	5.61	0.00	0.38	5.22
	Anacardiaceae	*Anacardium excelsum*	1.54	-1.48	66199.73	790.50	0.04	0.19	790.35
	Anacardiaceae	*Astronium graveolens*	1.15	-0.44	3939.02	45.08	0.34	0.00	45.42
	Anacardiaceae	*Spondias mombin*	2.06	-1.74	3243.11	49.98	0.00	0.00	49.98
	Annonaceae	*Malmea* sp [v. JAC-3209, tag. 167]	0.54	0.57	201.93	0.29	0.00	0.00	0.29
	Annonaceae	*Oxandra espintana*	0.20	0.63	87.49	2.60	0.00	0.00	2.60
	Annonaceae	*Pseudomalmea* sp [v. RLC-15595, tag. 7]	0.14	-0.56	1012.64	23.11	0.20	17.00	6.32
	Annonaceae	*Rollinia mucosa*	1.41	-1.20	134.12	13.26	1.08	2.56	11.78
	Apocynaceae	*Aspidosperma* sp1 [v. RLC-15602, tag. 30]	0.05	0.03	0.00	0.00	0.00	0.00	0.00
	Apocynaceae	*Tabernaemontana grandiflora*	-1.33	-1.63	798.04	18.76	2.09	17.88	2.97
	Apocynaceae	*Tabernaemontana markgrafiana*	-1.58	-1.10	2.09	0.11	0.00	0.00	0.11
	Bignoniaceae	*Jacaranda caucana*	0.58	-1.31	1599.37	0.06	0.97	0.00	1.03
	Bignoniaceae	*Tabebuia rosea*	0.86	-0.35	3805.51	28.44	0.38	58.03	-29.21
	Boraginaceae	*Cordia alliodora*	0.47	-0.05	16.16	11.77	0.00	0.00	11.77
	Boraginaceae	*Cordia bicolor*	1.68	-1.83	8.98	1.72	1.96	0.00	3.68
	Burseraceae	*Protium tenuifolium*	1.23	-0.41	157.68	10.92	0.00	3.15	7.78
	Chrysobalanaceae	*Licania* sp1 [v. RLC-15703, tag. 678]	-1.46	-0.34	6.08	0.42	0.00	0.00	0.42
	Ebenaceae	*Diospyros* sp1 [v. RLC-15612, tag. 23]	-0.43	-1.21	0.00	0.00	0.00	0.00	0.00
	Euphorbiaceae	*Acalypha diversifolia*	0.18	0.13	2.56	0.43	0.00	0.00	0.43
	Fabaceae	*Albizia* sp2 [v. RLC-15687, tag. 254]	2.07	-0.07	9.85	0.13	0.00	0.00	0.13
	Fabaceae	*Brownea ariza*	0.90	0.62	23.06	0.00	0.00	0.00	0.00
	Fabaceae	*Cassia* sp [tag. 623]	-0.02	-2.26	0.71	0.55	0.00	0.00	0.55
	Fabaceae	*Enterolobium* sp1 [v. RLC-15687, tag. 476]	1.01	-1.11	370.61	4.26	0.00	0.00	4.26
	Fabaceae	*Inga* sp1 [v. RLC-15590, tag. 73]	0.83	-0.44	693.54	58.36	3.34	12.71	48.99
	Fabaceae	*Inga* sp4 [v. RLC-15634, tag. 181]	1.74	-0.55	53.80	3.90	0.00	0.00	3.90
	Fabaceae	*Inga* sp6 [v. RLC-15589, tag. 87]	1.64	-1.06	2930.90	59.78	32.08	78.20	13.67
	Fabaceae	*Machaerium capote*	1.13	0.10	2032.30	86.52	6.19	0.00	92.70
	Fabaceae	*Platymiscium pinnatum*	-0.27	-1.63	0.00	0.00	0.00	0.00	0.00
	Fabaceae	*Senegalia* sp1 [v. RLC-15669, tag. 510]	1.01	-0.90	250.80	11.90	10.79	0.00	22.69
	Fabaceae	*Styphnolobium sporadicum*	0.86	-0.35	56.14	2.44	0.00	0.00	2.44

Study sites	Family	Species	PC1	PC2	Standing Biomass	BG_S	BG_R	BM	NBC
	Fabaceae	*Swartzia simplex*	0.94	1.44	1128.24	0.00	0.00	0.00	0.00
	Fabaceae	*Swartzia* sp1 [v. RLC-15604, tag. 31]	1.64	0.67	2486.80	35.44	0.00	0.00	35.44
	Lamiaceae	*Callicarpa acuminata*	-0.34	-1.34	26.98	5.44	1.24	2.13	4.55
	Lauraceae	*Nectandra* sp [v. RLC-15618, tag. 116]	0.66	0.03	242.35	16.87	7.01	6.65	17.23
	Lecythidaceae	*Gustavia hexapetala*	-1.02	0.20	490.78	14.84	0.00	16.96	-2.12
	Lecythidaceae	*Gustavia superba*	0.23	-0.91	110.43	2.34	0.00	0.00	2.34
	Malvaceae	*Apeiba tibourbou*	0.19	-2.82	34.91	14.40	0.00	1.35	13.04
	Malvaceae	*Guazuma ulmifolia*	-0.40	-1.43	348.90	2.06	0.00	0.00	2.06
	Malvaceae	*Hampea thespesioides*	0.36	-2.20	65.79	18.52	4.08	4.32	18.27
	Malvaceae	*Herrania laciniifolia*	0.08	-1.49	0.00	0.00	0.00	0.00	0.00
	Malvaceae	*Ochroma pyramidale*	0.02	-2.94	1441.24	72.10	0.00	42.79	29.31
	Malvaceae	*Pachira quinata*	0.83	-0.13	1414.20	3.67	0.19	54.15	-50.30
	Malvaceae	*Pseudobombax septenatum*	0.07	-2.83	4.70	0.94	1.06	0.00	2.00
	Meliaceae	*Guarea* sp1 [v. RLC-15645, tag. 230]	1.37	0.80	30.82	1.26	0.32	0.00	1.58
	Meliaceae	*Trichilia hirta*	0.06	-1.47	576.64	14.65	0.00	0.00	14.65
	Moraceae	*Brosimum alicastrum*	0.50	-0.37	681.37	691.79	0.00	0.00	691.79
	Moraceae	*Ficus* sp [tag. 24]	-0.12	-0.15	0.00	0.00	0.00	0.00	0.00
	Moraceae	*Helianthostylis sprucei*	0.48	0.34	2872.28	52.11	0.16	46.12	6.15
	Moraceae	*Maclura tinctoria*	-0.31	-1.92	7.93	1.38	0.35	0.00	1.74
	Moraceae	*Sorocea* sp [v. RLC-15598, tag. 39]	1.47	0.35	372.33	4.19	0.33	6.11	-1.59
	Myrtaceae	*Eugenia* sp3 [v. JAC-3196, tag. 479]	-0.47	0.35	467.60	17.91	0.00	0.00	17.91
	Myrtaceae	*Eugenia* sp4 [v. RLC-15644, tag. 217]	0.54	0.57	729.97	5.53	0.65	0.00	6.17
	Nyctaginaceae	*Neea macrophylla*	-0.15	-2.37	192.32	7.48	0.00	10.23	-2.75
	Piperaceae	*Piper* sp6 [v. RLC-15584, tag. 1]	-0.07	-0.79	443.93	28.87	36.04	23.05	41.86
	Polygonaceae	*Coccoloba obovata*	0.41	0.02	2.18	0.59	1.23	0.00	1.82
	Polygonaceae	*Ruprechtia* sp1 [tag. 768]	-0.18	1.33	9.33	1.47	0.00	0.00	1.47
	Polygonaceae	*Triplaris melaenodendron*	0.89	-0.32	391.87	40.92	0.00	7.96	32.96
	Rubiaceae	*Alseis blackiana*	-0.80	-0.69	3140.66	100.95	4.55	0.00	105.50
	Rubiaceae	*Ixora* sp [v. RLC-15721, tag. 899]	-0.42	-0.49	186.04	5.17	7.94	0.00	13.11
	Rubiaceae	*Ladenbergia* sp [v. RLC-15578, tag. 47]	-0.56	-1.27	1090.69	2.56	0.00	0.00	2.56
	Rubiaceae	*Randia dioica*	-0.93	-0.03	1451.78	26.92	1.74	7.69	20.97
	Rubiaceae	*Randia* sp [v. RLC-15620, tag. 99]	-0.44	-0.70	2.32	0.38	0.00	0.00	0.38
	Rubiaceae	*Simira cordifolia*	-0.77	-0.24	1122.33	29.12	0.27	0.00	29.39
	Rutaceae	*Zanthoxylum rhoifolium*	0.16	-1.40	0.56	0.09	0.00	0.00	0.09
	Salicaceae	*Banara ibaguensis*	-1.11	0.14	16.33	0.34	0.00	0.00	0.34
	Salicaceae	*Casearia aculeata*	-0.83	-0.40	6.74	0.18	0.00	0.00	0.18
	Salicaceae	*Casearia praecox*	-1.02	-0.18	124.59	13.41	21.42	4.99	29.84

Study sites	Family	Species	PC1	PC2	Standing Biomass	BG_S	BG_R	BM	NBC
	Sapindaceae	*Allophylus nitidulus*	0.33	0.03	19.94	0.65	0.00	2.22	-1.57
	Sapindaceae	*Cupania cinerea*	-1.26	-0.10	0.98	0.12	0.00	0.00	0.12
	Sapindaceae	*Dilodendron costaricense*	0.68	-0.36	1585.88	6.30	0.04	65.79	-59.44
	Sapindaceae	*Matayba* sp1 [v. RLC-15587, tag. 10]	0.76	0.57	2168.33	17.56	0.12	0.00	17.68
	Sapotaceae	*Pouteria* sp5 [v. RLC-15728, tag. 770]	0.28	0.50	94.72	17.07	0.00	1.53	15.54
	Solanaceae	*Solanum lepidotum*	-0.73	-1.29	1.15	0.00	0.00	0.47	-0.47
	Ulmaceae	*Ampelocera* sp1 [v. JAC-3203, tag. 865]	1.14	0.88	41.44	3.37	1.06	0.00	4.43
	Urticaceae	*Cecropia peltata*	0.20	-2.62	1640.81	48.66	0.00	77.06	-28.40
	Urticaceae	*Myriocarpa stipitata*	-0.42	-2.66	288.93	7.62	0.00	8.64	-1.02
	Urticaceae	*Urera caracasana*	-0.62	-3.33	791.45	17.34	16.62	78.32	-44.36
	Violaceae	*Rinorea* sp1 [v. JAC-3197, tag. 843]	-1.44	0.13	8.14	0.57	0.00	0.00	0.57
Taminango Research Station									
	Bignoniaceae	*Handroanthus chrysanthus*	0.66	0.87	17265.44	1115.92	16.42	210.68	921.66
	Burseraceae	*Bursera tomentosa*	0.55	-1.39	65.58	1.15	0.40	3.98	-2.42
	Capparaceae	*Cynophalla flexuosa*	-0.45	0.68	640.83	14.77	0.00	9.69	5.08
	Erythroxylaceae	*Erythroxylum jaimei*	-0.95	0.76	16.35	0.06	0.00	0.00	0.06
	Euphorbiaceae	*Jatropha gossypiifolia*	-0.22	-3.22	4.19	0.65	0.67	0.34	0.98
	Fabaceae	*Caesalpinia cassioides*	0.27	0.45	135.86	1.92	2.13	3.21	0.85
	Fabaceae	*Vachellia pennatula*	1.65	0.33	153.92	5.65	0.24	6.25	-0.36
	Rutaceae	*Zanthoxylum fagara*	-0.72	0.73	1562.63	41.00	0.36	13.27	28.09
	Verbenaceae	*Lippia origanoides*	-0.33	1.09	21.01	0.26	0.00	1.97	-1.71
El Vinculo Regional Park									
	Achatocarpaceae	*Achatocarpus nigricans*	-0.41	-0.16	1552.08	64.76	2.33	18.92	48.16
	Anacardiaceae	*Anacardium excelsum*	1.44	-1.08	2794.51	13.44	0.00	0.00	13.44
	Annonaceae	*Annona muricata*	1.56	-0.84	16.65	0.31	0.00	0.00	0.31
	Asteraceae	*Verbesina* sp [v. VLL-224, tag. D67]	-0.43	-3.68	6.38	0.00	0.26	1.49	-1.23
	Capparaceae	*Cynophalla amplissima*	0.33	0.14	3123.39	92.40	0.00	28.23	64.17
	Erythroxylaceae	*Erythroxylum ulei*	-0.73	0.29	25.89	0.98	0.42	0.00	1.39
	Euphorbiaceae	*Croton gossypiifolius*	1.17	0.03	56.12	0.25	2.03	13.77	-11.49
	Euphorbiaceae	*Euphorbia cotinifolia*	-0.78	-3.36	86.64	0.48	0.00	7.47	-6.99
	Fabaceae	*Enterolobium* sp1 [v. VLL-228, tag. E24]	0.09	-2.19	3442.38	20.16	0.00	0.00	20.16
	Fabaceae	*Gliricidia sepium*	0.91	-1.58	714.11	22.47	0.00	0.00	22.47
	Fabaceae	*Machaerium capote*	0.74	0.23	4513.18	200.13	0.11	4.08	196.16
	Fabaceae	*Pithecellobium dulce*	0.40	-1.97	68.54	2.34	0.00	0.00	2.34
	Fabaceae	*Pithecellobium lanceolatum*	1.11	-0.24	4259.99	108.38	0.43	62.22	46.59
	Fabaceae	*Pseudosamanea guachapele*	1.58	-0.10	28.99	3.20	0.00	0.00	3.20
	Fabaceae	*Senna spectabilis*	1.81	-1.22	37.33	0.20	0.00	0.00	0.20

Study sites	Family	Species	PC1	PC2	Standing Biomass	BG_S	BG_R	BM	NBC
	Fabaceae	*Vachellia farnesiana*	-0.13	1.63	15.41	0.66	0.00	0.00	0.66
	Lauraceae	*Ocotea veraguensis*	0.36	0.21	7704.26	359.17	2.01	3.64	357.54
	Malpighiaceae	*Bunchosia pseudonitida*	-0.93	0.68	260.20	14.04	0.82	2.90	11.96
	Malpighiaceae	*Malpighia glabra*	-0.60	-0.43	105.17	4.94	0.00	0.00	4.94
	Malvaceae	*Ceiba pentandra*	0.21	-1.54	199.03	11.11	0.00	0.00	11.11
	Malvaceae	*Guazuma ulmifolia*	0.19	-1.50	2967.65	40.96	0.00	37.52	3.44
	Meliaceae	*Trichilia pallida*	-0.81	-0.71	27.81	1.38	0.09	0.00	1.47
	Moraceae	*Brosimum alicastrum*	0.88	0.19	2154.56	134.82	3.70	1.31	137.21
	Moraceae	*Ficus zarzalensis*	-0.21	-0.67	7.75	0.72	0.00	0.00	0.72
	Moraceae	*Sorocea trophoides*	0.52	0.11	1136.64	35.97	3.46	7.50	31.93
	Myrtaceae	*Eugenia monticola*	-0.25	0.84	1100.86	53.69	6.10	51.80	7.99
	Myrtaceae	*Eugenia procera*	-0.79	0.86	10038.93	586.20	47.36	32.98	600.58
	Myrtaceae	*Psidium guineense*	-0.77	0.34	1.09	0.00	0.00	0.00	0.00
	Nyctaginaceae	*Guapira* sp1 [v. VLL-187, tag. O129]	-0.26	-0.43	2704.48	100.50	5.00	29.35	76.15
	Piperaceae	*Piper amalago*	-0.83	-0.73	2.47	0.05	0.00	0.00	0.05
	Rubiaceae	*Chiococca alba*	-0.16	-0.53	422.31	9.17	1.11	0.58	9.69
	Rubiaceae	*Coffea arabica*	-0.87	0.31	2.94	0.03	0.10	0.00	0.13
	Rubiaceae	*Genipa americana*	0.12	-0.19	346.39	30.92	0.11	7.12	23.91
	Rutaceae	*Amyris pinnata*	-0.61	0.12	2143.52	19.79	0.77	100.86	-80.31
	Rutaceae	*Zanthoxylum fagara*	-0.29	0.57	6.27	0.48	0.00	0.00	0.48
	Rutaceae	*Zanthoxylum rhoifolium*	-0.14	-1.07	182.77	5.06	0.00	0.00	5.06
	Rutaceae	*Zanthoxylum schreberi*	-0.61	-0.37	2987.50	130.46	7.88	20.89	117.45
	Rutaceae	*Zanthoxylum verrucosum*	-0.26	-1.18	1199.99	58.49	1.85	0.00	60.34
	Salicaceae	*Casearia aculeata*	-1.37	0.01	297.68	15.83	0.07	3.08	12.81
	Salicaceae	*Xylosma intermedia*	-1.43	-0.19	67.91	4.29	0.00	1.68	2.61
	Sapindaceae	*Cupania* sp1 [v. VLL-230, tag. E72]	0.27	0.00	3107.66	56.90	0.00	86.01	-29.11
	Sapindaceae	*Sapindus saponaria*	0.98	-0.28	1481.37	6.03	0.00	33.45	-27.43
	Thymelaeaceae	*Daphnopsis* sp [v. VLL-243, tag. L150]	-0.18	-0.71	196.68	7.66	0.00	0.00	7.66
	Urticaceae	*Urera simplex*	-0.38	-3.44	21.71	0.33	0.23	2.44	-1.88
	Verbenaceae	*Citharexylum kunthianum*	0.56	-0.11	373.58	5.70	0.29	26.38	-20.39
Dry Savannas									
Tuparro National Park									
	Achariaceae	*Lindackeria paludosa*	-0.51	-0.14	74.64	10.24	0.00	0.00	10.24
	Achariaceae	*Mayna odorata*	-1.27	-0.79	1.68	0.08	0.03	0.38	-0.27
	Anacardiaceae	*Astronium graveolens*	0.95	-0.38	130.31	8.33	0.00	0.19	8.14
	Anacardiaceae	*Spondias mombin*	0.68	-0.83	12.33	0.54	0.00	0.00	0.54
	Annonaceae	*Duguetia odorata*	-0.26	0.29	115.85	6.99	0.00	0.00	6.99

Study sites	Family	Species	PC1	PC2	Standing Biomass	BG$_S$	BG$_R$	BM	NBC
	Annonaceae	*Guatteria metensis*	1.56	0.48	20.99	0.37	0.00	1.36	-0.99
	Apocynaceae	*Himatanthus articulatus*	-0.05	-1.20	1867.66	49.40	1.44	24.62	26.22
	Bignoniaceae	*Handroanthus barbatus*	1.56	1.00	693.35	5.75	0.00	26.94	-21.19
	Bixaceae	*Cochlospermum orinocense*	1.75	-2.31	262.20	6.44	0.00	0.00	6.44
	Burseraceae	*Bursera simaruba*	0.74	-1.60	382.90	7.79	0.00	1.53	6.25
	Burseraceae	*Protium guianense*	0.51	0.28	10057.62	271.40	0.26	0.00	271.66
	Capparaceae	*Capparidastrum sola*	-0.99	0.25	10.10	0.19	0.00	0.00	0.19
	Chrysobalanaceae	*Hirtella racemosa*	0.92	1.11	68.18	2.17	0.00	0.00	2.17
	Chrysobalanaceae	*Licania apetala*	0.74	0.94	531.98	16.13	0.00	0.00	16.13
	Chrysobalanaceae	*Licania micrantha*	1.32	1.20	7600.18	192.13	0.00	0.54	191.59
	Chrysobalanaceae	*Licania parvifructa*	1.62	1.22	399.74	4.98	0.00	0.00	4.98
	Chrysobalanaceae	*Licania* sp [v. RG-2387, tag. 116]	2.58	0.74	154.17	4.45	0.00	0.00	4.45
	Chrysobalanaceae	*Licania* sp2 [v. RG-2367, tag. 35]	0.80	0.82	712.47	12.98	0.00	0.00	12.98
	Clusiaceae	*Clusia umbellata*	0.72	1.06	31.49	0.81	0.00	0.00	0.81
	Combretaceae	*Terminalia amazonia*	1.34	0.19	594.60	30.11	0.00	0.00	30.11
	Connaraceae	*Connarus ruber*	0.48	0.46	31.85	1.14	0.00	0.00	1.14
	Erythroxylaceae	*Erythroxylum macrophyllum*	-0.06	0.87	415.09	15.66	0.00	0.00	15.66
	Euphorbiaceae	*Mabea trianae*	0.20	-0.22	33.16	0.93	0.00	0.00	0.93
	Euphorbiaceae	*Sapium glandulosum*	1.51	-1.53	2290.53	55.65	0.00	22.72	32.93
	Fabaceae	*Clathrotropis macrocarpa*	1.27	-0.05	301.34	29.14	0.00	2.41	26.72
	Fabaceae	*Enterolobium schomburgkii*	1.53	0.06	765.43	8.70	0.00	0.58	8.12
	Fabaceae	*Inga gracilifolia*	1.48	1.26	3107.58	171.98	0.05	43.69	128.33
	Fabaceae	*Inga laurina*	1.00	1.20	235.64	0.96	0.00	0.00	0.96
	Fabaceae	*Inga* sp [v. RG-2433, tag. 692]	1.03	1.21	1800.61	113.10	0.00	51.81	61.29
	Fabaceae	*Machaerium biovulatum*	-0.01	-2.58	114.22	3.11	0.00	0.00	3.11
	Fabaceae	*Pterocarpus* sp4 [v. RG-2420, tag. 389]	1.12	0.02	695.79	10.18	0.00	0.00	10.18
	Fabaceae	*Tachigali guianensis*	1.88	0.18	442.68	86.53	0.00	0.00	86.53
	Indet	Morf sp4 [v. RG-2430a, tag. 107]	0.74	-1.50	6063.79	132.92	0.00	0.00	132.92
	Lamiaceae	*Vitex orinocensis*	-0.06	0.62	322.24	3.97	0.00	0.00	3.97
	Lauraceae	*Ocotea schomburgkiana*	0.70	0.53	216.84	12.51	0.38	2.65	10.25
	Lecythidaceae	*Eschweilera tenuifolia*	1.17	1.19	8005.90	284.92	0.00	49.02	235.90
	Lecythidaceae	*Gustavia augusta*	-0.31	-0.67	2370.81	43.24	0.29	10.54	33.00
	Lecythidaceae	*Lecythis chartacea*	0.87	0.06	468.58	10.39	0.61	0.00	11.00
	Malvaceae	*Apeiba tibourbou*	0.90	-0.31	2067.01	28.11	0.00	0.00	28.11
	Malvaceae	*Pachira nukakica*	2.21	-2.43	4015.82	119.42	0.00	0.00	119.42
	Melastomataceae	*Graffenrieda rotundifolia*	0.88	-1.42	47.52	3.40	0.00	1.50	1.91
	Melastomataceae	*Miconia splendens*	-0.86	-0.22	10.64	0.63	1.48	0.00	2.12

Study sites	Family	Species	PC1	PC2	Standing Biomass	BG$_S$	BG$_R$	BM	NBC
	Meliaceae	*Guarea glabra*	-0.36	0.05	578.66	23.83	0.00	2.37	21.46
	Moraceae	*Brosimum guianense*	0.79	0.28	504.68	9.00	0.00	0.00	9.00
	Moraceae	*Clarisia racemosa*	1.88	0.33	5.69	0.81	0.00	0.00	0.81
	Moraceae	*Ficus americana*	1.97	-0.94	3569.14	84.94	0.00	4.40	80.54
	Moraceae	*Ficus* sp [v. RG-2396, tag. 186]	1.67	-1.15	1.22	0.37	0.00	0.00	0.37
	Moraceae	*Ficus* sp1 [tag. 495]	2.16	-0.88	725.85	0.00	0.00	0.00	0.00
	Moraceae	*Ficus trigona*	2.30	0.81	734.31	0.00	0.00	0.00	0.00
	Moraceae	*Pseudolmedia* sp1 [v. RG-2361, tag. 189]	0.93	0.31	399.61	9.22	0.00	1.81	7.41
	Moraceae	*Sorocea muriculata*	0.75	0.20	6.18	0.21	0.00	0.00	0.21
	Myrtaceae	*Calyptranthes multiflora*	0.83	-0.57	4.19	0.00	0.00	1.05	-1.05
	Myrtaceae	*Eugenia florida*	0.84	0.67	172.88	1.75	0.00	0.00	1.75
	Myrtaceae	Morf sp2 [v. RG-2372, tag. 47]	-1.58	0.05	227.82	7.49	0.00	0.00	7.49
	Myrtaceae	Morf sp3 [v. RG-2458, tag.]	-0.63	0.75	320.37	9.47	0.00	0.00	9.47
	Myrtaceae	*Myrcia* sp1 [v. RG-2378, tag. 69]	-0.52	0.66	1306.41	59.27	0.29	0.37	59.19
	Myrtaceae	*Myrcia* sp2 [v. RG-2416, tag. 341]	-0.03	0.82	2.71	0.40	0.00	0.31	0.09
	Nyctaginaceae	*Neea ignicola*	-0.96	0.28	5.27	0.19	0.00	0.00	0.19
	Ochnaceae	*Ouratea* sp [v. RG-2380, tag. 83]	-0.01	0.91	67.03	5.14	0.10	0.00	5.23
	Olacaceae	*Heisteria acuminata*	1.30	1.15	1107.08	32.93	0.00	21.44	11.49
	Phyllanthaceae	*Amanoa guianensis*	1.63	1.67	408.97	13.12	0.00	0.00	13.12
	Rubiaceae	*Amaioua corymbosa*	-0.36	-0.15	109.98	2.96	0.00	2.56	0.41
	Rubiaceae	*Cordiera myrciifolia*	-0.45	0.85	11.70	0.57	0.09	0.00	0.66
	Rubiaceae	*Coussarea paniculata*	-1.04	-0.74	8.54	0.33	0.00	0.00	0.33
	Rubiaceae	*Palicourea rigida*	-1.14	-1.02	75.98	5.01	0.00	0.00	5.01
	Rubiaceae	*Rudgea crassiloba*	-1.50	-0.53	123.27	9.28	1.24	0.00	10.52
	Rubiaceae	*Simira rubescens*	-0.67	0.39	229.34	3.17	0.09	0.00	3.26
	Sapindaceae	*Matayba* sp [v. RG-2382, tag. 117]	0.26	0.99	2352.02	72.45	0.23	6.33	66.35
	Sapotaceae	*Elaeoluma* sp [v. RG-2392, tag. 163]	0.29	0.51	82.88	6.64	0.00	0.00	6.64
	Sapotaceae	*Pouteria plicata*	-0.23	0.38	1095.64	22.98	0.00	2.29	20.68
	Sapotaceae	*Pouteria* sp4 [v. RG-2406, tag. 234]	-0.31	0.20	1275.92	59.13	0.08	0.00	59.21
	Siparunaceae	*Siparuna guianensis*	-0.17	-0.11	185.49	14.78	0.04	6.55	8.27
	Urticaceae	*Cecropia peltata*	2.63	-1.40	23.70	4.51	0.00	1.24	3.27
	Verbenaceae	*Petrea* sp [v. RG-2371, tag. 44]	0.13	-0.76	482.12	16.81	0.29	0.00	17.10
	Violaceae	*Rinorea pubiflora*	-1.31	0.01	35.50	0.20	0.06	5.88	-5.63
	Vochysiaceae	*Vochysia vismiifolia*	0.19	0.18	60.27	3.77	0.00	0.42	3.35

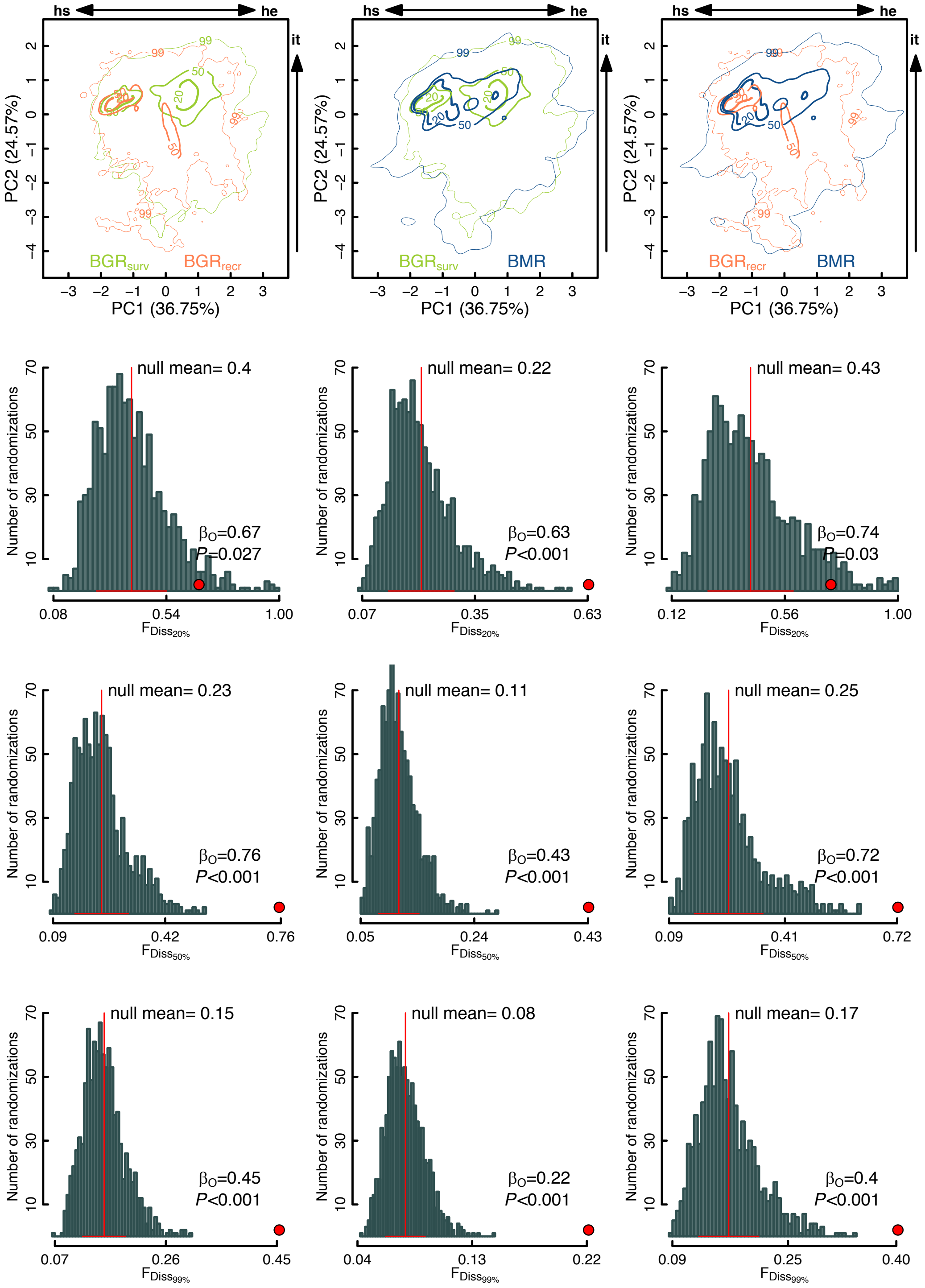


Figure S3. Null models for functional dissimilarity (F_{Diss}) between biomass growth and mortality TPD's at thresholds 20%, 50%, and 99% of probability. Significant β_O ($P<0.001$) indicated that dissimilarity between paired TPD demographic dimensions was more significant than expected by chance (999 randomizations). Hydraulic safety (hs); hydraulic efficiency (he); investments in tissues (it).

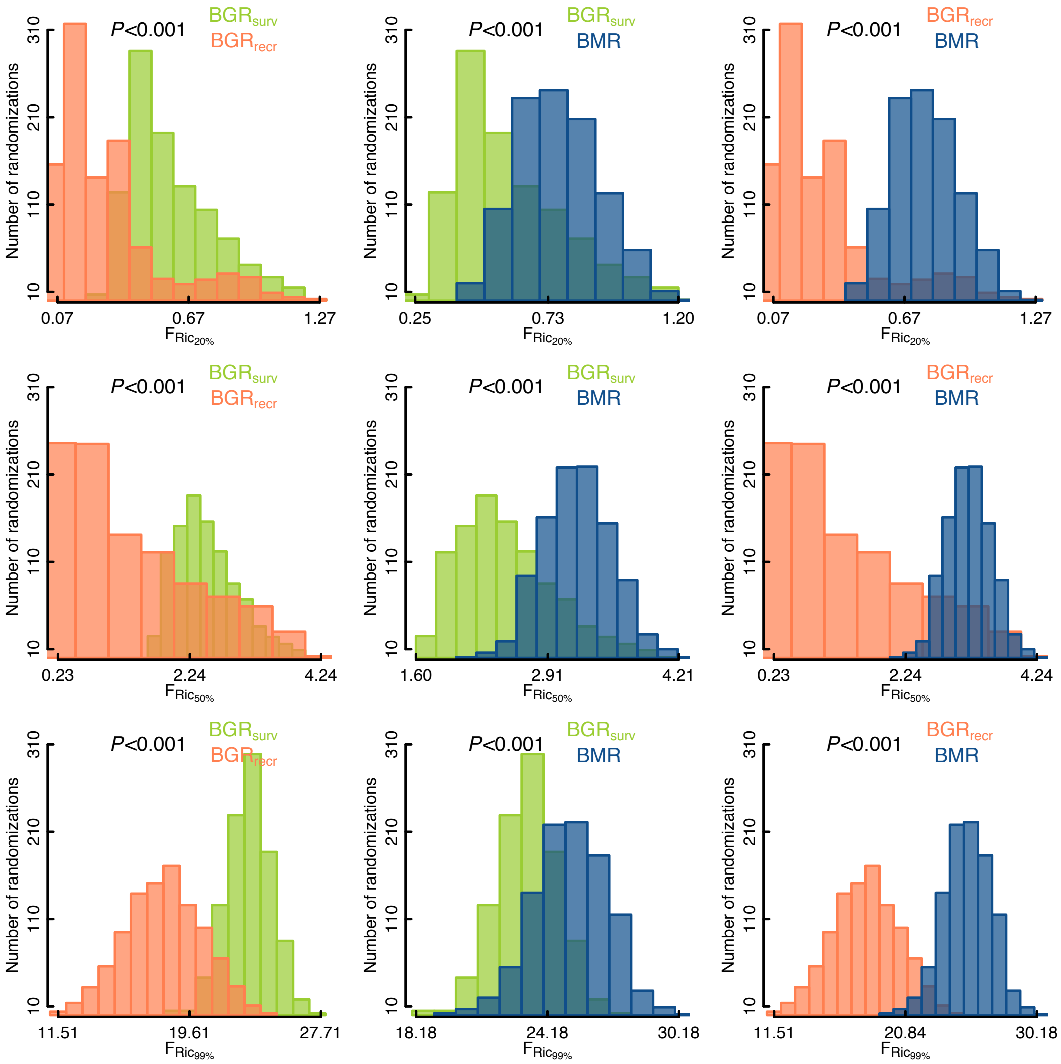
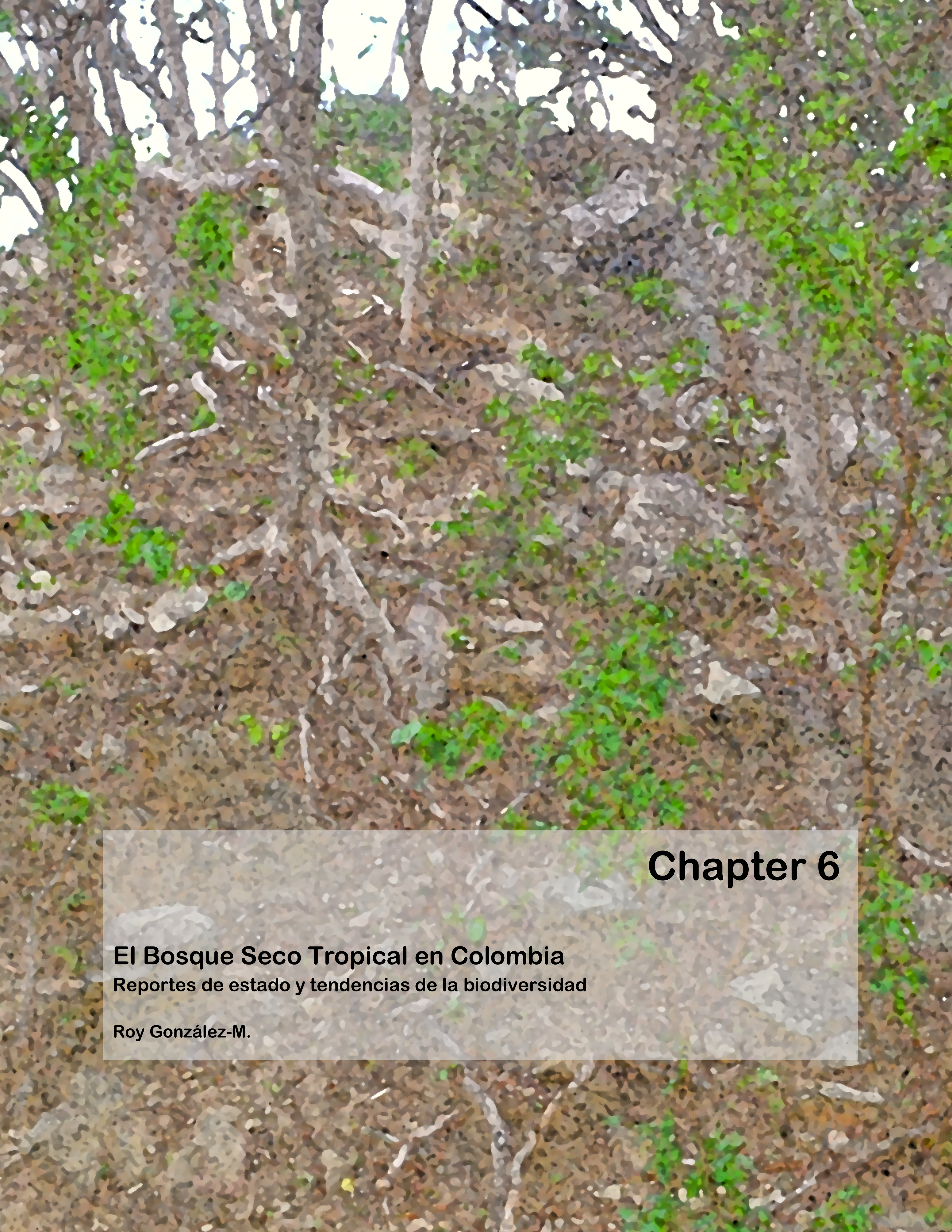


Figure S4. Functional richness (F_{Ric}) between biomass growth and mortality TPD's at thresholds 20%, 50%, and 99% of probability. Significant differences between paired frequency distributions indicated different F_{Ric} of contrasted TPD's demographic dimensions ($P<0.001$, 999 randomizations). Biomass growth of survivors (BG_S), biomass growth of recruits (BG_R), and biomass mortality (BM).



Chapter 6

El Bosque Seco Tropical en Colombia

Reportes de estado y tendencias de la biodiversidad

Roy González-M.

El Bosque Seco Tropical en Colombia: Distribución y estado de conservación

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Síntesis

El bosque seco se encuentra en un estado crítico de fragmentación y degradación en Colombia. La mayoría de sus áreas están expuestas a presiones antropogénicas como la ganadería, la infraestructura humana y la agricultura.

Reporte

El Bosque Seco Tropical (BST) se encuentra en tierras bajas (0-1000 msnm) y se caracteriza por presentar una fuerte estacionalidad de lluvias con al menos tres meses de sequía (<100 mm de precipitación). Este ecosistema sostiene una diversidad única de plantas, animales y microorganismos, cuyas especies se han adaptado a condiciones extremas. El BST contiene aproximadamente 2.600 especies de plantas (Pizano *et al.* 2014b), al menos 230 de aves (Gómez & Robinson 2014) y 60 de mamíferos (Díaz-Pulido *et al.* 2014), con 83, 33 y 3 especies exclusivas, respectivamente. Adicionalmente, el BST presta servicios fundamentales, tales como la regulación hídrica, la retención de suelos y la captura de carbono (Maass *et al.* 2005; Wall *et al.* 2011). La distribución del BST en suelos relativamente fértiles y en condiciones climáticas específicas ha convertido sus áreas en escenarios históricos de asentamiento humano. En consecuencia, es considerado como uno de los ecosistemas más amenazados del Neotrópico (Janzen 1988b); tanto así, que fue declarado como estratégico para la conservación de la biodiversidad por el Ministerio del Medio Ambiente y Desarrollo Sostenible.

Hasta ahora, la imposibilidad de contar con un insumo cartográfico detallado había impedido la gestión integral del BST. Por tal razón, fue necesario cuantificar su distribución y determinar cuáles eran las presiones antropogénicas que más lo afectaban (**Figura 1**). La situación actual refleja una severa fragmentación, que se traduce en un número exiguo de remanentes boscosos que podrían limitar la provisión de servicios ecosistémicos. Teniendo en cuenta que el BST constituye un porcentaje muy pobre de las áreas del Sistema Nacional de Áreas Protegidas (García *et al.* 2014) (SINAP) (6.4%), y que las 9.000.000 ha que cubría originalmente, solo queda el 8%, es imperante establecer estrategias integrales para su gestión (García *et al.* 2014). Estas deben considerar zonas prioritarias para la conservación, la restauración ecológica mediante enriquecimiento de áreas degradadas (rastrojos y bosques secundarios) y la conectividad de fragmentos estratégicos en territorios productivos (Urbina-Cardona *et al.* 2014; Vargas & Ramírez 2014). De tal forma, es necesario adelantar acciones inmediatas: (a) orientar una agenda de investigación y monitoreo para enfocar mejor los esfuerzos de restauración; (b) revisar aquellos insumos cartográficos oficiales que registren remanentes menores a 25 ha; (c) lograr una mayor representatividad en el SINAP con base en las áreas de distribución original y no en los remanentes actuales; (d) incluir áreas de BST en figuras regionales de protección y en instrumentos de ordenamiento territorial; y (e) articular los esfuerzos de la red de reservas de la sociedad civil por medio de estrategias complementarias (Miles *et al.* 2006; Chazdon *et al.* 2009).

Para poner en práctica las recomendaciones mencionadas, se debe garantizar un esfuerzo colectivo que involucre al Gobierno, a las entidades ambientales, a la Academia y al sector privado. Esto permitirá estudiar este ecosistema en mayor detalle y orientar las decisiones necesarias para conservar lo que queda del mismo.

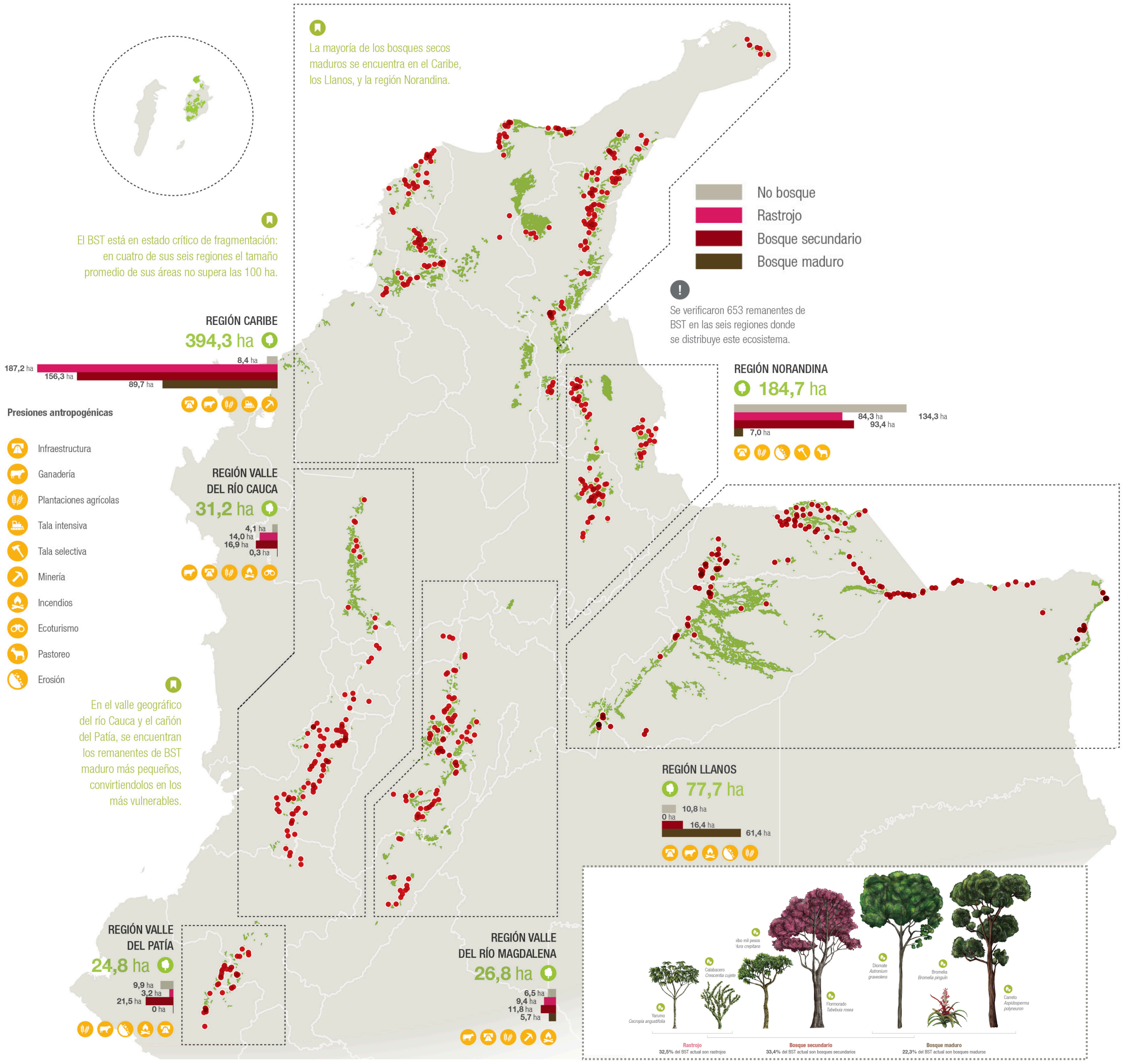

Figura 1. Distribución actual y estado de conservación del bosque seco tropical en Colombia. Las barras de color indican el área total de cobertura para los sitios de muestreo (653 remanentes de bosque seco) valorados en tres estados sucesionales: (i) rastrojo (coberturas en estadio de sucesión temprana, color fucsia), (ii) bosques secundarios (coberturas en estadios de sucesión intermedia, color magenta claro) y (iii) bosques maduros (coberturas en estadios de sucesión tardía, color magenta oscuro). La cobertura evaluada sin presencia de vegetación se representa en color gris. Los iconos color naranja indican las presiones antropogénicas identificadas en campo para los sitios de muestreo.

Monitoreo de la vegetación en los bosques secos de Colombia: Una herramienta para el análisis y la gestión integral de este ecosistema a escala de país

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Síntesis

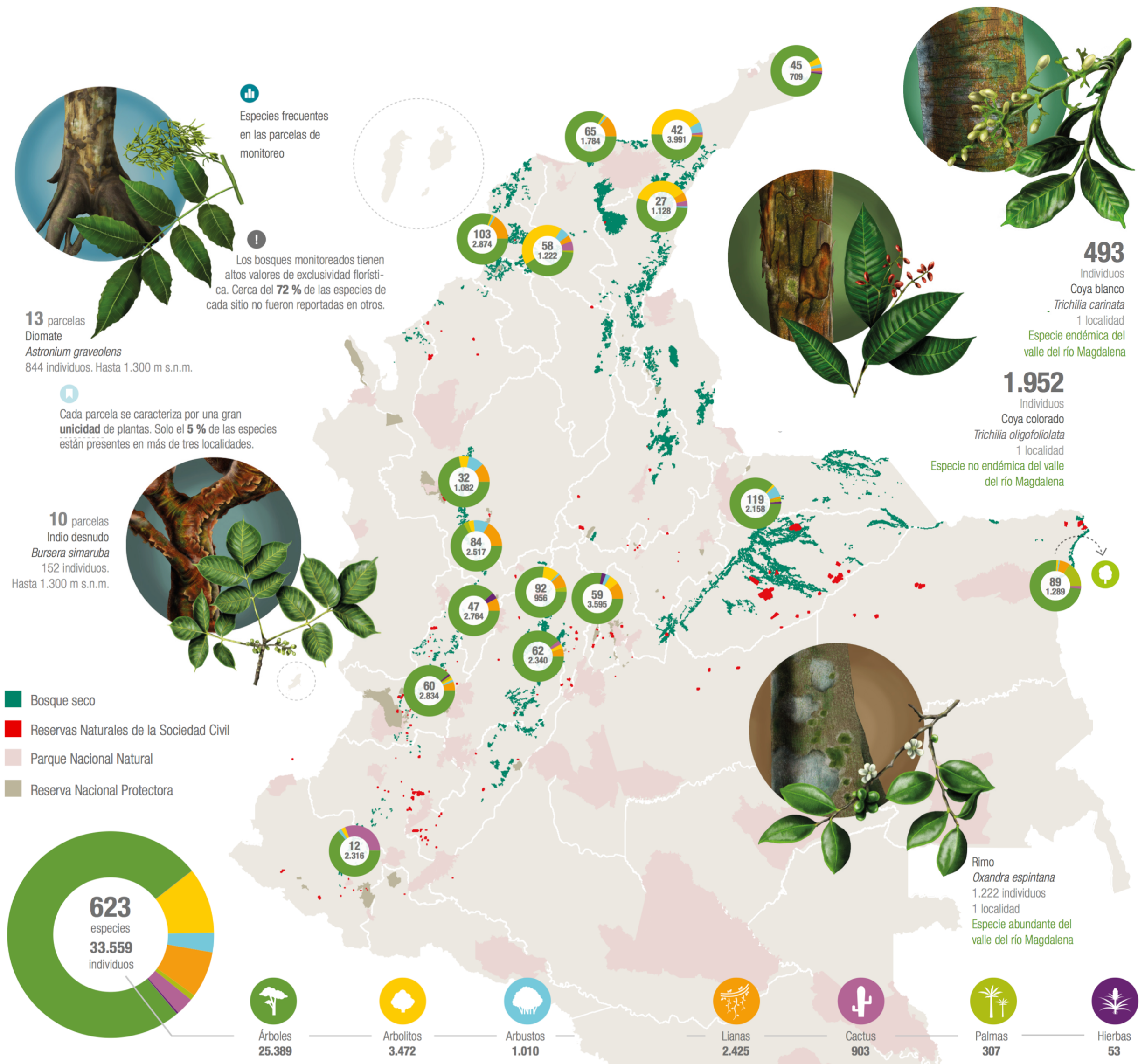
El monitoreo permanente en ecosistemas con prioridad de conservación, como el bosque seco, es fundamental para comprender las dinámicas ecológicas y proponer medidas de manejo para su gestión integral.

Reporte

En el Neotrópico los bosques secos son considerados ecosistemas con alta prioridad para la conservación1, en ellos se encuentran especies exclusivas de estos ecosistemas, que resisten altas temperaturas y fuertes limitaciones de agua durante gran parte del año (Pizano & García 2014; DRYFLOR *et al.* 2016). Sin embargo, las áreas donde se distribuye este ecosistema han albergado tradicionalmente grandes asentamientos humanos, lo que le confiere una larga historia de transformación y perdida de su biodiversidad (Miles *et al.* 2006; DRYFLOR *et al.* 2016). Alarmados por el grado de amenaza que sufren estos bosques en Colombia (Pizano *et al.* 2016) y la falta de conocimiento sobre su dinámica y funcionamiento (Sánchez-Azofeifa *et al.* 2005a; Parrado-Rosselli *et al.* 2016), en 2013 investigadores regionales iniciaron, una estrategia nacional para el monitoreo de la vegetación del bosque seco (Red BST-Col), cuyo objeto es generar datos científicos relevantes para la gestión integral de este ecosistema de cara a los motores de cambio que enfrenta y los escenarios socioecológicos complejos que presenta (García *et al.* 2014).

Estos esfuerzos de monitoreo aportan información de alta calidad que debe ser la base para la toma de decisiones en términos de su conservación. Se considera, entonces, que el monitoreo permanente de la vegetación se traducirá en un proceso sistemático de toma y análisis de datos, que no solo explorará las tendencias de cambio de los atributos propios de las especies y comunidades vegetales en el tiempo, sino que también permitirá verificar como los diferentes esquemas de conservación que Colombia tiene para este ecosistema aportan a la gestión integral de su biodiversidad. Hasta el momento, a partir del análisis de la información registrada para la primera toma de datos, 623 especies de plantas (33.559 individuos) entre árboles, arbustos, palmas, lianas y cactus, están siendo monitoreadas en todas las parcelas (62±29 especies ha^{-1}) (**Figura 1**). Al sobreponer las parcelas con el Sistema Nacional de Áreas Protegidas (SINAP), se encontró que tanto las áreas con medidas de protección estricta como las áreas con iniciativas de conservación privada resguardan un mayor número de especies respecto a los bosques sin figuras de manejo. Para los Parques Nacionales Naturales y Parques Regionales se registra ~72 especies ha^{-1}), para las Reservas Privadas de la Sociedad Civil ~74 especies ha^{-1} y en predios privados ~51 especies ha^{-1} . Sin embargo, independientemente de la figura de manejo, llama la atención la alta exclusividad y unicidad florística de cada sitio de monitoreo, sumado a la presencia de especies endémicas para la mayoría de las regiones.

Lo anterior resalta la importancia del SINAP para la gestión integral de la biodiversidad en los bosques secos y la necesidad de proponer alternativas para la conservación de las plantas en las áreas privadas que no cuentan hoy en día con alguna figura de manejo y sobre la base del acoplamiento con los escenarios productivos que subyacen a cada sitio. Aunque esta iniciativa está en su fase preliminar, en el futuro, y gracias al monitoreo permanente, se podrán puntualizar necesidades de conservación derivadas de los análisis sobre la dinámica, el funcionamiento y la capacidad de respuesta de las plantas ante diferentes motores de transformación.


Especies frecuentes en las parcelas de monitoreo

Los bosques monitoreados tienen altos valores de exclusividad florística. Cerca del **72 %** de las especies de cada sitio no fueron reportadas en otros.

Cada parcela se caracteriza por una gran **unicidad** de plantas. Solo el **5 %** de las especies están presentes en más de tres localidades.

Figura 1. Sistema de monitoreo permanente de la vegetación en los bosques secos de Colombia. Los diagramas en anillo para cada parcela permanente de 1 ha indican el porcentaje de individuos correspondientes a especies de árboles, arbolitos, arbustos, lianas, cactus palmas y hierbas.

Diversidad funcional en los bosques de Colombia

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Síntesis

Los rasgos funcionales de las plantas leñosas son claves para entender la vulnerabilidad de los bosques frente al cambio climático, su capacidad para ofrecer servicios ecosistémicos y para garantizar su adecuado manejo y conservación. Sin embargo, existen grandes vacíos de información para todos los ecosistemas forestales del país.

Reporte

Los bosques de Colombia abarcan cerca del 53 % del territorio nacional (FAO 2002) y ofrecen servicios ecosistémicos tan importantes como la regulación del clima o del ciclo hidrológico, de los cuales depende el bienestar de la población humana. La oferta de estos servicios está relacionada con los procesos de los ecosistemas, los cuales están influenciados por las características de las especies arbóreas que ahí habitan. Es decir, la oferta de servicios ecosistémicos está determinada por la diversidad funcional, que hace referencia a la variedad de formas y estrategias que tienen las plantas para usar los recursos y transformar con su actividad el ambiente (Salgado Negret 2015). Los rasgos funcionales de las plantas pueden agruparse de acuerdo a su función en: (1). Rasgos de las hojas, relacionados con la captura de carbono y relaciones hídricas de las plantas; (2). Rasgos del tallo, relacionados con la función hidráulica y el sostenimiento mecanico; (3). Rasgos de raíces, importantes para el transporte de agua y nutrientes; 4. Rasgos reproductivos, asociados al establecimiento y dispersión de los individuos (**Figura 1**).

Aunque todavía no existen datos consolidados ni un análisis a escala regional sobre los rasgos funcionales de las plantas leñosas en Colombia, los estudios en diversidad funcional en los ecosistemas forestales del país se han incrementado en los últimos años. Esta ficha evidencia el creciente interés por incorporar esta dimensión de la diversidad en los estudios de ecología en los bosques del país. Este análisis se elaboró a partir de la información colectada por cerca de 60 investigadores en 2265 especies de árboles distribuidas en los diferentes bosques del país. Los rasgos foliares fueron los mejor representados en todos los bosques estudiados y son importantes por su influencia en la productividad primaria, la descomposición de la hojarasca y el ciclaje de nutrientes (Pérez-Harguindeguy *et al.* 2013). Llama la atención la poca información que se encuentra sobre los rasgos radiculares en los todos los ecosistemas forestales del país.

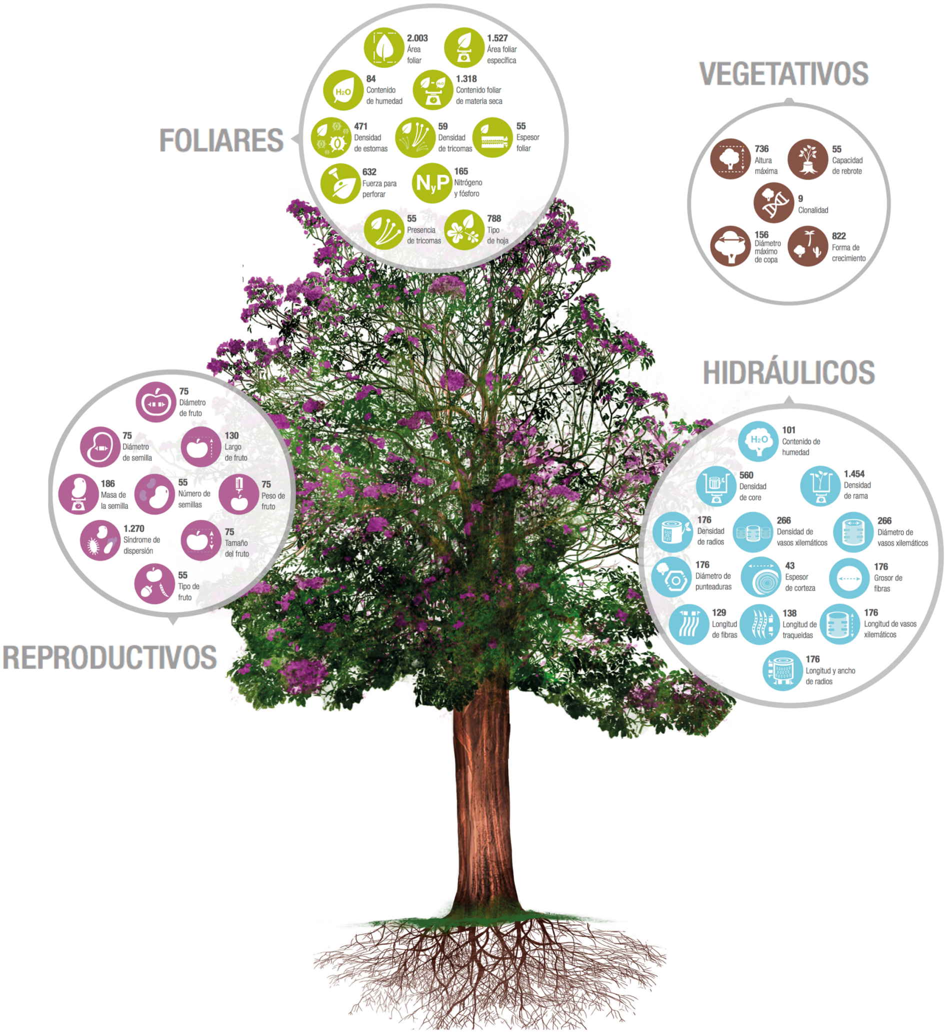


Figura 1. Diversidad de rasgos funcionales de las plantas leñosas en los bosques de Colombia y número de especies medidas por cada rasgo funcional. *Rasgos foliares*: Los rasgos foliares hacen referencia a los caracteres fisiológicos o morfológicos de las hojas de las plantas. Son probablemente los más sensibles a la variación ambiental e influencian procesos de los ecosistemas como la productividad primaria, la descomposición de hojarasca y el ciclaje de nutrientes. *Rasgos reproductivos*: Los rasgos reproductivos pueden ser tanto sexuales como vegetativos y proveen información sobre las estrategias de regeneración y dispersión, así como la capacidad de los individuos de colonizar diferentes ambientes. *Rasgos hidráulicos*: Son los rasgos funcionales del tronco se han estudiado principalmente desde su relación con la conductividad hidráulica de la planta. *Rasgos vegetativos*: Los rasgos vegetativos están relacionados con el potencial de establecimiento de las especies en nuevos ambientes y determinan la posición de la planta en el gradiente vertical, así como su vigor competitivo. Hacen referencia a las características propias de la planta, como su altura máxima, forma de crecimiento, entre otros.

El bosque seco es el ecosistema que tiene el mayor número de especies con información funcional (**Figura 2**). Mientras que los rasgos de tallo y vegetativos fueron muestreados principalmente en bosques andinos, los reproductivos en los bosques húmedos del Pacífico. Es importante destacar que la densidad de madera fue el rasgo mejor representado en todos los bosques debido principalmente a la reciente necesidad de estimar el carbono en muchos proyectos nacionales. Los rasgos foliares fueron los mejor representados en todos los bosques estudiados. Sin embargo, los rasgos vegetativos fueron muestreados principalmente en los bosque andino y bosque seco. Los ecosistemas con mayor número de rasgos reproductivos medidos fueron los bosques húmedos del Pacífico y bosque seco.

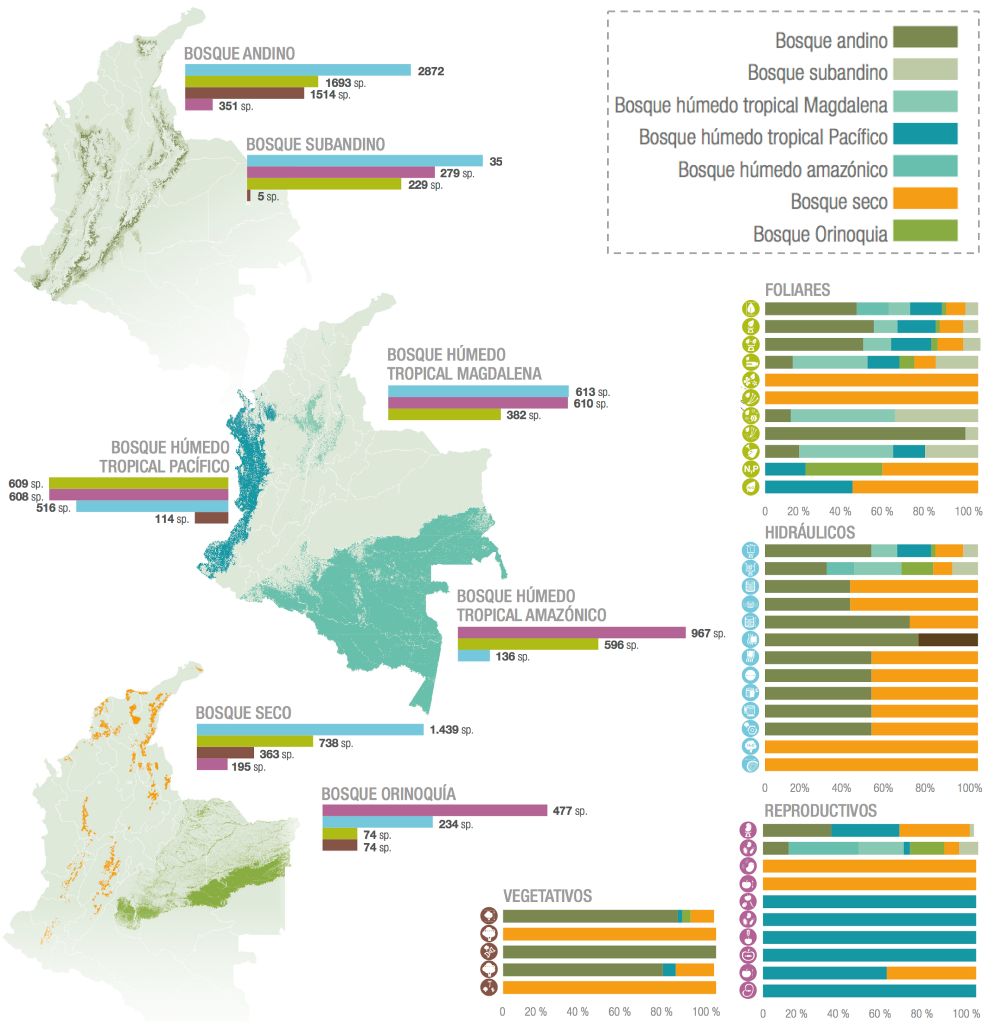
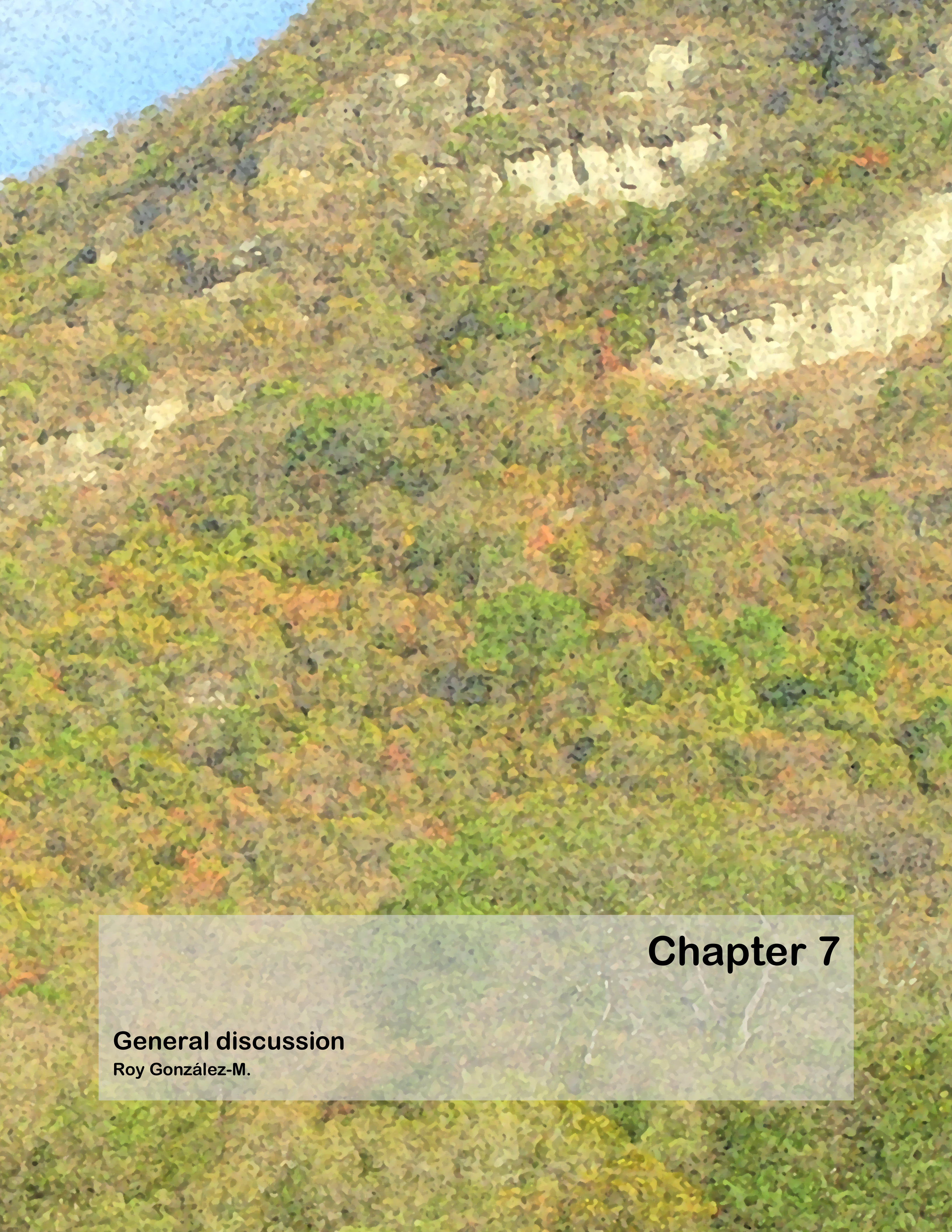


Figura 2. Síntesis de información sobre rasgos funcionales en los principales ecosistemas de Colombia e intensidad de muestreo.

La diversidad funcional para la gestión de la biodiversidad

Aunque el enfoque de ecología funcional ha sido adoptado por muchas instituciones en Colombia, aún hay grupos de rasgos clave y ecosistemas con poca información en el país. El reto actual no solo consiste en aumentar el número de especies y ecosistemas con información de rasgos funcionales sino en enlazar estos conocimientos a preguntas de investigación y gestión a diferentes escalas biológicas como la identificación de áreas prioritarias para la conservación, la restauración de ecosistemas enfocada en la recuperación de los procesos de los ecosistemas, el manejo de las invasiones biológicas, adaptación al cambio climático, entre otras. Esta información debe estar a disposición de la comunidad científica, traducida e integrada en recomendaciones que apunten a disminuir la pérdida de las funciones ecosistémicas del territorio.



Chapter 7

General discussion

Roy González-M.

Discussion outline

The objective of this thesis was to identify the factors determining environmental harshness in Tropical Dry Forests (TDF) of Colombia and to study its influence on plant community attributes and functioning. Additionally, this thesis evaluated how the extreme "El Niño" Southern Oscillation drought of 2015 ($ENSO_{2015}$) affected biomass dynamics of this ecosystem. Overall, we found that: (1) Colombian TDF are widely heterogeneous in their climate, soil, and land-cover transformation and that the interaction of these factors is what determines the environmental harshness in this ecosystem (**Chapter 2**). (2) Environmental harshness drives changes in species composition (**Chapter 2**), species diversity and forest structure (**Chapters 3**), and trait community composition and biomass productivity (**Chapter 4**) of TDF. (3) TDF tree species are adapted to cope with environmental harshness via different functional trait combinations (**Chapters 3** and **5**); nevertheless, all tree species seem to be sensitive to extreme droughts (**Chapter 5**). Accordingly, extreme drought events cause negative net biomass balances, particularly for species having traits associated with high hydraulic efficiency and 'cheap' tissue investments (**Chapters 4** and **5**). This dissertation provides new information about the drivers of environmental harshness and their ecological consequences on TDF diversity and functioning (**Chapters 2-5**), with clear implications for a comprehensive management of the most threatened ecosystem in Colombia (**Chapter 6**).

The complexity of environmental harshness driving plant community attributes in TDF

Rainfall seasonality determines plant community attributes of TDF, where variations in frequency, intensity, or length of drought conditions are commonly suggested as the most substantial controllers of environment harshness for this ecosystem (Murphy & Lugo 1986; Allen *et al.* 2015, 2017a; Dexter *et al.* 2018). Multiple studies have shown how differences in drought conditions drive species turnover (Muenchow *et al.* 2013; Neves *et al.* 2015), species diversity and forest structure (Gillespie *et al.* 2000; Marcelo-Peña *et al.* 2007; Pineda-García *et al.* 2007), and trait community composition (Fauset *et al.* 2012; Ouédraogo *et al.* 2016; Álvarez-Dávila *et al.* 2017; Aguirre-Gutiérrez *et al.* 2019). However, TDF have important variations in other environmental conditions such as temperature, isothermality, solar radiation, soil fertility, and even in land-cover transformation (Portillo-Quintero & Sánchez-Azofeifa 2010; Peña-Claros *et al.* 2012; Muenchow *et al.* 2013; Neves *et al.* 2015). This motivated us to evaluate how these multiple environmental conditions may also be responsible for 'environmental harshness' and its role in shaping plant community attributes in TDF.

We found that TDF in Colombian are widely distributed across six biogeographical regions with contrasting climatic, soil, and land-transformation conditions. For instance, forests in the Inter Andean valleys have two dry periods per year (3-4 continuous dry months twice a year), where precipitation in each dry period reaches between 178 and 191 mm, while Caribbean forests only experience one dry period (5-8 dry months) where total seasonal precipitations reach 69 mm on average. In addition, Inter Andean valley forests are not exposed to high temperatures like Caribbean forests or to low soil water retention as Orinoquía forests. Nevertheless, all six regions showed fragments highly irregular in shape and comprising mostly early and intermediate successional stages, with some mature forest concentrated in the Caribbean region (see details in **Chapter 2**). These results not only show the high environmental heterogeneity of Colombian TDF but also reinforce the idea that the attributes of plant communities may be determined by the interaction of multiple environmental conditions (Peña-Claros *et al.* 2012; Muenchow *et al.* 2013; Neves *et al.* 2015; Ouédraogo *et al.* 2016). The results of **Chapters 2-4**, show how the combined effects of these factors exert important controls on TDF plant community attributes (e.g., species turnover and diversity, forest structure and trait community composition), demonstrating that environmental harshness in this ecosystem is more complex than just rainfall seasonality claimed for several studies (Dexter *et al.* 2015, 2018).

In particular, we found strong climatic and soil control on floristic turnover among (dissimilarity >80%) and within regions (between 67% and 88%) (**Chapter 2**). Floristic composition in the Caribbean region was characteristic of forests with more arid conditions and prolonged droughts, with coastal marine influence, where the most common species are predominantly fast deciduous (e.g., *Piptadenia* spp. and *Pithecellobium roseum*), mesomorphic water-storing (e.g., *Pereskia guamacho*) and 'bombacoids' (e.g., *Pachira quinata*), with water-stress avoidance strategies for long and hot drought seasons (Rangel-Ch *et al.* 1997; Rojas-P. & León-H. 2020), or adapted to tolerate saline conditions (e.g., *Caesalpinia coriaria*; IRENA 1992). In contrast, Inter Andean valley forests floristic composition changed along more fertile soil gradients and were exposed to moister conditions, with a bimodal drought regime, when compared to Caribbean forests. In this region, we found local-dominances and unique species that were restricted to these particular environmental conditions (e.g., *Trichilia carinata, Trichilia oligofoliolata*; Villanueva Tamayo *et al.* 2015), but also common generalist species (e.g., *Casearia sylvestris*, *Croton* spp. *Cecropia, Leucaena leucocephala, Zanthoxylum fagara*) that were favored by the predominance of secondary forests in the landscape (García *et al.* 2014). Finally, in the Orinoquía region, species turnover was determined by high temperatures, and sandy and infertile soils that result from nutrient leaching induced by high annual precipitations. Across this region, the most common species (e.g., *Spondias mombin, Vitex orinocensis*) are associated with riparian habitats and have adaptations for water dispersal (Duvall 2006), but also to have sclerophylly due to infertile soil (Amaya 2014; Cabrera-Amaya & Rivera-Díaz 2016). Several environmental harshness factors were driving species diversity and forests structure. We found that increases in climate severity (*i.e.*, high aridity, solar radiation, wind speed, and temperature, but low precipitation) and greater land-cover transformation (*i.e.*, narrow forests with low area, and location in a highly transformed landscape) had synergic effects that reduced species richness and diversity, basal area, and canopy height (**Chapter 3**). Interestingly, the plant community attributes for legumes and deciduous species did not change along those gradients (discussed below), with the exception of diversity for deciduous species (**Chapter 3**). Several studies have shown that soils with a low water supply and high temperatures may limit the persistence of tall tree species that demand water for supporting their size, but low nutrient availability can also limit growth and impair osmotic regulation (Sperry 1995; Ryan & Yoder 1997; Tao *et al.* 2016), which could explain why basal area and canopy height decreased in arid environments. In addition, the influence of land-cover transformation on species diversity, basal area, and canopy height may be the result of an increase in temperature, wind exposure, and solar radiation due to increases in forest edge effects and forest isolation that affected species with low mechanical resistance (van Bloem *et al.* 2006) or low tolerance to water-stress (Sperry 1995).

Two main conclusions were derived from these results. First, we identified the need that future studies in TDF take an 'environmental harshness' approach to comprehensively understand processes underlying changes in plant community attributes. Second, we showed the importance of including land-cover transformation, which we found was one of the most important drivers shaping the composition, structure, and functioning of forests given the broad and global human degradation of ecosystems (Lindborg & Eriksson 2004; Stein *et al.* 2014; Baynes *et al.* 2016).

Functional traits strategies of TDF tree species

It has widely suggested that TDF tree species are adapted to cope with environmental harshness, particularly to drought conditions, via multiple functional strategies (Markesteijn *et al.* 2011a; Méndez-Alonzo *et al.* 2012; Pineda-García *et al.* 2015). However, different studies have also shown that TDF species may be at their limits of drought tolerance (Choat et al. 2012; Allen *et al.* 2015, 2017), and therefore, it is a priority to explore the mechanisms underlying species drought responses. Additionally, as we previously discussed, species not only respond to drought but also to soil conditions and land cover change. Thus, another motivation of this study was also to relate the functional strategies of TDF tree species in response to environmental harshness, and identify the mechanisms responsible for changes in plant community attributes across gradients.

Overall, we found that dominant TDF tree species are characterized by having traits with high investment in tissues (*i.e.*, dense leaves and wood; see **Chapter 5**) but to have a broad range of traits along the hydraulic safety-efficiency trade off. We found species with the expected hydraulically-safe and costly tissues (i.e., *Aspidosperma*, *Cynophalla*, *Eugenia*, *Trichilia*), but, interestingly and contrary to general expectation, we also found species with hydraulically-efficient and costly tissues (e.g., *Astronium graveolens*, *Platymiscium pinnatum*, *Lonchocarpus* spp. and *Machaerium* spp.). This last finding contrasts with studies suggesting that species having high hydraulic-efficiency, commonly associated with deciduous leaf habits and high cavitation risk under water constraints, have consequently low investment in tissues due to their low leaf lifespan and high nutrient concentration which enable them to maximize growth rates in their reduced growing season (Brodribb *et al.* 2010; Markesteijn *et al.* 2011a, b; Méndez-Alonzo *et al.* 2012). Thus, one of the main finding of this dissertation was the finding that species with hydraulically efficient vessel and dense tissues (in leaves and woods) are dominant, highlighting the importance of 'costly' tissues in response to harshness conditions in TDF. Costly tissue investments, such as high wood density and thick fiber walls prevent cell collapse caused by negative xylem potentials (Salleo & Nakdini 2000; Hacke *et al.* 2001a), but can also increase mechanical resistance to external forces such as strong winds (Chave *et al.* 2009; Beeckman 2016; Díaz *et al.* 2016), while small, dense and rigid leaves have can have lower wilting risks (Niinemets 2001; Poorter *et al.* 2009). Additionally, this result may help understand why under increasing harsh conditions, species richness and basal area of legumes and deciduous species did not decrease in our forests (**Chapter 3**). Legumes, having denser leaves with smaller surfaces (see Powers & Tiffin 2010), reduce their wilting risks and transpiration surface under water limitations (Niinemets 2001), which in combination with their resource acquisition abilities (nitrogen-fixing bacteria, Sprent 2009; Adams *et al.* 2016) can maintain a high photosynthetic capacity under harsher conditions. On the other hand, deciduous (non-legume) species, that make costly investments in their tissues may benefit from higher protection against herbivores during the rainy seasons (Turner 1994; Cunningham *et al.* 1999), reduce cavitation risk during unexpected droughts that can occur during the growing season (Powers & Tiffin 2010; Lopezaraiza-Mikel *et al.* 2013) and retard leaf shedding during the onset of the dry seasons, increasing the carbon gain window.

However, we also found that about half of the TDF tree species have trait combinations differing from the dominant functional strategies (**Chapter 5**). This result highlight that plants have evolved different strategies to cope with harsh conditions. For instance, a group of species with intermediate dominance, were characterized by a high hydraulic efficiency, low investments in tissues, a high content of water at maximal capacity and predominance of deciduous leaf habits (e.g., *Cavanillesia platanifolia*, *Bursera simaruba*, *Pachira quinate*, *Pseudobombax septenatum*). These species are known as resource acquisitive but fugaciously deciduous, or water storage species (Méndez-Alonzo *et al.* 2012). Another group of species, evergreen with low dominance, made low investments in leaf tissues but had intermediate hydraulic safety-efficiency (e.g., *Croton punctatus*, *Guazuma ulmifolia*, *Jatropha gossypiifolia* and *Aralia excelsa*), which may be associated with pioneer ecological guilds (Markesteijn *et al.* 2011a). Our results are also in agreement with the idea that some trait combinations would be non-viable or would be related to very poor performance in TDF (Méndez-Alonzo *et al.* 2012; Gleason *et al.* 2016). For instance, species with low tissue investments and high hydraulic safety such as *Tabernaemontana* spp (**Chapter 5**) showed the lowest dominance.

Overall, these results suggest that there are multiple trait combinations that may emerge as alternative responses to environmental harshness in TDF, and that interspecific variations may blur functional community patterns along environmental gradients. In agreement with this idea, the weak relationships found between traits and environment when analyses were performed at community-weighted level (CWM, **Chapter 4**) can be related explained by species differing in their functional trait combinations in response to environmental harshness. Specifically, we demonstrated that using CWM trait failed to detect relationships in about 96.9% of 464 models evaluating the effects of climate, soils and land-cover transformation on 15 functional traits (**Chapter 4**). Additionally, we found that communities account for the lowest fraction of explained variance for the studied traits (9.6±9.2%), with the exception of specific leaf area that reached 35.7%. Our results highlight the importance of improving sampling design to gain a comprehensive understanding of the ecological mechanisms that drive plant community attributes and functioning of tropical forests (Baraloto *et al.* 2010b; Carmona *et al.* 2015), and suggest that new studies should (i) sample traits of both dominant and 'rare' species, and (ii) make important efforts to take into account trait variability within and among communities, for an adequate trait characterization. As an important methodological contribution of this dissertation, we proposed a new trait sampling scheme based on the species abundance-weighted efforts (see details in **Chapter 4**).

Explaining biomass changes in TDF through functional traits and environment

The interaction between functional traits and environmental conditions play an important role in determining the functioning of tropical forests (Brown & Lugo 1982; Ruiz-Jaen & Potvin 2010; Poorter *et al.* 2015). For instance, both traits and environment have effects on biomass productivity (Finegan *et al.* 2015b; Poorter *et al.* 2017), and it has been suggested that environments with favorable conditions (*e.g.*, high light intensity, water supply and soil nutrient availability) favor species with 'acquisitive' resource use strategies (*e.g.*, high hydraulic efficiency, and high specific leaf area, among others), with fast growth but also high mortality rates, which in turn have high biomass stands (Poorter *et al.* 2008, 2010, 2017; Finegan *et al.* 2015b). This generalization is not necessary true for ecosystems with harsh environmental conditions, where plants may display contrasting ecological strategies to overcome environmental limitations (Marks & Lechowicz 2006; Méndez-Alonzo *et al.* 2012). It is the case of TDF, where high standing biomass and growth have been associated with the dominance of acquisitive species (*i.e.*, large canopy height and low wood density; Conti & Díaz 2013) or species with conservative traits (e.g., low specific leaf area, high wood density) (Prado-Junior *et al.* 2016). In this sense, we explore the functional mechanisms behind biomass demographic rates in TDF, and the effects of environmental harshness on net biomass productivity for this ecosystem.

Biomass demographic changes (i.e., survival, mortality and recruitment) were strongly determined by traits related to the hydraulic safety-efficiency trade-off and by investment in tissues (**Chapter 5**). We found that the growth of surviving trees after a strong drought, caused by el Niño 2015 event, was stronger in trees that were already dominant before the drought, supporting the hypothesis that dominant trait combinations would perform better under particularly harsh conditions. Tree recruitment occurred in species with a broad range of traits related to the hydraulic safety-efficiency trade-off that had "costly" tissues, but also in species with "cheap" tissues that were nor dominant before the drought. Unexpectedly, however, tree mortality was widespread and affected species that invest in costly tissues (**Chapter 5**). Net biomass balances following el Niño showed that the most negative balances were associated to species that produced cheap tissues. More importantly, negative net balances of biomass were more widespread in the functional space than positive net balances.

These findings confirmed that positive biomass changes in TDF are strongly determined dense tissues (Prado-Junior *et al.* 2016), where high investments is one of the most critical mechanisms to cope with water-constraints in this ecosystem. However, the results also revealed the high sensitivity of TDF to future drier climatic scenarios (Allen *et al.* 2015, 2017a). Extreme droughts, such as that TDF experienced during the 2015 el Niño, can cause widespread mortality and significantly reduce the biomass gain of species (Condit *et al.* 1996; Slik 2004; Allen *et al.* 2010; Maza-Villalobos *et al.* 2013). In our forests, the predominance of species with 'costly tissues' driving biomass productivity may even be at a disadvantage under drier scenarios. Investment in costly tissues is energetically expensive and require long payback times (Chave *et al.* 2009; Osnas *et al.* 2013) and an increase in the frequency and intensity of extreme droughts can play against species with these traits. Changes in these climatic conditions may cause significant reductions in aboveground biomass stock in forests (Venturas *et al.* 2016; Powers *et al.* 2020) and accelerate the risk of extinctions and permanent changes of this ecosystem in the next 50 years (Rowland *et al.* 2019).

Ecological knowledge for decision-makers

Fifteen years ago, Sánchez-Azofeifa *et al.* (2005) called the attention of the need for including human transformation in ecological studies of TDF. Their publications highlighted the existence of widespread efforts to generate information for a comprehensive management of TDF, which are ecosystems that are restricted to a few sites worldwide in comparison with other tropical ecosystems (Sánchez-Azofeifa *et al.* 2005a, b). The most important priorities identified by authors were: i) integrate land-cover transformation and climatic change as the main drivers of TDF future, ii) improve the ecological approaches for understanding responses to the drivers of transformation of these ecosystems, and, iii) to communicate the level of threat and ecological significance of this ecosystem to decision-makers. In Colombia, TDF underpin the wellbeing of many rural populations, but have suffered intensive land-cover transformation which, in combination to the intensification of drier conditions, can trigger cascading effects that could lead to desertification and affect food security (Norden *et al.* 2020). However, the interest of researcher to support conservation actions in Colombian TDF only became relevant in 2013 (Pizano *et al.* 2017), while one of the most important challenge has been to translate the research findings to a flexible language for decision makers.

In this sense, each chapter of this thesis had the purpose of filling gaps in our knowledge of TDF and to be the base for an infographic offprint for decision-makers, indicating the importance of scientific knowledge for the conservation of TDF and to take informed management decisions. In 2016 we made a report on the distribution and conservation status of this ecosystem in Colombia (**Chapter 6** – Infographic offprint 1). This offprint was the first extensive fieldwork sampling effort for this ecosystem, where the recorded information revealed its current extent across six important regions of the country, and its degradation derived from human infrastructure, cattle ranches, agriculture, and others anthropogenic pressures. This information is currently included in the list of ecosystems that are a conservation priority in the Environmental Ministry of Colombia, and guides mining moratorium in this ecosystem. In 2017 we published in the national biodiversity report our 1-ha permanent plots network for monitoring TDF (**Chapter 6** – Infographic offprint 2), highlighting the importance of long-term monitoring strategies that will evaluate the response on TDF to future climatic change. Currently, this information is part of the socio-ecological monitoring platform for the comprehensive management of TDF in Colombia (Norden *et al.* 2020), and it has been included in the monitoring programs for National and Regional Parks, and the Biodiversity Information System of Colombia. Additionally, we reported the status of knowledge of functional diversity in Colombian forests and the trait sampling effort (**Chapter 6** – Infographic offprint 3, 2017), where we emphasizing in the importance of plant functional traits to evaluate the responses of forests to future climatic change scenarios, and the direction for its adaptive conservation. That infographic offprints not only had the purpose of communicating the current ecological knowledge on TDF in Colombia, but also to inform decision-makers about the significance of conserving this ecosystem for the country.

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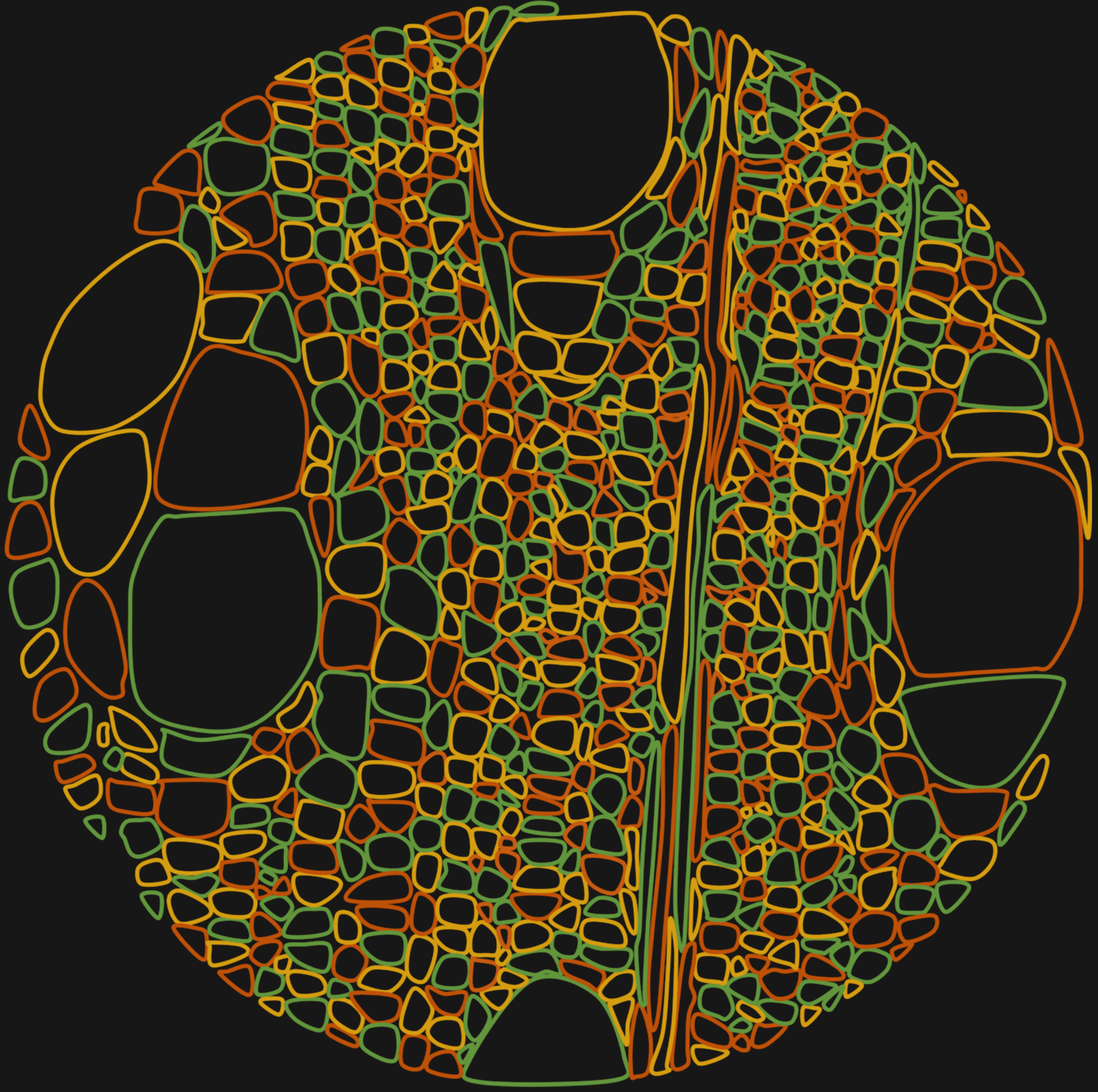

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