FUNCTIONAL ANALYSIS OF SECONDARY TROPICAL DRY FORESTS IN A REGION OF THE COLOMBIAN CARIBBEAN

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ABSTRACT

Secondary tropical forests are increasingly recognized for their role conserving biodiversity in agricultural landscapes and this role is especially important for seasonally dry tropical forests (SDTF), one of the most threatened tropical forested ecosystems. The conservation value of secondary forest is increased by its capacity to maintain ecosystem properties and provide services to humans; which has been hypothesized to have positive links to the species and functional diversity of ecosystems. However very little information is available on the occurrence of this relationship in secondary forests. This dissertation makes an important contribution to the ecological knowledge of secondary SDTF and describes changes in plant species and functional diversity by using a stratified design considering different successional stages along an environmental gradient in a region of the Caribbean coast of Colombia and a multi-trait approach to study functional diversity at three scales: species, communities and landscape.

The analysis of the variation in functional traits of SDTF trees at the species level allowed me to support the hypothesis of coordination between leaves and stem traits. Three dimensions of correlated variation were identified: the first related to leaf and stem economy, the second to leaf thickness and organization and the third to the trade-offs between leaf size, stem density and bark thickness. Secondary forests showed high species turnover during succession and increasing diversity from early to late forests. Species composition similarity was higher among late successional forest than early and intermediate stage forests, showing that environmental characteristics are influencing successional trajectories. Frequency distributions of species in the three successional stages showed evidence of functional trait similarity among species and underlined the importance of changes in species abundances determining functional composition during succession. A shift in abundance from individuals with traits that favour survival after disturbance to individuals with denser stems and a more conservative resource use profile was observed from early to late stages of succession. Functional composition was also strongly influenced by environmental variables, especially leaf traits, and a shift of traits from acquisitive to conservative type species was observed with increasing nutrient content and flooding, proxies of water availability.

Assessment of ecosystem services was conducted using two independent approaches: semi-structured interviews and field data. A high richness of useful woody plants was recorded and the provision of services was related to a high variability in functional traits among species. The provision of the ecosystem services determined by the presence and abundance of useful species showed significant differences between stages. The relationships observed between ecosystem sevices and functional and species diversity indices were not consistent. In contrast species richess showed significant negative relationships at the plot level with most of the ecosystem services assessed, showing a trade-off among the conservation of species richness and the maintenance of service provision. Overall, this research provides novel insights into the dynamic relationships between biodiversity, ecosystem function and ecosystem services in this globally important, but under-researched forest type.

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LIST OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

AUTHOR'S DECLARATION

I confirm that the work presented in this thesis is my own work. The work is original and no part of the dissertation has been submitted for any other degree or examination in any other university.

CHAPTER 1 INTRODUCTION

Secondary tropical forests have increasingly been recognized for their important role in the conservation of biodiversity (Chazdon et al. 2009; Dent and Wright 2009). This recognition has been influenced by evidence of a recent increase in the area of secondary forests in some regions of the tropics by a process of forest recovery (Wright and Muller-Landau 2006; Aide et al. 2013), as well as the limited success of conservation initiatives that have focused only on protected areas (Laurance et al. 2012). The fact that secondary forests are usually surrounded by agricultural land use increases the conservation value of modified landscapes, which have been shown to conserve a high diversity of populations and functions, especially when spatial heterogeneity is increased (Gordon et al. 2004; Harvey et al. 2006; Chazdon et al. 2011). In this context, the protection of secondary forests as part of the sustainable management of modified landscapes is a promising approach for the conservation of tropical biodiversity, especially for forest types that have been subject to considerable reductions of their original area.

1.1 SEASONALLY DRY TROPICAL FORESTS

Seasonally dry tropical forests (SDTF) occur in lowland regions where the rainfall is less than c. 1600 mm year^{-1}, with a period of at least 4–6 months receiving less than 100 mm (Gentry 1995, Dirzo et al. 2011a). SDTF are widely distributed in the Neotropics but most of their remaining area is composed of fragments of small size (Miles et al. 2006). Globally it is estimated that 48.5% of its original area has been transformed and only 7.6% is protected (Hoekstra et al. 2005). Like other tropical forest types, SDTF have also shown signs of recovery especially in the neotropics (Arroyo-Mora et al. 2005). However, high deforestation rates are still observed in many regions and secondary forests have also been widely subjected to forest degradation processes instead of forest recovery (Rey-Benayas et al. 2011; Kolb and Galicia 2012; Bianchi and Haig 2013).

A number of important contributions have been made to the knowledge of the biodiversity and ecology of SDTF in recent decades (Stoner and Sánchez-Azofeifa 2009; Dirzo et al. 2011b). SDTF have shown high regional and local floristic diversity, as well as high species turnover (Gentry 1995; Linares-Palomino et al. 2011), which are strongly influenced by water availability (Trejo and Dirzo 2002; Espinosa et al. 2011). SDTF have also shown high natural regeneration ability, with secondary forests achieving similar structural characteristics and biomass to conserved forests in less than four decades following disturbance (Lebrija-Trejos et al. 2008; Becknell et al. 2012). However, floristic

composition takes much longer to recover and varies considerably in relation to management (Griscom and Ashton 2011). This high variability has supported the need to consider succession as a multi-directional process, influenced by management as well as environmental factors, and to describe it based on the functional attributes of species (Chazdon et al. 2007; Quesada et al. 2009). It has also highlighted the importance of studying this ecosystem throughout its natural range, especially in poorly researched regions (Sánchez-Azofeifa et al. 2005).

1.2 FUNCTIONAL DIVERSITY AND COMMUNITY ASSEMBLY

Functional diversity is an attribute of ecosystems that can be more informative in ecological terms than species diversity, to understand the factors that determine plant community assembly (Weiher et al. 1998; Kraft et al. 2008). Taxonomic classifications are based on a set of the morphological attributes that characterize plant species, however their link with species performance and relationship to the environment is not easily determined. In addition, other sets of attributes have been suggested for classifying species, focusing on their performance under natural conditions, strategy of resource use, response to disturbance and effects on the ecosystem (Grime 1977; Díaz and Cabido 1997). The functional identity of a plant species is characterized by the set of morphological, physiological and reproductive attributes that determine plant functions and underpin their adaptations to the environment (Noble and Slatyer 1980; Lavorel et al. 2007). The study of these attributes has gained considerable attention and there is now information available on a wide set of functional traits and species (Kattge et al. 2011). Global scale studies of these traits have shown that common patterns of variation can be found among species (Díaz et al. 2004; Wright et al. 2004; Chave et al. 2009) and there is now great interest in describing these patterns at the community level and identifying the external factors that influence them (Wright et al. 2005; McGill et al. 2006).

In principle, species from a regional pool successfully establish in areas where they can overcome biological and abiotic constraints. Biological constraints refer to the effects of biological interactions limiting species co-occurrence, in such a way that functionally similar species can co-occur until limiting resource increase inter-specific competition (Macarthur and Levins 1967). Functionally dissimilar species can co-occur by exploiting resources in different ways (Silvertown 2004). Abiotic constraints refer to the environmental characteristics of a site that limit species presence at different scales, from climatic to habitat variables (Díaz et al. 1998; Bello et al. 2013). The integrated effect of these factors is hypothesized to determine the range and abundance of functional traits found in a

19

community and has been referred to as assembly rules (Wilson 1999; Luzuriaga et al. 2012). The studies that have tested the strength of these rules try to detect non-random patterns of trait distribution, where higher variation than expected of coexisting species traits is interpreted as limiting similarity, whereas higher convergence of traits is interpreted as habitat filtering (Kraft et al. 2008; Cornwell and Ackerly 2009; Pillar et al. 2009). However, in natural communities where the number of factors that can be controlled is limited, the distinction between the effects of biotic or abiotic filters has been difficult to achieve (Götzenberger et al. 2012).

In species-rich communities such as tropical forests, testing assembly rules is a challenging task. An alternative approach to study the factors that influence community assembly is to analyse the associations between functional traits at the community level and environmental and management variables (Dray and Legendre 2008; Kleyer et al. 2012). The underlying mechanisms determining these distribution patterns relate to the strategies of species to deal with limiting resources and to respond to changes in the environment. Studies dealing with this question have found strong associations between functional traits of species and environmental and management characteristics (Swenson and Enquist 2009; Lebrija-Trejos et al. 2010; Kröber et al. 2012), although these have generally been considered independently. The risk of confounding factors in this type of analysis is high, as management regimes also alter environment conditions (Lebrija-Trejos et al. 2011). Studies that consider different factors concurrently are therefore needed, especially in natural communities (Campetella et al. 2011). However, the same importance that is given to the factors studied must be given to the selection of traits, which should represent the functional variation of the regional species pool and reflect differences in species performance in the ecosystem of study (Violle et al. 2007).

1.3 SHADE AND DROUGHT TOLERANCE IN TROPICAL TREES

For tropical trees, the most important factors determining plant functional variation have been recognized as the vertical and horizontal availability of water and light (Denslow 1987; Holbrook et al. 1995; Poorter 2005). Variation in these resources has partially explained temporal and spatial patterns of species distributions and has allowed the recognition of groups of species that present similar functional responses to the environment (Comita and Engelbrecht 2009; Maharjan et al. 2011). Light variation in natural tropical forest is determined by the vertical structure of trees and the dynamic of gaps created by tree falls and small-scale disturbances (Chazdon and Fetcher 1984; Canham et al. 1990; Montgomery and Chazdon 2001). In addition, leaf phenology can play an important role in determining light

levels, especially in SDTF where a high percentage of trees in the canopy are deciduous during the dry season (Lebrija-Trejos et al. 2011). Traditionally, tropical trees were classified as pioneer and non-pioneer species according to their light requirements for establishment and position in the forest canopy (Bazzaz and Pickett 1980; Swaine and Whitmore 1988). However, analysis of functional traits at the whole plant level have found that plant variation in relation to light is better described as a continuum of shade tolerance determined by a trade-off between traits that allow rapid growth under high light availability conditions, such as low wood density, long –lived leaves and high specific leaf area, and traits that reduce mortality under low light availability especially at the seedling stage (Popma and Bongers 1988; Poorter and Bongers 2006; Wright et al. 2010).

In contrast, local variation in water availability has been related to soil and topographic characteristics and annual variation in precipitation (Becker et al. 1988; Markesteijn et al. 2010). Classification of species in terms of their drought tolerance has not received as much attention as shade tolerance until relatively recently (Holbrook et al. 1995). However, drought has also been shown to be a determining factor of tree species distribution and trait variation, especially in SDTF (Condit et al. 1996; Poorter and Markesteijn 2008; Balvanera et al. 2011). Two mechanisms by which species can cope with water scarcity have been identified: desiccation tolerance and avoidance (Ackerly et al. 2002; Engelbrecht and Kursar 2003). The ability of tropical trees to use these mechanisms has been shown recently to relate to the trade-off between traits that allow plants to reduce water loss or increase water uptake, such as deep roots, water stem storage and leaf shading, and traits that reduce their risk of stem embolism during the dry season (Pineda-García et al. 2013).

Research integrating the combined response of plants to light and water has not been commonly conducted and there is no clear understanding of whether adaptations between these factors generate trade-offs (Smith and Huston 1989; Markesteijn and Poorter 2009). Identifying the dimension of plant trait variation among coexisting species can provide evidence of these trades-offs and reflect different strategies of resource use (Westoby and Wright 2006). For example, in a study of dry forest in Argentina, Easdale et al. (2007) found that species could be differentiated in a multidimensional space of three axes independent of each other: shade tolerance, population turnover and ability to colonize harsh environments, in declining order of importance. In SDTF, recent evidence suggests that plants have a coordinated adaptation to availability of light and water and that trait adaptation can be better explained along a continuum from plants with an acquisitive use of resource to a conservative strategy (Markesteijn et al. 2011; Sterck et al. 2011). Additional local-scale

studies are required to test this resource strategy model and its implications for the community dynamics of this ecosystem.

1.4 BIODIVERSITY AND ECOSYSTEM SERVICES

The negative impacts of human activities on biological diversity are well documented (Dirzo and Raven 2003; MEA 2005), especially in the tropics, which sustain two-thirds of the species on the planet (Pimm and Raven 2000). The view that these negative effects also affect human well-being was not initially considered explicitly. However, increasing evidence has shown that biodiversity has a strong effect on ecosystem functions and it relates directly to several of the benefits that people rely on (Díaz et al. 2006; Cardinale et al. 2012). This finding, together with the high rates of species loss associated with current rates of forest transformation and degradation (Pimm et al. 1995), have motivated questions in relation to the number and identity of the species that are most important to conserve (Naeem et al. 2002).

Biodiversity has many components, and it is still unclear whether genes, species or functional types have the strongest effects on ecosystem function. Studies in controlled and natural environments have shown positive effects of species richness on some ecosystem functions (Balvanera et al. 2006), especially productivity. However, the mechanisms explaining this link are not completely understood, and other components including phylogenetic and functional diversity are starting to be considered to explain the richness effect on ecosystem functions (Flynn et al. 2011). The inclusion of plant functional traits in the assessment of ecosystem functions and services at a landscape scale has been shown to be a promising approach, and a common conceptual framework has been developed (Díaz et al. 2007; Lavorel et al. 2011). In this context, functional diversity has been hypothesized to influence ecosystem function by two mechanisms: a higher complementarity in resource use with higher species richness, or by differences in the functional identity of dominant species that have a determining effect on functions (Hooper and Vitousek 1998; Lavorel and Garnier 2002). The importance of each mechanism has been shown to be dependent on the system under study, although few non-manipulative studies have been undertaken, especially in species rich natural communities (Mokany et al. 2008; Roscher et al. 2012). Environmental variables and disturbance can also influence the relationship between species, functional diversity and ecosystem functions, but studies that consider this effect are lacking in the literature (Mayfield et al. 2010; Sutton-Grier et al. 2011).

Ecosystem functions, including processes and structure, that are used by people are considered as ecosystem services (ES) and benefits (Lamarque et al. 2011). This recognition has made it possible to identify the possible contributions of natural or modified ecosystems to human well-being (Ehrlich and Ehrlich 1992). The assessment of ecosystem services, whether in monetary or non-monetary terms, is necessary to identify the pressures acting on these services and the users that will potentially be affected by changes in their provision due to different management actions (Busch et al. 2012). The biological scale at which this information is recorded varies depending on the type of ES measured and their area of influence. Plant communities are often the main unit of assessment, as they integrate different ecological processes and properties that have been successfully linked to several services. For example community-aggregated traits associated with the leaf economics spectrum have been related to forage availability and litter accumulation in alpine grasslands (Quétier et al. 2007). Spatial scales also influence the assessment of ES. Local scales facilitate the collection of information and analysis but are not usually the scale at which management action takes place. Landscape-scale analyses on the other hand allow consideration of several ecosystem services and trade-offs among them, which can help direct regional management actions (Bennett et al. 2009; Newton et al. 2012).

1.5 THESIS OVERVIEW

The main objective of this research was to determine the relationship between anthropogenic disturbance and environmental variables on species and plant functional diversity of secondary tropical dry forests and their potential effects on the provision of ecosystem services. In this research, such impacts were examined by using a stratified design considering different successional stages along an environmental gradient and a multi-trait approach to study functional diversity at three scales: species, communities and landscape.

The following questions will be addressed:

- Does variation in plant traits at the species level support coordinated tolerance of trees to both shade and drought?
- Do environmental factors influence species composition during successional trajectories in a SDTF landscape?
- Do changes in functional composition of SDTF reflect changes in species composition in relation to the successional process and environmental gradients?
- How does functional diversity relate to the provision of ecosystem services of secondary forests differing in successional stage?

These questions were addressed in the following chapters, ordered in increasing scales of analysis from traits at the species level to variation in species and functional composition at the community level. In chapter 2, I present an analysis of the variability of plant functional traits in a large set of tropical dry forest species. Previous studies have underlined the importance of trade-offs between functional traits as the main drivers of diversification of plant strategies. Major dimensions of trait variation were identified and used to validate the hypothesis that traits that have been related to both light and drought tolerance in tropical trees were correlated in a community of SDTF. In addition, I evaluated the adequacy of different functional classifications in accounting for the observed variation, and their potential use to simplify plant communities in this ecosystem.

In chapter 3, I describe changes in plant community composition and structure during SDTF recovery and determine values of alpha and beta diversity in the region. I conducted this analysis to test whether environmental variables or differences in successional stages better explained the variation in species composition at the landscape scale. My hypothesis was that in areas subject to similar management, local environmental heterogeneity could result in different routes towards late successional communities, particularly when high regional species richness is present

Chapter 4 deals with the relationship between functional composition of secondary forests and successional and environmental gradients. Considering the importance of water availability in this ecosystem, I hypothesized that different sets of traits were related to each gradient considered, and that environmental conditions would have a stronger filtering effect on plant traits than successional stage. This approach also allowed me to assess functional regeneration patterns of highly diverse ecosystems and their relation to species diversity.

Chapter 5 explores the relationship between species diversity and functional diversity in the provision of ecosystem services of secondary forest differing in successional stages. Previous studies analysing this link have focused on field data measures that do not take into account cultural services and user preferences. For this purpose, I used two different assessment methods that focused independently on the services provided by the woody species and the plant community. I hypothesized that higher plant functional diversity is positively related to the provision of ecosystem services, following the assumption that niche complementarity among species increases efficiency of resource use. I also hypothesized that ecosystem services that have been previously related to plant traits would be provided differentially by plant functional groups, whereas cultural services that are not expected to relate to a particular functional profile would be evenly provided among them.

24

1.6 STUDY AREA

The biological, environmental and social information used in this dissertation was collected in the lowlands of the Caribbean region at the north of Colombia. The Colombian Caribbean was originally covered by seasonally dry tropical forests (SDTF) but at present only a few fragments of this ecosystem remain. Most of the territory has been transformed for livestock grazing and now the region presents the highest risk of desertification in the country, a situation that not only threatens biodiversity but also human populations, food security and housing.

The study area is located geographically in the region of influence of the Totumo swamp, a marine lagoon that is watered by the permanent and temporal creeks of the surrounding area (Fig 1.1). This heterogeneous landscape of nearly 300 km^2 encompasses three of the most important fragments of seasonally dry tropical forest identified in the Atlántico and Bolívar departments. These fragments correspond to late secondary SDTF that were allowed to recover and are found in private farms currently managed for livestock pastures and annual crops. The sites selected for this study encompass the forest fragments and the neighbouring areas, providing secondary forest of different successional stages that result from similar management regimes.

At present, as a result of the collaborative work between the local environmental authorities and NGOs, two of the sites have been declared as regional protected areas and one is in the process of being declared as such. During the planning process associated with the declaration of the three sites, local actors have been involved in conservation initiatives and detailed biological and socio-economic information has been produced as well. Given these conditions, the region represents a great opportunity to develop management plans that meet both biodiversity conservation goals and the interests of local people, addressing processes and threats at a landscape-scale. To achieve this aim, ecological information at different scales, from plant species to ecosystem processes, is required and the results of this project are expected to fill some of these gaps.
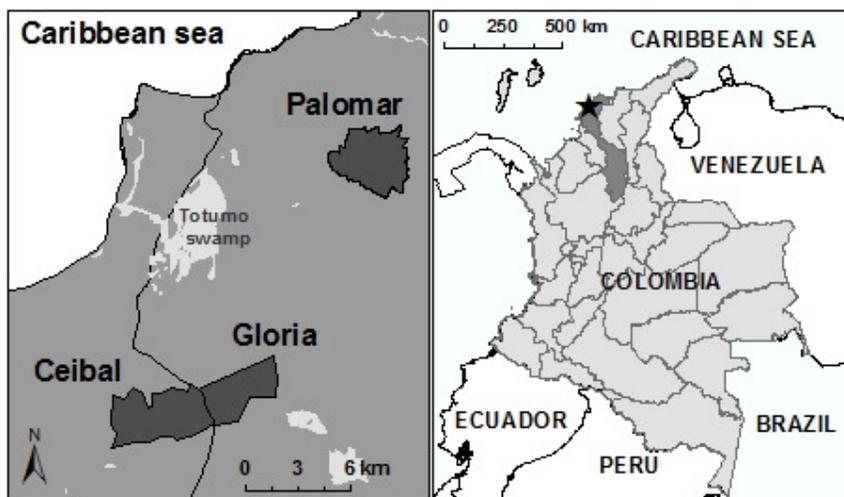
Figure 1.1. Location of the study sites in the Caribbean region, north of Colombia

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CHAPTER 2 TRAIT VARIATION AND PLANT FUNCTIONAL TYPES IN 113 WOODY SPECIES OF A SEASONALLY DRY TROPICAL FOREST

2.1 ABSTRACT

Tropical forest plants present a high variation in functional traits that reflect different adaptations to the environment. In seasonally dry tropical forest (SDTF) plant trait variation has been related to light and water availability and a coordinated tolerance of plants to shortage of both resources has been proposed. In this study I tested this hypothesis by analysing the relationship between eleven leaf and stem functional plant traits related to shade and drought tolerance in a set of 113 species. In addition, the use of different types of functional classifications to describe plant trait variation was evaluated. Plant trait variation was high and for most of the traits it was explained to a great extent by differences between species. A principal component analysis showed that traits that confer shade and drought tolerance were correlated and three axes of variation were identified. The first axis described leaf and stem economy, the second was related to leaf thickness and organization and the third was related to the trade-offs between leaf size, stem density and bark thickness. Stem density was correlated strongly with several plant traits, emphasizing its key role in explaining variation in life history strategies of SDTF species. Significant differences were found between functional groups categorized by phylogenetic group and leaf phenology although high overlap was observed in the ordination space, whereas for life forms differences were only observed for palms and woody grasses. Classification by cluster analysis identified ten functional groups that described better the variation in plant traits although its use in other plant communities is limited by the low stability of some groups.

2.2 INTRODUCTION

The classification of plant species in relation to their morphological and life-history characteristics has been a keystone for the development of plant ecology. The use of plant functional types has allowed simplification of the analysis of species distribution in relation to environmental and management characteristics (Chazdon et al. 2010; Laliberté et al. 2010; Enquist and Enquist 2011), the relationship between plant functional diversity and ecosystem functioning (Díaz and Cabido 1997; Wardle et al. 2000; Ward et al. 2009; Finn et al. 2013)

and the response of ecosystems to global change (Fry et al. 2013). Particularly, the use of plant functional traits has been shown to be a promising approach to group species with similar response to the environment or effect on the ecosystem (Lavorel et al. 2007). The main assumption of trait analyses is that plant trait combinations are limited and that life history strategies are associated with trade-offs that confer fitness to certain environmental conditions at the expense of others (Westoby et al. 2002; Díaz et al. 2004; Wright et al. 2004; Westoby and Wright 2006). For example, Grime (1977) proposed a triangular scheme to describe variation in plant life history strategy according to the relative importance of adaptations to competitive ability, stress and disturbance tolerance. In contrast Westoby (1998) described plant trait variation along a scheme in which each axis represented a trait (leaf, height and seed) that reflects an accepted trade-off for light and reproductive constraints.

More recently, evaluation of worldwide databases of plant traits has identified that the major axis of leaf trait variation is the fundamental trade-off between a set of plant attributes that allow rapid acquisition of resources at the expense of longevity, and another set that permits conservation of resources within well-protected tissues (Díaz et al. 2004; Wright et al. 2004). This trade-off agrees with previous results of Grime et al. (1997), which indicated that the major axis of variation of plants in Great Britain was the adaptive specialization in resource dynamics. In a parallel manner, a wood economic spectrum has been suggested where wood density is a key integrator trait that reflects trade-offs in mechanical support, growth and hydraulic conductivity among species (Chave et al. 2009). However, the generality of these resource use axes describing variation in plant traits has not been completely resolved and global studies have also observed high within-site variation (Wright et al. 2007). Although some general patterns may be identified, trait differentiation results from environmental-specific conditions and multiple axes of differentiation may explain community functional diversity (Westoby et al. 2002; Ackerly 2004; Silvertown 2004; Hillebrand and Mathiessen 2009). Considering that the data analysed to date represents only a portion of the wide array of ecosystems found in nature, further studies in a wider range of ecological communities are required.

In tropical forested ecosystems, the gradient of resource use variation in plant leaf and stem traits has been related to species light requirement and performance. Shade intolerant species tend to have higher growth rates, higher seedling survival rates and low mass density and shorter lived leaves compared to shade tolerant species (Poorter and Bongers 2006). Wood anatomical traits on the other hand have been found to relate to light gradients, plant stature and to influence growth and survival in the field (Kraft et al. 2010; Poorter et al.

2010; Wright et al. 2010). These relationships, however, can vary depending on the climatic conditions of the forest. For example, Wright and Westoby (2002) found that the magnitude of the relation between leaf lifespan and leaf mass per area is different in species of dry sites compared to wet. In addition, comparisons in Bolivia showed that shade-tolerance groups in dry forest do not present differences in carbohydrate storage related to differences in survival, contrary to what is observed in wet forest (Poorter and Kitajima 2007). Furthermore, a shift in the importance of leaf functional traits that determine plant performance has been observed to occur in dry forest compared to wet, from attributes that determine growth and survival to those that improve growth under light or shade conditions (Poorter 2009). Light availability in dry forest increases considerably during the dry season generating medium to high irradiance for all plants in the understory (Lebrija-Trejos 2009), suggesting that there may be other factors than light availability that better describe plant trait variation in this ecosystem compared to wet forest.

Water availability, in addition to light gradients, has being suggested as a major driver of plant variation in tropical forests (Poorter 2005). Drought tolerance influencing plant communities is especially important in dry forests, which are characterized by three or more months of severe drought during the year (Mooney et al. 1995). In these forests, plant species possess characteristics that allow them to cope with water shortage and that can be segregated along an axis going from drought avoidance to drought resistance (Pineda-Garcia et al. 2013). Deciduous species, categorized to have a drought avoidance strategy that reduces water loss, have been found to be more efficient at water transport and carbon gain than evergreen species (Markesteijn et al. 2011) and to experience lower herbivory rates (Pringle et al. 2010). However, they have also been show to be more vulnerable to drought-induced embolism (Choat et al. 2005). In contrast, drought tolerant species have developed characteristics like deep roots and tough tissues that allow them to function under low soil and plant water potentials (Ackerly 2004; Poorter and Markesteijn 2008). Drought related adaptations have also been observed in specific life forms or phylogenetic groups. This is the case of lianas, an important structural component of neotropical forest that have shown high densities in dry forests (Gentry 1995) and for which higher drought resistance has been hypothesized without consistent results (Schnitzer and Bongers 2002; Van der Sande et al. 2013). Lianas have also shown lower specific leaf area and assimilation rates than trees in lowland forest, supporting the view that classification in plant life-forms can help to simplify functional diversity of this ecosystem (Santiago and Wright 2007). The family Fabaceae, which is highly dominant in seasonal dry forest, is also characterized by a group of traits that favour establishment in dry conditions such as compound leaves, high N leaf content and

low specific leaf area and has been nominated as a better criterion to classify species in this ecosystem than leaf phenology (Powers and Tiffin 2010).

The relative importance of shade and drought tolerance in explaining the variation in functional traits of tropical dry forest species is still unresolved. A decoupled adaptation of plant traits to both factors has been suggested in tree species of dry and moist tropical forest of Bolivia, where shade tolerance was related mainly to variation in leaf resource economy traits (Poorter 2009), whereas drought tolerance was strongly related to leaf organization, deciduousness and to stem and root traits (Poorter and Markesteijn 2008, Markesteijn and Poorter 2009). In agreement, an orthogonal variation among both leaf and stem traits has been observed in an extensive sample of neotropical wet forest species (Baraloto et al. 2010; Fortunel et al. 2012). On the contrary, strong associations between stem and leaf traits have been observed in seasonally dry forests species (Easdale et al. 2007). Some of these traits have also been related to hydraulic conductivity, which has been observed to strongly associate with a coordinated tolerance of trees in this ecosystem to shade and drought (Markesteijn et al. 2011). No further studies have been conducted in dry forests to test these relationships and there is therefore a need for further research on the functional ecology of this ecosystem (Chatuverdi et al. 2011). Using a set of 113 woody species of dry forest in a region of the Colombian Caribbean this study will test the hypotheses that leaf and stem traits related to drought and shade tolerance are not correlated and describe different axes of adaptation in plants. With this aim, I will analyze the variation in functional traits related to shade and drought tolerance and the relative importance of each trait explaining the variation between species. Additionally, I will test the adequacy of a priori plant functional classifications commonly used for SDTF describing plant variation in the region compared to the use of a posteriori classifications.

2.3 METHODS

2.3.1 Study area

The research was conducted in the Totumo region in the Caribbean coast of Colombia. The landscape in the region is heterogeneous and the main land cover type is pastures for cattle. Other land cover types include shrubland and secondary forest derived from abandoned agricultural fields, forest fragments and cultivated crops (mostly maize and yuca). The climate is characterized by a mean annual temperature between 24 and 27.5 °C with maximum temperatures of 38 °C (IGAC 2004, 2008). Mean annual precipitation is around

900 mm distributed in a rainy season from April to December, with a decrease in precipitation during June and July, followed by a 5 month dry season. Forests in the region have been described as neotropical dry forests (Gentry 1995), which reach an average canopy height of 15 m. The most diverse families in the region are Fabaceae, Rubiaceae and Bignoniaceae and some of the most important genera found are *Capparis*, *Euphorbia*, *Melicoccus*, *Paullinia*, *Senna* and *Solanum.*

2.3.2 Study species

A total of 113 species were included in the study on the basis of vegetation assessments conducted during 2011 in three sites located in the municipalities of Santa Catalina (10° 38.36'' N, 75° 14.61'' W), Luruaco (10° 38.85'' N, 75° 13.15'' W) and Piojó (10° 47.62'' N, 75° 09.5'' W), to the west of the Magdalena river base level. The species selected were those that contributed to 70% of the basal area of at least one of 123 10 x 10 m plots randomly distributed among the three sites, where all individuals with a DBH > 2.5 cm were identified and recorded. The assessments included three types of forest cover that were differentiated on the basis of satellite image and field observations, namely early, intermediate and late secondary forests, so a wide variety of species were included in terms of life history traits. Nomenclature follows that of the Missouri Botanical Garden (Tropicos.org. September 2013 <http://www.tropicos.org>).

2.3.3 Plant trait selection and measure

Functional traits are the characteristics of an organism that are considered relevant to its response to the environment and/or effect on ecosystem function (Díaz and Cabido 2001). Plant traits include various life history, morphological, physiological and biochemical characteristics, which may not always be easily measured. In practical terms, they have been divided into soft and hard traits; the former includes those that can be easily measured in the field or by simple laboratory procedures, while the latter request more complex methods or long periods of time (Cornelissen et al. 2003; Weiher et al. 1999). Selection of traits was conducted after a detailed literature review and the critera used were that the trait had been previously related to shade and drought tolerance, survival and growth performance of plants and that its measurement was feasible in the field conditions. The traits selected correspond to soft traits that are expected to be sufficiently fixed to characterize species despite intra-specific variability.

Field collections were made from June to September 2011. Leaf characteristics were measured, if possible, in 5 individuals per species following the recommendations of minimum sample size of Cornelissen et al. (2003). For a few relatively rare species it was not possible to attain this sample size but not less than three samples per species were considered in those cases. Variation associated with the development stage and the effects of light environment were reduced by selecting healthy mature leaves from the outer leaf layer of the crown that were exposed to full sunlight at least during a few hours of the day. This last criterion was not considered for species whose individuals were found primarily in the understory. Fully expanded leaves without epiphylls and significant herbivore damage were collected, including the corresponding petioles. The leaves were stored in sealed plastic bags with a wet tissue and maintained in the shade to avoid dehydration until measurement; all measures were taken on the same day of collection.

For each individual 5 leaves were measured for fresh mass, lamina thickness and force to punch. For compound leaves, individual leaflets were measured. Lamina thickness (LT) was measured with a digital calliper avoiding visible primary and secondary veins in two different sections of the lamina. The force-to-punch a leaf was measured using a push and pull gauge (rod diameter 3.18 mm, Chatillon 516-1000, AMETEK TCI Division, Chatillon Force Measurement Systems) following Pringle et al. (2010). Although the use of punch tests has been criticized (Sanson et al. 2001) as it does not actually measure leaf toughness directly, the results obtained with this technique are consistent with those using other shearing instruments as long as the diameter of the punch is specified and the measure is corrected for the length or thickness of the leaf (Kitajima and Poorter 2010; Onoda et al. 2011). It is also a valid technique for comparative studies that do not analyse in detail biomechanical properties. The rod head was therefore positioned to avoid primary and secondary veins and measures were taken in two positions of the leaf blade. The mass at the moment of penetration of the leaf was converted to punch force by converting grams to N and dividing by the rod circumference (Fp, $N.mm^{-1}$). The use of the circumference instead of rod area to normalize the data has been recommended to reduce sensitiveness to the size of the punch diameter (Onoda et al. 2011). Fp was subsequently divided by the lamina thickness to calculate the specific force-to-punch (Fps, $N.mm^{-2}$).

Additionally, a digital picture was taken of each leaf after locating it in a white background between two laminas of glass and marking the scale. The pictures were analysed with pixel-counting software to calculate the area of the lamina and the petiole (Rasband, W.S., ImageJ, U. S. National Institutes of Health, Bethesda, Maryland, USA, http://imagej.nih.gov/ij/, 1997-2011). Leaf area (LA) considered the area of the lamina blade

without the petiole; for compound leaves leaf area was calculated by multiplying leaflet areas by the mean number of leaflets. Compoundness was recorded in three states: simple leaves, pinnate and bipinnate. Species were assigned to one of two leaf habits, deciduous or evergreen, based on field observations, local interviews and a literature review (Appendix 1). Although deciduous species have been shown to vary in the timing and length of the leafless period no distinction was made as no detailed information was available for all species.

Seeds were collected from one to three individuals, according to availability, and from each individual at least 10 seeds were measured for dry biomass. Leaves, leaflets and seeds were dried for a minimum of 48 h at 60-70 °C to record dry mass. Samples were dried in a sealed room using a gas oven at the installations of the University of Atlántico, Colombia, were they were located approximately 70 cm over the oven on an aluminum table and were protected using a cardboard sheet. Temperature was constantly monitored using laboratory thermometers. To assure that samples had lost all water content, a few samples were weighed, placed again inside the room and weighed a few hours later to check if the biomass continued decreasing. If this was the case all the material was dried for additional hours, until a constant dry mass was obtained. Based on the measurements the following variables were calculated: leaf dry matter content (LDMC = dry mass per unit of fresh mass) and specific leaf area (SLA in $cm^2.g^{-1}$ = total leaf area / leaf dry mass) and seed mass (SM in g).

Stem density (SD) was measured in five individuals per species as the dry weight (g) per unit volume (cm^3). Most of the species possessed hard, woody stems, for which samples were collected by cutting a section of the trunk. In the case of relatively soft-stemmed species, such as *Bursera simaruba*, *Ceiba pentandra* and *Hura crepitans* an increment borer was used to take a stem sample for analysis. For lianas and plants with stem diameters >6 cm and height >4 m, the samples were taken at approximately 1.3 m height. For plants with thin main stems (diameter <6 cm) or smaller than 4 m height, a section was cut at approximately one third of the stem height. Volume was calculated using the water displacement method (Chave 2005). Bark thickness (BT) was measured in stem sections using a digital calliper; for some of the species measures were taken in dried samples and the values may therefore be relatively low owing to tissue contraction. Samples were kept in a cool place until oven-dried for at least 48 h at 60-70 °C, as previously described for leaf samples, and dry mass recorded.

Height, estimated visually by the field team, and crown exposure of each individual, were also recorded. Crown exposure index (CE) values were obtained through visual assessment following Poorter and Kitajima (2007): CE is assigned a value of 1 if the tree

does not receive any direct light, 2 if it receives lateral light, 3 if it receives overhead light on part of the crown, 4 when it receives full overhead light on the whole crown and 5 when it has an emergent crown that receives light from all directions. Considering that a species could potentially be found in different light environments during different growth stages, the highest value of crown exposure recorded in the field was used for analysis.

Spinescense records follow the categorical classification of Cornelissen et al. (2003): 0) no spines, thorns or prickles; 1) low or very local density of soft spine equivalents of <5 mm length; 2) high density of soft spine equivalents or intermediate density of spine equivalents of intermediate hardness- or else low density of hard, sharp spine equivalents >5 mm length; 3) intermediate density of hard, sharp spine equivalents >5 mm length; 4) intermediate density of hard, sharp spine equivalents >20 mm length and 5) intermediate density of hard, sharp spine equivalents >100 mm length.

2.3.4 Data analysis

Traits measured in the field presented two levels of sampling, species and individual trees. To explore which of these levels was the largest source of variation, a linear mixed effect model was fitted to the data considering each level of sampling as a random factor. Variation between individuals in seed mass only considered a few species, as for most species all the seeds were collected from one individual. Ttaits that did not meet the assumptions of the analysis were transformed by means of the natural logarithm. Significance of each level of grouping (species, individuals) was analysed by means of simple ANOVAs or Kruskall-Wallis on aggregated data to account for the unbalanced sampling effort.

Species-specific trait values were calculated using an arithmetic mean and the resulting variables were tested for normality using the Shapiro-Wilk test. Traits that differed from a normal distribution were transformed by means of the natural logarithm to reduced skewness. Relations between the traits were analysed by calculating multiple correlations using the Pearson's coefficient. Because of very high differences in maximum and minimum value for LA, Fp and Fps, these variables did not fit normal distribution after transformation and correlations were analysed using Spearman's coefficient.

A principal components analysis was carried out on the correlation matrix to explore the relations between traits and the distribution of species along the reduced ordination axis. SLA, LA, LT, Fps and BT were transformed before the ordination to reduce skewness and Fp was excluded due to high correlation with Fps. Considering the high number of missing

cases for SM, the analyses were performed using all the species sampled and excluding the seed variable. Missing values were replaced by mean values in two cases, bark thickness for *Hura crepitans* and *Ceiba pentandra*. Compoundenss and spinescense were considered as quantitative ordinal variables. SM, maximum height and CE were correlated with the axis scores of the first three principal components. Only species that possessed data of 10 or more individuals of maximum height and CE were included in the correlations to avoid estimations from a low sampling number.

To test for differences between functional groups three *a priori* classifications were considered; species were classified according to leaf phenology, life form and phylogenetic clade. In terms of phenology, species were classified as evergreen or deciduous and no discrimination was made between different levels of deciduousness considering the heterogeneous sources of information. For life form, the categories considered were tree, liana and palms or tall grasses. This study included 14 species of lianas and 6 of palms and grasses that are an important structural element of the forest in the region. For phylogenetic clade four groups were considered following the AGP III system (2009): monocots (commelinids), eudicots, Fabaceae as a special case of eudicots and magnoliids.

Additionally, a cluster analysis was conducted on the initial matrix to test for *a posteriori* functional groups. The euclidean distance on the normalized variables was used to calculate the distance matrix and groups were defined using the complete linkage agglomerative cluster method, which attained the highest correlation coefficient between the cophenetic distance and the original distance. Compoundnes and spines were considered as ordinal variables. The final number of clusters was selected considering the average distance within groups, the Calinski–Harabasz pseudo-F index and the ecological meaning of the clusters. Clustering stability was assessed by calculating the mean Jaccard similarity of the original clusters with those obtained by resampling data through bootstraping (Henning 2007). The cactus *Pereskia guamacho* was not included in the analysis as it formed an independent cluster with all methods. An analysis of variance using distance matrices was conducted to test for differences between the functional groups; dissimilarity between species was calculated as the Euclidean distance and the significance was assessed with 200 permutations. In addition, differences in functional traits between the groups of *a priori* and *a posteriori* classifications were tested by means of an analysis of variance and Kruskal-Wallis when variables were not normalized after transformation. For these analyses only Fabaceae and Eudicots were considered among phylogenetic groups and lianas and trees among life forms, due to the small number of samples for the other functional groups. These

analyses were conducted using the packages vegan, cluster and fpc within R (version 2.15.1, R Core Team 2012).

2.4 RESULTS

Plant traits recorded in the field varied widely among the species (Table 2.1). Leaf area (LA) showed the highest variation with values varying by four orders of magnitude. This can be explained by the high leaf area of palms and other species included in the study such as *Sterculia apetala*, *Cecropia peltata* and *Cavallinesia platanifolia*. Other traits that showed high variation among values were SLA (one order of magnitude), Fp (one order of magnitude) and Fps (three orders of magnitude). LDMC and SD showed especially low minimum values, which correspond respectively to the cactus species *Pereskia guamacho* that possess very succulent leaves, and to the species *C. platanifolia* common in dry forests and characterized by a water storage trunk.

Table 2.1. Summary statistics for eight functional traits of a set of 113 species of seasonally dry tropical forests. Leaf dry matter content (LDMC), leaf thickness (LT), specific force to punch (Fps), leaf area (LA), specific leaf area (SLA), stem density (SD), bark thickness (BT) and seed mass (SM).

	Min	**Max**	**Mean**	**St.dev.**	**Median**
LDMC	0.08	0.61	0.32	0.10	0.33
LA (cm^2)	6.66	47338.00	996.30	5777.39	67.11
SLA (cm^2.g^{-1})	67.96	589.78	198.98	85.57	186.13
SD (g.cm^{-3})	0.13	0.85	0.54	0.14	0.57
LT (mm)	0.06	0.58	0.19	0.07	0.18
Fps (N.mm^{-2})	0.36	536.32	34.79	79.50	11.89
BT (mm)	0.26	7.30	2.89	1.50	2.670
SM (g)	0.00	15.96	0.76	2.41	0.05

Interspecific differences were the major source of variation for all plant traits (Table 2.2) and both levels of variation were significant in all cases ($P < 0.001$). For LA, LDMC, Fps, SD and SM the percentage of variation explained by species differences was high (71-

96%). Whereas for SLA and BT an important percentage of variation was explained by differences between individuals or remained unexplained. Considering other variables, 62% of the species included in the study have simple leaves, 28% pinnate leaves and 10% bipinnate leaves. For spinescense most of the species do not possess spines (85%) and when present, high variability was observed, from very low densities to high densities of hard spines (e. g. *Bactris guianensis*).

Table 2.2. Percentage of variance explained by species and individuals in a set of eight functional traits. Both levels of variation were significant for all traits. Based on 113 species and 523 individuals, except seed mass (49 species, 101 individuals), stem density (109 species, 500 individuals) and bark thickness (109 species, 477 individuals). For functional traits abbreviations and units see Table 2.1.

	LDMC	LT	Fps	LA	SLA	SD	BT	Seed
Species	68.90	72.71	71.75	91.68	52.38	77.58	52.92	95.39
Individual	12.00	20.13	17.09	4.41	30.10	-	-	3.23
Residual	19.1	7.2	11.2	3.9	17.5	22.4	47.1	1.4

Significant correlations were found for all plant traits (Table 2.3). LDMC was negatively correlated with SLA ($P < 0.001$) and leaf thickness ($P < 0.001$) and positively correlated with SD ($P < 0.001$), Fps ($P < 0.001$) and compoundness ($P < 0.001$). Other significant correlations were found between seed dry mass, LA, SLA and Fps. The high correlation between LA and SM is maintained when removing palms from the analysis, which presented the highest values for both traits. Results suggest that species with higher seed mass (SM) are characterized by larger leaves, low SLA, and high Fps and that species with high SD are also characterized by high LDMC and Fps, and less strongly by low BT and LT.

The first three components of the PCA explained 25%, 24% and 15% of plant trait variation (Table 2.4). The first component was highly correlated to LDMC, Fps and SLA, and more weakly to SD, locating on the negative side of the first axis of the ordination species with high investment in leaf and stem tissues (Figure 2.1). The second component was highly correlated with leaf thickness and compoundness, and more weakly to SLA, locating species with compound and thin leaves on the positive side of the second axis. The third component was highly negatively correlated to LA and with a lower magnitude to SD,

44

bark thickness and compoundness. Maximum height, SM and crown exposure (CE) were correlated with the species coefficient along the third component, whereas SM was also correlated with species coefficient along the first component (Figure 2.2).

Table 2.3. Pair-wise relationships amongst 10 functional traits of 113 tropical dry forest species. Values indicate Pearson's coefficient for relationships between LDMC, SLA, SD and BT; for all other relationships Spearman's coefficient. N = 45 for correlations with seed mass. Significant correlations at $P < 0.001$ are indicated in bold, in bold and italics $P < 0.05$. For trait abbreviations and units see Table 2.1, except Maximum height- Mheight (m) and Compoundness- Comp.

	LDMC	LA	SLA	SD	LT	Fps	BT	Spines	Comp.	Seed
LDMC										
LA	0.05									
SLA	**-0.39**	-0.08								
SD	**0.54**	***-0.21***	-0.16							
LT	**-0.35**	0.02	**-0.33**	***-0.24***						
Fps	**0.41**	0.14	**-0.65**	***0.22***	0.28					
BT	-0.06	0.16	-0.1	***-0.24***	0	-0.04				
Spines	0.05	0.03	0.15	-0.07	-0.09	0	-0.12			
Comp.	0.34	0.4	0.13	0.06	**-0.49**	-0.13	0.07	0.14		
Seed	0.28	**0.62**	**-0.48**	<0.01	-0.05	**0.58**	0.19	-0.05	0.28	
Mheight	-0.11	0.23	-0.01	***-0.35***	0.09	0.12	0.23	-0.03	-0.05	0.11

Table 2.4. PCA components (variance explained) and loadings of plant traits for a set of 113 species of SDTF. For trait abbreviations and units see Table 2.1, except Compoundness- Comp.

	LDMC	SD	Spines	Comp.	LA	SLA	LT	Fps	BT
PC1 (24.5%)	-0.53	-0.37	-0.01	-0.03	-0.17	0.52	0.00	-0.53	0.07
PC2 (23.9%)	0.32	0.30	0.11	0.52	-0.04	0.34	-0.57	-0.24	-0.16
PC3 (15.3%)	-0.01	0.46	-0.20	-0.35	-0.71	0.01	0.06	-0.08	-0.34
PC4 (12.7%)	0.12	0.06	-0.74	0.06	-0.07	-0.10	-0.15	-0.14	0.61
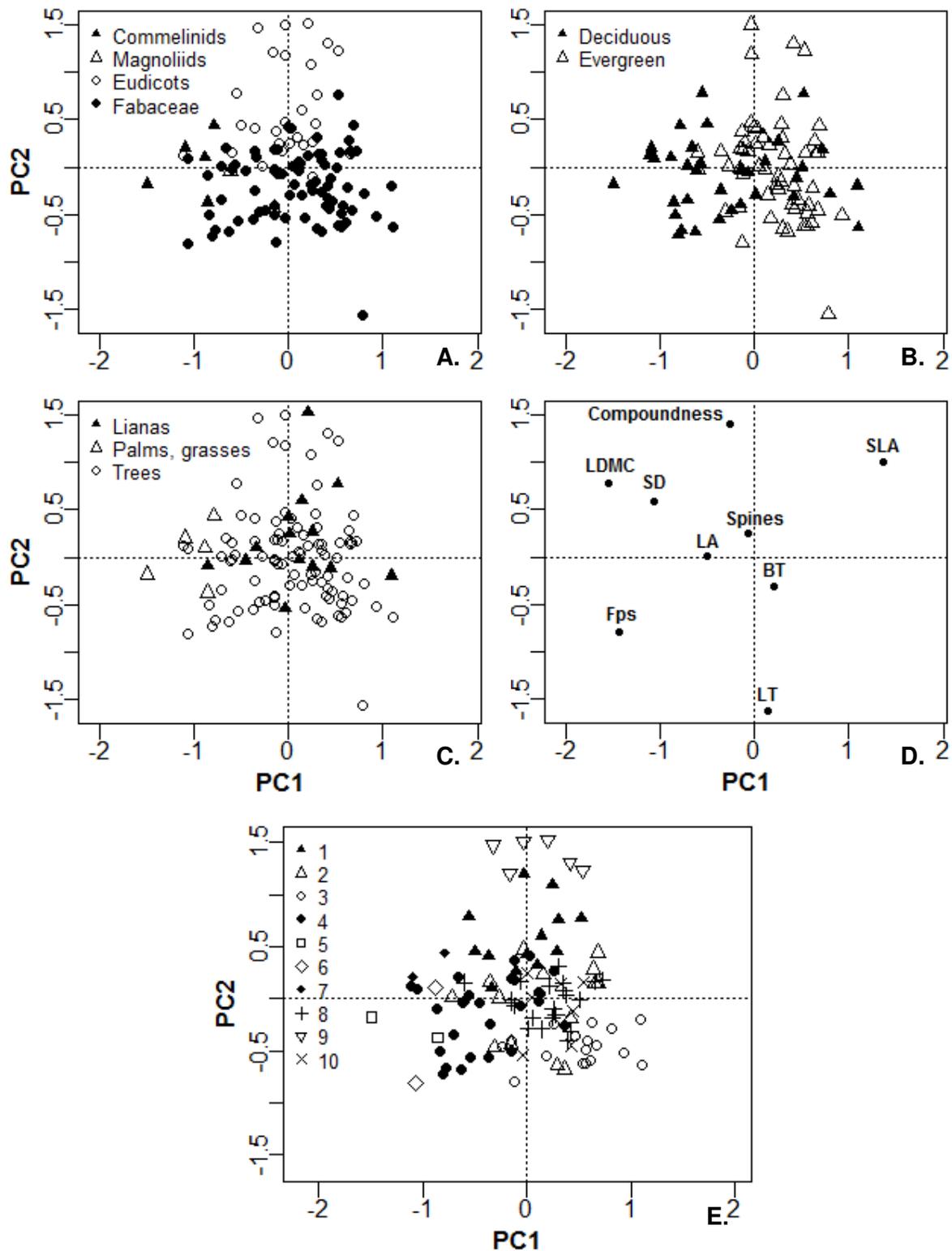
Figure 2.1. Principal component analysis biplot of functional trait data for 113 species of SDTF. Different symbols indicate grouping by different functional classifications: A.) phylogenetic clade, B.) leaf phenology, C.) life form and E.) cluster analysis. D.) Scores of plant functional trait on the first and second axis.

46
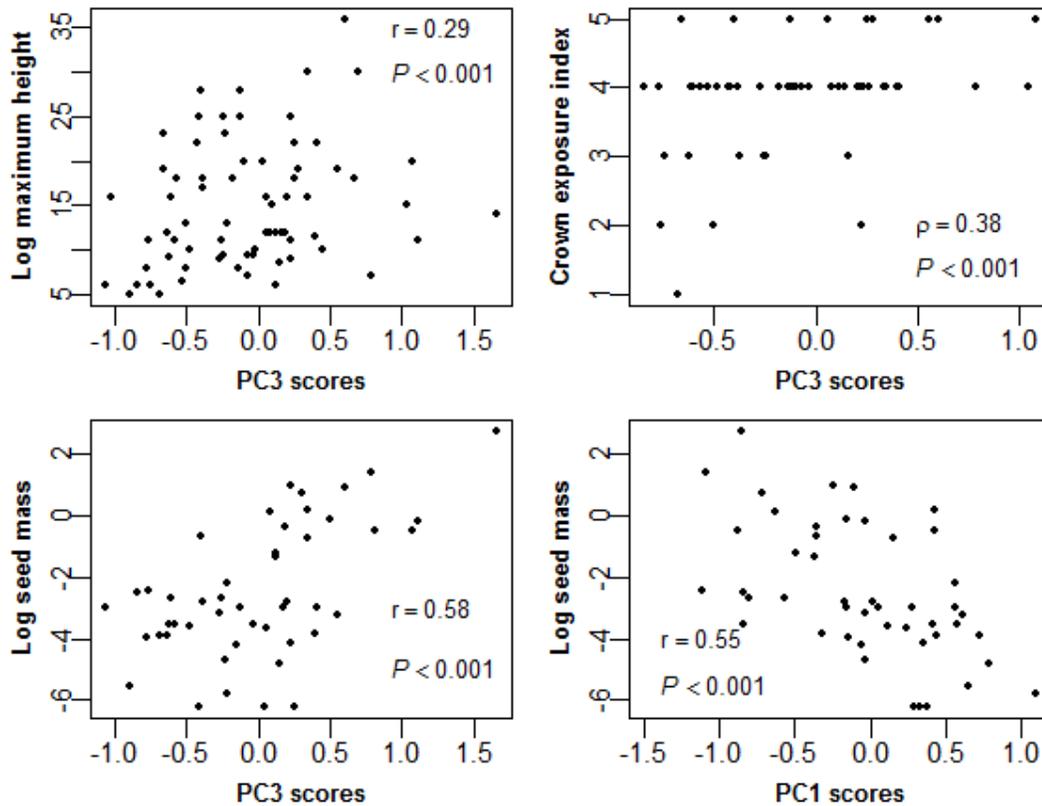
Figure 2.2. Scatterplot of significant relationships between plant functional traits and species scores along the first and third axes of a principal component analysis. Pearson (r) and Spearman (ρ) coefficients and significance levels are given. N is 46 species for crown exposure correlations, 68 for maximum height and 45 for seed mass.

Significant differences were found between legumes (Fabaceae) and the remaining Eudicots by means of an analysis of similarities (F = 13.7, df 1, P = 0.005). Legumes were located on the top of the second axis and were characterized by compound leaves, low LT and high SLA (Fig. 2.1). These results were confirmed by significant differences in analysis of individual plant traits with legumes presenting higher LDMC and SLA and lower Fps and LT than the remainder Eudicots (Table 2.5). Considering leaf phenology significant differences were also found by means of the analysis of similarities (F = 7.2, df 1, P = 0.005). Deciduous species presented significantly lower LDMC, and Fps and higher SLA and BT than evergreen, as well as a higher number of compound-leaved species (Table 2.5). No differences were found between life forms (F = 1.7, df 1, P = 0.13), lianas covered the same range of trait characteristics as trees (Figure 2.1, Table 2.5); grasses and palms on the other hand were located in the extreme right of the distribution in the first axis, reflecting their high LDMC and Fps.

Table 2.5. Features of functional groups classified by leaf phenology, life form and phylogenetic clade. Mean values for continuous functional traits and median values for categorical traits. Differences between groups were analysed by means of t-test or Wilcoxon rank sum test for continuous data and chi-squared test for categorical data. Analysis of life form only considered lianas and trees and of phylogenetic clade only considered Eudicot and Fabaceae. Leaf dry matter content (LDMC), leaf thickness (LT, mm), Fps (Specific force to punch, $N.mm^{-2}$), LA (leaf area, cm^2), SLA (specific leaf area, $cm^2.g^{-1}$), SD (stem density, $g.cm^{-3}$), BT (bark thickness, mm). Spines categories follow Cornelissen et al. (2003) and Comp. (compoundness): 1. Simple, 2. Pinnate and 3. Bipinnate.

Classification	FG	N	LDMC	LA	SLA	SD	LT	Fps	BT	Spines	Comp.
Phenology	Evergreen	36	0.36	2731.40	163.89	0.59	0.19	62.53	2.41	1	1
	Deciduous	57	0.29	201.26	213.32	0.48	0.19	15.04	3.36	1	2
			t=3.4	W=825	t=-4.0	t=3.6	W=1105.5	W=1523	t=-2.9	X^2=3.5	X^2=3.3
		P	<0.001	0.114	<0.001	<0.001	0.533	<0.001	0.005	0.476	0.189
Life form	Palms, grasses	5	0.44	19148.92	121.52	0.55	0.16	260.37	1.62	5	2
	Lianas	14	0.33	137.96	238.95	0.52	0.17	18.03	2.15	1	2
	Trees, shrubs	94	0.32	158.57	197.14	0.55	0.19	25.28	3.06	1	1
			t=0.7	t=-0.49	t=1.6	t=-0.637	W=559	W=626	t=-2.0	X^2=11.5	X^2=1.6
		P	0.491	0.624	0.112	0.5254	0.367	0.773	0.046	0.022	0.457
Phylogeny	Commelinids	5	0.44	19148.92	121.52	0.55	0.16	260.37	1.62	5	2
	Magnoliids	2	0.38	100.88	157.61	0.58	0.16	107.91	5.13	1	1
	Fabaceae	27	0.38	176.21	247.35	0.59	0.13	10.20	2.88	1	2
	Eudicots	79	0.30	150.35	188.39	0.53	0.21	27.06	2.91	1	1
			t=4.1	t=0.7	t=2.7	t=2.0	W=349	W=713	t=0.165	X^2=11.0	X^2=50.3
		P	<0.001	0.501	0.009	0.048	<0.001	0.011	0.869	0.027	<0.001

The classification of 112 species by means of cluster analysis permitted the differentiation of ten groups. Analysis of similarities showed significant differences between groups although only four of the ten clusters can be considered stable and three have values of the Jaccard coefficient over 0.5. Significant differences were found between groups for all individual traits, except LA (Table 2.6). Four groups with conservative type traits values were located in the negative side of the first axis of the PCA and the distinction among these groups along the second axis was mainly related to differences in leaf area and toughness. Group 4 included mainly thick and simple-leaved species; wheras groups 5, 6 and 7 included palms, grasses and very thick-leaved species, with increasing SLA and presence of spines. Three groups with intermediate type trait values were identified on the center of the first axis. Group 9, located on the positive side of the second axis, included bipinnate species with the highest SLA and lowest LT and Fps. Groups 1 and 8, towards the centre of the second axis, included respectively mostly compound species with intermediate LT and species with high LT and low LDMC. Cluster 3 in the positive side of the first axis was characterized by medium to high LT and low SD and LDMC. Group 10 and 2 were dispersed in the ordination space and we characterized respectively by the presence of spines and the highest bark thickness, as well as low LDMC and SD.

Table 2.6. Features of functional groups classified by complete clustering. Mean values for continuous functional traits and median values for categorical traits. Differences between groups analysed by means of analysis of variance or Kruskal-Wallis test. For abbreviations and units see Table 2.5.

FG	N	LDMC	LA	SLA	SD	LT	Fps	BT	Spines	Comp.
1	13	0.37	198.40	235.99	0.59	0.13	14.24	2.55	1	2
2	14	0.29	275.82	184.23	0.45	0.17	30.07	5.68	1	2
3	17	0.23	205.43	202.27	0.37	0.23	12.22	3.22	1	1
4	28	0.39	104.26	142.34	0.66	0.19	33.07	2.57	1	1
5	2	0.46	43377.50	80.90	0.44	0.18	268.85	2.56	1	2
6	2	0.40	1289.22	118.24	0.64	0.21	506.24	2.82	3	1.5
7	2	0.47	3229.55	144.57	0.64	0.14	113.91	0.57	6	1.5
8	21	0.27	120.04	*220.82*	0.56	0.19	13.57	1.76	1	1
9	6	0.43	132.43	418.84	0.65	0.07	1.55	2.50	3	3
10	7	0.27	86.07	193.28	0.45	0.20	14.23	2.29	5	1
		F=13.70	H=17.4	F=11.60	F=12.20	H=44.7	H=33.6	H=56.4	X^2=193.8	X^2=95.9
	P	<0.001	0.044	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

2.5 DISCUSSION

The variability of morphological traits among plant species was very high as expected from the numerous and diverse sample of woody plants included in the study. The assumption that interspecific variation was higher than intraspecific variation was confirmed by the results and a great percentage of the variation in functional traits was explained at the species level, with the exception of specific leaf area (SLA) and bark thickness (BT). The measurement of SLA is subject to high natural variability in relation to the light environment, leaf age and sampling errors (Wilson et al. 1999); factors that may not have been completely controlled in this study. In the case of BT the high percentage of variation that remained unexplained could be partially related to differences in individual tree diameter, which have been shown to strongly influence this trait and were not controlled in this study (Paine et al. 2010).

2.4.1 Relations among stem and leaf traits

The strong negative correlations between traits suggests that trade-offs occur between the morphological traits measured. The association of traits in the three major axis of variation identified by the ordination analysis did not provide evidence of decoupling between traits that are reported to determine shade and drought tolerance. These results support the hypothesis that functional trait variation of woody species in dry forests can be explained better in terms of acquisitive traits that allow high resource use under high light or water availability conditions versus conservative traits that provide tolerance to both shade and drought (Markesteijn et al. 2011; Sterck et al. 2011). The first axis of the ordination, related to leaf density and toughness, was determined by the strong negative relation between SLA, Fps and LDMC. This axis of variation has also been identified for other lowland forest as part of the shade tolerance strategy where species with tougher and denser leaves were also characterized by longer lifespan, lower palatability, low sapling relative growth rate and high survival (Kitajima and Poorter 2010). The second component was related to leaf organization and thickness, traits that can favour both growth and drought tolerance. Compound leaves have been suggested to decrease branching and allow rapid increases in vertical growth for both shade-tolerant and pioneer species (Malhado et al. 2010). They have also shown higher C:N ratios compared to simple leaves, which are related to less energetic cost with no detrimental effect in herbivory defence (Warman et al. 2010). Leaf thickness on the other hand has been observed to vary independently of leaf toughness and LDMC and was related to leaf lifespan in woodlands of Australia (Wright and Cannon 2001), although this relation was not observed in moist forests of Bolivia (Kitajima and Poorter 2010).

Leaf area was not correlated with any other leaf trait but it was negatively related to SD, determining the third component of trait variation. This link between SD and LA has been explained by plant hydraulics, as species with lower wood density have on average higher hydraulic conductivity and will be able to transport more water to the leaves (Wright et al. 2007). A significant relationship between these two traits has also been observed in multi-species analysis of lowland neotropical forests (Malhado et al. 2009, Baraloto et al. 2010). Moreover, our results agree with the predicted relationships of plant traits in low rainfall locations provided by Baraloto et al. (2010), where they expected: 1) a decoupling of leaf area from leaf toughness accompanied by lower probability of herbivore damage risks to tissue, and 2) a stronger association between leaf area and stem economics because of increased risk of cavitation with increased transpiration surface. This axis was also weakly correlated with BT and compoundness, reflecting their positive correlation with the main traits mentioned. The negative relationship between BT and SD could be related to a lower need of denser stems for external herbivory defence (as suggested by Paine et al. 2010) and to fire resistance (Brando et al. 2012). In terms of leaf organization, there was a tendency for compound leaves to have higher leaf size and these differences were significant when treating compoundness as a factor in an independent analysis; specifically pair-wise comparisons showed that simple leaves had a smaller area than pinnate leaves. Differences in LA between simple and compound species have not been documented and previous analyses have only considered leaflet size for comparisons between them (Warman et al. 2010); although a consistent positive relation between leaf and leaflet area has been observed (Patiño et al. 2012). Nevertheless, a higher investment in biomass has been observed in compound leaved compared to simple leaved species (Niinemets et al. 2006), which would favour area expansion without increasing photosynthetic area prone to desiccation, allowing compound species to exploit high light availability but also to tolerate drought.

Stem density was correlated strongly with the first and third component, and to a lesser extent to the second, underlying its key role in dry forest species variation. SD was also negatively correlated with maximum height supporting the trade-off between rapid growth versus high survival and investment in structural tissues (Wright et al. 2010). Furthermore, wood density and maximum height have been identified as the principal traits that determine species growth rate and its variation in relation to changes in light availability and size (Rüger et al. 2012).Wood density has also been shown to determine species drought tolerance by its close relation to stem hydraulic conductivity and vulnerability to cavitation (Markesteinj et al. 2010). Considering the relationships of SD with other leaf traits, the strong positive correlation with LDMC has also been observed in other dry forests (Poorter and Markesteinj 2008; Markesteinj et al. 2011); species with a conservative use of resources

present a higher mass investment in plant tissues including leaves, stem and roots at the expense of a more efficient hydraulic system. However, these authors also found a strong relation between SD and SLA contrary to our results, whereas an independent variation of SLA in relation to SD has been more common in wet tropical forests (Wright et al. 2007; Baraloto et al. 2010).

2.4.2 Seed size and light environment

Seed size has been identified as one of the independent strategy dimensions of plant traits (Wright et al. 2007), as well as leaf size and SLA. Our results, however, showed high correlation of this trait with species scores on the first axis of variation that relates to the dry mass investment in leaves and stem, suggesting that SDTF species with high individual seed mass (SM) also have a tendency for high cost leaves. In agreement, higher seed mass has been observed in shade tolerant compared to shade intolerant species of dry forest in India (Khurana et al. 2006). Maximum height and crown exposure (CE) on the other hand did not correlate with this axis, suggesting that different resource strategies can be present at different light environments. These results agree with observations in moist forests where leaf traits were better related to the regeneration rather than the adult light niche, when measured as maximum height and average adult crown exposure (Poorter 2007).

Maximum height and CE are proxies of the vertical position of the species in the forest and these were correlated with the third component of the PCA, determined by LA and SD. The relations between CE and the third component however showed high variation and the pattern observed is better explained as a tendency for trees with low crown exposure to present small leaves, whereas trees with high CE present high variation in leaf size. Trees with larger leaves and lower stem density are then expected to be observed in gaps and in higher vertical stratums of these forests. These results agree with observations by Poorter (2009) in tropical forest of Bolivia, where light-demanding species were characterized by large leaves as well as large internode cross-sectional area, long petioles, and a large biomass fraction in petioles. Leaf area has also been found to explain changes in response of relative growth rate to light (Rüger et al. 2012).

The strong relationship observed between SM and LA determined the former correlation with the third component of the ordination analysis. This link corresponds with one of the main patterns of specialization identified by Díaz et al. (2004) using a world wide database of temperate ecosystems and agrees with the positive relation between seed size and leaf area, not maximum height, found in moist forests in Panama (Rüger et al. 2012). In

contrast, for trees of Amazonian wet forests seed size was related to maximum height and not to leaf areas (Wright et al. 2007; Patiño et al. 2012). In seasonally dry forest, wind dispersed species with seeds usually of small size are more abundant than in wet forest (Gentry 1995; Khurana et al. 2006) and this characteristic could weaken the relation between seed size and maximum height in this ecosystem. On the other hand, the sample we used to analyse relationships with seed size was smaller than for other traits and most of the collection of fruits was conducted during the wet season, so an underrepresentation of fruit dispersed during the dry season could have occurred. It is possible that a larger sample could weaken the relationships observed but it is unlikely that the general pattern would change.

2.4.3 Functional types

Classification of species according to leaf phenology and phylogenetic clade revealed different strategies of plaint trait coordination. Deciduous species differed from evergreen species in their distribution along the first component of the ordination and showed a tendency to have an acquisitive use of resources with higher SLA and lower LDMC, Fps and SD. These results agree with studies in other neotropical seasonally dry forest, where differences in stem density and leaf density, toughness and dry matter content were observed between both leaf habits (Easdale et al. 2007; Pringle et al. 2010; Markesteijn et al. 2011). Timing of leaf shading and extent can vary considerably among species in relation to soil water potential due to differences in stem water content and hydraulic conductivity (Pineda-Garcia et al. 2013). As wood density has been shown to relate closely to both of these traits (Pineda-Garcia et al. 2011; Markestein et al. 2011) its consideration is expected to reflect some of this variation. However, there was an evident overlap of trait values reflecting the difficulty of classifying species based solely on this trait in agreement with observations of Powers and Tiffin (2010) and Chatuverdi et al. (2011).

In a complementary manner, phylogeny was an important factor differentiating species along the second axis of variation that considers leaf organization and thickness. Although a broad classification approach was used, my results confirm that Fabaceae is a distinctive group in this ecosystem and that legumes have developed a series of characteristics that favor drought tolerance and could explain their high abundance (Powers and Tiffin 2010). A great proportion of the legumes registered in the area were deciduous and except for one all were compound-leaved, they also presented a lower LT and higher SLA than the remaining Eudicots. Compound species have been related to faster diameter growth rates and lower wood density in wet forests (Malhado et al. 2010), which would allow legumes to take advantage of high light availability conditions. Furthermore, among

tree species of the Amazon, Fabaceae were also characterized by thin leaves with high mineral nutrients concentrations, whereas a wide variation in wood density was observed (Baraloto et al. 2010).

In terms of life forms, classification of species specifically in lianas and trees did not reflect variation in leaf and stem morphological traits. Considering that some of the traits measured are associated with the growth-survival trade-off (Wright et al. 2010), our results agree with other studies in which no differences in slope or range of this trade-off was observed between these two life forms (Gilbert et al. 2006). In addition, no differences in physiological and morphological functional traits between lianas and trees were observed at the sapling stage by Van der Sande (2013), although lianas did present lower cavitation resistance and higher hydraulic conductivity than trees. These authors suggested that this may change in later ontogenetic stages when lianas would invest less in stem biomass and more in photosynthetic leaf area, however our results on adult morphological traits did not find differences between these two life forms either and both showed a wide trait variability.

A posteriori functional groups can be a site and community specific alternative to general classifications that do not take into account all the variation in a community. Especially when the use of a priori classification schemes explaining ecosystem functions has proven in some cases to give results not better than using random grouping (Wright et al. 2006). Likely, more detailed classification schemes have been recommended to benefit the use of forest landscape and stand level growth models that require a higher number of functional groups (Fyllas et al. 2011). In this study clustering of species resulted in ten functional groups that were distributed along the first two dimensions identified in the PCA. The classification successfully described variation from acquisitive to conservative type species on one hand and from compound thin leaves to simple and thicker leaves on the other. The low stability of some of the clusters nevertheless reflects the high variation in functional traits among species and limits its use to describe other plant communities.

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CHAPTER 3 ENVIRONMENTAL HETEROGENEITY INFLUENCES SUCCESSIONAL TRAJECTORIES IN COLOMBIAN SEASONALLY DRY TROPICAL FORESTS

3.1 ABSTRACT

Environmental characteristics have a major influence on the species composition of seasonally dry tropical forests, however their effect on the secondary succession of this ecosystem has been little considered. In this research, I tested the hypothesis that local environmental heterogeneity influences successional trajectories of secondary forests in a region of the Colombian Caribbean. Changes in species composition and structure were described in 126 vegetation plots differing in stand age and located along a topographical and soil nutrient gradient. Variation in community composition was partitioned between successional stage, environment and spatial components using mantel tests and redundancy analyses. High species turnover was observed during succession and species composition similarity was higher among late successional forest than early and intermediate age stands. Species composition was better explained by environmental characteristics than successional stage whereas low spatial structure was detected. Our results suggest that variation in the successional trajectories is occurring due to environmental and management characteristics, as well as other unmeasured processes.

3.2 INTRODUCTION

Seasonally dry tropical forests (SDTF) are widely distributed in the Neotropics but most of their remaining area is composed of fragments of small size (Miles et al. 2006). This patchy distribution is the result of both a naturally fragmented distribution at the regional scale (Pennington et al. 2009) and the intense human disturbance to which this ecosystem has been subject (Murphy and Lugo 1986; Trejo and Dirzo 2000; Fajardo et al. 2005). Neotropical SDTF have also been identified as a biome that is relatively old, with high niche conservatism and phylogenetic geographic structure (Pennington et al. 2009). Such factors have an important role in determining the diversity and composition of woody plants in this ecosystem, characterized by high endemism and beta diversity at regional and continental scales with low species similarity between its major floristic nuclei and few widespread species (Gentry 1995; Trejo 2005; Gordon and Newton 2006; Linares-Palomino et al. 2010).

The biological distinctiveness of SDTF, coupled with its highly threatened status (Sánchez-Azofeifa and Portillo-Quintero 2011), makes it a priority to protect this ecosystem throughout its range and to produce local information that contributes to understanding of the factors that influence variation in species composition at different scales.

Environmental conditions, in addition to the distinctive evolutionary history, have a major influence in community composition of SDTF. Variability in species composition has been strongly related to precipitation gradients and evapotranspiration at continental and regional scales (Gentry 1995; Trejo and Dirzo 2002). Likely, environmental variables that influence water availability during the year at local scales are important drivers of species turnover. For example in Brazil, canopy openings and topographic and edaphic characteristics were found to influence species composition (Oliveira-Filho et al. 1998) whereas in Ecuador species composition was related to altitude, climate, soil variables related to water availability, soil nitrogen and slope (Espinosa et al. 2011). Furthermore, distributions of individual species in Mexico have been explained by variation in elevation, isolation and slope (Lott et al.1987, Balvanera et al. 2011).

Disturbance can also be an important factor affecting species composition of SDTF remnants, as observed by Wiliams-Linera and Lorea (2009) in Mexico. Secondary SDTF forests can possess high diversity but their composition and structure depend on the disturbance regime of the area and age since abandonment (Gordon et al. 2004, Molina and Lugo 2006, Larkin et al. 2012). For example in Puerto Rico, Roth (1999) observed that early successional stages of SDTF were characterised by shrubby vegetation dominated by native and exotic opportunists. In contrast, in areas of Mexico subject to low intensity disturbance, secondary vegetation showed high similarity in composition to conserved forest (Kalacska et al. 2004). However, the influence of environmental variables on successional trajectories at a local scale has been very little studied in tropical forests (Quesada et al. 2009; Guariguata and Ostertag 2001). For example, in SDTF of Costa Rica regional variation in species composition and diversity was better explained by stand age and forest types than soil properties (Powers et al. 2009) whereas in SDTF of Mexico soil properties explained more variation in plant composition than stand age (Dupuy et al. 2012). No other studies have tested the effect of environment on successional trajectories in this ecosystem, although potentially in areas subject to similar management local environmental heterogeneity could result in different routes towards late successional communities, particularly when high regional species richness is present.

This study will test this hypothesis by measuring the variation of SDTF composition in relation to both successional stage and environmental characteristics in a region of the Caribbean coast of Colombia. The aims of this study are to: (1) describe changes in plant community composition and structure during SDTF recovery; (2) examine the relationship between environmental variables and species composition in different successional stages; and (3) determine values of alpha and beta diversity in the region. We hypothesize that the environmental gradient will influence successional trajectories and result in increased regional beta diversity.

3.3 METHODS

The research was conducted in the Totumo region in the Caribbean coast of Colombia. The climate in the region is characterized by a mean annual temperature between 24 and 27.5 °C with maximum temperatures of 38 °C (IGAC 2004, 2008). Mean annual precipitation is around 900 mm distributed in a rainy season from April to December, with a decrease in precipitation during June and July, followed by a 5 month dry season. The landscape is characterized by small hills and foothills, which range in altitude between 30 and 200 m.a.s.l. On the hills, land relief is steep, with slopes between 10-75%, and is subject to moderate erosion (IGAC 2004, 2008). The main soil types are Typic Haplustepts and Ustorthents and Lithic Haplustolls, which are freely draining and have high base saturation. In the foothills and plains, the relief is flat and soils are developed from recent alluvial and fluvio-marine deposits. The dominant soil types are Haplustepts, Typic Argiustolls and Sodic Haplusterts, which have high base saturation and are poorly to moderately well drained

The region is characterized by a heterogeneous landscape where the main land cover type is cattle pasture. Other land cover types include shrubs and secondary forest derived from abandoned agricultural fields, remnant forest fragments and cultivated crops (mostly maize and yuca). Three sites ranging in area between 3 and 18 km^2, offering secondary vegetation of different ages and similar patterns of land use were selected for the study. The sites El Ceibal (10°37.19′ N, 75°14.28′ W) and La Gloria (10°37.78′ N, 75°12.56′ W) correspond to two privately owned farms that possess forest fragments of nearly 300 ha. The site El Palomar (10° 45.39' N, 75°09.22′ W) is composed of several privately owned farms that possess fragments of forest of approximately 60 ha each. Late forest remnants are relatively undisturbed although surrounding secondary vegetation is subject to cattle grazing and is periodically cleared for pastures and subsistence agriculture in the three sites. Forests in the area have been described as neotropical dry forests (Gentry 1995), with a mean canopy

height of 20 m. The most diverse families reported for the region are Leguminosae, Malvaceae and Bignoniaceae and some of the most abundant genera are *Cordia*, *Coccoloba*, *Senna*, *Paullinia*, *Trichilia*, *Acacia* and *Cynophalla* (Rodríguez et al. 2012).

3.3.1 Vegetation assessment along successional gradients

Vegetation sampling was conducted during 2011 using a stratified random design applied to existing land cover maps derived from remote sensing imagery. Random points were located in three forest cover types at each site. At each point, a 10 x 10 m plot was established and the vegetation surveyed. The age of abandonment and the disturbance regime of each plot were determined by interviews with local inhabitants. Using this information plots were differentiated according to years since abandonment, as either late (>40 years), intermediate (15-25 years) and early secondary vegetation (<12 years). A total of 126 vegetation plots were assessed, 15 per land cover type and site. Exceptions were the late secondary vegetation in the Cerro El Palomar where only 11 plots were established and the early and intermediate secondary vegetation in La Gloria where 12 plots were established in each cover type. A minimum combined sample size of 0.1 ha was used, as this has been used previously to describe floristic diversity in neotropical forests and is also expected to provide a reliable indication of the most abundant species in the area (Gentry 1995).

In each plot all individuals with a diameter at breast height (DBH) > 2.5 cm were recorded and identified. Height was estimated visually and when the species could not be determined in the field, plant samples were collected and processed in the Colombian National Herbarium (COL), where voucher collections were deposited. Voucher collections for most of the species are available at COL. Environmental characteristics of each plot were recorded including elevation, slope, flooding level during the wet season and proximity to seasonal and permanent water bodies based on field observations and cover maps (Supplementary information, Table 3.7). Measures of anthropogenic disturbance were also recorded in the field and from local testimonies, including: canopy cover measured as the mean value of four densitometer readings per location facing the cardinal points, fire frequency measured as the presence of burnt trees and ashes on the forest floor, grazing intensity measured as the presence of livestock faeces and trails and proximity to productive systems. Other field measures adapted from Tongway and Hindley (2005) included percentage of ground surface covered by bare soil and rock, soil crust brokenness, soil erosion type, soil surface roughness and surface nature (resistance to mechanical disturbance).

A mixed sample of surface soil (10 cm) was collected in each plot for analysis. The samples were periodically sent for analysis to the Soil and Water Laboratory of the Faculty of Agronomy at the National University of Colombia (Bogota). Organic oxidizable carbon (OC) was determined by the Walkley and Black procedure and colorimetric quantification, total nitrogen was estimated from OC by a factor of 0.0862, available phosphorus was determined by the Bray II procedure, exchangeable bases (Ca, Mg, K and Na) were determined by the ammonium acetate method and quantification by atomic absorption spectrometry, cationic exchange capacity was determined by the NN4 displacement method with NaCl and interchangeable acidity was determined by extraction with KCl 1M. Soil texture class, including percentage of sand, loam and clay, were determined following the Bouyoucos procedure and pH was measured in a 1:1 soil and water suspension by means of a potentiometer. Additionally, a core sample of 180.8 mm^3 of soil was extracted to calculate apparent density as the ratio between the oven-dried soil mass and the specified volume.

3.3.2. Data analysis

Environmental heterogeneity in the region was assessed by evaluating differences in environmental variables between sites and stages using a factor analysis of variance, with post-hoc Tukey tests applied when appropriate. Percentages variables were transformed using the logit function in the package car for R (Fox and Weisberg 2011) and variables that did not fit the assumptions of the analysis were log transformed. Those variables that did not meet the assumptions of the analysis after transformation were analysed by means of a Kruskal-Wallis test. Categorical variables were related to stage and site using a log-linear model, with subsequent reduction of terms to explore conditional dependence. To evaluate relations between variables a multiple correlation analysis was performed using Pearson's correlation coefficient. Relationships with crown cover, altitude and slope (which were not normally distributed, even after transformation) were analysed using Spearman's correlation coefficient. An analysis of principal components was carried out on the correlation matrix to explore the relations between environmental variables and the distribution of plots along the reduced ordination axis. For this analysis highly correlated variables were removed and no ordinal or categorical variables were included, for a total of 12 variables included in the ordination. These analyses were conducted using the software R (version 2.15.1, R Core Team 2012).

Changes in plant species composition during forest recovery were described as variations in the most abundant species as well as exclusive and shared species. Differences in forest structure between successional stages were evaluated by conducting analyses of

variance on the mean values of basal area, density of individuals and mean and maximum height; with post-hoc Tukey tests applied when appropriate. Individuals were also classified by DBH size into three categories: >30, 30-10 and <10 cm, and differences in the proportions of each category between successional stages were analysed by means of a Chi-squared test.

Species accumulation curves for each site were constructed using the Possion model on the sample-based abundance data (Colwell et al. 2012) and alpha diversity was estimated using the Shannon-Wiener index for each site and recovery stage, using the software EstimateS (v. 9.0.0, Colwell 2013). The Kruskal-Wallis test on aggregated data was used to compare the Shannon index of diversity between the three sites and stages. Beta diversity was estimated using the Chao abundance-based Jaccard index (Chao et al. 2005) on the dataset categorized by stand age and site. The relationships between plots on the basis of species composition were explored by means of a non-metric multidimensional scaling ordination.

In order to test the relationship between species composition and environmental variables, simple and partial Mantel tests were performed on the complete database and on subsets of each site. The species dissimilarity matrix was calculated using the Bray Curtis index on the log transformed data and the environmental data dissimilarity matrix was calculated using the Gower index, previously eliminating variables that were highly correlated. Partial tests controlled for the effect of spatial structure and stage category on the environmental variables and were included as independent matrices in the analysis. Differences in stage were calculated using the Gower index for a nominal variable and the spatial structure of the data was analysed by calculating the euclidean distance matrix from the latitude and longitude plane coordinates of the plots. Correlations were conducted using the Pearson coefficient, except for distance where the Spearman coefficient was used, and run with 1000 permutations.

To identify which environmental variables explained better the variation in species composition, a redundancy analysis was conducted on the species abundance data. This analysis was conducted on the complete dataset and on subsets categorized by successional stage. Uniques and singletons were removed from the data and the Hellinger transformation was applied to the abundance matrix to reduce the weight of rare species as recommended by Legendre and Gallagher (2001). Missing values in environmental variables were replaced by the mean in eight cases. Forward selection of the explanatory variables in the environmental data set was conducted using the ordistep function of the package vegan (Oksanen et al.

2011). The spatial structure was included as an additional data matrix composed of the nine terms of the polynomial function of the geographical coordinates. Variation partitioning was conducted following the subtractive procedure proposed by Borcard et al. (1992), which conducts three redundancy analyses of the abundance data to calculate the fraction of variance explained by the spatial data, the environmental data and both data together (Peres-Neto et al. 2006). All analyses were conducted using the vegan and cluster packages of the software R (Oksanen et al. 2012, Maechler et al. 2012).

3.4 RESULTS

3.4.1 Environmental and management characteristics

Analysis of variance of the environmental variables showed significant interactions between the factors stage and site in various cases (Table 3.1). All soil variables were significantly different between sites ($P < 0.001$). Soil textural characteristics were similar for El Palomar and La Gloria, but both sites differed from El Ceibal, demonstrating their higher apparent density, sand content and rock cover, and lower silt and clay content. This relates to the higher mean values of slope and altitude for the former sites (Table 3.1). On contrast organic matter content and cation concentrations were higher in El Ceibal, followed by La Gloria and El Palomar. Crown cover was significantly different between sites although these differences were small and only four plots presented values lower than 90 percent.

Fewer soil variables differed significantly when plots were grouped by successional stage ($P < 0.01$). Late-stage plots presented higher sand content and apparent density and lower silt content, Na and K than early forests and were located in higher slope areas, although these differences were mainly driven by the effect of the site La Gloria. They were also charcaterized by higher sand content and apparent density and lower silt content than early and intermediate stands. Ordinal variables that were associated with site were fire, proximity to productive systems, surface nature, roughness and erosion type; and only aspect was associated with successional stage. Flooding, water proximity and grazing were both associated with site and stage.

66

Table 3.1. Two-way analysis of variance of environmental variables recorded in 126 vegetation plots in a region of tropical dry forest. Probabilities ≤0.01 indicated in bold, P ≤0.05 in italics and bold. Values grouped by the same letter are not significantly different at P ≤ 0.05. Abbreviations: OC (organic carbon), EA (exchangeable acidity), ECEC (effective cation exchange capacity in meq/Hg), CEC (cation exchange capacity in meq/Hg), AD (apparent density), Soilc (bare soil cover), Rockc (soil rock cover), Ldepth (litter depth), Ccover (crown cover). Stage: early (E), intermediate (I) and late (L).

	Site				Stage				Site:Stage
	G	P	C	*P*	E	I	L	*P*	*P*
Altitude (m a.s.l.)	149.4a	81.3 b	30.8c	**<0.001**	79.9	87.7	90.5	0.368	**<0.001**
Slope (°)	19.9 b	20.2 b	7.2 a	**<0.001**	10.5 b	14.7 ab	21.2 a	**<0.001**	**<0.001**
pH	6.7 a	6.1 b	6.3 b	**<0.001**	6.20	6.30	6.60	0.089	***0.019***
OC (%)	2.09 b	1.58 b	2.97 a	**<0.001**	2.40	2.18	2.12	0.981	**0.002**
N (%)	0.18 b	0.14 b	0.26 a	**<0.001**	0.21	0.19	0.18	0.984	**0.003**
Ca (meq/Hg)	15.74 b	10.14 c	23.68 a	**<0.001**	17.99	15.77	16.38	0.696	**0.002**
K (meq/Hg)	0.54 b	0.31 c	0.81 a	**<0.001**	0.71 a	0.51 a	0.47 a	**0.002**	**0.002**
Mg (meq/Hg)	4.64 b	3.53 c	8.68 a	**<0.001**	6.28 a	5.71 a	5.14 a	***0.043***	0.277
Na (meq/Hg)	0.19 b	0.18 b	0.25 a	**0.002**	0.27 a	0.21 a	0.14 b	**<0.001**	0.567
EA (meq/Hg)	0 a	0.1 a	0.01 a	**0.005**	0.07 a	0.02 a	0.01 a	***0.016***	0.370
ECEC	21.12 b	14.267 c	33.44 a	**<0.001**	25.32	22.23	22.15	0.289	**0.003**
CEC	19.40 b	16.01 b	34.47 a	**<0.001**	26.43	23.26	21.21	0.076	0.243
P (mg/Kg)	18.31 b	9.84 b	29.76 a	**<0.001**	24.94	16.77	17.02	0.507	**0.007**
Clay (%)	13.1 b	16.4 ab	19.8 a	**<0.001**	17.86	17.02	14.88	0.247	0.528
Silt (%)	19.8 b	18.2 b	31.5 a	**<0.001**	25.2 a	24.4 ab	20.6 b	***0.011***	0.367
Sand (%)	67.1 a	65.5 a	48.4 b	**<0.001**	56.8 b	58.5 ab	64.4 a	***0.028***	0.528
DA (g/cm^3)	1.17 a	1.23 a	1.06 b	**<0.001**	1.11 b	1.15 ab	1.21 a	***0.008***	0.705
Soilc (%)	11.6 b	18.5 a	12.3 b	**<0.001**	15.3	14.1	13.0	0.504	**0.006**
Rockc (%)	3.0 ab	3.6 a	0.6 b	**0.006**	1.1 b	2.0 ab	4.0 a	***0.012***	**<0.001**
Ldepth (cm)	3.4 c	1.4 a	2.1 b	**<0.001**	1.9	2.4	2.6	0.050	***0.021***
Ccover (%)	95.7 b	98.6 a	96.2 b	**<0.001**	96.8	96.3	97.5	0.248	**<0.001**

Highly significant correlations were observed between environmental variables (Supplementary information, Table 3.8). Relationships between all cations (Ca, Mg and K) and the cation-exchange capacity were strong (*P* <0.001, r >0.7). High correlation

coefficients were also observed between N and organic C, and between nutrients concentrations, pH and the percentages of textural classes ($P < 0.001$). Altitude and slope showed significant correlations with all soil variables ($P < 0.001$), except Na. An ordination of the plots by principal component analysis explained 65% of the variation of the data in the three first axes (Figure 3.1). Loading of the environmental variables showed that the first axis was positively related to altitude, slope and sand content, and negatively to the interchangeable cation exchange capacity (ICEC) and K content; plots from El Ceibal were visibly differentiated from El Palomar and La Gloria in this axis. The second axis was positively related to N and litter depth and negatively to Na and bare soil cover. The third axis was negatively related mainly to pH and secondarily to P and rock cover.
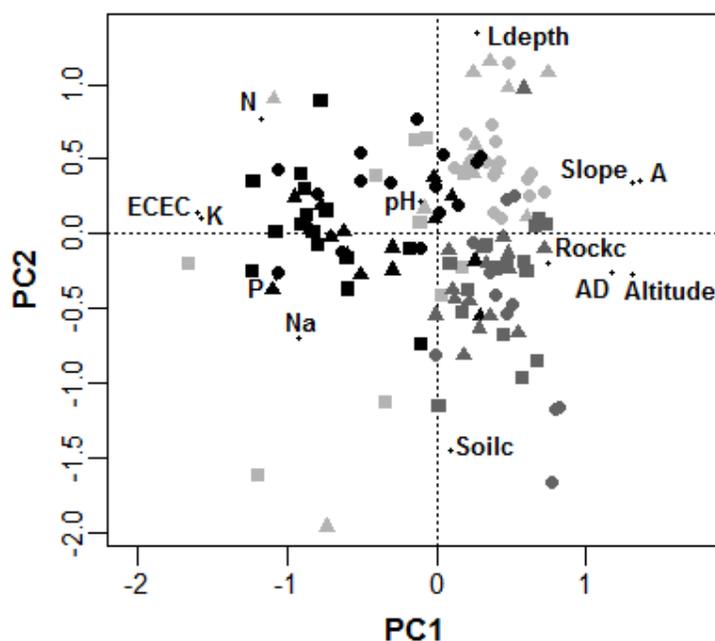
Figure 3.1. Correlation biplot of 13 environmental and soil variables in 126 field plots in a region of seasonally dry tropical forest in Colombia. Different colours indicate site: light grey (La Gloria), dark grey (El Palomar) and black (El Ceibal). Different signs indicate successional stage: square (early), triangle (intermediate) and circle (late).

3.4.2 Richness and composition

A total of 241 species from 57 families were recorded in the field survey (176 trees, 57 lianas, 4 palms, 2 cactus, 1 grass and 1 herb); eight species were identified to family and 20 as morphospecies. A similar number of species was recorded in all successional stages and

the lowest number of exclusive species was recorded in the intermediate successional forests, which also shared more species with both early and late forests (Table 3.2). Richness increased from early to late successional forests of El Ceibal whereas the opposite was observed in forests of El Palomar, forests of La Gloria showed highest richness in the intermediate stage. In terms of the sites, the highest number of species was recorded in El Palomar, which also showed the highest number of exclusive species and shared less species with the other two sites (Table 3.2). Similar numbers of individuals were recorded in all sites and the species accumulation curves did not reach an asymptote in either of the sites, reflecting the high number of rare species and a higher richness at the landscape scale than that observed in the plots (Figure 3.2). 75 species were found only in one of the plots and 56 species were recorded only as one individual.

Table 3.2. Species richness of SDTF classified by successional stage and site in a region of the Colombian Caribbean. Diagonal values indicate exclusive species and lower triangle values indicate shared species. N is 42, 43 and 41 plots of 10 x 10 m for early (E), intermediate (I) and late (L) successional stage forests, respectively. N is 39, 45 and 42 plots of 10 x 10 m for the sites La Gloria (G), El Ceibal (C) and El Palomar (P), respectively

	Stages					Sites			
	E	**I**	**L**	**Total**		**G**	**C**	**P**	**Total**
E	40			155	**G**	24			136
I	22	26		153	**C**	30	31		138
L	11	23	37	153	**P**	20	15	59	156
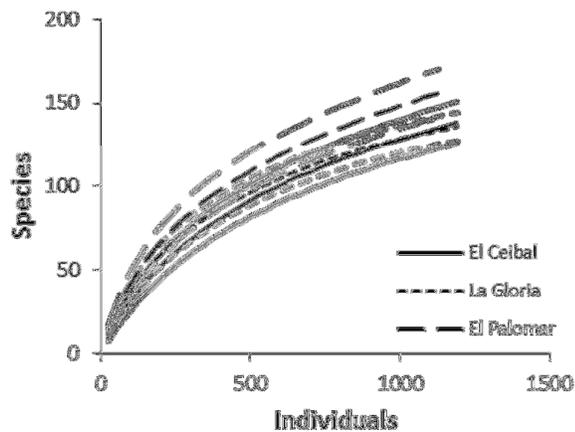
Figure 3.2. Individual sampled-based accumulation curves of three seasonally dry tropical forests in three sites of the Caribbean coast of Colombia. Grey lines show 95% confidence intervals.

The most important families in terms of the number of species in early and intermediate successional forests were Fabaceae, Bignoniaceae, Capparaceae and Rubiaceae, whereas in late successional forests Malvaceae reached the third place in importance. In terms of individuals, the most abundant families in early stage forests were Fabaceae, Lecythidaceae, Malvaceae and Bignoniaceae; in intermediate Fabaceae, Bignoniceace, Lecythidaceae and Capparaceae; and in late stands Fabaceae, Moraceae, Capparaceae, and Bignoniaceae. The 10 most abundant species differed markedly between sites and forest types (Table 3.3). Most of the species were abundant in one or two consecutive successional stages and usually showed a change in ranking position between the stages, which suggests dynamic species turnover during succession. Species important in early successional forest common to at least two sites were *Guazuma ulmifolia*, *Cordia collococca, Coursetia ferruginea* and *Pithecellobium lanceolatum*. In intermediate forest, common species were *Astronium graveolens*, *Capparidastrum frondosum* and *Lecythis minor*. In late stage stands, *Brosimum alicastrum*, *C. frondosum*, *Cynophalla verrucosa*, *Hura crepitans* and *Carpotroche grandifolia* were abundant species.

Table 3.3. The ten most abundant species in different successional stages of secondary seasonally dry tropical forests in three sites located in the Caribbean coast of Colombia. Abundance is expressed as number of individuals, and species are organized according to the frequency in age and site. Stages: early- E., intermediate- I., and late- L.

Scientific name	El Ceibal E	El Ceibal I	El Ceibal L	La Gloria E	La Gloria I	La Gloria L	El Palomar E	El Palomar I	El Palomar L
Capparidastrum frondosum		33	15		13	25		16	8
Astronium graveolens			16		19		25	19	7
Coursetia ferruginea	6	11					31	17	
Guazuma ulmifolia	41	23		25			19		
Lecythis minor	251	84	10		21				
Brosimum alicastrum					15	80			24
Carpotroche grandifolia		20	54			14			
Cordia collococca	41	17		17					
Cynophalla verrucosa						19		17	13
Hura crepitans						12		14	12
Memora patula				17	18	18			
Pithecellobium lanceolatum	13			31	28				
Trichila acuminate		9	11						25
Arrabidaea mollissima							10	12	

70

Species	1	2	3	4	5	6	7	8	9
Bauhinia glabra							19	16	
Bursera simaruba			9	8					
Caesalpinia coriaria							10		7
Centrolobium paraense			9	12					
Martinella obovata		8						13	
Machaerium microphyllum	9	7							
Tabebuia ochracea	5	11							
Acacia macracantha							11		
Acacia polyphylla					14				
Albizia niopoides				9					
Aspidosperma polyneuron								18	
Bignonia pubescens							13		
Bourreria cf. cumanensis						13			
Calycophyllum cf. candidissimum			15						
Clytostoma pterocalyx						14			
Combretum fruticosum									8
Cordia gerascanthus									7
Croton niveus								23	
Cynophalla flexuosa			11						
Guetarda cf. malacophylla									7
Inga cf. hayessi					13				
Lippia Americana				11					
Lonchocarpus cf. sanctae-marthae					16				
Maclura tinctoria				12					
Myrospermum frutescens	20								
Oxandra laurifolia				8					
Paullinia fuscescens							15		
Pradosia colombiana									8
Pterocarpus officinalis							10		
Ruprechtria ramiflora							20		
Sapium glandulosum	6								
Seguieria Americana						12			
Sorocea spruce									8
Swartzia simplex			9						
Tabebuia rosea	11								
Tabernaemontana grandiflora					21				
Talisia oliviformis						12			

3.4.3 Structure

Basal area and density of individuals did not show significant differences between successional stages whereas mean and maximum height did ($F = 27.14$, df $= 2$, $P < 0.001$; $F = 8.7$, df $= 2$, $P < 0.001$), which corresponds to grouping of early and intermediate forest stands on one side and late on the other (Table 3.4). The proportion of individuals present in the three DBH size categories differed from the expected frequencies ($X^2 = 23.35$, df $= 4$, $P < 0.001$) in each successional stage. The analysis of residuals showed that lower values than expected were observed of individuals with DBH < 10 cm in the late forest stands, of individuals with DBH between 10-30 cm in intermediate forests, and of individuals with DBH > 30 cm in early forests (Figure 3.3).
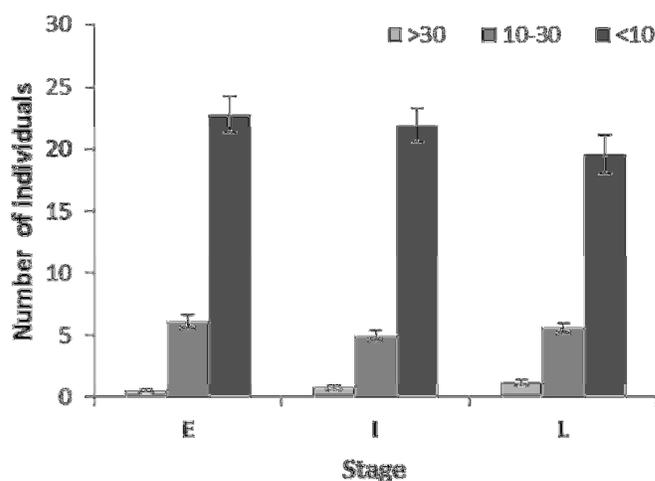
Figure 3.3. Number of individuals ($\overline{x} \pm$ S.E) in different DBH (cm) categories in three successional stages of tropical dry forests. E (early), I (intermediate) and L (late).

Lianas were an important structural component of the community and made up to 14.4% of the total of individuals recorded in early forest stands, 18.5% of intermediate and 14% of late. The mean percentage of total basal area contributed by lianas in a plot was of 5.1%, 6.7% and 3.8% in each successional stage, respectively (Table 3.4). In terms of species representation, lianas corresponded to 35 of the species found in early stands, 37 in intermediate and 31 in late. However, there was also a significant effect of site determining liana abundance. In terms of sites the overall number of lianas as a percentage of total number of individuals was clearly lower in El Ceibal (9%) compared to El Palomar (22%) and La Gloria (17%), and changes in abundance between stands varied in each site. Density

of lianas increased from early to late successional forests in La Gloria, decreased in El Palomar and was higher in intermediate stands in El Ceibal.

Table 3.4. Summary of structural characteristics of three successional stages of seasonally dry tropical forests. Values of basal area and number of stems indicate $\bar{x} \pm$ SE. N is 42, 43 and 41 plots of 10 x 10 m for early, intermediate and late stage, respectively. Rows with different letter in the same column indicate significant differences at $P < 0.05$.

Stage			Total		Lianas	
	Maximum height (m)	Mean height (m)	Basal area (m²/ha)	N. stems (ha)	Basal area (m²/100m²)	N. stems (100m²)
Early	12 ± 0.6 b	5.7 ± 1.1 b	24.7 ± 3.8	2942 ± 454	5.2 ± 1	5.5 ± 0.6
Intermediate	14.1 ± 0.8 b	6.1 ± 0.3 b	27.4 ± 4.2	2772 ± 428	7.6 ± 1.7	5.3 ± 0.5
Late	19 ± 0.7 a	7.0 ± 1.7 a	35.4 ± 5.5	2646 ± 408	4.8 ± 1.4	4.6 ± 0.6

3.4.4 Diversity

Species diversity evaluated by means of the Shannon diversity index showed a significant interaction between successional stage and site (H = 44.6, $P < 0.001$, df 8). Diversity in the site El Ceibal increased from early to late succesional stage forests, whereas it decreased slightly in El Palomar and La Gloria (Figure 3.4). Mean plot species diversity did not show difference between successional stages (H = 5.4, $P = 0.07$, df 2); although diversity increased slightly from early (3.94), to intermediate (4.36) and late (4.27) successional stages when pooling all vegetation plots. Between sites, species diversity showed significant differences (H = 24.5, $P < 0.001$, df 2), specifically between El Ceibal, showing the lowest mean plot diversity (1.75), and El Palomar and La Gloria (2.4 and 2.2, respectively).

Overall, composition similarities were high between early and intermediate and between intermediate and late successional stages forests (0.788 and 0.78, respectively), whereas similarity was lower between early and late stages (0.638). The highest species similarity was observed between stages in each site, except for early and late successional stage forest in El Ceibal, and the lowest was observed between early and late stage forests of different sites (Table 3.4). Mean similarity between late stage forests of all sites was higher than between intermediate and early age stages, with the highest value recorded between El

73

Ceibal and La Gloria. Ordination of the plots based on species composition and abundance located late successional plots of the three sites in the left of the first axis, showing species similarity among them (Figure 3.5). Early and intermediate plots on the contrary showed a more distinct composition with plots from El Ceibal mainly located in the right of the first axis and plots from El Palomar on the centre; plots from La Gloria showed a more disperse distribution.
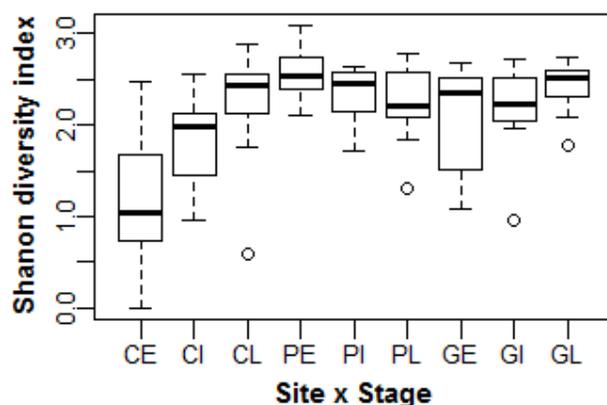
Figure 3.4. Shannon diversity index of seasonally dry tropical forest grouped by successional stage and site in the Caribbean coast of Colombia. The analysis was conducted in a subset of 11-15 plots per site and stage. Bars indicate standard deviation. Site = El Ceibal (C), El Palomar (P) y La Gloria (G). Stage = early (E), intermediate (I) and late (L).

Table 3.5. Species similarity between different successional stages and sites expressed by the Chao abundance-based Jaccard index. E (early), I (intermediate) and L (late).

		Gloria			Palomar			Ceibal	
		E	I	L	E	I	L	E	I
Gloria	E								
	I	0.681							
	L	0.558	0.584						
Palomar	E	0.363	0.374	0.373					
	I	0.389	0.396	0.457	0.626				
	L	0.264	0.307	0.439	0.502	0.658			
Ceibal	E	0.517	0.419	0.144	0.322	0.271	0.169		
	I	0.504	0.46	0.432	0.5	0.527	0.507	0.563	
	L	0.283	0.471	0.591	0.353	0.438	0.441	0.24	0.569
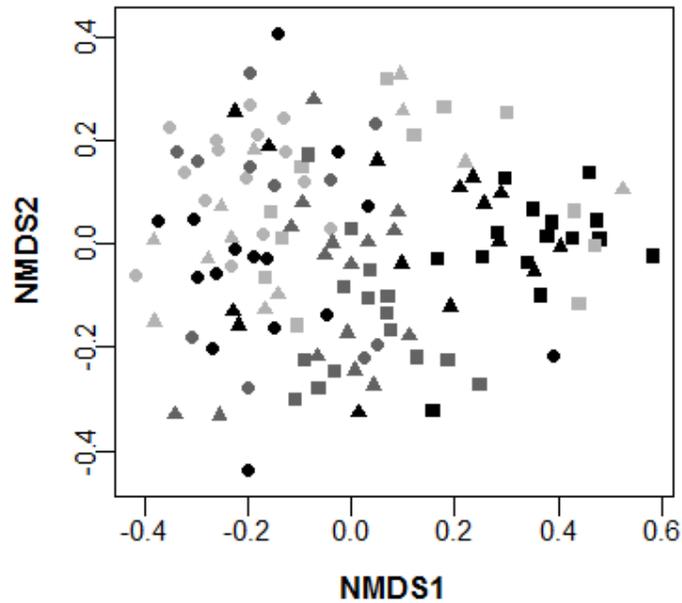
Figure 3.5. Non metric multidimensional scaling of vegetation plots using Chao abundance-based Jaccard index. Stress value: 0.22. Different symbols indicate successional stage: early (square), intermediate (circle) and late (triangle) secondary forests. Different colours indicate sites: El Ceibal (black), La Gloria (dark grey) and El Palomar (light grey).

3.4.5 Composition and environmental variables

The results of the Mantel tests showed that correlation between species composition dissimilarity displayed a high correlation with environmental variables dissimilarity in all cases (Table 3.6). The correlation of species composition with forest successional stage was also significant but with a lower coefficient. Low spatial structure was detected for the species composition and the environmental variables when considering the complete dataset, whereas it was not significant in any site.

The explanatory power of the redundancy analysis was significant in all cases and the variables maintained by forward selection for the complete data set reflected the topographic gradient observed in the region and its effect on soil properties. The variables maintained by forward selection varied when considering data for each successional stage separately and no variable was shared among the three stages (Table 3.7). The fraction of variance explained by the environmental variables was similar between stages, whereas the spatial structure and the variation explained jointly by both data sets reached the highest values for the early stage forest data.

75

Table 3.6. Simple Mantel correlation coefficients and one-sided p-values for associations between species composition, environmental variables, stand age, and space (top). Partial Mantel correlation coefficients for associations between species composition and soil properties or stand age controlling the effects of space and stand age (bottom). In bold probabilities ≤ 0.01.

	All		Gloria		Ceibal		Palomar	
	R	*P*	r	*P*	r	*P*	r	*P*
Species*Space	0.11	**0.001**	-0.05	0.777	-0.05	0.862	-0.01	0.504
Species*Env.	0.33	**0.001**	0.59	**0.001**	0.41	**0.001**	0.19	**0.002**
Species*Stage	0.17	**0.001**	0.18	**0.001**	0.33	**0.001**	0.15	**0.002**
Env.*Stage	0.05	**0.001**	0.09	**0.008**	0.17	**0.001**	0.02	**0.185**
Env.*Space	0.15	**0.001**	-0.04	0.659	-0.04	0.771	0.05	0.235
Stage*Space	0.00	0.313	-0.02	0.778	0.10	**0.009**	0.01	0.314
Species*Env./Stage	0.33	**0.001**	0.58	**0.001**	0.38	**0.001**	0.18	**0.002**
Species*Env./Space	0.33	**0.001**	NA	NA	NA	NA	NA	NA
Species*Stage/Space	0.17	**0.001**	NA	NA	0.34	**0.001**	NA	NA
Species*Space/Env.	0.06	**0.002**	NA	NA	NA	NA	NA	NA

Table 3.7. Variance partitioning of 126 vegetation plots in a region of SDTF explained by environmental variables and spatial structure. Analyses were conducted using the complete data set and categorized by successional stage.

	Environment		Spatial			
	R^2_{adj}	*P*	R^2_{adj}	Intersection	Residual	Variables
All	0.11	0.001	0.03	0.06	0.80	K, stage, pH, soil cover, slope, Na, ECEC, roughness, altitude, fire, sand, crown cover, soil apparent density
Early	0.13	0.001	0.07	0.12	0.69	ECEC, N, pH, rock cover, altitude, surface nature, soil cover
Intermediate	0.10	0.001	0.04	0.02	0.85	K, litter depth, aspect, grazing
Late	0.11	0.001	0.01	0.06	0.82	pH, altitude, sand, K, Na, roughness, soil apparent density, ECEC

76

3.5 DISCUSSION

In the study area examined here, an environmental gradient was identified from low and flat areas in Ceibal, with high concentration of soil nutrients and low sand content, to higher and steeper areas in Gloria and Palomar with lower concentration of nutrients and higher sand content. This gradient is likely to be associated with variation in water availability, given the variation in soil water potential associated with topography observed in other SDTF (Markesteijn et al. 2010). Soils on steeper slopes will retain water for less time during the dry season, whereas in low-lying areas, increased water availability can result from flooding events during the rainy season. Results of this investigation showed few relationships between successional stage and edaphic characteristics. The decrease in concentration of Na and K from early to late stage forests agrees with observations during the first 20 years of succession in other SDTF (Leiva *et al*. 2009a, Toniato and Oliveira-Filho 2004), whereas the increasing soil sand content and apparent density observed in late stage forest relates to their tendency to be located on higher slopes.

3.5.1 Community composition and stand age

The total number of species recorded here was similar to other chronosequence studies of SDTF in Mexico (236, González-Iturbe *et al*. 2002), but higher than studies in Costa Rica (159, Kalacska *et al*. 2004) and Providencia Island (72, Ruiz *et al*. 2005). The mean number of species recorded in 0.1 ha of intermediate- and late-stage stands (70) was similar to other forests of this type in Colombia (60, Mendoza-C 1999) and the neotropics (mean 64, Gentry 1995). Additionally, 18 endangered plant species previously reported in the region were recorded in this study (Rodríguez *et al*. 2012). The highest number of total and exclusive species observed in Palomar, the site that showed the lowest soil nutrient concentration and the highest soil cover, disagrees with results obtained in Costa Rica, where lowest richness of species was observed in low fertility soils (Powers *et al*. 2009).

Changes in composition during the successional process were substantial. Some 60 percent of the species were abundant in just one stage / site category and 25 percent in more than three. Although most of the exclusive species in each successional stage were recorded from only one individual, I also observed some abundant species such as *Bravaisia integerrima*, *Colubrina heteroneura*, *Sapium glandulosum* and *Pterocarpus officinalis* in early stands; *Lonchocarpus* cf. *sanctae-marthae* in intermediate; *Gyrocarpus americanus* and *Guettarda* cf. *malacophylla* in late stands. There was also a group of frequent species

that were present in plots of all stages. These consisted of a group of regionally distributed species including *C. ferruginea*, *L. minor*, *C. verrucosa* and *C. frondosum*, and a group of widespread species that includes *G. ulmifolia*, *H. crepitans*, *A. graveolens*, *Swartzia simplex*, *Tabebuia ochracea*, *Bauhinia glabra, Bursera simaruba*, *B. alicastrum* and *Talisia oliviformis*. Interestingly, some of the species in this latter group have been classified as ecological generalists that can be present in other ecosystems (*sensu* Linares-Palomino et al. 2011), whereas four of the species exclusive of late stage forests, *Aspidosperma cuspa*, *Pterocaprus rohrii*, *Trichilia hirta* and *Luehea candicans*, are widespread seasonally dry forest specialists. The results suggest that as succession progresses the presence and importance of both SDTF generalist and specialist species can increase; a suggestion that requires further verification. For example, Capparaceae, a dry forest specialist family (Gentry 1995), increased considerably in abundance from early to intermediate and to late-stage stands in all sites.

The density of individuals was expected to peak in early successional stages as a result of the rapid recruitment of pioneer species followed by high mortality in intermediate and late stages (Kalacska et al. 2004, Lebrija-Trejos et al. 2010, Chazdon et al. 2010). This pattern, as well as a significant increase in basal area between early and late stands, was not observed. This may be because the very early stages of succession were excluded, where rapid changes in structural variables have been observed in other studies. The value of basal area observed in late-stage stands was similar to the values reported for 40-60 year-old and mature SDTF in Costa Rican and Bolivia (Kennard 2002, Leiva et al. 2009b).

Liana diversity and abundance has been observed to increase with disturbance and rainfall seasonality (Schnitzer and Bongers 2002, 2011; Wright et al. 2004). Additionally to these factors, topography could be influencing the differences in abundance between sites in our study area. Plots of El Ceibal, located in flat areas with higher nutrient content and availability of water during the wet season, showed less lianas compared to sites characterized by steeper slopes like Palomar and Gloria. Higher abundances of lianas in intermediate forests in El Ceibal agree with observations by Madeira et al. (2009) in Brazilian SDTF occurring also in a flat topography area. These authors explained their observation by a trade-off between light and support availability during regeneration with late stage forest presenting the highest number of large trees for support but the lowest light availability. In contrast, higher abundance of lianas in late stage forest agrees with observation by Sánchez-Azofeifa et al. (2009) in SDTF located in hilly sites of Mexico. The decrease in liana abundance at late stands in El Palomar can be explained by the higher disturbance observed, which can limit understory vegetation growth.

3.5.2 Alpha and beta diversity

The highest similarity between stands was observed between intermediate- and late-stage stands in each site. This supports observations in other SDTF indicating higher similarity as succession progresses (Lebrija-Trejos et al. 2008). The higher mean similarity of late stands between sites is also notable, and suggests that variation in the successional trajectories owing to environmental characteristics and disturbance regime is higher at initial stages. Similarity values for late stands recorded here were much higher than those obtained for forest fragments in Mexico (Williams-Linera & Lorea 2009), which were smaller and more isolated than those examined here. In contrast, these values are lower than those reported between late stage forests of 60 to >100 years in Costa Rica (Leiva et al. 2009b). These authors also found, in contrast to our results, very high similarity between early and intermediate sites, even when considering different soil types.

No differences were observed in species diversity between plots differing in successional stage. When pooling all the plots sampled, lower diversity was observed in early compared to intermediate and late successional stage forest, result that agrees with observations in SDTF in Mexico (Kalacska et al. 2004). However, there was a high influence of the site on the diversity patterns observed during succession. The continued increase in diversity during succession observed in El Ceibal can be explained by the decreasing dominance of *L. minor*, a native species with high sexual and vegetative reproductive success, which has likely been favoured by disturbance and flooding in this site. The decrease in diversity observed in late forests in La Gloria can be explained by the dominance of *B. alicastrum,* whereas in El Palomar this might have been influenced by the considerable decrease in the number of individuals observed (271 versus 433 and 427 in early and intermediate stages, respectively). This decrease can be related to the clearing of understory, a common practice to facilitate livestock access, however, it is interesting that the considerable decrease in stem density was not reflected in species richness, which was highest at this site.

3.5.3 Community composition and environment

A significant correlation between species composition and environmental variables was consistently observed in this investigation, even when controlling for the effects of successional stage and spatial structure. These results agree with Dupuy et al. (2012) underlining the stronger effect of soil properties compared to stage shaping this plant community, in contrast to observations by Powers et al. (2009) in Costa Rica. The strength

of the relationship between environmental characteristics and species composition at each site seems to be increased by the influence of the successional stage on both.

A number of different processes may account for the portion of variation not explained by the environment, including dispersal limitation (Legendre et al. 2009, Tuomisto et al. 2003) and differences in disturbance regime that were not captured by the field survey. Both factors would be expected to be represented in the spatial structure of the data; however, the percentage of variation explained by the spatial structure of the data was low. The influence of environmental filtering on the plant community can also potentially change during succession (Campetella *et al.* 2011). For example, the relationship between environmental variables and plant species composition in SDTF has been observed to vary when different diameter categories are considered (Wiliams-Linera and Lorea 2009; Toniato and Oliveira-Filho 2004). In this study, when considering the successional stages separately, a higher portion of variation was explained for early stage forest owing to an increase of the importance of the spatial structure. Variables relating to anthropogenic disturbance were selected when considering the intermediate stands and the complete dataset, reflecting the effects of grazing and the occasionally fire spread into the forest during charcoal production reported by the local inhabitants. The effect of livestock determining community composition and richness has also been detected in SDTF in Mexico (Williams-Linera and Lorea 2009).

An additional factor that has been observed to explain composition variation in secondary SDTF is the degree of forest fragmentation (López-Martínez *et al*. 2013) which was not taken into account in our study. Moreover, at the species level the importance of environmental variables, historical events and local dispersal limitation can vary (Svenning et al. 2006). It is possible that the complexity of these processes cannot be fully explained by the orthogonal axes provided by the canonical ordination employed here.

In conclusion, species composition varied among sites and a higher portion of this variation was explained by environmental characteristics than successional stage. The high beta diversity observed was favoured by the environment and management characteristics. Overall, our results suggest than different groups of species can be favoured by local conditions especially at early and intermediate stage forests influencing successional trajectories. Species turnover between successional stages also suggested a shift from ecological generalists present in other ecosystems to species characteristic of SDTF.

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3.7 SUPPLEMENTARY INFORMATION

Table 3.8. Units and categories of environmental variables considered in this study.

Soil variables	Units	Soil variables	Units
pH	Continuous	*Cation exchange capacity (CEC)*	Continuous (meq/Hg)
Organic oxidizable carbon (OC)	Continuous (%)	*Effective cation exchange capacity (ECEC)*	Continuous (meq/Hg)
Nitrogen (N)	Continuous (%)	*Phosphorus (P)*	Continuous (mg/Kg)
Calcium (Ca)	Continuous (meq/Hg)	*Clay content (C)*	Continuous (%)
Potassium (K)	Continuous (meq/Hg)	*Silt content (Si)*	Continuous (%)
Magnesium (Mg)	Continuous (meq/Hg)	*Sand content (S)*	Continuous (%)
Sodium (Na)	Continuous (meq/Hg)	*Apparent density (AD)*	Continuous (g/cm^3)
Exchangeable acidity (EA)	Continuous (meq/Hg)		

Site and management variables	Units
Altitude	Continuous (m a.s.l.)
Aspect	north, east, south, west
Canopy cover (Ccover)	Continuous (%)
Flooding level	0 = does not present flooding, 1 = flooding lower than 50 cm or for short time (hours), 2 = flooding higher than 50 cm or long time (days)
Grazing	0 = no evidence or local testimonies, 1 = local testimonies declare grazing occurred more than 10 years ago, 2 = No evidences found but local testimonies declare grazing occurs actually or recently (less than 8 years), mainly in places where livestock moves during the dry season looking for food, 3 = Evidences (sighting, tracks, faeces)

Water bodies proximity	0 = Less than 50 m from a permanent stream, pond or lake; 1 = Less than 50 m from a seasonal creeck; 2 = More than 100 m from a permanent stream, pond or lake, 3 = More than 200 m from a permanent stream, pond or lake; 4 = No near water bodies
Fire	0 = No fire evidences; 1 = Testimonies from local residents dating previous fires, no evidences found; 2 = Fire evidences (burned logs, carbonized soil)
Productive systems proximity	1 = Less than 100 m from pastures or crops, 2 = More than 100 m from pastures or crops, 3 = No near productive systems

Surface variables (measured in five 1 x 1 m quadrants per plot).

Surface cover	Continuous. Percentage of bare soil (Soilc) and rock cover (Rockc).
Litter depth (Ldepth)	Continuous (cm)
Erosion type	0 = Nil, 1 = Run-off, 2 = Rills, 3 = Pedestalling and/or terracetes
Surface roughness	0 = Shallow depressions, less than 25 mm; 1 = Moderate depressions, 25 < 100 mm; 2 = Deep depressions >100 mm
Surface nature	0 = Surface not crusted or weak crust, sub-crust not-coherent; 2 = Crust moderately or very hard, breaking into amorphous fragments, sub-crust coherent

Table 3.9. Correlation among a set of environmental variables of 126 plots in a region of seasonally dry tropical forest. Lower cells show Pearson correlation coefficient and upper cell show probability values; except for altitude, slope, ccover and rockc for which Spearman coefficient is presented. For abbreviations and units see table S1.

	pH	OC	N	Ca	K	Mg	Na	EA	ECEC	CEC	P	C	Si	S	AD	Altitude	Slope	Ccover	Soilc	Rockc	Ldepth
pH		0.457	0.456	0.000	0.085	0.019	0.008	0.000	0.045	0.367	0.000	0.000	0.546	0.030	0.657	0.005	0.345	0.298	0.620	0.158	0.017
OC	-0.07		0.000	0.000	0.000	0.000	0.046	0.035	0.000	0.000	0.000	0.009	0.001	0.000	0.000	0.000	0.000	0.091	0.001	0.044	0.037
N	-0.07	1		0.000	0.000	0.000	0.048	0.039	0.000	0.000	0.000	0.009	0.001	0.000	0.000	0.000	0.000	0.088	0.000	0.044	0.031
Ca	0.34	0.58	0.58		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	0.010	0.199	0.003	0.376
K	0.15	0.61	0.62	0.82		0.000	0.000	0.087	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.009	0.868	0.012	0.759
Mg	-0.21	0.4	0.4	0.68	0.64		0.000	0.582	0.000	0.000	0.029	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.034	0.000	0.464
Na	-0.23	0.18	0.18	0.4	0.47	0.7		0.113	0.000	0.000	0.019	0.000	0.000	0.000	0.000	0.000	0.000	0.410	0.376	0.012	0.008
EA	-0.45	-0.19	-0.18	-0.32	-0.15	-0.05	0.14		0.013	0.446	0.116	0.076	0.969	0.267	0.030	0.028	0.633	0.121	0.013	0.570	0.006
ICEC	0.18	0.56	0.56	0.97	0.82	0.84	0.54	-0.22		0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.004	0.132	0.000	0.801
CEC	-0.08	0.5	0.5	0.79	0.73	0.83	0.59	-0.07	0.87		0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.050	0.230	0.000	0.372
P	0.45	0.4	0.4	0.59	0.68	0.19	0.21	-0.14	0.52	0.37		0.159	0.000	0.000	0.003	0.000	0.000	0.387	0.011	0.471	0.478
AR	-0.32	0.23	0.23	0.42	0.5	0.65	0.52	0.16	0.54	0.59	0.13		0.000	0.000	0.003	0.003	0.001	0.270	0.499	0.001	0.038
L	-0.05	0.31	0.31	0.66	0.62	0.76	0.62	0	0.75	0.75	0.34	0.61		0.000	0.000	0.000	0.000	0.036	0.977	0.000	0.133
S	0.19	-0.31	-0.31	-0.62	-0.66	-0.79	-0.66	-0.1	-0.74	-0.77	-0.31	-0.86	-0.92		0.000	0.000	0.000	0.063	0.997	0.000	0.027
AD	0.04	-0.44	-0.44	-0.5	-0.5	-0.46	-0.41	0.19	-0.52	-0.47	-0.26	-0.26	-0.48	0.44		0.000	0.000	0.378	0.049	0.000	0.833
Altitude	-0.17	-0.46	-0.46	-0.68	-0.71	-0.61	-0.42	0.2	-0.7	-0.6	-0.54	-0.32	-0.58	0.51	0.41		0.000	0.000	0.610	0.000	0.386
Slope	0.06	-0.34	-0.34	-0.48	-0.59	-0.49	-0.45	-0.04	-0.53	-0.51	-0.41	-0.4	-0.55	0.53	0.44	0.67		0.146	0.607	0.000	0.001
Ccover	-0.12	-0.26	-0.27	-0.24	-0.24	-0.26	-0.11	0.14	-0.27	-0.18	-0.05	-0.02	-0.14	0.08	0.11	0.38	0.13		0.041	0.000	0.000
Soilc	0.04	-0.31	-0.31	-0.12	-0.02	-0.19	0.08	0.22	-0.13	-0.11	0.23	-0.06	0	0	0.18	0.02	-0.09	0.1		0.004	0.000
Rockc	0.14	-0.29	-0.28	-0.4	-0.37	-0.51	-0.3	0.05	-0.47	-0.46	-0.11	-0.38	-0.5	0.48	0.44	0.44	0.66	0.32	0.29		0.742
Ldepth	0.23	0.3	0.3	0.13	0.05	-0.06	-0.3	-0.24	0.05	-0.06	-0.08	-0.19	-0.12	0.19	-0.06	-0.08	0.29	-0.33	-0.51	-0.03	

CHAPTER 4 SUCCESSIONAL AND ENVIRONMENTAL GRADIENTS INFLUENCE PLANT FUNCTIONAL TRAIT COMPOSITION IN TROPICAL DRY FOREST

4.1 ABSTRACT

The study of the recovery of tropical forests following disturbance has centred on the description of changes in species composition and structure. However, the changes in functional composition that occur during this process are not well understood. This study addressed the following questions: How does plant functional trait composition change over successional and environmental gradients in a region of seasonally dry tropical forests? What is the relationship between functional composition and species richness in forest stands of different successional stage? Plant community data were obtained from 123 vegetation plots randomly located in three sites in the Caribbean coast of Colombia and categorized by successional stage: namely early, intermediate and late. Environmental and management characteristics were also recorded in each plot and functional trait information was recorded for those species that contributed to 70% of basal area. The analysis of community weighted mean (CWM) values by means of analysis of variance showed significant differences between stages for stem related traits, whereas most leaf traits differed between sites. Comparisons of species' trait frequency distribution only showed differences between stages for stem density, whereas no differences were observed between sites. The assessment of the relationship between CWM trait values and environmental variables by means of a redundancy analysis and the fourth-corner method showed that functional composition was strongly influenced by environmental characteristics and a shift of traits from acquisitive to conservative type species with increasing nutrient content and flooding, proxies of water availability. From the early to late stages of succession a similar shift was observed, particularly in stem density, as well as a decrease in the frequency of traits that favour survival after disturbance. These results present evidence of similar functional trait diversity between stages and suggest that differences in functional composition were due to changes in species abundances.

4.2 INTRODUCTION

The widespread depletion of biodiversity in tropical ecosystems has raised concerns about the consequences of species loss on ecosystem function and the role of species identity in modulating this effect. It has been widely accepted that the functional characteristics of species should be addressed when considering their effects on ecosystem function (Hooper and Vitousek 1997; Lavorel and Garnier 2002; Hillebrand and Mathiesssen 2009) and that species' abundance is an important factor influencing this effect (Aarssen 1997; Huston 1997; Grime 1998; Conti and Díaz 2013). In the tropics, forested ecosystems are subjected to strong disturbance pressures, which range from selective harvesting of trees to complete clearing. Secondary forests observed after the abandonment of cropland or pastures are typically characterized by a lower number of species than relatively undisturbed areas (Kalacska et al. 2004; Kupfer et al. 2004; Lebrija-Trejos et al. 2008). They may also be characterized by different species composition even if structural characteristics and species richness are similar to those of relatively undisturbed forests (Aide et al. 2000). However, a key question that remains unresolved is whether secondary forests are associated with a similar functional diversity compared to mature forests and whether they can accomplish the same ecosystem functions.

Plant trait analysis is a useful approach to address this question as it allows the identification of different axes of variation and provides an understanding of the range of ecological strategies demonstrated by plants (Petchey and Gaston 2006; Westoby and Wright 2006). It is also a useful tool to predict responses to disturbance and to identify similarities among species in ecological behaviour (Grime et al. 1997). Traditionally, tropical plant species have been classified into two ecological groups based on their regeneration strategy, namely pioneer species whose seeds can only germinate under light conditions and non-pioneer species whose seeds can geminate in the shade (Swaine & Whitmore 1988). However, increasing availability of plant functional trait information has shown that between these two extremes there is a wide variety of plant strategies and the establishment of species with particular traits is not completely restricted to one phase of the successional process (Martínez-Garza et al. 2005; van Breugel et al. 2007; Bongers et al. 2009, Chazdon et al. 2010). Global analyses of plant functional trait variation have found evidence of a common dimension of variation related to resource use (Wright et al. 2004; Díaz et al. 2004), which for tropical trees has mainly been related to a continuum of adaptive response to light availability (Denslow 1987). Position of plant species along this continuum, where variation in leaf traits plays an important role, has been closely correlated with plant performance and mortality (Poorter and Bongers 2006; Wright et al. 2010). In dry forests, traits conferring

adaptation to low water availability also have been shown to have a major influence on survival (Ackerly 2004; Poorter and Markjesteijn 2008). Furthermore, it has been observed that different sets of plant traits can be related to plant performance along different resource gradients in the same location (Easdale et al. 2007; Markesteijn and Poorter 2009), and that correlations between traits of tree species can vary depending on whether a successional or a vertical light gradient is considered (Falster and Westoby 2005). Reproductive traits have also been observed to play an important role in influencing species presence and abundance at the earliest stages of succession (Viera and Scariot 2006; Quesada et al. 2009), whereas in undisturbed conditions or in late-successional forest, they show wide variation (Cornwell and Ackerly 2010; Wright et al. 2010).

In a heterogeneous landscape subject to disturbance, both successional and environmental gradients can potentially influence plant functional diversity. Changes in community trait values are therefore expected to shift with the functional identity of its dominant species in association with changing environmental conditions (Cornwell and Ackerly 2009) and the successional process (Lebrija-Trejos et al. 2010). Under these circumstances, functional composition found at a specific location will depend on the filtering action of both the biotic and abiotic gradients (Díaz et al. 1999; Kraft et al. 2008). For example, Lohbeck et al. (2013) observed that successional changes in wet and dry forests were characterized by different suites of traits, which they related to differences in the environmental filters acting on the communities. In addition, in species-rich ecosystems high functional redundancy is expected to occur (Fonseca and Ganade 2001), given that natural variation of plant traits is limited by trade-offs and life history strategy mechanisms (Westoby and Wright 2006). It is therefore possible that a forest recovering after a major disturbance (such as clearance for agriculture) might recover its functional diversity more rapidly than its species richness (Guariguata and Ostertag 2001). However, few studies have examined how variation in plant species traits relates to species richness during succession. In tropical rain forests of Mexico, Lohbeck et al. (2012) found that weighted functional and species diversity increased linearly in the 25 years following disturbance. Further data are needed to understand this relationship, particularly in seasonally dry tropical forests (SDTF) where no previous studies have considered simultaneously the effect of both successional and environmental gradients.

The aim of this investigation is to assess the plant functional composition of secondary STDF differing in successional stage and examine the variation of plant functional traits in relation to environmental characteristics in a region of the Caribbean coast of Colombia. The research addressed the following questions: a) how does plant functional trait composition

change along a successional chronosequence in a region of tropical dry forest? b) what is the relationship between functional trait composition and species richness in different stages of succession? c) how do plant functional traits relate to environmental characteristics along a topographic gradient? Specifically, this research tests the hypothesis that different sets of traits will be related to the successional and topographic gradients considered and that environmental conditions, especially those related to water availability, will have a strong effect on plant traits. Additionally, assuming that species-rich communities tend to have high functional redundancy (Naeem 1998; Fonseca and Ganade 2001), similar functional trait diversity will be expected between secondary forests differing in successional stage despite differences in species richness.

4.3 METHODS

4.3.1 Study area

This study was conducted in the Totumo region of the Caribbean coast of Colombia to the west of the Magdalena river. The climate is similar through the region and is characterized by a mean annual temperature between 24 and 27.5 °C with maximum temperatures of 38 °C (IGAC 2004, 2008). Mean annual precipitation is around 900 mm and is distributed during the year in a rainy season, from April to December with a decrease in precipitations during June and July, followed by a dry season from early December to late April.

Three small regional protected areas (3-18 km^2) that encompass relatively conserved forest fragments and differently aged secondary vegetation were selected for this study. The sites of El Ceibal (10°37.19′ N, 75°14.28′ W) and La Gloria (10°37.78′ N, 75°12.56′ W) correspond to two privately owned farms that possess forest fragments of nearly 300 ha, while the site El Palomar (10° 45.39' N, 75°09.22′ W) is composed of several privately owned farms that possess three fragments of forest of approximately 60 ha each and others of smaller size (>10 ha). The main land use in the region is pastures for cattle, followed by slash and burn agriculture of maize, yuca and other food crops. Cattle pasture is common in the secondary vegetation at the three sites although it is limited by land topography. Forests that originally dominated the region have been described as neotropical dry forests, and the most diverse families are Leguminosae, Malvaceae and Bignoniaceae (Gentry 1995; Rodríguez et al. 2012). The forest canopy has a mean height of 20 m and the most representative species are *Astronium graveolens*, *Capparidastrum frondosum*, *Lecythis*

minor, *Trichilia acuminata*, *Coursetia ferruginea*, *Guazuma ulmifolia*, *Cynophala verrucosa*, *Brosimum alicastrum* and *Hura crepitans*.

The landscape in the region is characterized by small hills and foothills, modelled on sedimentary materials, which vary between 30 and 200 m a.s.l. The main soil types are inceptisols and entisols and topographic variation in the landscape is associated with variation in soil characteristics (Chapter 3). Sites were selected to encompass most of the topographic and soil variation of the region. Two of the sites, La Gloria and El Palomar, are situated in the hills while El Ceibal is located in the foothills and plains.

4.3.2 Field survey

Vegetation sampling was conducted during 2011 using a stratified random design applied to existing land cover maps derived from remote sensing imagery. The age of abandonment and the disturbance regime of each plot were determined by interviews with local inhabitants. Using this information plots were differentiated according to years since abandonment, as either late (>40 years), intermediate (15-25 years) and early secondary vegetation (<12 years). A total of 123 vegetation plots of 10 x 10 m were assessed (~15 random points per land cover type and site) and all individual trees with a DBH > 2.5 cm, including lianas, were recorded and identified. When the species identity could not be resolved in the field, taxonomic samples were collected and processed in the National Herbarium of Colombia (COL). Environmental characteristics of each plot were recorded, including elevation, slope, flooding level during the wet season and proximity to seasonal and permanent water bodies. Measures of anthropogenic disturbance and local testimonies were also recorded, considering the extractive and productive activities carried out in all the sites. These measures included evidence of fire (by presence of burnt trees and ashes on the floor), wood extraction (presence of tree stumps), proximity to productive systems and grazing (by presence of animal faeces and livestock trails). Other field measures adapted from Tongway and Hindley (2005), and assessed visually, were percentage of ground surface covered by bare soil and rock, soil crust brokenness, soil erosion type, soil surface roughness and nature of the soil surface (resistance to mechanical disturbance) .

A mixed sample of surface soil (10 cm) was collected in each plot for analysis. The samples were periodically sent for analysis to the Soil and Water Laboratory of the Faculty of Agronomy at the National University of Colombia (Bogota). Organic oxidizable carbon (OC) was determined by the Walkley and Black procedure and colorimetric quantification, total nitrogen was estimated from OC by a factor of 0.0862, available phosphorus was

determined by the Bray II procedure, exchangeable bases (Ca, Mg, K and Na) were determined by the ammonium acetate method and quantification by atomic absorption spectrometry, cationic exchange capacity was determined by the NN4 displacement method with NaCl and interchangeable acidity was determined by extraction with KCl 1M. Soil texture class, including percentage of sand, loam and clay, were determined following the Bouyoucos procedure and pH was measured in a 1:1 soil and water suspension by means of a potentiometer. Additionally, a core sample of 180.8 mm^3 of soil was extracted to calculate apparent density as the ratio between the oven-dried soil mass and the specified volume.

4.3.3 Species selection and plant traits

The species selected for the analysis were the most abundant in each vegetation plot, which have been arbitrarily defined by Cornelissen et al. (2003) as those that make up about 70-80% of the standing biomass. In this study basal area was used as a proxy for biomass. This approach is based on the assumption that this proportion of the species provides a good representation of the community and that differences between communities will be detected with this sample. In total, 107 species were included in the survey. A total of 14 plant traits, including leaf, stem, reproductive and whole-plant traits were selected for analysis based on their ease of measurement in the field or by simple laboratory procedures, and the fact that they had previously been related to plant performance. The traits were measured on a sample of the population found in the study area assuming that plant traits are species-specific despite intra-specific variability. This was supported by a >70% of variance in trait values explained by species in comparison to individuals for most traits.

Field collections were made from June to September 2011. Leaf characteristics were measured when possible in five individuals per species following the recommendations of minimum sample size of Cornelissen et al. (2003). For a few relatively rare species it was not possible to attain this sample size and leaves were sampled in one individual for two species and in two individuals for eight; for the remaining species no less than three individuals per species were measured. Variation associated with development stage and the effects of light environment were reduced by selecting healthy mature leaves from the outer leaf layer of the crown that were exposed to full sunlight at least during a few hours of the day. This last criterion was not fulfilled for species whose individuals were found primarily in the understory. Fully expanded leaves without epiphylls and significant herbivore damage were collected, including the corresponding petioles. The leaves were stored in sealed plastic bags with a wet tissue and maintained in the shade to avoid dehydration until measurement; all measures were taken on the same day of collection. For each individual, five leaves were

measured for fresh mass, lamina thickness and force to punch; leaflets were used as a measuring unit for compound leaved species. Lamina thickness was measured with a digital calliper avoiding visible primary and secondary veins in two different sections of the lamina. The force-to-punch (Fp) a leaf was measured using a push and pull gauge (rod diameter 3.18 mm, Chatillon 516-1000, AMETEK TCI Division, Chatillon Force Measurement Systems) following Pringle et al. (2010). The rod head was therefore positioned to avoid primary and secondary veins and measures were taken in two positions of the leaf blade. The mass at the moment of penetration of the leaf was converted to punch force by converting grams to N and dividing by the rod circumference (Fp, $N.mm^{-1}$). Fp was subsequently divided by the lamina thickness to calculate the specific force-to-punch (Fps, $N.mm^{-2}$). Additionally, a digital picture was taken of each leaf after locating it in a white background between two laminas of glass and marking the scale. The pictures were analyzed with pixel-counting software to calculate the area of the lamina and the petiole (Rasband, W.S., ImageJ, U. S. National Institutes of Health, Bethesda, Maryland, USA, http://imagej.nih.gov/ij/, 1997-2011.). Leaf area (LA) considered the area of the lamina blade without the petiole; for compound leaves leaf area was calculated by multiplying leaflet areas by the mean number of leaflets. Compoundness was recorded in three categories: simple leaves, pinnate and bipinnate. Leaves and leaflets were dried for a minimum of 48 h at 60-70 °C to record dry mass and based on the measurements the following variables were calculated: leaf dry matter content (LDMC; dry mass per unit of fresh mass) and specific leaf area (SLA; total leaf area (cm^2) / leaf dry mass (g). Leaf phenology was determined by means of a literature review, field observations and local interviews.

Stem density (SD) of field adults was measured in five individuals per species as the relationship between dry mass (g) and fresh volume (cm^3). Most of the species possessed hard, woody stems, for which samples were collected by cutting a section of the trunk. In the case of relatively soft-stemmed species, such as *Bursera simaruba*, *Ceiba pentandra* and *Hura crepitans* an increment borer was used to take a stem sample for analysis. Following Cornelissen et al. (2003), for plants with stem diameters >6 cm and height >4 m, the sample was taken at approximately 1.3 m height. For plants with thin main stems (diameter <6 cm) or smaller than 4 m height, a section was cut at approximately one third of the stem height. Volume was calculated using the water displacement method (Chave, 2005). Bark thickness was measured in stem sections using a digital calliper and the mean value recorded. Samples were kept in a cool place until dried at least for 48 h at 60-70 °C and dry mass recorded. Spinescense was recorded following an adaptation of the categorical classification of Cornelissen et al. (2003), which was reduced to three categories. Presence of free flowing

latex, mean number of trunks and resprouting ability were recorded in the field during vegetation assessment.

4.3.4 Data analysis

Functional diversity is defined as the value and range of the functional traits of organisms or functional groups present in a given ecosystem (Díaz and Cabido, 2001). In this study, functional composition was considered in two ways, as the community abundance-weighted mean (CWM) of traits values in each plot and the species frequency distribution of trait values in each successional stage and site. The calculation of CWM trait values was conducted by multiplying the traits *vs* species and the species *vs* plot matrixes, considering only the species that contributed ≥70% of the basal area.

The effect of site and successional stage on the CWM trait values of the plots was analysed individually using a factorial analysis of variance followed by post-hoc comparisons when appropriate. Plant traits that did not fulfil the assumptions for analysis of variance were analysed by means of the Kruskal-Wallis test on the aggregated data by single and combined factors. Differences in species frequency distribution between stages and sites were analysed by means of a two sample Kolmogorov-Smirnov test for each trait, which has the advantage of making no assumption about the distribution of data. Categorical variables were analysed as frequencies, calculated using both species and individuals counts, and related to stage and site using a log-linear model with subsequent reduction of terms to explore conditional dependence.

The relationship between plant traits and environmental variables (soil, topography and management) was analysed using two approaches, the ordination of CWM trait values as proposed by Kleyer et al. (2012) and the analysis of extended tables using the fourth-corner method as proposed by Dray and Legendre (2008). Ordination of the data enabled shared relationships between traits and environmental characteristics to be identified, whereas the fourth-corner analysis was used to test the consistency of these relationships. A redundancy analysis was conducted on the traits *vs* plots and the variables *vs* plots matrices followed by forward selection of significant variables using as stopping criteria the R^2_{adj} and a threshold of $P<0.05$. For this analysis, compoundness and spines were included as numerical variables and categorical variables were not considered. Missing values were replaced by the mean in eight cases of the environmental matrix. The fourth-corner method relates a matrix of plots by untransformed environmental variables (R) and a matrix of species by traits (Q), linked by the plot by species abundances data (L), by means of correlation of inflated data tables.

Relationships between categorical variables are analysed using the X^2 statistic, the r coefficient between continuous data and the pseudo-F statistic between continuous and categorical data. Five permutation models have been proposed to test the three table relation (Dray and Legendre 2008). Here we used the sequential testing of two of the permutation models, Model II and Model IV, proposed by Ter Braak et al. (2012). Model II permutes the entire rows of table L to test the null hypothesis that species assemblages are randomly attributed to plots, irrespective of the plots' characteristics (table R). The number of plots occupied by a given species is kept constant and the link between the species and their traits (table Q) is maintained. Model IV permutes the entire columns of table L to test the null hypothesis that species are distributed according to their preferences for site conditions, but irrespective of their traits (table Q). The number of species present in a given site (i.e. species richness) is kept constant and the link between L and R is maintained during this analysis. The overall null hypothesis that relates Q and R is rejected when both individual null hypotheses are rejected. These analyses were conducted using the packages ade4, vegan and packfor of the software R (version 2.15.1, R Core Team 2012).

4.4 RESULTS

4.4.1 Functional diversity and successional stage

The effect of successional stage on functional diversity was expected to be observed as shifts in the CWM values of functional traits associated with species turnover and composition changes. CWM values differed between stage and site and significant interactions were observed for specific leaf area (SLA), leaf thickness (LT), bark thickness (BT) and leaf area (LA; Table 4.1). Significant differences of functional traits CWM values were observed between stages for stem density (SD), BT and number of trunks. Post-hoc tests indicated that differences between stands increased from early to late stage forests, showing the lowest SD and the highest BT and number of trunks in early stages. Interactions between stage and site for the five traits mentioned were related to the different patterns of variation between stages observed in El Palomar and La Gloria compared to El Ceibal, for which the difference of early vs later stages is generally much greater than for the other two sites (Supplementary information, Figure 4.4).

Species' frequency distributions were only significant for differences in SD values between early and late stands (Table 4.2), for which a higher frequency of high density species was observed in the late stage (Figure 4.1). The number of species included in these

analyses was similar between intermediate and late forest stands (84 and 88) and was lower in early stands (63). Species frequency distribution between sites did not show significant differences for any of the traits (Suplementary information, Table 4.5). The number of species included in these analyses was similar between El Palomar and La Gloria (80 and 88, respectively) and was lower in El Ceibal (65).

Table 4.1. Results of two way analyses of variance analysing variation in plant functional traits, presented as community weighted mean values, of 123 plots on three sites and successional stages in a tropical dry forest region. E (early), I (intermediate) and L (late). N= 41 for all stand ages. Bold values indicate $P<0.05$. LDMC (leaf dry matter content), LA (leaf area), SLA (specific leaf area), SD (stem density), LT (leaf thickness), Fps (specific force to punch, measure of leaf toughness), BT (bark thickness), Ntrunks (mean number of trunks).

Functional Trait	Site				Stand age				Site:Stage
	Ceibal	Gloria	Palomar	*P*	E	I	L	*P*	*P*
LDMC	0.34 a	0.30 b	0.32 ab	**0.033**	0.32	0.33	0.31	0.403	0.133
LA (cm^2)	606.16	357.63	139.00	0.331	150.12	420.84	561.72	0.811	**0.023**
SLA (cm^2.g^{-1})	163.49 b	199.49 a	197.21 ab	**<0.001**	177.92	185.33	193.54	0.405	**<0.001**
SD (g.cm^{-3})	0.55	0.54	0.55	0.874	0.51 b	0.56 a	0.56 a	**0.003**	0.051
LT (mm)	0.21 a	0.18 b	0.18 b	**0.003**	0.20	0.19	0.19	0.543	**<0.001**
Fps (N.mm^{-2})	39.32 a	22.47 b	26.32 b	**0.007**	24.40	33.95	31.21	0.251	0.480
BT (mm)	3.94 a	2.82 b	3.16 ab	**0.005**	4.09 a	3.19 b	2.74 b	**<0.001**	**0.026**
Ntrunks	2.1 a	1.9 ab	1.5 b	**0.006**	1.9	2.3	1.5	0.060	**0.908**

Table 4.2. Kolmogorov-Smirnov test *D* and *P* values from comparisons of species frequency distributions for eight functional traits between secondary SDTF differing in successional stage. For each stage, data from 41 plots distributed in three sites was pooled. E (early), I (intermediate) and L (late). For trait abbreviations and units see Table 4.1.

Stages		LDMC	Log(LA)	SLA	SD	LT	Log(Fps)	BT	Log(Ntrunks)
E – I	*P*	0.181	0.766	0.971	0.222	0.939	0.366	0.900	0.993
	D	0.18	0.11	0.08	0.18	0.09	0.15	0.10	0.07
I – L	*P*	0.922	0.465	0.999	0.076	0.829	0.174	0.391	0.287
	D	0.09	0.14	0.06	0.21	0.10	0.18	0.15	0.16
E – L	*P*	0.555	0.907	0.999	0.828	0.868	0.962	0.397	0.865
	D	0.12	0.09	0.06	0.10	0.09	0.08	0.14	0.09
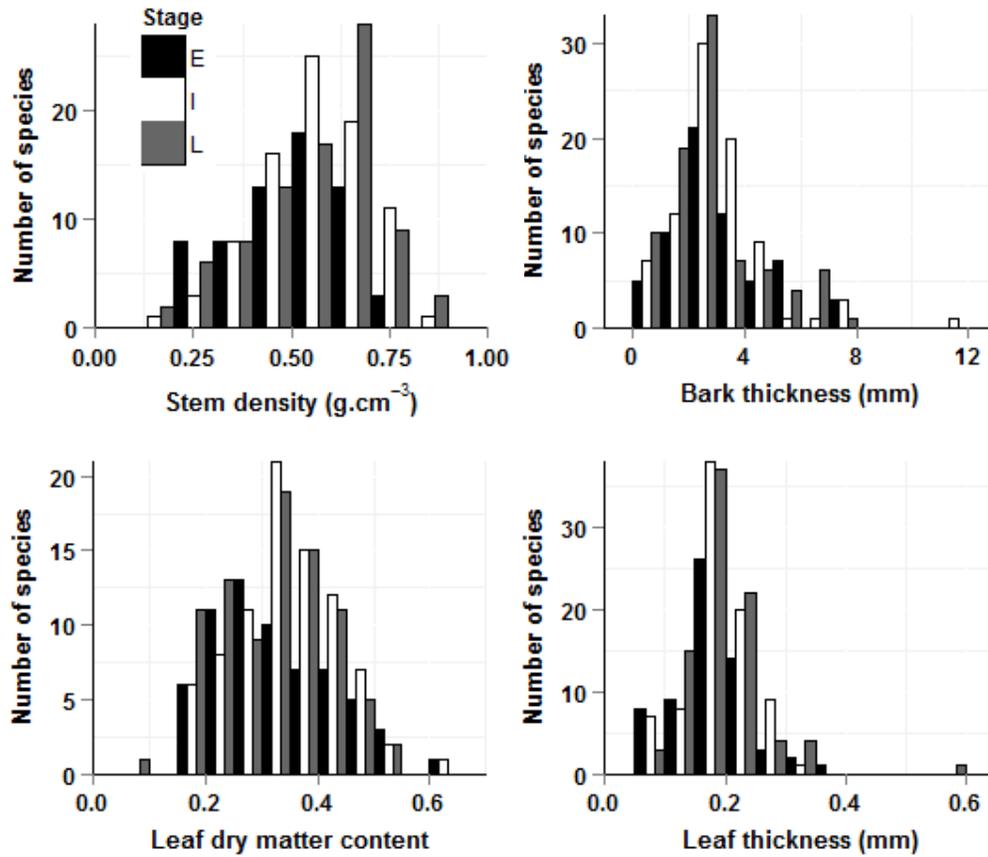
Figure 4.1. Species frequency distributions plots for stem density, bark thickness, leaf dry matter content and leaf thickness of secondary SDTF differing in successional stage. The x axis indicates counts of species in discrete size classes. For each stage, data from 41 plots distributed in three sites was merged. E (early), I (intermediate) and L (late).

Log-linear models of the categorical traits showed that when considering species counts all categorical variables were independent of each other whereas when considering individual's counts complete dependence was observed for all of the traits (all terms in the saturated model were significant). Third degree interactions can be explained by the lack of a common pattern of change during succession in the individual's frequency proportion of the traits' levels in the three sites, with the exception of resprouting ability and latex (Figure 4.2). For these traits, a decrease in the number of individuals of resprouting species was observed from early to late stands in the three sites, whereas higher frequencies of number of individuals from species presenting latex was observed in late stands. Additionally, La Gloria and El Palomar showed similar results for phenology and compoundness. For these sites the number of individuals of evergreen and simple leaved species increased from early to late stands (Figure 4.2).
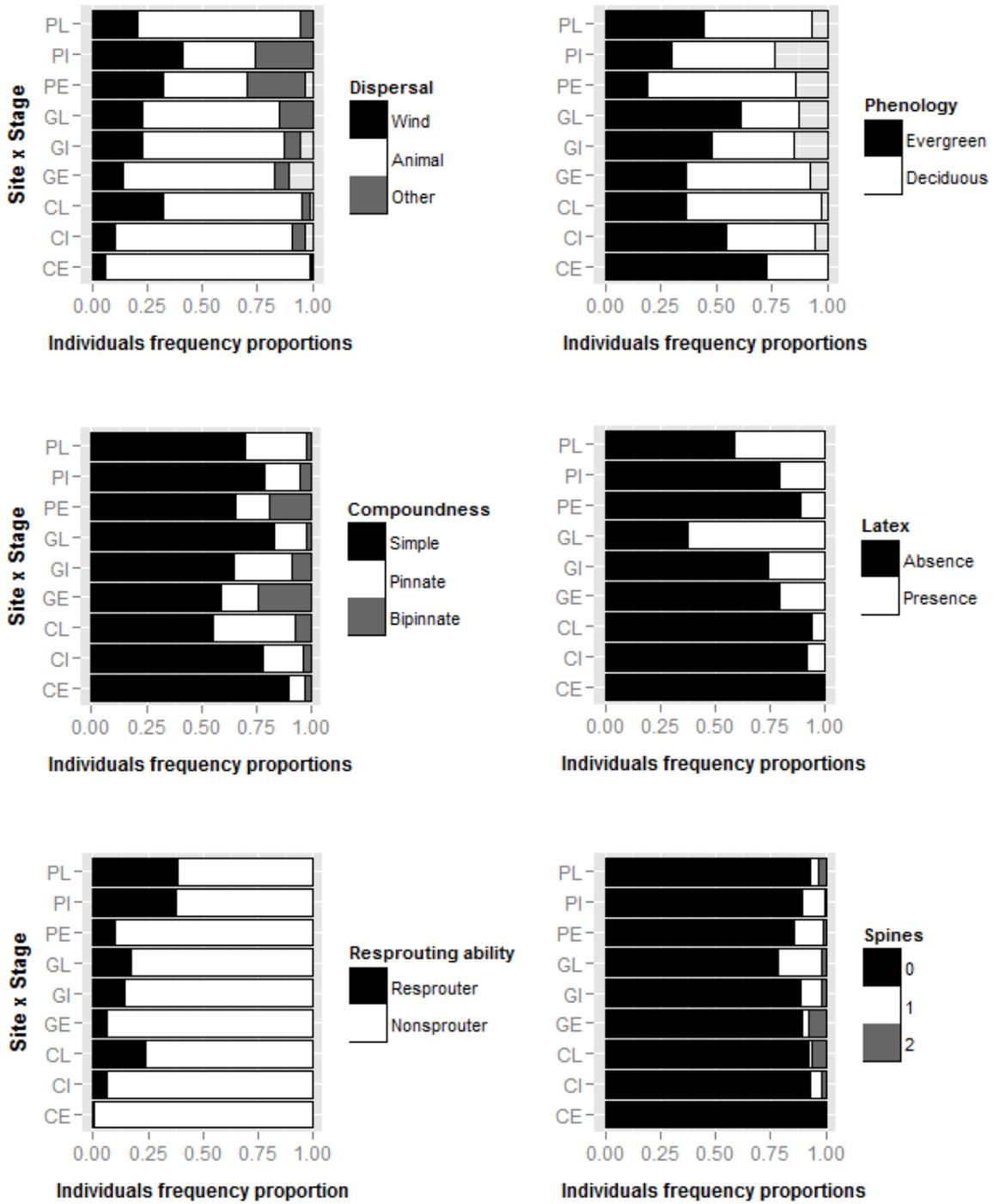
Figure 4.2. Individuals' frequency bar plots of dispersal mode, phenology, compoundness, latex presence, resprouting ability and spines in three stages and three sites of a region of tropical dry forests. Site = P (Palomar), G (Gloria), C (Ceibal). Stage = E (early), I (intermediate) and L (late). Areas without fill (light gray background) indicate species for which no information was available on these traits.

4.4.2 Functional diversity and environmental variables

Four of the five plant traits that changed significantly between sites (namely LDMC, SLA, LT, and Fps) were related to leaf characteristics (Table 4.1), and were correlated at the plot level (Supplementary information, Table 4.4). Post-hoc tests showed that the most distinct site was El Ceibal, which is located mainly in flat areas and is subject to flooding during the wet season, and characterized by higher values of LDMC, LT, Fps and BT and lower values of SLA. The opposite was observed in La Gloria and El Palomar, sites with higher slopes and soil sand content.

The CWM trait values of the vegetation plots showed significant correlations with several environmental variables (Table 4.3). Soil variables presented the highest number of significant correlations with plant functional traits, especially LDMC, SLA, BT and Ntrunks. LDMC, BT and Ntrunks presented positive correlations with nutrient concentrations and negative relationships with sand content and soil apparent density, whereas SLA showed the opposite. LT and Fps were also related to nutrients' concentrations, whereas LA was correlated with P, bare soil cover and litter depth. Slope and altitude were positively related to SLA and negatively to LT, BT and Ntrunks.

The redundancy analysis showed a significant linear relationship between the CWM values and the explanatory variables (p = 0.001, R^2_{adj} = 0.19), and the first three canonical axes explained 76% of the constrained variance. The ordination showed that soil N, flooding level and erosion type were related to the distribution of sites along the first three axes. Na was correlated with the second and third axes, and apparent density and grazing were correlated only with the second. Forward selection of the redundancy analysis retained four variables: flooding level, erosion type, Na and N; the simplified model using these variables had an R^2_{adj} = 0.19. Distribution of plots across the RDA ordination space showed that plots with high risk of flooding, characterized by low slope, high content of nitrogen and nutrients and low sand content, were associated with plant species with high LDMC, Fps, BT and number of trunks, and low SLA (Fig. 4.3).
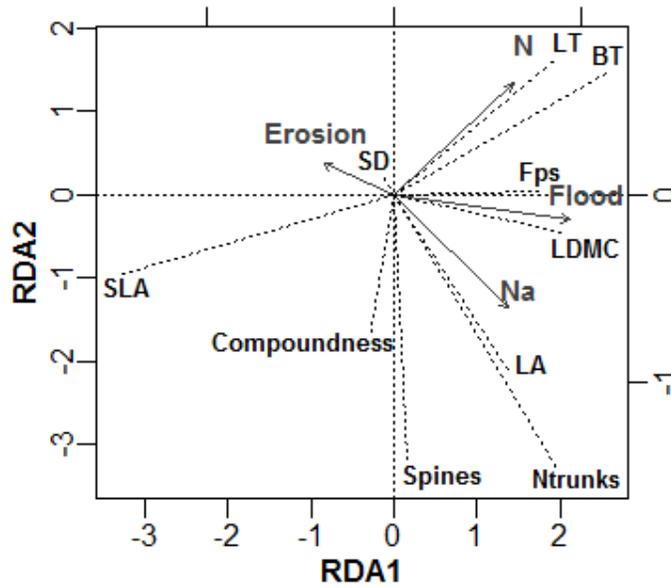
Figure 4.3. RDA ordination (distance scaling) of the CWM trait values of 10 plant traits in 124 plots located in a region of tropical dry forest. Arrows indicate explaining environmental variables. For trait abbreviations and units see Table 4.1. Erosion was included as a quantitative variable to facilitate display but in the analysis was considered as a factor. Flooding level (Flood.).

The fourth-corner analysis tested the consistency of these relationships and allowed analysis of relationships between categorical variables. The results were consistent with the correlation analysis of CWM values for leaf related traits, in addition bark and leaf thicknesses were related to fire events (Figure 4.4., Supplementary information Table 4.5). Presence of latex also showed significant relationships with pH, sand content and litter depth, whereas resprouting ability was related to pH, N and proximity to productive systems.

Table 4.3. Spearman rank correlation coefficients between environmental variables and CWM values of ten plant functional traits. For units of functional traits see Table 4.1. *** $P < 0.001$, ** $P < 0.05$. N = 123 vegetation plots. Interchangeable cation exchange capacity (ICEC), sand (S), apparent density (AD), bare soil cover (soilc), rock cover (rockc) and litter depth (Ldepth).

| | Functional traits | | | | | | | | | |
Variables	Leaf dry matter content	Leaf area	Specific leaf area	Stem density	Leaf thickness	Specific force to punch	Bark thickness	Spines	Comp.	Number of trunks
pH	-0.14	-0.12	0	0	0.15	0.13	-0.2**	0.1	-0.22**	-0.05
N (%)	0.24**	0.01	-0.25**	0.02	0.28**	0.26**	0.24**	-0.27**	-0.09	0.2**
K (meq.Hg^{-1})	0.26**	-0.18	-0.36***	-0.11	0.32***	0.26**	0.26**	-0.12	-0.13	0.29**
Na (meq.Hg^{-1})	0.43***	-0.1	-0.32***	0.08	0.07	0.06	0.27***	-0.17	0.05	0.36***
P (mg.Kg^{-1})	0.19**	-0.24**	-0.4***	-0.12	0.43***	0.36***	0.18**	-0.1	-0.22**	0.24**
ECEC (meq.Hg^{-1})	0.33***	-0.05	-0.35***	0.02	0.3***	0.29**	0.28**	-0.19**	-0.05	0.3***
S (%)	-0.37***	0	0.27**	0.08	-0.15	-0.17	-0.28**	0.21**	-0.05	-0.26**
AD (g.cm^{-3})	-0.31***	-0.02	0.29***	0.02	-0.13	-0.24**	-0.24**	0.1	-0.11	-0.32***
Altitude (m.a.s.l.)	-0.17	0.13	0.2**	0.15	-0.26**	-0.15	-0.18**	0.13	0.08	-0.36***
Slope (DG)	-0.24**	0.23**	0.24**	0.21**	-0.25**	-0.13	-0.37***	0.25**	0.06	-0.32***
Soilc (%)	0.01	-0.27**	-0.28**	-0.08	0.19**	0.2**	0.03	-0.11	-0.21**	0.06
Rockc (%)	-0.24**	-0.05	0.05	0.12	-0.09	-0.06	-0.29**	0.05	-0.12	-0.26**
Ldepth (cm)	-0.08	0.22**	0.16	0.13	-0.12	-0.05	-0.2**	0.14	0.03	-0.04
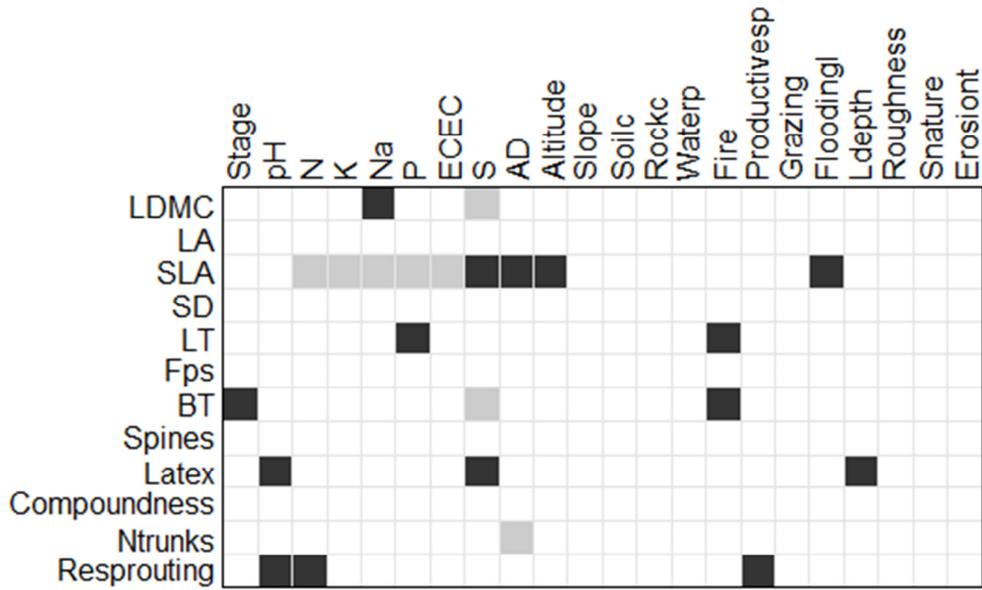
Figure 4.4. Output of the Fourth Corner Analysis for a set of 123 vegetation plots of seasonally dry tropical forest. Significance levels $P < 0.05$. For continuous traits black indicates positive correlations and grey negative, otherwise black indicate a significant association between categorical or mixed traits. For abbreviations of functional traits see Fig. 4.1. Effective cation exchange capacity (ECEC), sand (S), apparent density (AD), bare soil cover (Soilc), rock cover (Rockc), proximity of water bodies (Waterp), proximity of productive systems (Productivesp), flooding level (Floodingl), litter depth (Ldepth), soil surface roughness (Roughness), soil surface nature (Snature), erosion type (Erosiont).

4.5 DISCUSSION

This study presents a comprehensive analysis of the effect of environmental variables and the successional process on the functional composition of a tropical dry forest community. The results showed significant relationships between community plant traits and environmental variables, especially for traits related to mass investment in leaf tissues, soil characteristics and topography. With respect to succession, the effect of stage was significant for stem density and traits related to survival after disturbance, namely bark thickness and number of trunks. The filtering effect of environmental variables and stage in functional composition was stronger when considering species abundances in the vegetation

103

plots, as species with similar plant traits were found along both successional and environmental gradients.

4.5.1 Plant trait and successional stage

In species-rich ecosystems like tropical forests, it is possible that functional diversity is recovered before species richness after a disturbance (Guariguata and Ostertag 2001). In the STDF studied we expected an overlap of plant functional traits values, especially between intermediate- and late-stage stands, due to the limited plant ecological strategies that can establish in this ecosystem. Our results support these hypotheses as no differences were observed when comparing trait frequency distributions for species between stages (Table 4.2), except for stem density (SD). The lack of significant differences of species frequencies between successional stages for most traits can be explained by a) a low turnover of species during succession, b) replacement of species with similar trait values, or c) establishment of species with traits values already present in the community. As changes in species composition during succession were observed in each of the sites together with an increase in species richness (see Chapter 2), there is evidence of species turnover, so the process explaining our results is probably the addition and replacement of functionally similar species.

We also expected a shift of plant trait values from early- to late-stage stands resulting from changes in the dominance of species (Lebrija –Trejos et al. 2010). This prediction was partly supported by differences between CWM values for stem density, bark thickness and mean number of trunks (Table 4.1). These results underline the importance of considering abundance when studying functional assembly of plant communities. In agreement, previous functional analysis of tropical dry forests in Mexico only found a significant effect of environmental filtering when considering weighted community values (Lebrija-Trejos et al. 2010), concluding that although species can be present in the variety of environmental conditions found during succession, only the best-suited species are abundant.

Both stem density and bark thickness showed differences between the early-stage forests on one side and the intermediate- and late-stage stands on the other, supporting the prediction of greater functional similarity of communities as succession advances (Lebrija-Trejos et al. 2010). Wood density has previously been identified as a key functional trait determining plant performance and is highly related to the growth-survival trade-off (Wright et al. 2010). High wood density species are characterized by a conservative strategy of resource use with high investment in tissues that increase longevity (Poorter el at. 2008;

104

Markesteijn et al. 2011). Its increment along succession was a consistent result, which suggests a replacement of individuals from rapid acquisitive species in early stands by more resource-use-efficient species in intermediate- and late-stage stands. An increase of low growth rate species during succession has also been observed in tropical wet forests accompanied by an increasing mortality of moderate to fast growth species (Chazdon et al. 2010). Variation in frequency distribution also showed a tendency for an increase in the number of individuals with dense and thick leaves during succession, traits characterizing conservative-type species. Differences in leaf trait functional composition between successional stages of seasonally dry forest were also observed by Alvarez-Añorve et al. (2012), who described shifts from traits that maximize heat dissipation and minimize water loss in early stages (e.g. high leaf density, low SLA) to traits that favour light acquisition and water conservation in late stages.

Our results differ from those from a previous analysis of variation in functional composition of a dry forest in Mexico (Lohbeck et al. 2013), where a decrease in wood density and an increase in LT was observed during succession following a a shift from early conservative- to late acquisitive- species, which this authors relate to higher water availability with increasing forest structure and cover. However, a higher number of deciduous and compound leaved individuals in early-stage forests was also observed in the last study, which agrees with our observations in El Palomar and Los Rosales. These traits could therefore favour establishment and be relatively common in the early successional stage of dry forests due to their relationship with higher drought-tolerance and rapid growth (Poorter and Markesteijn 2008, Malhado et al. 2010). Presence of latex, which increased in frequency of individuals of late stage in Gloria and Palomar, has been related to chemical defences to small mandibulated insects (Agrawal and Konno 2009), which might have a stronger effect on late successional forests. These results agree with observations made in SDF of Mexico, where presence of exudates also increased with forest succession (Lebrija-Trejos et al. 2010). The contrasting results observed in El Ceibal across successional stages could relate to the flat topography of this site and the expected higher water availability during the dry season, although further research on these site-specific effects is required to verify this.

Differences in bark thickness, resprouting ability and number of trunks between the stages showed a higher dominance of individuals with traits that favour survival after disturbance. Stem cutting and controlled fire are common management practices to clear secondary forest and release nutrients before cropping in our study area, and it was expected

105

that these may have influenced the plant community. Additionally, BT and LT were related to fire whereas resprouting ability was related to productive system proximity. A thicker bark has been related to lower susceptibility to fire damage in tropical dry and wet forest trees (Pinard and Huffman 1997, Brando et al. 2012). A general defensive role of thicker bark has also been suggested but there is still little data to support this hypothesis owing to great intra-species variability in tropical trees (Paine et al. 2010). The importance of resprouters on the other hand is a common characteristic of early secondary dry forest subject to disturbance, and it is an ability widely present in species of this ecosystem (Kennard et al. 2002; Viera et al. 2006; Maza-Villalobos et al. 2011, Lévesque et al. 2011). A decrease in the importance of resprouting species as succession advances can also be related to the lower mean number of trunks per individual in late-stage stands, as has been observed in other dry forests (Lévesque et al. 2011).

4.5.2 Relation of environmental variables and plant traits

The study area presents a strong topographic gradient that determines differences in slope, altitude and soil texture between sites that is also correlated with concentrations of nitrogen, organic content and nutrients in the soil. Higher temporal variation in water availability, as expected on steeper slopes, has been observed to influence nutrient cycling and availability in other tropical dry forests (Anaya et al. 1997) and can explain the differences in nutrients observed. The topographic gradient can be used as an indirect proxy of water availability, which we expected to influence community plant trait values. The analysis of CWM trait values supported this hypothesis as several plant traits related to investment in leaf tissue were correlated with soil characteristics strongly associated with altitude and slope. The fact that these variables did not differ between stages gives additional support to the stronger filtering effect of the environmental gradient on trait values. These results agree with observations by Enquist and Enquist (2011), who found a stronger effect of variation in precipitation compared to the recovery process from disturbance shaping functional composition of seasonally dry forest in Costa Rica. The variables selected by the RDA forward selection were also consistent with this interpretation and represented the nutrient concentration gradient (N and Na), water storage capacity (flooding level) and soil loss (erosion type) gradient in the area.

In summary, plant communities of individuals with leaves with high toughess, thickness and high mass content per area, thicker bark and higher number of trunks occurred in plots with higher concentration of soil nutrients and lower soil sand content. SLA, in contrast, decreased with increasing nutrient content and decreasing sand content, altitude and

106

slope. Following a gradient of resource use, species with high LDMC and low SLA possess a conservative use of resources and invest in long-lived leaves, whereas acquisitive species present high carbon gain rates at the expense of short–lived tissues (Wright et al. 2004, Poorter and Bongers 2006). High leaf toughness and thickness has been related to lower rates of herbivory and resistance to damage that in turn are consistent with a higher investment in tissues for longer-lived species (Wright and Cano 2001, Pringle et al. 2010). Low LDMC, on the other hand, has also been correlated with low wood density and high hydraulic conductivity, traits that favor short-term gain in high availability environments at the expense of long term survival (Markesteijn et al. 2011). Interestingly, SD was only related to slope in this study, although a significant relationship of this trait with leaf thickness and toughness at the species and community level was observed.

Our results suggest that individuals from acquisitive type species were more common in low resource availability conditions as may be found in steeper slopes during the dry season. These results agree with the observation by Sterck et al. (2011) and Pineda-Garcia et al. (2011) in dry forests of Bolivia and Mexico, where acquisitive species, characterized by a higher hydraulic conductivity and carbon gain were located in areas with lower water availability during the year. According to these authors, this pattern may be explained by a more efficient carbon gain in the wet season that allows lower activity during the dry season. Additionally other studies in Australian forests have found non-conservative species to occur preferentially in low fertility or low rainfall sites (Fonseca et al. 2000). On the contrary, an association between species with low leaf mass per unit area and high leaf nutrient concentrations with high soil fertility has been observed in the wet Amazon basin (Fyllas et al. 2011), showing the different trait-environment relationships that occur in both ecosystems.

In conclusion, the filtering effect of environmental variables was stronger than successional stage for most of the traits, especially those related to mass investment in leaf tissues. Nonetheless, a shift in abundance from individuals with traits that favor survival after disturbance to individuals with a more conservative type of resource use was observed along succession. These differences are expected to have a significant effect on ecosystem processes and highlight the functional distinctiveness of conserved forest. The strong relationships between trait and environment described in this study also contribute to the understanding of the effect that changes in water availability can have on this ecosystem. Finally, this study provides evidence of species functional redundancy in secondary forests, attribute that has been related to increasing resilience and efficiency to capture limiting

resources (Cardinale et al. 2011), and that can benefit the management and conservation of this ecosystem.

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4.7 SUPPLEMENTARY INFORMATION
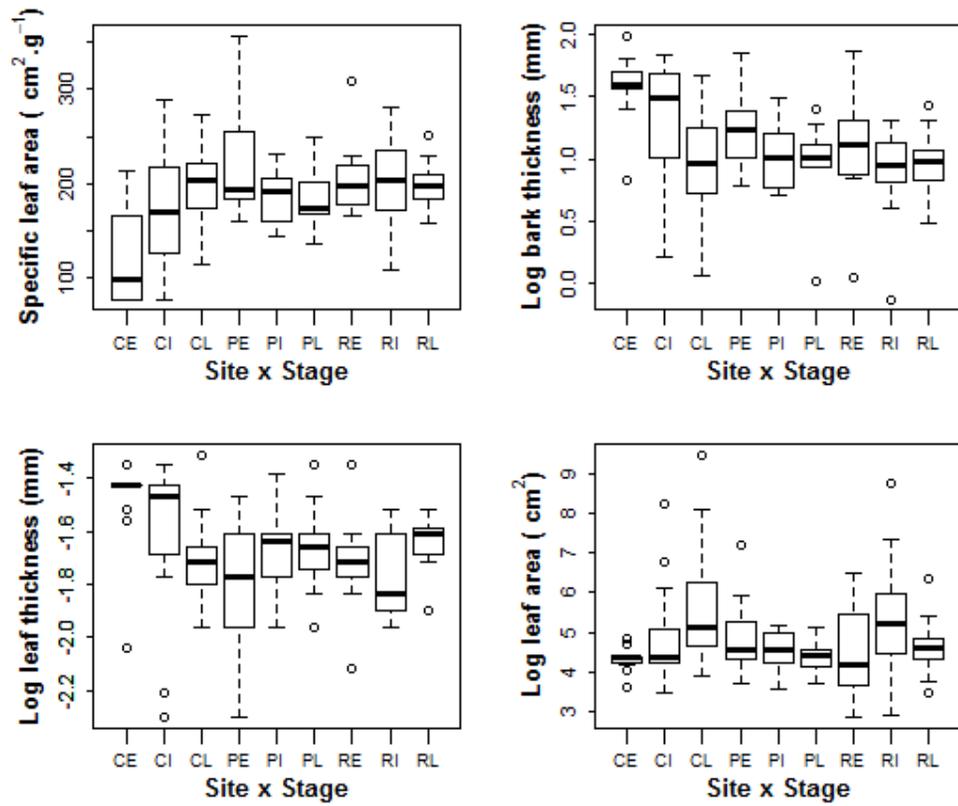
Figure 4.5. Functional traits weighted mean values of nine stage x site categories in a region of seasonally dry tropical forest. Site = C (Ceibal), P (Palomar) and G (Gloria). Stage = E (early), I (intermediate) and L (late). N for each category is 11-15 plots. Three plots with extreme values of number of trunks were removed from the data.

Table 4.4. Spearman rank correlation coefficients between plant functional traits CWM trait values of 123 vegetation plots. Upper triangle cells show probability values and lower triangle cells show correlation coefficient. Leaf dry matter content (LDMC), leaf area (LA), specific leaf area (SLA), stem density (SD), leaf thickness (LT), specific force to punch (Fps), bark thickness (BT), compoundness (Comp.), mean number of trunks (Ntrunks),.

	LDMC	LA	SLA	SD	LT	Fps	BT	Spines	Comp.	Ntrunks
LDMC		0.553	0.000	0.000	0.286	0.001	0.407	0.024	0.024	0.191
LA(cm^2)	0.05		0.263	0.571	0.007	0.699	0.079	0.032	0.000	0.265
SLA (cm^2.g^{-1})	-0.47	0.1		0.698	0.000	0.000	0.000	0.001	0.000	0.004
SD (g.cm^{-3})	0.51	-0.05	-0.04		0.001	0.374	0.000	0.555	0.064	0.308
LT(mm)	-0.1	-0.24	-0.55	-0.3		0.000	0.000	0.011	0.000	0.011
Fps (N.mm^{-2})	0.31	-0.04	-0.7	0.08	0.57		0.017	0.043	0.000	0.479
BT (mm)	0.08	-0.16	-0.36	-0.39	0.36	0.22		0.001	0.029	0.000
Spines	-0.2	0.19	0.3	0.05	-0.23	-0.18	-0.29		0.012	0.082
Comp.	0.2	0.42	0.42	0.17	-0.65	-0.36	-0.2	0.23		0.063
Ntrunks	0.12	-0.1	-0.26	-0.09	0.23	0.06	0.34	-0.16	-0.17	

Table 4.5. Kolmogorov-Smirnov test *D* and *P* values from comparisons of species frequency distributions for eight functional traits between secondary SDTF in three sites in a region of the Caribbean coast of Colombia. El Ceibal (C), La Gloria (G) and El Palomar (P). Data from 45, 39 and 39 vegetation plots distributed in three successional stages was pooled for each site respectively. For trait abbreviations and units see Table 4.4.

		Trait							
Sites		**LDMC**	**Log(LA)**	**SLA**	**SD**	**LT**	**Log(Fps)**	**BT**	**Log(Ntrunks)**
C-G	*P*	0.396	0.146	0.684	0.872	0.887	0.041	0.862	1.000
	D	0.15	0.19	0.12	0.10	0.09	0.23	0.10	0.05
C-P	*P*	0.968	0.395	0.651	0.754	1.000	0.162	0.937	1.000
	D	0.08	0.15	0.12	0.11	0.05	0.19	0.08	0.05
G-P	*P*	0.472	0.973	0.949	0.942	0.943	0.893	0.093	0.796
	D	0.13	0.08	0.08	0.08	0.09	0.09	0.08	0.10

Table 4.6. Output of the fourth corner analysis, involving randomization tests of rows and columns of a species by plot matrix, for the assessment of the relationship between a set of 22 environmental variables and 12 functional traits. A total of 123 vegetation plots were considered for the analysis. $P \leq 0.01$ highlighted in bold, $P \leq 0.05$ in bold and italics. For trait abbreviations and units see Table 4.4, except resprouting ability (Respro.). Environmental variables: Effective cation exchange capacity (ECEC), sand percentage (S), apparent density (AD), bare soil cover (soilc), rock cover (rockc) and litter depth (Ldepth).

Var. R	Var. Q	Stat.	Value	Prob.	Var. R	Var. Q	Stat.	Value	Prob.
Stage / LDMC		F	10.56	0.699	K / LDMC		R	0.31	0.101
Stage / LA		F	2.15	0.763	K / LA		r	0.03	0.165
Stage / SLA		F	34.09	0.283	K / SLA		r	-0.47	**0.002**
Stage / SD		F	37.37	0.315	K / SD		r	-0.11	0.337
Stage / LT		F	16.21	0.489	K / LT		r	0.32	0.082
Stage / Fps		F	0.97	0.93	K / Fps		r	0.14	0.113
Stage / BT		F	116.82	*0.031*	K / BT		r	0.34	0.098
Stage / Spines		F	8.00	0.576	K / Spines		r	-0.10	0.496
Stage / Latex		Chi2	160.96	0.08	K / Latex		F	75.40	0.291
Stage / Comp.		F	3.66	0.879	K / Comp.		r	0.05	0.357
Stage / Ntrunks		F	4.28	0.621	K / Ntrunks		r	0.18	0.065
Stage / Respro.		Chi2	35.02	0.556	K / Respro.		F	188.56	0.139
pH / LDMC		R	-0.14	0.109	Na / LDMC		r	0.29	*0.035*
pH / LA		r	0.02	0.4	Na / LA		r	0.02	0.251
pH / SLA		r	0.04	0.38	Na / SLA		r	-0.30	*0.014*
pH / SD		r	-0.01	0.445	Na / SD		r	-0.02	0.423
pH / LT		r	0.10	0.186	Na / LT		r	0.09	0.298
pH / Fps		r	0.02	0.428	Na / Fps		r	0.06	0.181
pH / BT		r	-0.11	0.181	Na / BT		r	0.22	0.122
pH / Spines		r	0.06	0.286	Na / Spines		r	-0.01	0.684
pH / Latex		F	62.85	*0.05*	Na / Latex		F	80.19	0.137
pH / Comp.		r	-0.05	0.329	Na / Comp.		r	0.17	0.162
pH / Ntrunks		r	-0.01	0.438	Na / Ntrunks		r	0.17	0.056
pH / Respro.		F	75.35	*0.044*	Na / Respro.		F	97.68	0.126
N / LDMC		r	0.32	0.143	P / LDMC		r	0.18	0.143
N / LA		r	0.02	0.275	P / LA		r	0.02	0.297
N / SLA		r	-0.47	**0.006**	P / SLA		r	-0.30	**0.005**
N / SD		r	0.01	0.536	P / SD		r	-0.14	0.192
N / LT		r	0.28	0.154	P / LT		r	0.28	*0.033*
N / Fps		r	0.14	0.111	P / Fps		r	0.12	0.112
N / BT		r	0.34	0.138	P / BT		r	0.21	0.098
N / Spines		r	-0.19	0.097	P / Spines		r	-0.08	0.411
N / Latex		F	99.07	0.185	P / Latex		F	26.39	0.48
N / Comp.		r	-0.04	0.623	P / Comp.		r	0.05	0.336
N / Ntrunks		r	0.07	0.122	P / Ntrunks		r	0.12	0.082

Var. R	Var. Q	Stat.	Value	Prob.	Var. R	Var. Q	Stat.	Value	Prob.
N / Respro.		F	499.07	**0.002**	P / Respro.		F	38.61	0.354
ICEC / LDMC		R	0.34	0.077	Altitude / LDMC		r	-0.09	0.369
ICEC / LA		R	0.05	0.12	Altitude / LA		r	-0.04	0.222
ICEC / SLA		r	-0.45	**0.002**	Altitude / SLA		r	0.29	0.06
ICEC / SD		r	-0.08	0.373	Altitude / SD		r	0.13	0.288
ICEC / LT		r	0.29	0.106	Altitude / LT		r	-0.29	0.088
ICEC / Fps		r	0.14	0.105	Altitude / Fps		r	-0.08	0.171
ICEC / BT		r	0.35	0.09	Altitude / BT		r	-0.29	0.105
ICEC / Spines		r	-0.09	0.48	Altitude / Spines		r	0.05	0.494
ICEC / Latex		F	155.98	0.157	Altitude / Latex		F	114.19	0.202
ICEC / Comp.		r	0.10	0.319	Altitude / Comp.		r	0.01	0.585
ICEC / Ntrunks		r	0.20	0.056	Altitude / Ntrunks		r	-0.15	*0.05*
ICEC / Respro.		F	181.71	0.129	Altitude / Respro.		F	115.32	0.24
S / LDMC		r	-0.32	*0.029*	Slope / LDMC		r	-0.18	0.233
S / LA		r	-0.04	0.174	Slope / LA		r	-0.02	0.302
S / SLA		r	0.35	**0.009**	Slope / SLA		r	0.33	*0.042*
S / SD		r	0.14	0.265	Slope / SD		r	0.20	0.229
S / LT		r	-0.23	0.108	Slope / LT		r	-0.28	0.102
S / Fps		r	-0.11	0.108	Slope / Fps		r	-0.10	0.164
S / BT		r	-0.33	*0.023*	Slope / BT		r	-0.40	*0.038*
S / Spines		r	0.09	0.38	Slope / Spines		r	0.10	0.303
S / Latex		F	225.46	*0.022*	Slope / Latex		F	166.19	0.178
S / Comp.		r	-0.04	0.35	Slope / Comp.		r	-0.01	0.428
S / Ntrunks		r	-0.16	0.057	Slope / Ntrunks		r	-0.15	0.058
S / Respro.		F	125.01	0.119	Slope / Respro.		F	168.15	0.187
AD / LDMC		r	-0.30	0.057	Soilc / LDMC		r	-0.05	0.297
AD / LA		r	-0.05	0.168	Soilc / LA		r	-0.04	0.333
AD / SLA		r	0.34	*0.013*	Soilc / SLA		r	-0.06	0.307
AD / SD		r	0.03	0.434	Soilc / SD		r	-0.08	0.217
AD / LT		r	-0.16	0.196	Soilc / LT		r	0.06	0.276
AD / Fps		r	-0.12	0.108	Soilc / Fps		r	0.07	0.199
AD / BT		r	-0.26	0.113	Soilc / BT		r	0.09	0.197
AD / Spines		r	0.02	0.622	Soilc / Spines		r	-0.07	0.238
AD / Latex		F	133.95	0.127	Soilc / Latex		F	5.52	0.573
AD / Comp.		r	-0.08	0.308	Soilc / Comp.		r	0.00	0.54
AD / Ntrunks		r	-0.22	*0.027*	Soilc / Ntrunks		r	0.08	0.142
AD / Respro.		F	147.35	0.092	Soilc / Respro.		F	15.26	0.312
Rockc / LDMC		r	-0.16	0.086	Psystems / LDMC		F	13.87	0.435
Rockc / LA		r	-0.02	0.308	Psystems / LA		F	0.71	0.869
Rockc / SLA		r	0.10	0.194	Psystems / SLA		F	10.50	0.495
Rockc / SD		r	0.09	0.266	Psystems / SD		F	15.39	0.385
Rockc / LT		r	-0.10	0.184	Psystems / LT		F	1.65	0.88
Rockc / Fps		r	0.01	0.465	Psystems / Fps		F	2.49	0.697
Rockc / BT		r	-0.20	*0.043*	Psystems / BT		F	13.67	0.415

Var. R	Var. Q	Stat.	Value	Prob.	Var. R	Var. Q	Stat.	Value	Prob.
Rockc / Spines		r	-0.01	0.462	Psystems / Spines		F	12.25	0.302
Rockc / Latex		F	61.80	0.087	Psystems / Latex		Chi2	52.53	0.224
Rockc / Comp.		r	-0.07	0.276	Psystems / Comp.		F	4.96	0.686
Rockc / Ntrunks		r	-0.08	0.07	Psystems / Ntrunks		F	1.31	0.801
Rockc / Respro.		F	19.04	0.395	Psystems / Respro.		Chi2	89.58	*0.038*
Waterp / LDMC		F	9.12	0.653	Graizing / LDMC		F	21.15	0.405
Waterp / LA		F	0.75	0.931	Graizing / LA		F	5.97	0.363
Waterp / SLA		F	25.95	0.189	Graizing / SLA		F	45.90	0.1
Waterp / SD		F	7.75	0.672	Graizing / SD		F	8.72	0.664
Waterp / LT		F	11.09	0.476	Graizing / LT		F	27.91	0.224
Waterp / Fps		F	5.08	0.563	Graizing / Fps		F	11.23	0.316
Waterp / BT		F	22.94	0.263	Graizing / BT		F	51.49	0.096
Waterp / Spines		F	4.31	0.702	Graizing / Spines		F	7.23	0.572
Waterp / Latex		Chi2	23.75	0.531	Graizing / Latex		Chi2	138.45	0.107
Waterp / Comp.		F	1.15	0.99	Graizing / Comp.		F	3.19	0.904
Waterp / Ntrunks		F	4.78	0.47	Graizing / Ntrunks		F	14.05	0.143
Waterp / Respro.		Chi2	97.78	0.089	Graizing / Respro.		Chi2	120.98	0.154
Fire / LDMC		F	20.60	0.286	Floodingl / LDMC		F	63.53	0.354
Fire / LA		F	0.85	0.887	Floodingl / LA		F	1.78	0.836
Fire / SLA		F	26.69	0.171	Floodingl / SLA		F	219.70	*0.025*
Fire / SD		F	26.66	0.221	Floodingl / SD		F	8.04	0.78
Fire / LT		F	57.47	*0.035*	Floodingl / LT		F	76.00	0.199
Fire / Fps		F	7.35	0.429	Floodingl / Fps		F	20.96	0.258
Fire / BT		F	71.88	*0.015*	Floodingl / BT		F	176.28	0.072
Fire / Spines		F	6.17	0.668	Floodingl / Spines		F	8.87	0.665
Fire / Latex		Chi2	77.64	0.061	Floodingl / Latex		Chi2	63.25	0.333
Fire / Comp.		F	1.58	0.902	Floodingl / Comp.		F	5.03	0.93
Fire / Ntrunks		F	2.82	0.634	Floodingl / Ntrunks		F	32.21	0.064
Fire / Respro.		Chi2	45.04	0.28	Floodingl / Respro.		Chi2	234.52	0.057
Ldepth / LDMC		r	-0.06	0.228	Erosiont / LDMC		F	3.80	0.829
Ldepth / LA		r	0.01	0.369	Erosiont / LA		F	4.54	0.341
Ldepth / SLA		r	-0.01	0.496	Erosiont / SLA		F	23.03	0.178
Ldepth / SD		r	0.09	0.153	Erosiont / SD		F	14.23	0.405
Ldepth / LT		r	-0.03	0.357	Erosiont / LT		F	34.52	0.091
Ldepth / Fps		r	-0.04	0.36	Erosiont / Fps		F	7.73	0.365
Ldepth / BT		r	-0.08	0.193	Erosiont / BT		F	31.48	0.127
Ldepth / Spines		r	0.10	0.122	Erosiont / Spines		F	3.43	0.746
Ldepth / Latex		F	44.95	*0.032*	Erosiont / Latex		Chi2	48.65	0.282
Ldepth / Comp.		r	-0.13	0.062	Erosiont / Comp.		F	6.88	0.687
Ldepth / Ntrunks		r	-0.03	0.399	Erosiont / Ntrunks		F	10.06	0.173
Ldepth / Respro.		F	0.18	0.915	Erosiont / Respro.		Chi2	69.03	0.215
Roughness / LDMC		F	8.10	0.403	Snature / LDMC		F	57.79	0.216
Roughness / LA		F	0.44	0.929	Snature / LA		F	2.26	0.643
Roughness / SLA		F	20.56	0.215	Snature / SLA		F	60.19	0.144

Var. R	Var. Q	Stat.	Value	Prob.	Var. R	Var. Q	Stat.	Value	Prob.
Roughness / SD		F	3.77	0.63	Snature / SD		F	0.00	0.996
Roughness / LT		F	2.23	0.818	Snature / LT		F	16.23	0.468
Roughness / Fps		F	2.90	0.655	Snature / Fps		F	0.01	0.979
Roughness / BT		F	14.01	0.296	Snature / BT		F	84.75	0.119
Roughness / Spines		F	5.16	0.539	Snature / Spines		F	14.00	0.429
Roughness / Latex		Chi2	39.57	0.148	Snature / Latex		Chi2	60.78	0.165
Roughness / Comp.		F	5.23	0.556	Snature / Comp.		F	11.04	0.68
Roughness / Ntrunks		F	3.57	0.527	Snature / Ntrunks		F	0.35	0.867
Roughness / Respro.		Chi2	12.48	0.652	Snature / Respro.		Chi2	69.85	0.146

CHAPTER 5 LINKING PLANT FUNCTIONAL DIVERSITY AND ECOSYSTEM SERVICES PROVISION OF SECONDARY TROPICAL DRY FORESTS

5.1. ABSTRACT

The important role of species diversity determining ecosystem processes and services is well supported and differences in species functional traits have been proposed as one of the mechanisms that influences this link. In this research, I tested the hypothesis that plant functional diversity is positively related to the provision of ecosystem services (ES) in secondary seasonally dry tropical forests. This was tested by assessing plant species and functional diversity of different successional stage forests in a region of the Caribbean coast of Colombian, together with a quantification of the services these forests provide by two independent approaches: semi-structured interviews and field data. During the interviews 173 useful species were recorded and species importance was estimated as the proportion of their records for each service in relation to the total number of interviews. Species for which functional information was available were classified into ten plant functional groups (PFG) previously developed for the region. An overall importance value (OIV) was estimated by adding the importance values of the species present in each successional stage and PFG. Species mean importance values differed significantly between PFG and more than five groups, on average seven, made uneven contributions to each ecosystem services. ES provision based on useful species presence and abundance percentage of species that provide food source for an endangered species showed significant differences among stages. Functional and species diversity indices showed significant relationships with five and seven estimates of ES, respectively, although these were not consistent. Positive and significant relationships were found between differet types of ES at the plot level; but a trade-off was observed between these estimates and species richness. These results showed that the contribution of secondary forest to the provision of ES in the region is high, widely distributed across different stand ages and supported by the high species diversity and functional observed.

5.2 INTRODUCTION

Analysis of the provision of ecosystem services (ES) has become a central approach for evaluating the consequences of biodiversity loss for human livelihoods (de Groot et al. 2002). This concept has allowed linkage of ecological and social information at different scales and has increased awareness of the potential impacts of ecosystems loss and degradation on human well-being (Foley et al. 2005; Díaz et al. 2006). The central framework of this approach has been represented as a cascade that relates the ecosystem's biophysical structures or processes to the final services and benefits that human receive (Haines-Young and Potchin 2010). At present, the identification of the properties of an ecosystem that have a major influence on the provision of services is a major area of research. Species richness has been the most common candidate and considerable evidence supports the hypothesis that biodiversity has a positive effect on ecosystem functions and services (Gamfeldt et al. 2013; Maestre et al. 2012a; Costanza et al. 2007). Although research on these links has focused on terrestrial plants, the results have been shown to be consistent with other ES providers (Quijas et al. 2010; Cardinale et al. 2011). However, the ecological mechanisms that explain this relationsip are still not fully understood and other community attributes, like species evenness and spatial pattern, have been shown to influence this relationship (Maestre et al. 2012b).

Other measures of diversity can have an important effect on the provision of ES and special attention has been given to functional diversity, a measure of the value and range of the functional traits of organisms or functional groups present in a given ecosystem (Díaz and Cabido 2001). The study of functional diversity (FD) allows exploring alternative hypotheses that have been proposed to explain an increase in ecosystem function, and potentially of service provision, with higher species richness. Ecosystem function can increase due to higher efficiency in resource use due to functional complementarity among species or by a higher probability of including a species with an important functional effect when more species are present (Loreau and Hector 2001; Tilman et al. 2001) Three components of FD have been identified for this purpose (Díaz et al. 2007): the traits of the most abundant species, the range of traits in the community and the presence of important functional species. Studies addressing these components have supported its use and have shown that functional diversity can be related simultaneously or independently to several ecosystem services (Lavorel and Grigulis 2012; de Bello et al. 2010; Conti and Díaz 2013).

In the assessments of the relation between biodiversity and ES an important distinction has been made between supply and delivery. The former referring to the potential

beneficial contributions of ecological or biophysical elements whereas the second considers the actual contact of this potential supply with human populations (Balvanera et al. 2012). The estimation of ES supply can be derived from ecological information, for example community functional traits and measures of litter decomposition and productivity are considered estimates of nutrient cycling and fodder production (Lavorel and Garnier 2002; Garnier et al. 2004; Grigulis et al. 2013). ES delivery on the other hand requires independent information on how people use resources, which can be more challenging. This may be one of the reasons why recent reviews have identified that the assessment of the relationship between functional traits and the delivery of ecosystem services has focused on regulating and supporting services (*sensu* MEA 2005), whereas provision and cultural services require further research (de Bello et al. 2010).

In tropical forests the study of the links between FD and ES has been scarce, despite the fact that these ecosystems provide numerous services to the local communities. Moreover, present studies have shown that in forested areas land-use can modify community assembly processes and have different effects on species and functional diversity depending on the local context (Mayfield et al. 2010). In this study I present a novel approach to link functional diversity with the ecosystem services provided by plants in secondary seasonally dry tropical forests (SDTF). These forests are located in highly populated areas and local communities have exploited historically the different resources provided by this ecosystem (Bye 1995; Murphy & Lugo 1995; Albuquerque et al. 2005). Previous assessments have identified several ecosystem services provided by tropical dry forests at the local and regional scale (Maass et al. 2005; Birch et al. 2010). Conserved dry forests remnants, however, are scarce and highly fragmented (Miles et al. 2006) and secondary vegetation has been highlighted as an opportunity for conservation of biodiversity and ecosystem services provision (Becknell et al. 2012). Additionally, this type of vegetation is located in the drylands of the world, which are vulnerable to land degradation due to the interdependent effect of the different drivers of climate change, risking their capacity to provide benefits to the local communities (Reynolds et al. 2007; Dregne 2002; Maestre et al. 2012c). Land use in tropical ecosystems is one of these major drivers and there is no information available on the provision of ES by different stage secondary forests and its relation to changes in species and functional diversity.

This study addressed the following questions: (i) What ecosystem services are provided by the woody plant community in a region of seasonally dry tropical forest? (ii) Are these provided differentially by plant functional groups? (iii) How does this provision change between forest differing in successional stage and how does it relate to the plant

functional diversity of theses forests? To test this link I applied the concept of ecosystem service provider to both plant communities and species (Luck et al. 2009). Woody plants were chosen as an object of study, as functional trait information was available for this group and it is assumed to be the major determinant of community processes. We hypothesized that higher plant functional diversity is positively related to the provision of ecosystem services following the assumption that niche complementarity among species increases efficiency of resource use (Tilman et al. 2001). I also hypothesize that cultural services that are not expected to relate to a particular functional profile were evenly provided among plant functional groups, in contrast to provisioning ES which are strongly determined by ecosystem processes and have been related to specific plant functional attributes (Garnier et al. 2004).

5.3 METHODS

5.3.1 Study area

The research was conducted in the Totumo region in the Caribbean coast of Colombia. The region is characterized by a heterogeneous landscape where the main land cover type is pastures for cattle. Other land cover types include shrubs and secondary forest derived from abandoned agricultural fields, remnant forest fragments and cultivated crops (mostly maize and yuca). Three small areas (3-18 km^2) that encompass relatively conserved forest fragments and differently aged secondary vegetation were selected for this study. These sites have been or are in the process of being declared regional protected areas. The sites El Ceibal (10°37.19′ N, 75°14.28′ W) and La Gloria (10°37.78′ N, 75°12.56′ W) are contiguous and correspond to three extensive privately owned farms (approx. 1000 ha) that possess forest fragments of nearly 300 ha, whereas the site El Palomar (10° 45.39' N, 75°09.22′ W) is distanced by 12 km and is composed of 19 medium sized privately owned farms that include three fragments of forest of approximately 60 ha each and others of smaller size (>10 ha). Forests in the area are categorized as neotropical dry forests (Gentry 1995), with a mean canopy height of 20 m. The most diverse families reported for the region are Fabaceae, Bignoniaceae, Capparaceae and Malvaceae and some of the most diverse genera are *Machaerium*, *Cordia*, *Cynophalla*, *Trichilia*, *Coccoloba* and *Tabebuia*.

5.3.2 Vegetation sampling and functional traits

The species functional and occurrence data used in this chapter originated from fieldwork conducted in 2011 and described in detail in previous chapters. Tree successional stages were differentiated in each site on the basis of satellite image and field observations, namely early, intermediate and late secondary forests. A total of 123 10 x 10 m plots, ~45 vegetation plots per stage, equally distributed among sites were assessed and all individuals with a diameter at breast height (DBH) > 2.5 cm were measured and identified. Additionally, a mixed sample of surface soil (up to 10 cm depth) was collected in each plot for soil analysis. Functional trait information was collected for all species that contributed >70% of the basal area in each plot, which are expected to have an important influence on ecosystem processes (Chapter 4). The traits selected are associated with plant performance and are related to the environmental and successional gradient present in the region. Measures included leaf dry matter content, specific leaf area, leaf thickness, leaf toughness, leaf organization, stem density, bark thickness and presence of spines (for details see chapter 2). A total of 113 species were classified by means of clustering analysis into ten functional groups (FG) based on these measures (for details see chapter 2).

5.3.3 Ecosystem services assessment

The provision of ES in the region was assessed using two approaches: semi-structured interviews with local residents and landowners and estimation of ecosystem functions based on field data. For the interviews, the administrators or proprietaries of the farms encompassed by each site and residents of the towns in the area of influence were considered. These included the towns of Cerrito (80 habitants) and Hibacharo (2000 habitants), in the vicinity of the site El Palomar, and Los Límites (183 habitants) and Pendales (1531 habitants) in the area of influence of the sites El Ceibal and La Gloria. A high percentage of the population in these towns subsists by working for the day in private farms in the region and conducting small scale agriculture and livestock farming, however they differ in the type of tenure of the agricultural land. In the towns surrounding El Palomar the farmers are owners of the land they work, usually parcels of 15 ha on average, whereas in the latter two the farmers work in lands that are leased for periods of 1-2 years located mainly in the farm El Ceibal. Despite these differences, participants were mainly selected based on their experience working in the rural areas and knowledge of native plants, as well as recommendations of a local guide and other participants from the communities. A total of 55 interviews were conducted during September 2012, of which 75% male and 25% female. The gender imbalance is due to the fact that in the region men are mostly responsible for

farming activities whereas women are in charge of activities at home. Ages ranged from 17 to 80 years, although 84% of the participants were older than 30 years, and the mean age of the men and women interviewed were 54 and 44 years respectively. Interviews were conducted mostly in the participants' homes and a few were conducted in their location of work or on roads.

The interviews were conducted to obtain information about the woody plants more commonly used in the region and the services for which they are recognized. Species were recorded by their common names and the identification of their scientific name was conducted based on field work, floristic lists available for the three study sites (Rodriguez et al. 2012, Rodríguez and Banda 2012) and other regional and national databases (Jiménez-Escobar and Estupiñán-González 2011, IAvH 2013, Bernal et al. 2013). Twelve common names were associated with more than one species of the same genus and therefore were assignated the higher taxon (Appendix 2). Five common names that were associated with more than one scientific name were excluded from the analysis.

Nine services were selected to include provisioning, regulatory and cultural benefits: timber, charcoal production, medicine, food, livestock fodder, scenic beauty, association with water sources, resource for wild fauna and landslide control. Participants were asked to identify the species they commonly recognized as useful for each one of these uses. Timber and charcoal are the main uses for wood extracted from the forest or the surrounding vegetation but they differ in their impact on the ecosystem. In this study timber included all the stems that were selectively harvested for construction, fencing and carpentry without clearing of the vegetation. Charcoal production in contrast usually involves the clearing of 1 to 3 ha of secondary forest in preparation for annual crops. The stems are grouped by size and burned for a few days until the charcoal is ready. The product is packed in bags and sold to intermediaries that transport it to restaurants in the city of Barranquilla, an hour's drive away. This activity is discouraged by local authorities and local NGOs but it is still an important source of income for many inhabitants. Livestock husbandry is the most important economic activity in the area and is the principal driver of forest clearing. Farms in the region vary in sizes and topographic characteristics that determine the number of animals that can be sustained. During the dry season livestock are allowed to pasture in the secondary forest as a supplementary source of fodder and farmers also recognize the importance of remnant trees to provide shade and food to the animals. The seasonal availability of water makes this resource very valuable during the dry season and at the same time the high precipitation during the rainy season makes the area vulnerable to flooding and landslides. Although regulatory services are mainly assessed at the ecosystem scale, I

included the association with water sources and landslide control in the interviews to examine if the species associated with these benefits were found differentially among successional stages. During the interviews, uses were recorded that had not been identified at the onset but were mentioned by respondents. These were grouped in another mixed category including tying up furniture (lianas), wrapping food, handcrafts, ceilings of houses and huts (palms), heels of shoes, protection of house and bird catching.

In addition, two ecosystem services associated with the plant community were estimated from vegetation assessment data: aboveground carbon storage and potential provision of food sources for the cotton-top tamarin monkey *Saguinus oedipus*, which is a species of high conservation concern within the region. Above-ground carbon storage was estimated by assuming a 50% fixed fraction of carbon in biomass, which was estimated for species that contributed to 70% or more of thec basal area in each vegetation plot. Stem density was available for these species (Chapter 4) and biomass of each individual was calculated using the model type II.1 formula developed for tropical dry forest in Colombia (Alvarez et al. 2012). The cotton-top tamarin monkey *S. oedipus* is a critically endangered species that has suffered a severe reduction in population in recent years owing to destruction of habitat (Savage and Causado 2013). Its distribution is restricted to north-western Colombia and a few of the remaining populations are found in the study area. The conservation of this species has been an important factor for the conservation of forest remnants in the region and it has been identified as a potential flagship species for ecoturism, reason why the provision of resources to the species was considered a relevant ES. Potential resource offer in each vegetation plot was estimated as the abundance percentage of species that have been identified as part of *S. oedipus* diet (Proyecto Tití 2013). For these analyses all the species with a DBH > 2.5 cm were considered.

5.3.4 Statistical analysis

In order to analyse differences in the provision of ES based on the social survey of useful species, the importance value for a plant species was estimated as the proportion of the specific number of records in relation to the total for each ecosystem service. This measure was design to provide an estimation of the frequency of use and/or quality of the plants providing each service independently. For the analysis of provision of ES by functional groups, 71 of the species for which functional trait data was available and used in the classification were found useful and were considered for the analysis. The portion of the species recorded that they represented varied among services. For the analysis of successional stages, ecosystem service provision was estimated based on presence and

abundance data. Species presence in each stage was calculated based on the data recorded during the vegetation assessment and available literature (Macías and Bardford 2000, Rodríguez 2001, Cárdenas and Salinas 2008, Rodríguez et al. 2012). This was conducted with the purpose of considering species that were known to be present in these forests but were not recorded in the vegetation plots. In addition, provision of services at the plot level was estimated by adding the importance value of the useful species present weighted by their abundance, for which only the species recorded in the vegetation assessment were considered.

Mean importance value of the species included in each successional stage and functional groups was calculated for all ES and differences were analysed by means of non-parametric Kruskal-Wallis rank sum test as values were not normally distributed after transformation. Summing the importance of all the species found in a functional group or successional stage (early, intermediate and late) resulted in an overall importance value (OIV) limited between 0 and 1, 1 being the highest importance if all the species identified for each service were included. The contribution in biomass of each species considered in the analysis corresponded to the average of all the plots in which it was recorded, differences in this contribution between the species included in each functional group were analysed by means of an analysis of variance on the log transformed data.

At the plot level, differences between successional stages were analysed by means of non-parametric Kruskal-Wallis rank sum test, as values were not normally distributed after transformation. Post-hoc comparison of non-parametric data was conducted using the function kruskalmc of the package pgirmess for R. For other services derived from field data differences were analysed by means of analysis of variance, for which biomass values were log transformed and the logit function was applied to the abundance percentages of species consumed by *S.oedipus*. All the analyses were conducted using the software R (version 2.15.1, R Core Team 2012).

For the analysis of functional diversity, plots were grouped into nine categories by successional stage and site, as it was not possible to calculate indices for each plot owing to the limitations of singular functional species in plots with one or two species. Four distance-based measures of functional diversity were calculated based on the species that contributed >70% of the basal area: functional richness (FRich), Functional Evenness (FEve), Functional Divergence (FDiv) and Functional Dispersion (FDis) indices (Mason et al. 2005; Villéger et al. 2008; Laliberté and Legendre 2010). Functional evenness and divergence are independent of community richness and allow comparison between

communities with different numbers of species. The Gower distance coefficient was used to produce the species distance matrix with the Podani formula for ordinal variables and the Cailliez correction for negative PCoA eigenvalues (Laliberté & Legendre 2010). The number of PCoA axes to be used as traits followed the $s \geq 2^t$ condition and FRich was standardized by the global functional richness that includes all species so it is constrained between 0 and 1. Additionally, the Shannon-Wiener index was computed using the software EstimateS (v. 9.0.0, Colwell 2013) considering all the species recorded in each plot and for plots pooled by site and stage category. The relationships between diversity indexes and estimates of ES were analysed by means of correlation analysis; Pearson correlation was calculated for analyses between biomass and diet, for all other analysis the Spearman coefficient was used. The analyses were conducted using the FD package (Laliberté and Shipley 2011) using the software R.

5.4 RESULTS

Participants mentioned a total of 258 species, of which 230 were identified to genera or species. Categorized by life form I recorded 159 trees and shrubs, 8 lianas, 6 palms, 2 cactus and 54 herbs, grasses and vines. This last category was not considered in this study except for the woody bamboos *Guadua amplexifolia* and *Guadua angustifolia*. In total 173 species were included in the analysis of which 134 were native to the region. The number of species mentioned in each interview ranged between 20 and 56, with a mean of 35±8. The categories with the highest number of species identified were timber and scenic beauty (Table 5.1), whereas the categories with the lowest number were landslide control and other. The percetange of native species was higher than 80% for timber, charcoal, association with freshwater sources, landslide control and other uses. Similar percentages were obtained for medicine, fodder and fauna resources (~78%), whereas it was lowest for food and scenic beauty (~64%).

From the total, 40 percent of the species were recorded for one ES and 13 percent for more than five. The species with the highest numbers of uses (>8) were very common in the area and found in different stages of SDTF: *Guazuma ulmifolia*, *Mangifera indica*, *Crateva tapia* and *Samanea saman*. Twenty species were known for more than 6 uses, all of which were native except for *Eucalytpus* sp. The 10 most important species for each service varied considerably and of these only 9% were recorded for more than three services (Table 5.2). Five non-native species were shown to be important providers for the community and some

of them are now found in the secondary SDTF of the region: *M. indica*, *Prosopis juliflora*, *Crescentia cujete*, *Psidium guajava* and *Spondias purpurea*.

Table 5.1. Number of woody species recorded for different ecosystem services in a region of the Caribbean coast of Colombia. Species were categorized by origin and presence in three successional stages of SDTF, namely early-E., intermediate-I., and late-L. Values show number of species in each category, species shared between successional stages are also indicated.

		Ecosystem services									
		Timber	Charcoal	Medicine	Food	Fodder	Beauty	Water	Fauna	Land.	Other
Native		68	46	38	35	36	35	41	45	25	12
Non-native		9	6	11	21	11	24	5	13	6	0
	Stage	Species presence in SDF									
	E	5	3	1	3	0	2	2	1	1	1
Exclusive	I	0	0	2	0	3	2	5	6	1	1
	L	9	5	6	7	6	8	6	7	3	1
	I-L	12	5	5	4	2	4	5	3	2	2
Shared	E-I	5	5	3	2	5	4	7	3	3	0
	E-I-L	38	30	19	15	22	16	18	24	15	6

5.4.1 Plant functional groups

We observed significant differences between the mean important values of the species that constituted each functional group only for landslide control ($H = 27.2$, $P = 0.001$). The mean biomass that species contributed to the plots was not significantly different between PFG either (Fig. 5.1). In terms of the overall sum of the importance values of the species in each PFG, more than five groups (7.3 ± 1.5), contributed to each ecosystem services and contrasting contribution were observed between them. A high portion of the total useful species was achieved in the functional analysis for timber, charcoal, fodder and fauna resources (Table 5.3). Nevertheless, for food and other services the species considered in the functional groups did not represent a high portion of the ones recorded in the interviews.

128

Table 5.2. The tenth most recorded woody species for each of ten ecosystem services assessed in a region of seasonally dry tropical forests in the Caribbean coast of Colombia. Numbers indicate the number of interviews where the species were recorded, maximum 55, and species are ordered according to increasing number of uses. Origin (O) indicates if the species is native (N) or non-native (NN) in the area. Presence (P) indicates if the species is found in early (E), intermediate (I) and late (L) SDTF, pastures (P) or savannas (S).

Origin	P	Species	Timber	Char.	Med.	Food	Fodder	Beauty	Water	Fauna	Land.	Other
N	P,L	*Samanea saman*	29	11			21	7	7		4	
N	E,I,L	*Gliricidia sepium*	20	12	10		18				4	
N	E,I,L	*Spondias mombin*		8		19	7		4	19		
N	E-I	*Tabebuia rosea*	42	9				6	5			
N	E,I,L	*Cordia dentate*		8			5			8	2	
NN	P	*Mangifera indica*				44	12	9		10		
N	P, L	*Melicoccus bijugatus*				26		9		10		
N	E,I,L	*Sterculia apetala*	28							6		
N	E,I,L	*Hura crepitans*	27								3	
N	E,I,L	*Guazuma ulmifolia*		25			25					
NN	E-I	*Prosopis juliflora*		17			17					
N	E-I	*Acacia macracantha*		17			17					
N	E,I,L	*Bauhinia glabra*			14							8
N	E,I,L	*Bursera simaruba*			13							1
NN	P,E,I,L	*Crescentia cujete*			5		7					
NN	P	*Psidium guajava*				40				6		
NN	P	*Spondias purpurea*				25				7		
N	E,I,L	*Crateva tapia*						14	3			
N	E,I,L	*Quadrella odoratissima*						27				1
N	I-L	*Guadua angustifolia*							5		4	

Origin	P	Species	Timber	Char.	Med.	Food	Fodder	Beauty	Water	Fauna	Land.	Other
N	E	*Bravaisia integerrima*							12		3	
N	L	*Anacardium excelsum*							12		4	
N	P,I	*Attalea butyraceae*								9	4	
N	I-L	*Pachira quinata*	31									
N	E,I,L	*Cordia alliodora*	25									
N	E	*Tabebuia billbergii*	25									
N	E,I,L	*Calycophyllum* cf. *candidisimum*	20									
N	I-L	*Cedrela odorata*	19									
N	E,I,L	*Centrolobium paraense*	19									
N	E,I,L	*Astronium graveolens*		11								
N	E,I,L	*Albizia niopoides*		7								
N	E,I,L	*Pterocarpus acapulcensis*		7								
NN	P	*Eucalyptus* sp.			21							
N	I-L	*Croton malambo*			18							
NN	P	*Cajanus cajan*			9							
N	E,I,L	*Aristolochia inflate*			8							
N	E,I,L	*Quassia amara*			7							
NN	P	*Citrus x limon*			5							
N	L	*Annona muricata*				24						
NN	P	*Citrus* sp.				17						
N	L	*Malpighia glabra*				16						
N	E,I,L	*Manilkara zapota*				15						
NN	P	*Annona* sp.				14						
N	E-I	*Enterolobium cyclocarpum*					15					

Origin	P	Species	Timber	Char.	Med.	Food	Fodder	Beauty	Water	Fauna	Land.	Other
N	I-L	*Bulnesia arborea*						10				
NN	P	*Terminalia catappa*						9				
N	I-L	*Capparidastrum pachaca*						6				
NN	P	*Murraya paniculata*						6				
N	E,I,L	*Inga* sp.							7			
N	E,I,L	*Lecythis minor*							5			
N	E,I,L	*Coccoloba caracasana*							4			
N	E,I,L	*Brosimum alicastrum*								9		
N	E,I,L	*Talisia oliviformis*								9		
N	E,I,L	*Cordia collococca*								6		
N	L	*Ficus nymphaeifolia*									5	
NN	P	*Cocus nucifera*									3	
N	E,I,L	*Sabal mauritiiformis*										18
N	E,I,L	*Bignoniaceae*										18
N	I	*Bactris guineensis*										8
N	I-L	*Cordia gerascanthus*										8
N	I-L	*Gustavia superba*										8
N	S	*Copernicia tectorum*										2
N	L	*Macfadyena ungis-cacti*										2
N	E,I,L	*Combretum fruticosum*										1
N	E	*Sapium glandulosum*										1
N	I-L	*Stigmaphyllon dicotomum*										1

Table 5.3. Sum of the importance values of woody species classified into ten plant functional groups for each of the ecosystems services assessed. Total is the sum of the species considered in the functional analysis for each service, values range from 0 to 1, the maximum achieved when all the species recorded for a specific service are present. Abbreviations: N indicates number of species in each group. Char.- Charcoal, Med.- medicine and Land.- landslide control. The three highest contributors to each service are highlighted in bold.

FG	N	Ecosystem services									
		Wood	Char.	Med.	Food	Fodder	Beauty	Water	Fauna	Land.	Other
1	7	0.06	0.07	0.00	0.00	0.01	0.00	0.02	0.00	0.02	**0.02**
2	12	**0.20**	**0.33**	**0.09**	**0.12**	**0.34**	**0.14**	**0.12**	**0.21**	**0.14**	0.00
3	14	**0.12**	**0.09**	0.08	0.02	0.05	**0.08**	**0.14**	**0.12**	**0.10**	0.31
4	16	0.09	**0.09**	**0.13**	**0.05**	0.04	**0.19**	0.07	**0.16**	0.03	**0.02**
5	2	0.00	0.00	0.00	0.00	0.02	0.02	0.01	0.05	0.08	0.00
6	1	0.00	0.00	0.00	**0.03**	0.00	0.00	0.03	0.03	0.00	0.00
7	1	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.03	0.00
8	10	**0.12**	**0.09**	**0.21**	0.01	**0.11**	0.05	**0.09**	0.04	0.06	**0.04**
9	5	0.01	0.08	0.01	0.00	**0.10**	0.01	0.01	0.01	0.00	**0.02**
10	3	0.09	0.04	0.01	0.00	0.02	0.02	0.03	0.02	**0.10**	0.00
Total	71	0.69	0.80	0.51	0.23	0.69	0.51	0.50	0.64	0.56	0.40
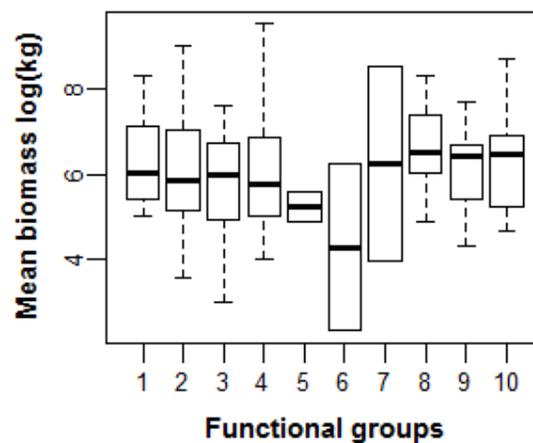
Figure 5.1. Mean biomass contribution of species included in each functional group. See table 5.3 for N in each functional group.

132

5.4.2 Successional stages

The provision of services by useful species at the plot level showed significant differences between stages for charcoal ($H = 37.4$, $P =$ <0.001), medicine ($H = 13.6$, $P = 0.001$), food ($H = 16.7$, P <0.001), livestock ($H = 40$, P <0.001), association with water ($H = 30$, P <0.001) and landslide control ($F = 23.2$, P <0.001). Post-hoc comparisons showed that provision of services decreased from early to late stages with the exception of food (Figure 5.2). In term of ecosystem services estimated from field data, significant differences between stages were found for abundance percentage and not for biomass; however, differences between site and interactions between site and stage were significant for these ecosystem services (Table 5.4).

The sum of importance values that considered only species presence in each successional stage showed differences between early to intermediate and late stages for medicine, food, scenic beauty, association with water, fauna and landslide control (Table 5.5). Not significantly different were observed in importance values of the species found or reported in the three stages for any ecosystem services. For timber, charcoal, fodder, fauna and landside control 40-60% of these species were reported in all stage forests (Table 1), whereas for the remaining categories the value was ~30%, and in all cases the species found only in intermediate and late forest comprised 11-20%. 13 native species lacked records in secondary vegetation either because they were common in other ecosystems (e.g. mangle) or were only found locally in pastures.

Table 5.4. Two-way analysis of variance of biomass (estimate of aboveground carbon storage) and abundance percentage (estimate of available food sources for *S. oedipus*) recorded in 126 vegetation plots in a region of tropical dry forest. Values grouped by the same letter are not significantly different at $P \leq 0.05$. *** indicates $P < 0.001$.

	Site				Stage				Site:Stage
	G	**P**	**C**	*P*	**E**	**I**	**L**	*P*	*P*
Biomass (kg)	897.0 b	1448.3 a	718.6 b	0.002	805.0	918.0	1296.6	0.481	0.001
Diet (%)	44.5 b	36.5 b	65.2 a	***	53.8	45.4	49.4	0.100	0.005
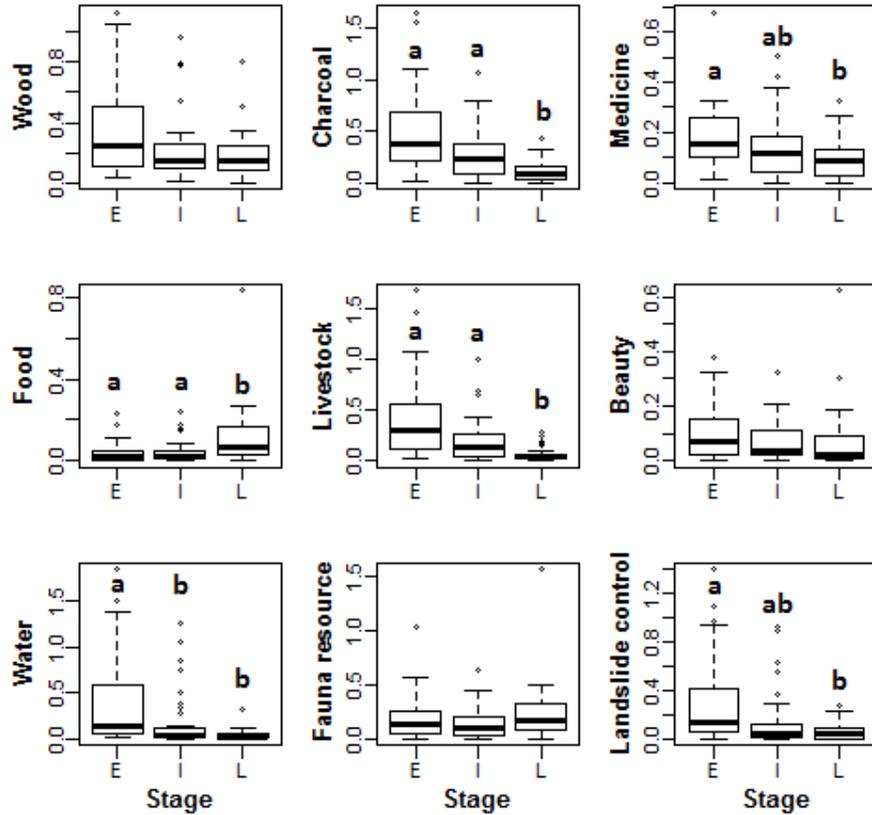
Figure 5.2. Provision of nine ecosystem services by the useful species present in ~45 vegetation plots of three successional stages: early (E), intermediate (I) and late (L). Provision estimated as the weighted sum of species importance value in each plot. Different letters indicate significant differences at $P \leq 0.05$ by means of Kruskall-Wallis tests.

Table 5.5. Sum of importance values of the species present in three successional stages of SDTF, namely early (E), intermediate (I) and late (L). Values range from 0 to 1, 1 being achieved when all the species recorded for a specific service are present. For abbreviations, see caption to Table 5.3.

Stage	Wood	Char.	Med.	Food	Fodder	Beauty	Water	Fauna	Land.	Other
E	0.76	0.86	0.51	0.21	0.69	0.42	0.58	0.54	0.51	0.61
I	0.81	0.84	0.66	0.28	0.73	0.52	0.60	0.67	0.62	0.90
L	0.77	0.69	0.64	0.36	0.57	0.57	0.68	0.66	0.70	0.80

5.4.3 Community plant diversity and ecosystem services

Provision of services by useful species, estimated as the abundance weighted sum of species importance values, showed significant relationhisps with functional and species diversity indices. Functional richness and functional evenness were negatively related to timber, association with water and landslide control, and positively to other services (Table 5.6). The Shannon-Wiener diversity index was negatively related to timber, charcoal, association with water, landslide control and other services (Table 5.6). Significant negative relationships were also observed between the abundance percentage of food source species and functional richness, functional eveness and the Shannon index (Table 5.6). However, early stage plots at El Ceibal showed extreme values for all functional indexes and ecosystem services exerting strong influence on the patterns observed (Supplementary information, Figure 5.9). When removing this value from the analysis several relationships became non-significant, especially between functional indexes and ES, whereas other became weaker (Table 5.6).

At the plot level, species richness showed negative significant relationships with six estimates of ES and one positive with the others service category. The opposite was observed for abundance percentage and no significant relationships were observed for biomass (Table 5.7).

5.5 DISCUSSION

The high species richness recorded and the dominance of native plants reflects high use levels of forests products by local habitants in the study area. The considerable variation in the most important species for each service and the low number of multi-functional species, capable of effectively supporting more than one function or ecosystem service (Sircely & Naeem 2012), also reflects a high complementarity among species in the services provided. The number of useful woody species recorded in this study was high compared to other ethno-botanical assessments of SDTF at a landscape scale but similar to values reported on a regional level (Suárez et al. 2012; Maldonado et al. 2013). The number of trees and shrubs recorded corresponded to 48% of the trees known to be useful in the Caribbean region of Colombia (Jiménez-Escobar and Estupiñán-González 2011).

Table 5.6. Pairwise correlations coefficients between diversity indexes and estimates of 12 ecosystem services. N = 9, each data point corresponds to a pooled sample of 15 plots. In brackets N = 8, data point from early plots in El Ceibal was eliminated due to its strong influence in the relationships observed. Abbreviations: FRic – functional richness, FEve – functional evenness, FDiv – functional divergence, FDis – functional dispersion. RichT – total richness. Significance values indicate * $P \leq 0.05$, ** $P \leq 0.01$ and *** $P \leq 0.001$.

	FRic	FEve	FDiv	FDis	Shanon	RichT
Biomass	-0.05 (-0.29)	0.07 (-0.13)	0 (0.18)	-0.37 (-0.59)	0.23 (0.37)	0.16 (0.09)
Diet	-0.70* (-0.22)	-0.79* (-0.39)	-0.57 (-0.14)	0.53 (-0.20)	-0.90*** (-0.92**)	-0.83** (-0.74*)
Wood	-0.78* (-0.38)	-0.89** (-0.66)	0.58 (-0.07)	-0.54 (-0.13)	-0.87*** (-0.63)	-0.69* (-0.22)
Charcoal	-0.65 (-0.14)	-0.58 (0.19)	0.46 (-0.23)	0 (0.81)	-0.68* (0.09)	-0.49 (0.13*)
Medicine	0.19 (0.57)	0.19 (0.71*)	-0.01 (-0.22)	0.31 (0.53)	0.05 (0.67)	0.37 (0.76*)
Food	-0.19 (-0.67)	-0.01 (-0.44)	0.25 (0.69)	-0.15 (-0.37)	0.11 (-0.35)	-0.02 (-0.3)
Livestock	-0.66 (-0.16)	-0.59 (0.15)	0.47 (-0.22)	-0.05 (0.74*)	-0.71* (-0.09)	-0.49 (0.13)
Beauty	0.06 (0.36)	0.26 (0.9**)	0.13 (-0.02)	0.3 (0.53)	-0.08 (0.31)	0.13 (0.41)
Water	-0.78* (-0.07)	-0.88** (-0.32)	0.6 (-0.54)	-0.49 (0.31)	-0.96*** (-0.69)	-0.78* (-0.3)
Fauna	-0.55 (-0.49)	-0.48 (-0.36)	0.61 (0.55)	-0.47 (-0.34)	-0.46 (-0.4)	-0.36 (-0.14)
Landslide	-0.71* (-0.24)	-0.79* (-0.4)	0.38 (-0.49)	-0.37 (0.18)	-0.81** (-0.48)	-0.64 (-0.16)
Other	0.68* (0.5)	0.76* (0.72*)	-0.38 (0.08)	0.46 (0.2)	0.72* (0.79*)	0.88** (0.85**)

Table 5.7. Pairwise relationships between estimates of five ecosystem services and species richness in 123 plots of STDF. Top triangle indicates P values, lower triangle indicates Pearson coefficients, except for relationships with richness for which Spearman coefficients were estimated. Bold indicates coefficient with $P \leq 0.001$.

	Richness	Diet	Biomass	Wood	Charcoal	Medicine	Food	Livestock	Beauty	Water	Fauna	Land.	Other
Richness		< 0.001	0.057	0.009	0.010	0.062	0.002	0.005	0.858	< 0.001	0.494	0.001	< 0.001
Diet	**-0.38**		0.812	< 0.001	0.021	0.924	< 0.001	< 0.001	0.137	< 0.001	< 0.001	< 0.001	< 0.001
Biomass	0.17	0.02		0.720	0.297	0.373	0.924	0.053	0.400	0.028	0.644	0.174	0.293
Wood	**-0.23**	**0.39**	0.03		< 0.001	0.374	0.006	< 0.001	0.001	< 0.001	< 0.001	< 0.001	0.001
Charcoal	**-0.23**	0.21	-0.09	**0.54**		< 0.001	0.073	< 0.001	< 0.001	< 0.001	0.240	< 0.001	0.179
Medicine	0.17	0.01	0.08	0.08	**0.43**		0.234	< 0.001	< 0.001	< 0.001	0.442	0.002	< 0.001
Food	0.28	**0.32**	0.01	**0.25**	-0.16	-0.11		0.917	0.862	0.730	< 0.001	0.673	0.881
Livestock	**-0.25**	**0.33**	-0.17	**0.55**	**0.87**	**0.44**	0.01		< 0.001	< 0.001	0.001	< 0.001	0.460
Beauty	0.02	0.13	0.08	**0.30**	**0.46**	**0.38**	0.02	**0.50**		< 0.001	0.027	< 0.001	0.031
Water	**-0.32**	**0.46**	-0.20	**0.57**	**0.72**	**0.32**	-0.03	**0.79**	**0.54**		0.001	< 0.001	0.038
Fauna	0.06	**0.55**	0.04	**0.54**	0.11	0.07	**0.83**	**0.30**	0.20	**0.30**		0.001	0.171
Lcontrol	**-0.30**	**0.48**	-0.12	**0.63**	0.63	0.27	-0.04	**0.68**	**0.44**	**0.82**	0.30		0.006
Other	**0.49**	**-0.37**	0.10	**-0.31**	**-0.12**	**0.52**	0.01	-0.07	0.19	-0.19	-0.12	**-0.25**	

Timber was the service for which most the species were recognized and was also among the services with the highest percentages of native species. The higher importance of introduced species for food and scenic beauty use, relates to the introduction of some of the most important crops in the region, including yuca (*Manihot esculenta*) and guandul (*Cajanus cajan*), as well as the widely used tropical trees *M. indica*, *P. guajaba* and *Citrus* sp. In the case of mango, this fruit tree has been extensively sown and dispersed in the area and adult individuals as well as seedlings are found inside the forest near houses or roads. These fruit trees are also valued for their scenic beauty like other introduced species that are known for their abundant and colourful flowers or their ability to provide shade (e.g. *Terminalia catappa*, *Platypodium elegans*, *Delonix regia*). Food and ornamental uses were identified by Bennett and Prance (2000) as important drivers for the introduction of non-native species in north South America, where they found that these were the principal uses when arrival for most of 216 introduced species currently used for medicinal uses by indigenous communities, of which 30% corresponded to trees and shrubs. Interestingly, one of the characteristics among species that were recorded for their scenic beauty was the ability to maintain their leaves during the dry season, for which various members of the family Capparaceae were recognized.

Social surveys can also provide ecological information of local species, including their preferences in distribution and rarity, which can be used to design forest conservation and management strategies. The species recorded in this study for their association with freshwater sources are commonly found in flooding areas and creeks and these can be targeted for restoration activities in these habitats. In addition, species recognized for their provision of resources for fauna are also of great importance as these are a potentially keystone resource for the functioning of this ecosystem (e.g. *S. mombin* and *B. alicastrum).*

5.5.1 Plant functional types

The results partially supported the hypothesis of an even provision of ecosystem services among plant functional groups, however contrasting contributions that strongly related to the number of composing species were observed between them. A high variability in the mean trait values of the functional groups that contributed most to the ES assessed was also observed, suggesting that native useful species in the region are not restricted to a certain set of traits for any service and that complementarity among functional groups in the provision of ES is ocurring. For example, functional groups two and four, that showed the highest contribution among services, were characterized by contrasting functional trait values. Functional group two was composed of deciduous trees with low stem density and high bark

thickness (details in Chapter 2), characteristics that have been related to a high stem growth rates, protection from fire and drought tolerance (Poorter et al. 2013), which can favour establishment and survival in early stages of succession (Chapter 4). Whereas functional group four was characterized mostly by evergreen species with high stem density and leaf dry matter content (details in Chapter 2), traits related to a conservative use of resources and more frequent in late forests (Poorter et al. 2008; Markesteijn et al. 2011).

The species included in the plant functional analysis were chosen considering their contribution to the basal area recorded in each plot, and a high representation of useful species among them could be understood as a positive relation between ecological importance and use. This was high for timber, charcoal, fodder and fauna, which indicates that species important for the provision of these services are also dominant in the forests. In the case of medicine, beauty, fauna and landslide control, the contribution of these species was lower and not surprisingly the lowest value of contribution was observed for food provision. Ecological characteristics of a species have been previously associated with their use, especially in wet forests where species ecological importance has been observed to positively relate to its use value (as proposed by (Phillips and Gentry 1993; Lawrence et al. 2005). This relation has been supported in SDTF of Mexico, where the use value of plant species was positively related to their ecological importance and frequency (Maldonado et al. 2013), whereas in SDTF of Brazil no apparent relationship has been found (Lucena et al. 2007). Patterns of use of plant species can also be influenced by cultural differences, for example in Mexico indigenous groups used more species for medicine, food and firewood, and had a stronger relationship between species use value and ecological importance than mestizo communities, which the authors related to a more profound knowledge of the area as a results of long history of contact with the ecosystem (Maldonado et al. 2013). In the study area, rural habitants are mestizos of relatively recent arrival in the area, which could explain the lower contribution of ecological important species to some services. Interestingly, the species mean biomass did not differ among functional groups, showing that differences in species abundance and size among groups is not reflected in differences in contribution to the biomass and possibly its effect on ecosystem processes.

5.5.2 Successional stages

The assessment of differences in the provision of ecosystem services between successional stages of SDTF was achieved by using two independent approaches: social surveys of useful plants and field data. The estimation of service provision using the information of useful woody plants showed significant differences between stages, although contrasting

importance values where obtained using species presence in comparison to abundance in plots. Higher provision in general was observed in early and intermediate stages when considering abundance data, whereas values calculated using species presence showed higher provision in late and intermediate stages for most services. These results suggest that abundance or presence of useful species is higher on average in early and intermediate plots, but that rare or non-dominant species that were not recorded in the vegetation plots can contribute significantly to service provision. For example, species such as *Cedrela odorata* and *Pachira quinata*, which are among the ten most important trees used for timber and are highly priced, are endangered and were not reported in the plots. The estimates of ES provision used in this study, however, more appropriately describe potential rather than actual delivery which can be influenced by other factors. For instance, in early successional stages trees have not reached an appropriate size to be harvested for timber and some of them may have not reached maturity to provide fruits. Significant differences between successional stages were also observed for aboveground carbon storage that increased from early to late successional forests in agreement with the increment in biomass observed with age in other SDTF (Becknell et al. 2012). However, a significant effect of site was observed, which is supported by the differences in topography and soil characteristics observed in the region.

Only a small portion of useful species was characteristic of intermediate and late forest stands whereas the greatest portion can be found in different successional stages or outside the forest. These results reflect the fact that as forest cover disappears and distance from forest remnants increases people rely on a reduced number of species that are common in early successional vegetation and disturbed areas (Lawrence et al. 2005). These species also present desirable characteristics for use, like high abundance and rapid growth, as observed for *G. ulmifolia*, *P. juliflora* and *Acacia macracantha* in young forest.

The overall importance value of each stage, which was on average higher for intermediate forest stands, can also provide information about redundancy in service provision, higher values indicating a better representation of the species recorded for that service at the specific stage (with the exception of medicinal uses that are specific to the type of illness). Redundancy of native utilitarian species has been identified as a desirable property to diminish the impacts of local extinction or scarcity of important species loss. For example in Madagascar, Brown et al. (2011) found a lower redundancy of utilitarian species in forest with higher basal area, closer to villages and with shorter height associated with higher harvesting rates. Unlike native species, in the current study the provision of services

140

by introduced species can be maintained by individuals located in the gardens close to the rural houses and farms.

5.5.3 Functional diversity and ecosystem services

The link between ecosystem services and functional diversity is not simple and these results showed a low number of significant relationships with either of the indices used. Functional trait similarity between species has been observed in the region (Chapter 4) and explains the results observed for the functional richnes index, which does not consider differences in abundance. However, variation in functional composition due to changes in species abundance has been observed along successional and environmental gradients, and these observations were not mirrored by differences in the other indices that consider this characteristic. Species diversity, measured by the Shannon diversity index, showed significant relationship with seven of the ecosystem services assessed; although these relationships became weaker when considering species richness for the site and succession stage categories compared to analysis at the plot level.

The widely reported positive relationship between biodiversity and ecosystem function has been mainly studied using species richness and measures of productivity, conditions under which this effect has been explained by a higher complementarity in diverse communities that optimize resource use (Cardinale et al. 2011; Tilman et al. 2001). In long-term studies, this effect has been shown to become increasingly non-saturating over time and has been related to a continuous increase of functional diversity (Reich et al. 2012). However, a higher number of species has also been suggested to increase competition among species and reduce the complementarity effect (Sircely and Naeem 2012). In this study, above-ground biomass was not related to species richness or any of the species and functional indices used. The number of species considered in this study was high in comparison to the number usually considered in other studies and differences in species richness between succession and site categories were proportionately low, except for early forest in El Ceibal. It is therefore possible that the levels of species loss required for a strong effect of species richness on biomass have not been reached and functional redundancy among species is conferring a certain degree of disturbance resilience to this ecosystem. Moreover, recent reviews have shown that a significant effect of species loss on productivity requires values of more than 20 percent reduction in species richness (Hooper et al. 2012). Following his line of argument, differences in biomass between stages could mainly be result of differences in the characteristic of the most abundant species (see Chapter 4).

Environmental conditions played an important role in influencing species diversity and some estimates of ecosystem services were better explained by differences in site than successional stage. This underlies the importance of considering environmental conditions in the provision of ecosystem functions and services especially in highly heterogeneous landscapes. In agreement, Isbell et al. (2011) found an increase in the proportion of species required to promote ecosystem functions when more factors were considered (e.g. time, space, and environment) as each assemblage of species appeared to be more efficient than others under specific scenarios. Differences in management can also influence the importance of species diversity and environmental variables on ecosystem functions. For example, an increased in abundance of multi-functional species can result from selection by local management in more disturbed vegetation and agricultural land, as could be observed in small parcels in the region, influencing the relation between diversity and function by increasing disproportionally the effect of species richness on functions (Sircely and Naeem 2012).

5.5.4 Relations between ecosystem services

Several positive relationships and trade-offs were observed between provisioning, regulatory and cultural services. With the exception of aboveground carbon storage that was only related to the successional stage. Surprisingly, relationships between species richness and ecosystem services were all negative, except for one case. These results give evidence of the positive effect of environmental and management variability promoting the provision of several ES at the landscape scale. However, they also contrast with previous studies that repoted high levels of correlation among biodiversity and ecosystem services (Bai et al. 2001) and exemplify the challenges for conserving biodiversity and maintaining ES in tropical agricultural landscapes.

5.5.5 Conclusions

The combination of socio-economic and field data methods in the assessment of the provision of ecosystem services proved to be a valuable approach to collect information on the different types of benefits offered by forests. A high number of useful species were recorded and high variability of functional traits was observed among them, showing that no specific functional profile has been selected for any of the services assessed. Differences in the provision of ecosystem services between stages were related to the presence of useful species, whereas field data showed differences in the abundance percentage of potential source food species for *S. oedipus*. Contrary to the predictions there was no consistent

142

support for the link between functional diversity and ecosystem provision, suggesting that in high diversity tropical forests the use of complementarity models to explain the relationship between biodiversity and ecosystem function and services is limited. The results also showed evidence of a negative relationship between species richness and the provision of ecosystem services at the plot level. The evidence of this trade-off in the region highlights the benefits of maintaining under sustainable use forests of different successional stage.

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5.7 SUPPLEMENTARY INFORMATION

Table 5.8. One-way analysis of variance of functional indices values for three successional stages of secondary seasonally dry tropical forest. N = 9, three sites per stage where each site is a grouped sample of 15 10 x 10 m plots.

	Early	**Intermediate**	**Late**	*F*	*P*
Richness	0.35	0.58	0.49	1.40	0.32
Evenness	0.98	0.98	0.98	0.17	0.85
Divergence	0.76	0.80	0.81	4.48	0.06
Dispersion	0.14	0.16	0.15	0.40	0.69
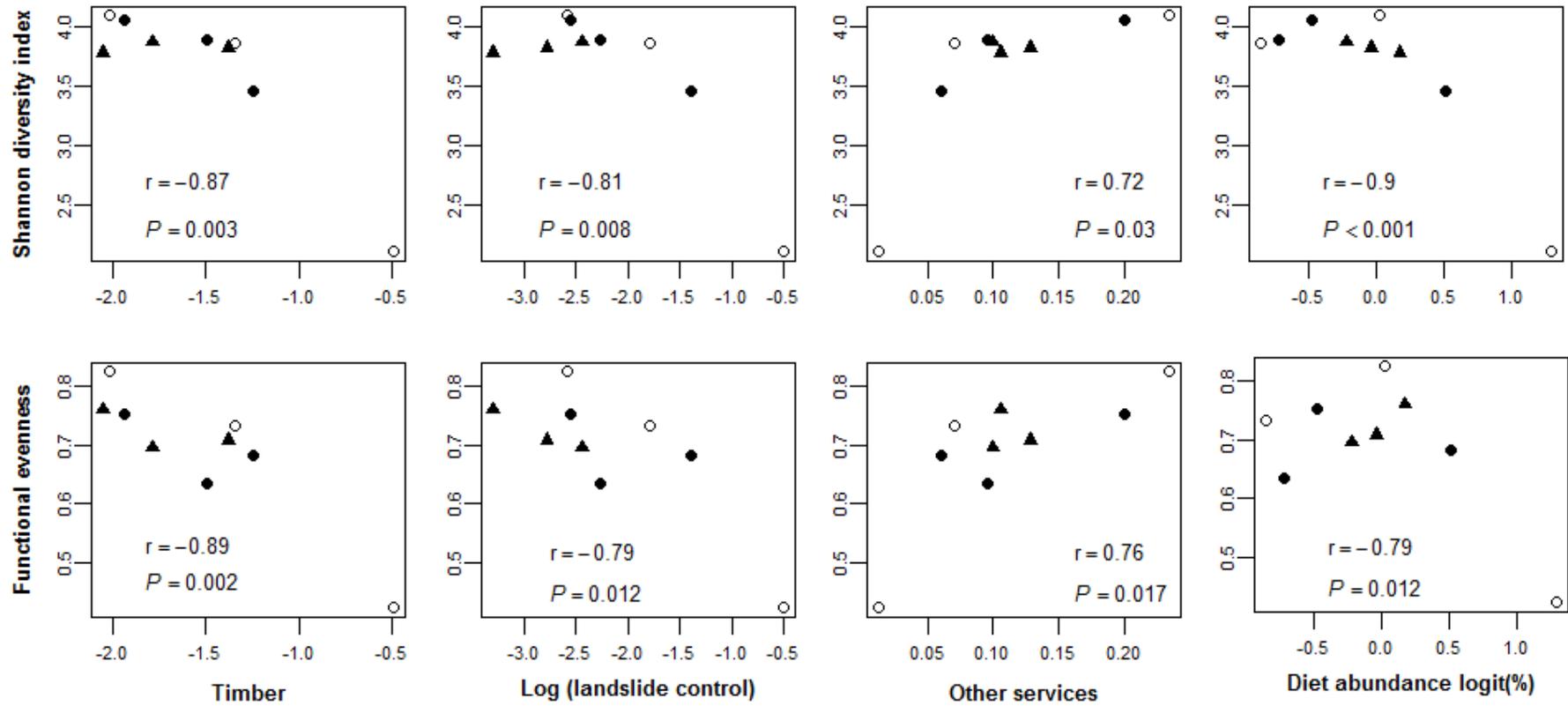
Figure 5.3. Relationships between functional evenness and Shannon diversity indexes and measures of timber, landslide control, other services and diet abundance (%) of SDTF. Each dot indicates the mean value of 15 plots per successional stage on three replicate sites.

148

CHAPTER 6 DISCUSSION AND SYNTHESIS

Secondary tropical forests result from the recovery of abandoned lands that were cleared generally for agriculture (Brown and Lugo 1990). They constitute a great percentage of the forested lands in the tropics (Trejo and Dirzo, 2000; ITTO 2002) and their extension is expected to increase if urbanization and slowing growth of human population continues (Wright and Muller-Landau 2006). These forests are an important component of agricultural landscapes and their protection and management can be a promising strategy for biodiversity conservation outside reserves. However, the varying environmental and management conditions under which they establish influence the different types of secondary forest found and there is great interest in understanding the different factors that control their conservation value.

In the case of seasonally dry tropical forest (SDTF), secondary vegetation plays a significant role as the area remaining of primary or old-growth forest is very scarce. These forests have been preferred for the establishment of human population due to the favourable climatic conditions where they are found and their relatively ease of management in comparison to wet forests (Murphy & Lugo, 1986). Although still understudied compared to other forest ecosystems of the tropics there is growing available information about their extension, diversity and ecology. It is now known that secondary SDTF can conserve high levels of biodiversity and share some of the species typically found in conserved forests (Kalacska et al. 2004; Lebrija-Trejos et al. 2008). The ability to recover this diversity after disturbance however is highly influenced by the time of use and management regime, as well as their proximity to forest fragments (Sabogal 1992; Molina-Colón and Lugo 2006; Romero-Duque et al. 2007).

The conservation value of these forests however goes beyond their capacity to sustain species and it is also desirable that they maintain ecosystem functions and provision of services to humans. SDTF provided a high variety of services to the local communities and these are threatened by continuous clearing and degradation (Balvanera and Maass 2010). Clearing of forests for agriculture disrupts species interactions, destroys the habitat of many species and modifies patterns of water capture and the pools of carbon and nutrients in the soil and aboveground (Kauffamn et al. 1993, Maass 1995). The recovery of these functions during succession has been observed to occur at different rates (Barlow et al. 2007; Campo et al. 2007; Vargas et al. 2008; Villa-Galaviz et al. 2012) and current evidence of the relationship between diversity and ecosystem function suggests that this recovery can be strongly influenced by the functional characteristics of the plant community (Bakker et al.

2013). However, the information about these aspects of secondary forests in general and in particular of SDTF is scarce. Very few studies have addressed the changes in functional composition of secondary SDTF forest and this dissertation makes a significant contribution in this matter. In addition, this research provides information about how the provision of ecosystem services differs among successional stages and how it relates to the species and functional diversity, an issue that until now had not been addressed.

6.1 DIMENSIONS OF PLANT TRAIT VARIATION IN SDTF

The coordinated variation of plant traits among species provides evidence of different resource use strategies at the whole-plant level and of the functional trade-offs that determine them. In chapter 2, I described the coordinated variation of leaf and stem traits in a set of 113 species of seasonally tropical dry forest. Plant performance in this ecosystem has been strongly related to the availability of water and light and I wanted to test if the relationships between this set of traits gave support to the hypothesis of a coordinated tolerance of drought and shade, as has been proposed recently (Sterck et al. 2010; Markesteijn et al. 2011).

High variability of trait values was observed among species and I found evidence of coordination among leaf and stem traits that potentially allow both shade and drought tolerance. A great percentage of variation (64%) was explained by the three first components of a multi-dimension analysis. These in order of importance described 1) differences in mass investment in leaves and stem, 2) leaf organization and thickness and 3) the relationship between leaf area and stem properties. My results differ from the orthogonal variation observed among stem and leaf traits in wet forest (Baraloto et al. 2010), supporting the different effects of environmental variables on trait variation between these ecosystems. The axes described also showed significant relationships with SM and height, traits that have been considered independent dimensions of plant variation (Westoby et al. 1998), providing evidence of coordination at the whole-plant level.

Classification of species based on the trait variation observed is desirable to simplify analysis of changes in the plant community in relation to environmental conditions and disturbance. I selected three common classification systems of species in this ecosystem and tested their capability to integrate the multi-trait space described. Significant differences were found between species classified by their leaf phenology and phylogenetic clade, however high overlap between groups was observed. Life form classification only showed functional differences for palms and woody grasses; whereas no differences were observed between lianas and trees. An *a posteriori* classification based on clustering of the functional

traits provided a better alternative but it is restricted to the specific community and location. One caveat of this analysis is that I did not test the relevance of the traits selected on plant performance, for example by recording field measures of drought and light tolerance and relating them to the traits used, or by considering species distribution along the environmental gradients. This last approach was used by Fyllas et al. (2011) to classify woody species of the Amazonian basin and gave an optimum classification of four functional groups to be used in global vegetation modelling. The inclusion of these measures will be considered in future analysis to improve the classification achieved.

Other factors that can influence trait analyses are intraspecific variation and ontogenetic changes. Intraspecific variation was considered in this research by quantifying the percentage of variation explained by species and individuals. For most of the traits a big portion of the variation was explained by differences between species, with the exception of specific leaf area and bark thickness, which were possibly influenced by differences in the adult stature or crown exposure (Markesteijn et al. 2007) and the size of the sampled individuals (Poorter et al. 2013), respectively. Future analysis considering these traits might require a bigger sample size or sampling at each plot to account for variation among individuals due to environmental factors. Ontogenetic changes can also influence the relationships between functional traits, for example Liu et al. (2010) found differences in the slope of the relationships between traits of small and large individuals of tropical trees in China. Studies that assess trait relationships at the seedling and sapling stages would provide information about the maintenance of the trade-offs observed in this study and their strength, and allow testing for differences in the influence of environmental factors at early stages.

6.2 DIVERSITY OF SECONDARY SDTF FORESTS

The functional variation observed among species in the plant community suggests that different trait combinations confer higher efficiency under different levels of water and light availability. In landscapes subject to seasonal precipitation water availability has been observed to vary with topography and to influence species distribution (Parker et al. 2005, Balvanera et al. 2011). Light levels on the other hand vary during the year due to the deciduousness associated with the dry season, although clearing and management of forest can intensify the levels of insolation and temperature on the understory and increase environmental heterogeneity (Lebrija-Trejos et al. 2011). In chapters 3 and 4, I tested the effect of successional and topographic gradients on the species and functional composition of secondary forests. The results contribute to the knowledge of the different types of

secondary forest found in modified landscapes and the factors that influence its plant community.

6.2.1 Do environmental factors influence species composition during successional trajectories in a SDTF landscape?

Species composition of secondary SDTF has been observed to vary considerably in relation to management regimes and age since abandonment. However, considering the strong effect of water availability in the distribution of species in this ecosystem, the effect of environmental variables in successional trajectories has been poorly documented. In chapter 3, I used stratified vegetation sampling to describe variation among successional stages along a topographic gradient that determines differences in nutrient content and soil texture and was considered as a proxy of water availability.

High species turnover was observed and dominant species varied considerably between stages at each site. Composition similarity among late successional stage forests was higher than between intermediate and late successional stages and overall the results showed evidence of the influence of environment conditions on successional trajectories. The variation in species composition explained by the environment was similar for all stages but the importance of the spatial structure was higher in early stage forests reflecting difference in dispersal limitations and favouring of species by management at each site.

My results also showed an increase of species diversity and height from early to intermediate and late stages, in agreement with other studies of secondary SDTF. However, no differences in basal area and density of individuals were observed, which I explain by the absence of younger stands where higher structure dynamics have been observed. This study has additional implications as it provides new evidence of the potential for conservation of secondary forests in heterogeneous landscapes, and makes available new floristic data that will complement the understanding of patterns of floristic diversity of SDTF in the neotropics.

6.2.2 Do changes in functional composition of STDF reflect changes in species composition in relation to the successional process and environmental gradients?

The relationship between species richness and functional diversity is a key element to understanding the mechanisms that link biodiversity and ecosystem function. A linear increase of species and functional diversity has been observed to improve efficiency of

resource use in an ecosystem due to complementarity in function, whereas a saturating relationship has been proposed to confer higher resilience to disturbances and species loss due to functional redundancy (Fonseca and Ganade 2011, Cadotte et al. 2011). In chapter 4 I described changes of recovery of functional composition of secondary SDTF and its relationship to species richness. Following the results of chapter 3 that supported the influence of succession and the topographic gradient shaping the plant community, I also wanted to analyse the filtering effect of these factors on the functional composition of these forests.

I did not find differences between stages in the distribution of species along the range of any of the traits studied, results that support the existence of functional redundancy in these forests. These results agree with observation by Mayfield et al. (2006) who found that functional diversity of herbaceous and shrubby plant communities in deforested habitats was not lower than for their counterparts in remnant forest habitats in the same landscapes and that few trait states common in forest remnants were completely absent from deforested components of these landscapes. Furthermore, the high turnover of species observed in Chapter 3 suggests that the replacement and addition of functional similar species is occurring during succession.

In contrast, when considering species abundance significant differences were observed between stages in the community weighted values of stem-related traits and the range distribution of all traits. These results highlight the importance of considering abundance when studying functional community assembly as it reflects not only the ability to establish in a location but also differences in performance advantage of sets of traits. Overall, from early to late stages I observed an increase of stem density and of individuals with latex, and a decrease of bark thickness, number of trunks and the number of individuals with resprouting ability. These shifts suggest changes in abundance of individuals with traits that favor regeneration after disturbance to individuals with a more conservative resource use strategy as succession progress.

Environmental characteristics on the other hand were strongly related to community weighted values of leaf related traits, suggesting that this set of traits are more responsive to the environment than succession. Areas with higher nutrient concentration, which in turn were found in lower altitudes and slopes, were related to a plant community with denser and tougher leaves, thicker bark and higher number of trunks. Leaf dry matter content and specific leaf area were traits strongly related with one of the dimensions of plant variation

identified in the community (Chapter 2) and its link with environmental variables support the importance of resource economy strategy shaping functional composition in this region.

The relationships among traits can also vary between the species and community level (Ackerly et al. 2002) and my results gave evidence of this decoupled response. For example, leaf thickness was found to be strongly linked with leaf dry matter content and stem density at the species level but not for community average values. These differences allowed some traits strongly linked at the species level to differ in their response to successional or environmental gradients at the community level. Kühner and Kleyer (2008) proposed that for a given landscape a limited set of functional traits would suffice to predict plant responses, but that this set would generally not be applicable across all scales and regions. In the region studied, traits that favour regeneration during disturbance and those related to the resource use strategy like stem density and leaf dry matter content, could suffice to describe functional variation in relation to management and abiotic factors.

Future analysis should address two issues that were not considered in this research: 1) the effect of spatial auto-correlation explaining variation in functional community assembly, which may be overestimating the relationships between traits and the environmental variables observed, and 2) changes in the importance of external factors in shaping plant community during succession. The latter was observed by Campetella et al. (2011) in the herbaceous community of beech forests, where an increase of the importance of abiotic factors and a decrease of the chance factor associated with dispersal occurred during succession. Multi-trait indices, which are an alternative to studying the relationship between functional diversity and abiotic factors, were not used in this section of my dissertation because their use can obscure independent relations of traits and environmental variables, which were one of the main interests of this part of the research.

6.3 MULTIFUNCTIONAL LANDSCAPES

Agricultural landscapes in the tropics consist of mixtures of land uses that provide several ecosystems services to local and regional communities. Secondary forests are a common components of these landscapes and their preservation value in comparison to other uses is very high as they can fulfill both the provision of services to humans and the conservation of biodiversity. Studying the link between these two purposes provides essential information to identify bundles of services and to direct management actions that maximize functioning of the landscape (Cimon-Morin et al. 2013). In chapter 5, I addressed this issue and used a novel approach to assess the capacity of different secondary forests to provide ecosystem

services and its link to their species and functional diversity. In these assessments it is crucial to include different type of services, including those that involve human preferences and knowledge like the use of medicinal plants. With this purpose I collected information in the field as well as from semi-structured interviews. This allowed me to have a better understanding of the value of secondary forest for the local communities.

I found that the provision of services estimated from the abundance of useful species in the plots assessed declined with successional stage. These results show that local people rely more on species abundant in early and intermediate forests to supply their demands for wood, charcoal, medicine and other common uses. This preference can result from the shortage of late and conserved forest in the region and also of the desirables characteristics of these species, like commonness, rapid growth and production of fodder. In contrast, when considering only species presence to calculate the importance value of each stage, which allowed me to include more than thirty species that were not registered in the plots but were recorded in secondary forests, I observed higher provision in intermediate and late forests. This discrepancy suggests that the contribution of rare species to the provision of services in these forests can be significant.

To link this provision with the functional diversity of these forests I used two approaches: the functional trait values of useful species and the variability of traits in the community. In terms of the functional identity of the useful species identified by respondents I observed a great variability of traits, showing that there was no specific profile selected for use by people. This was surprising in the case of wood, for which I was expecting a high representation of hard wooded species, but shows complementarity in the provision of services by the different functional types. The set of species that were used for this analysis was determined by their dominance in the forest plots, and their representation of the complete set of useful species varied with the service. Not surprisingly this was high for wood and charcoal, services that are linked to the size of individuals, but was lower for medicine, beauty, others and food that can be provided by non-dominant species or introduced plant that are found in farms and pastures.

The variation of plant traits was estimated using functional indices that measured different aspects of the functional diversity of the community: the size of the functional space (richness), the distribution of abundance in this space (functional evenness and divergence) and the mean distance of species to its centroid (dispersion). The results did not show a consistent relationship between any of these indices and the estimated services, in addition no differences in functional indices were observed between successional stages. The

155

evidence of species functional similarity shown in Chapter 4 can partially explain these results as similar traits values were observed in the three successional stages, suggesting that functional diversity has not been severely impoverished in the region to levels that affect ecosystem services. However, I did find differences in the functional composition between stages that were expected to be detected by the abundance weighted indices; this was not the case either. I did observe a strong influence of one of the data points in the significant relationships observed that limits their interpretation. A caveat of this analysis was that only nine data points were used due to the restricted number of dominant species in some plots, which impeded the calculation of functional indices and made necessary grouping plots by successional stage and site. A complete functional assessment of the community will increase this sample and allow a better understanding of the patterns observed. Species richness at the plot level showed stronger links with estimates of ecosystem services than functional indices. The significant relationships observed were however all negative, with the exception of other services, and in contrast to other studies, biomass was not related to any measure of species diversity.

My results have important implications for the future management of these areas, as they showed that for the conservation of both species richness and the provision of ecosystem services it is necessary to maintain different aged forests across the landscape. The relationships observed also make apparent the difficulty in generalizing the links between diversity and functions in species-rich systems like tropical forests. Future management decisions require the identification of stakeholder's interests and expectations on the benefits that the declaration of the studied area will bring.

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APPENDICES

Appendix 1. List of literature consulted to assign leaf phenology and seed dispersal syndrome to a set of SDTF plant species. Citations presented on the table and references provided below.

Scientific name	Literature consulted
Acacia macracantha	Casiva et al. (2004)
Aiouea vexatrix	Kubitzki & Renner (1982)
Albizia niopoides	Cordero and Boshier (2003), Toniato and Oliveira-Filho (2004), Wright et al. (2012)
Anemopaegma orbiculatum	Woodson et al. (1973)
Annona purpurea	Griscom et al. (2009), Powers (2010), Wright et al. (2012)
Antirhea trichantha	Condit et al. (2011), Wright et al. (2012), Proyecto Tití (2013)
Apeiba tibourbou	Pennington and Sarukhan (2005), Zuchowksi (2007), Powers and Tiffin (2010), Wright et al. (2012)
Arrabidaea mollisima	Woodson et al. (1973)
Aspidosperma polyneuron	Fonseca et al. (2004), Toniato and Oliveira-Filho (2004)
Astronium graveolens	Powers et al. (2009), Powers and Tiffin (2010), Wright et al. (2012)
Attalea butyraceae	Visser et al. (2004), Wright et al. (2012)
Bactris guineensis	Gargiullo et al. (2008), Wright et al. (2012)
Bactris major	Gargiullo et al. (2008), Wright et al. (2012)
Bauhinia glabra	Camacho et al. (2007), Zuchowski (2007) for *Bauhinia guianensis*, Griscom et al. (2009) for genus, Wright et al. (2012)
Bignonia dichotoma	Woodson et al. (1973)
Bourreria cf. cumanensis	Gottschling and Miller (2007)
Bravaisia integérrima	Frankie et al. (1974), Pennington and Sarukhan (2005)
Brosimum alicastrum	Rodriguez (2001), Zuchowski (2007), Powers et al. (2009), Powers and Tiffin (2010)
Brosimum guianense	Stevenson (2000), Rodriguez (2001), Condit et al. (2011), Wright et al. (2012)
Bunchosia diphylla	Martínez-Garza et al. (2011) for genus.
Bunchosia pseudonitida	Martínez-Garza et al. (2011) for genus.
Bursera simaruba	Trainer & Will (1984), Zuchowski (2007), Powers (2010), Wright et al. (2012)
Caesalpinia coriaria	Miller and Kauffam (1998), Cordero & Boshier (2003), Borges et al (2009), Wright et al. (2012)
Calycophyllum cf. *candidissimum*	Cordero and Boshier (2003), Griscom et al. (2009), Powers et al. (2009), Powers and Tiffin (2010), Wright et al. (2012)
Capparidastrum frondosum	Little et al. (1974), Rodriguez (2001), Wehncke et al. (2004)
Capparidastrum pachaca	Iltis (1965)
Capparis odoratissima	Rodríguez-Ferrardo and Sanz (2007), Ramírez and Valle (2011)

Scientific name	Literature consulted
Carpotroche grandiflora	Kelly (1995) for genus, Rodríguez (2001)
Casearia praecox	Kelly (1995) for genus, González-Ramírez et al. (2010)
Casearia sylvestris	Toniato and Oliveira-Filho (2004), Powers (2010), Wright et al. (2012)
Cavallinesia platanifolia	Condit et al. (2010), Wright et al. (2012)
Cecropia peltata	Zuchowski (2007), Powers et al. (2009), Powers and Tiffin (2010)
Ceiba pentandra	Zuchowski (2007), Wright et al. (2012)
Centrolobium paraense	Pirie et al. (2009)
Chamissoa altissima	Sánches and Válio (2002), Kelly (1995)
Chloroleucon mangense	Miller and Kauffman (1998), Borchert et al. (2004), Wright et al. (2012)
Chlorophora tinctoria	Rodríguez (2001), Cordero and Boshier (2003), Powers et al. (2009), Powers and Tiffin (2010), Wright et al. (2012)
Cochlospermum vitifolium	Zuchowski (2007), Powers et al. (2009), Powers and Tiffin (2010), Wright et al. (2012)
Combretum fruticosum	Exell (1958), Avalos et al. (2007), Wright et al. (2012)
Combretum spinosum	Exell (1958)
Cordia alliodora	Cordero and Boshier (2003), Zuchowski (2007), Powers and Tiffin (2010), Wright et al. (2012)
Cordia collococca	Cordero and Boshier (2003), Powers et al. (2009), Wright et al. (2012)
Cordia dentata	Cordero and Boshier (2003), Wehncke et al. (2004), Powers and Tiffin (2010), Wright et al. (2012)
Cordia gerascanthus	Cordero and Boshier (2003)
Coursetia ferruginea	Lavin (1988)
Crateva tapia	Guevara et al. (1986), Rodríguez (2001)
Croton malambo	Webster (1994)
Croton niveus	Webster (1994)
Cynophalla flexuosa	Sobral and Machado (2001), Little et al. (1974), Reyes (2003), Borchert et al. (2004)
Cynophalla verrucosa	Sobrado (1986)
Dalbergia brownei	Camacho et al. (2007), Wright et al. (2012)
Enterolobium cyclocarpum	Hunter (1989), Zuchowski (2007), Powers and Tiffin (2010), Proyecto Tití (2013)
Eugenia herrerae	Sobral and Machado (2001) for genus, Kimmel et al. (2010)
Gliricidia sepium	Zuchowski (2007), Powers et al. (2009), Powers and Tiffin (2010), Wright et al. (2012)
Guadua amplexifolia	Young and Judd (1992), Areta et al. (2009)
Guazuma ulmifolia	Zuchowski (2007), Griscom et al. (2009), Powers et al. (2009), Powers and Tiffin (2010), Wright et al. (2012)
Guettarda cf. malacophyla	Frankie et al. (1974), Loayza and Knight (2010) for *Guettarda viburnoides*, Croat et al. (2013) for *Guettarda foliaceae*
Gustavia superba	Aide (1992), Forget (1992), Muller-Landau et al. (2008)
Gyrocarpus americanus	Condit et al. (2011), Wright et al. (2012)

Scientific name	Literature consulted
Hiraea reclinata	Woodson et al. (1980)
Homalium racemosum	Sleumer (1980)
Hura crepitans	Corantioquia (2005), Condit et al (2010), Wright et al. (2012)
Hybanthus prunifolius	Augspurger (1979), Engelbrecht and Kursar. (2003), Condit et al. (2011), Wright et al. (2012)
Inga cf. Hayessi	Rodriguez (2001), Wright et al. (2012)
Labatia cf. glomerata	Pennington (1990), Andresen and Levey (2004)
Lecythis minor	Hammond and Brown (1995) for genus, Zuchowski (2007) for *Lecythis ampla*
Licania glabriflora	Hammond and Brown (1995) for genus, Anand and Langille (2010)
Lippia americana	
Lonchocarpus fendleri	Augspurger and Hogan (1983), Janzen et al. (1990) for genus
Luehea cf. candida	Cordero and Boshier (2003), Powers et al. (2009), Powers and Tiffin (2010), Wright et al. (2012)
Machaerium arboreum	Wright et al. (2012)
Machaerium biovulatum	Frankie et al. (1974), Dwyer and Hermann (1965) for genus.
Machaerium microphyllum	Griscom et al. (2009)
Matayba scrobiculata	Wright et al. (2012), Proyecto Tití (2013)
Melicoccus bijugatus	Cordero and Boshier (2003), Proyecto Tití (2013)
Memora patula	
Mimosa inaequalis	Hernández (1989), Zamora et al. (2000)
Myrospermum frutescens	Cordero and Boshier (2003), Wright et al. (2012)
Nectandra turbacensis	Rohwer (1993), Little et al. (1974)
Neea nigricans	Proyecto Tití (2013)
Ochroma pyramidale	Sandí and Flores (2002), Cordero and Boshier (2003), Kukowski (2007), Wright et al. (2012)
Ouratea guildingii	Hammond and Brown (1995) for genus.
Oxandra laurifolia	Little et al. (1974), Kelly (1995) for genus.
Paullinia fuscescens	Kelly (1995) for genus, Wright et al. (2012)
Pereskia guamacho	Edwards and Díaz (2006), Flores et al. (2011) for genus, Proyecto Tití (2013)
Phitecellobium lanceolatum	Rodriguez (2001), Wright et al. (2012)
Piptadenia viridifolia	Lopes et al. (2012) for genus.
Piscidia carthagenensis	López-Gómez et al. (2008)
Pouteria durlandii	Andresen and Levey (2004)
Pradosia colombiana	Pennington (1990)
Pseudobombax septenatum	Corantioquia (2005), Camacho et al. (2007), Condit et al. (2011), Wright et al. (2012)
Pseudopiptadenia pittieri	Lopes et al. (2012) for genus.
Pterocarpus acapulsensis	Augspurger (1986) for genus.
Pterocarpus rohrii	Little et al. (1974), Augspurger (1986), Pennignton and Sarukhán (2005) for genus

Scientific name	Literature consulted
Randia dioica	Frankie et al. (2004), Muller-Landau et al. (2008), Wright et al. (2012), Proyecto Tití (2013)
Rauvolfia littoralis	Zamora et al. (2000), Condit et al. (2011), Morales (2012)
Rondeletia purdiei	Little et al. (1974) for genus, Proyecto Tití (2013)
Ruprechtia ramiflora	Condi et al. (2011) for Ruprechtia costata
Sabal mauritiiformis	Tomlinson (1979), Rodriguez (2001), Kunz et al. (2011)
Samanea saman	Proyecto Tití (2013)
Sapindus saponaria	Cordero and Boshier (2003), Borchert et al. (2004), Wright et al. (2012), Proyecto Tití (2013)
Sapium glandulosum	Toniato and Oliveira-Filho (2004), Powers and Tiffin (2010), Wright et al. (2012)
Sciadodendron excelsum	Griscom et al. (2009), Valenta and Fedigan (2010)
Seguieria americana	Mirle and Burnham (1999)
Senna atomaria	Cordero and Boshier (2003)
Sorocea sprucei	Kelly (1995) for genus, Rodríguez (2001)
Spondias mombin	Powers et al. (2009), Powers and Tiffin (2010), Wright et al. (2012)
Sterculia apetala	Janzen (1972), Cordero and Boshier (2003), Condit et al. (2010), Wright et al. (2012), Proyecto Tití (2013)
Swartzia simplex	Cowan (1967), Zamora et al. (2000) for *Swartzia sumorum*, Rodriguez (2001), Camacho et al. (2007), Wright et al. (2012)
Tabebuia chrysea	Gentry (1970)
Tabebuia ochracea	Gentry (1970), Cordero and Boshier (2003)
Tabebuia rosea	Gentry (1970), Zuchowski (2007), Powers and Tiffin (2010), Wright et al. (2012)
Tabernaemontana grandiflora	Griscom et al. (2009), Wright et al. (2012)
Tabernamontana cymosa	Kelly (1995) for genus, Gargiullo et al. (2008) for *Tabernamontana alba*
Talisia oliviformis	Acevedo-Rodríguez (2003), Pennington and Sarukhán (2005), Proyecto Tití (2013)
Trichilia acuminata	Rodríguez (2001)
Trichilia hirta	Cordero and Boshier (2003), Condit et al. (2010), Wright et al. (2012), Proyecto Tití (2013)
Urera caracasana	Little et al. (1974), Zugliani and Oliveira-Filho (2004), Easdale and Healey (2009)
Vitex compressa	Acero (2007) for *Vitex orinocensis*, Proyecto Tití (2013)
Zanthoxylum caribaeum	Cordero and Boshier (2003), Toniato and Oliveira-Filho (2004)
Ziziphus heteroneura	Condit et al. (2011)
Zygia inequalis	Schongart et al. (2002)

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Appendix 2. List of the useful species recorded in the semi-structure interviews. Numbers indicate number of interviews where the species was mentioned and frequency (F.) indicates the number of uses recorded for each species. Charcoal- Char., medicine- Med., livestock- Live., landslide control- Land.

Scientific name	Common name	Wood	Char.	Med.	Food	Live.	Beauty	Water	Fauna	Land.	Other	F.
Acacia collinsii	Cachito			1								1
Acacia macracantha	Aromo	4	17	1		17	1	1	1			7
Acacia polyphylla	Baranoa	1										1
Acanthocereus tetragonus	Pitaya				3				2			2
Agonandra brasiliensis	Caimancillo								3			1
Albizia niopoides	Guacamayo	12	7								1	3
Anacardium excelsum	Caracoli	10	2					12	2	4		5
Anacardium occidentale	Marañon				9		1		1			3
Annona cherimola	Chirimoya				2							1
Annona muricata	Guanabana			1	24	1	1		1			5
Annona purpurea	Guanabana matimba			1	1							2
Annona sp.	Anon				14		1		1			3
Apeiba tibourbou	Algodoncillo	2				1						2
Aristolochia inflata	Contracapitana			8								1
Aspidosperma polyneuron	Carreto	12	2	1			1					4
Astronium graveolens	Quebracho	5	11	3		2						4
Attalea butyraceae	Palma de vino					3	2	1	9	4		5
Averrhoa carambola	Torombolo				1							1
Azadirachta indica	Nin			3		1	4			1		4
Bactris guineensis	Corozo				11	1		3	5		8	5
Bauhinia glabra	Bejuco cadena			14		1					8	3
Belencita nemorosa	Calabacillo						1		1			2
Bignonia pubescens	Bejuco colorado										1	1
Bougainvillea glabra	Buganvil						1					1
Bougainvilliea sp.	Veranera						1					1

Scientific name	Common name	Wood	Char.	Med.	Food	Live.	Beauty	Water	Fauna	Land.	Other	F.
Bourreria cf. cumanensis	Cajon	9	4									2
Bravaisia integérrima	Palo de agua	6	4					12		3		4
Brosimum alicastrum	Guaimaro	14			11	1			9			4
Bulnesia arbórea	Guayacan	7	1				10					3
Bursera graveolens	Caraña			3				1				2
Bursera simaruba	Resbalamono			13					3		1	3
Caesalpinia coriaria	Dividivi	1	1			3						3
Cajanus cajan	Guandul			9	2	1			1			4
Calycophyllum cf. candidisimum	Guayabo	20	3		2	1		1	1			6
Capparidastrum frondosum	Sincogollo			1								1
Capparidastrum pachaca	Calabacilla	2			1	1	6	1	2			6
Capparis odoratissima	Olivo	9	2	2			27	2	3		1	7
Capsicum spp.	Aji				3	1						2
Carica papaya	Papaya				13				1			2
Cariniana pyriformis	Abarco	1										1
Cassia grandis	Cañafistula	5		1	5	1	1	1				6
Cavallinesia platanifolia	Macondo	1		1					3			3
Cecropia peltata	Guarumo			3		1						2
Cedrela odorata	Cedro	19	1					1				3
Ceiba pentandra	Ceiba bonga	8	1			1	2	2		2		6
Centrolobium paraense	Colorado	19	3			1						3
Chloroleucon mangense	Viva seca	1										1
Chlorophora tinctoria	Mora	17	4	1		2			3	1		6
Chrysophyllum caimito	Caimito				7							1
Citrus máxima	Pomelo				4							1
Citrus reticulata	Mandarina				3							1
Citrus sp.	Naranja			2	17	2	3					4
Citrus x limón	Limon			5	10		3					3

169

Scientific name	Common name	Wood	Char.	Med.	Food	Live.	Beauty	Water	Fauna	Land.	Other	F.
Citrus x limonia	Limon mandarina				1		1					2
Coccoloba caracasana	Uvero							4				1
Coccoloba coronata	Juan garrote	1	1		2							3
Coccoloba uvifera	Uva playera				1							1
Cocus nucifera	Coco				13		1			3		3
Combretum fruticosum	Bejuco chupa chupa		1						1		1	3
Copernicia tectorum	Palmiche										2	1
Cordia alliodora	Canalete	25	1						1			3
Cordia colococca	Arato	12	1		1				6			4
Cordia dentata	Uvita	11	8		2	5		1	8	2		7
Cordia gerascanthus	Vara de humo	1										1
Cordia sp.	Canalete real	1										1
Coursetia ferruginea	Cucuiro					2						1
Crateva tapia	Naranjito	4	4	2		4	14	3	3	1		8
Crescentia cujete	Totumo	2	2	5		7	1	2	2			7
Croton malambo	Malambo			18								1
Croton niveus	Plateado			3								1
Cryptostegia grandiflora	Veinte de julio			1								1
Delonix regia	Acacia						1					1
Elaeis oleífera	Palma corozo								1	1		2
Enterolobium cyclocarpum	Carito	14	5		1	15	3	2		1		7
Erythrina fusca	Cantagallo							1				1
Erythroxylum densum	Coca			2								1
Erythroxylum havanense	Guayabo prieto								1			1
Eucalyptus sp.	Eucalipto	9	1	21			2		1	1		6
Euphorbia arenaria	Pita morrea			1								1
Ficus nymphaeifolia	Cope			1			2	3	1	5		5
Ficus sp.	Higueron				1	1	1	3				4

Scientific name	Common name	Wood	Char.	Med.	Food	Live.	Beauty	Water	Fauna	Land.	Other	F.
Ficus trigonata	Laurel						2					1
Genipa americana	Jagua							1	4			2
Gliricidia sepium	Mataraton	20	12	10		18	2		1	4		7
Gmelina arbórea	Melina	2					1	1				3
Guadua amplexifolia	Caña brava							1		2		2
Guadua angustifolia	Guadua							5		4		2
Guaiacum officinale	Guayacan extranjero						1					1
Guazuma ulmifolia	Guacimo	12	25	3	3	25	4	3	5	1		9
Gustavia superba	Membrillo			2	5				2		8	4
Gyrocarpus americanus	Banco			1								1
Hura crepitans	Ceiba blanca	27	3			1	2	1	1	3		7
Hymenaea courbaril	Algarrobo	1			3	2						3
Indigofera suffruticosa	Añi			1		1						2
Inga hayessi	Guamito				1							1
Inga sp.	Guama			1	9		1	7	1			5
Jacaranda caucana	Gualanday			1								1
Jatropha gossypiifolia	Tuatua			1								1
Labatia cf. glomerata	Yaya de cajon	1										1
Lecythis minor	Olla de mono	15	3	1		2		5	1	2		7
Leucaena leucocephala	Leucaena					2			1			2
Libidibia corymbosa	Granadillo	1										1
Lonchocarpus sp.	Bollo limpio	1										1
Ludwigia leptocarpa	Guayabito							1				1
Macfadyena ungis-cacti	Bejuco uñita										2	1
Malpighia glabra	Cereza		1		16	1		2	4			5
Mammea americana	Mamey				2				1			2
Mangifera indica	Mango	2	2	1	44	12	9		10	1		8
Manihot esculenta	Yuca				1	1			1			3

171

Scientific name	Common name	Wood	Char.	Med.	Food	Live.	Beauty	Water	Fauna	Land.	Other	F.
Manilkara zapota	Nispero	1			15		1	1	1			5
Melicoccus bijugatus	Mamon	3	3		26	1	9		10			6
Mimosa inaequalis	Guama arroyera							1				1
Muntingia calabura	Guayuyo				1	1		2	3	1		5
Murraya paniculata	Azahar de la india						6					1
Myroxylon balsamum	Balsamo	2	1									2
Nicotiana tabacum	Tabaco	1										1
Opuntia sp.	Tuna				1							1
Oxandra laurifolia	Yaya de sangre	5										1
Pachira quinata	Ceiba roja	31	2					1	1			4
Parathesis sp.	Fruta de pava			1								1
Parkinsonia praecox	Brea			1								1
Pereskia guamacho	Guamacho		1	1	2		1		1	2		6
Persea americana	Aguacate				2							1
Piptadenia viridifolia	Bocachico	1										1
Pithecellobium lanceolautm	Tiribuche	1	2					1				3
Pittoniotis trichanta	Maretiro	1										1
Platymiscium pinnatum	Trebol	8	1					1				3
Platypodium elegans	Mataraton ex.					1						1
Pouteria sapota	Sapote				1	1	1					3
Pouteria sp.	Zapotillo	1	1									2
Pouteria durlandii	Nispero monte	1			2							2
Pradosia colombiana	Mamon de tigre	1							2			2
Prioria copaifera	Cativo	1										1
Prosopis juliflora	Trupillo	16	17			17	1	1		2		6
Pseudobombax septenatum	Majagua			1				2				2
Pseudopiptadenia pittieri	Chicharron	5	4									2
Psidium friedrichsthalianum	Guayaba agria				2							1

Scientific name	Common name	Wood	Char.	Med.	Food	Live.	Beauty	Water	Fauna	Land.	Other	F.
Psidium guajava	Guayaba			2	40	4	4		6			5
Pterocarpus acapulsensis	Sangregao	2	7								1	3
Quassia amara	Cruceta			7								1
Rauvolfia sp.	Solita			2								1
Ricinus communis	Higuereta			1								1
Ruprechtia ramiflora	Volador	2	3									2
Sabal mauritiiformis	Palma amarga					1	1			1	18	4
Salix viminalis	Mimbre							1				1
Samanea saman	Campano	29	11		2	21	7	7	3	4		8
Sapindus saponaria	Pepo	1	1				1					3
Sapium glandulosum	Piñique	2	1	1					2		1	5
Sciadodendron excelsum	Maduraplatano								2			1
Senna atomaria	Chibato	1										1
Senna reticulata	Majaguito								1			1
Senna siamea	Abeto						1					1
Spondias mombin	Jobo	17	8		19	7		4	19	1		7
Spondias purpurea	Ciruela		1		25	4	3		7			5
Sterculia apetala	Camajoru	28	1		5		1	1	6	2		7
Stigmaphyllon dichotomum	Bejuco San Juan										1	1
Swartzia simplex	Corocito					1			1			2
Swinglea glutinosa	Swinglia	1					3			1		3
Tabebuia billbergii	Coralibe	25	5				2	1				4
Tabebuia chrysea	Cañaguate	7					1					2
Tabebuia ochracea	Polvillo	8	1				2					3
Tabebuia rosea	Roble	42	9			5	6	5		1		6
Talisia oliviformis	Mamon de mico	1			8	1	1		9			5
Tamarindus indica	Tamarindo		1		10							2
Tectona grandis	Teca	1										1

Scientific name	Common name	Wood	Char.	Med.	Food	Live.	Beauty	Water	Fauna	Land.	Other	F.
Terminalia catappa	Almendro	2					9		1			3
Thespesia populnea	Clemon						1					1
Trichilia acuminata	Negrito	2							2			2
Triplaris americana	Vara santa							1				1
Urera caracasana	Pringamosa			1								1
Various	Vara de piedra	2	1									2
Various	Bejuco blanco					1		1				2
Various	Pino							1				1
Various	Mangle							1				1
Various	Vara blanca							1				1
Vitex compressa	Aceituno	3	1									2
Ziziphus angolito	Mondonguito				1				1			2
Ziziphus mauritiana	Guinda Guinda				2							1