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A Functional Trait Approach to Understanding Natural Regeneration and Restoration of Neotropical Forests

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A Functional Trait Approach to Understanding Natural Regeneration and Restoration of Neotropical Forests

Vanessa K.S. Boukili, Ph.D.

University of Connecticut, 2013

Over half of the Neotropical forests have been damaged by human activity, often converted to pasture or agriculture. Under the right conditions, second-growth forests can naturally regenerate once these lands are abandoned, providing a means of recuperating biodiversity and ecosystem services. However, the mechanisms of community assembly during the process of natural regeneration are not fully understood. Here I assess the relative influences of environmental filtering and stochasticity in the regeneration of pre-montane moist forest and lowland wet forests in Costa Rica. I quantify the ecological characteristics of trees and palms with leaf and stem functional traits, which are species-specific morphological and physiological attributes. I explore changes in species composition and functional trait composition over successional time, both across four pre-montane old-fields in the first 11 years of natural regeneration, and among two old-growth and six second-growth stands ranging in age from 10–40 years after abandonment of pasture in the lowland wet tropical forest region. I also compare patterns of taxonomic and functional beta diversity over time within each set of forest stands (pre-montane and lowland wet) to assess if functional characteristics of the communities are converging at a different rate from the species composition. Finally, I use an experimental approach to test the ability of species with different functional traits to survive and grow under three habitat treatments (pasture, second-growth forest, and old-growth forest) representing restoration scenarios.

A Functional Trait Approach to Understanding Natural Regeneration and Restoration of
Neotropical Forests

Vanessa K.S. Boukili

B.A., University of California, Berkeley, 2003

A Dissertation

Submitted in Partial Fulfillment of the
Requirements for the Degree of Doctor of Philosophy
at the
University of Connecticut

2013

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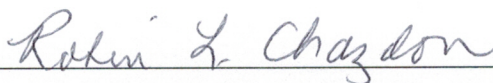
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A Functional Trait Approach to Understanding Natural Regeneration and Restoration of
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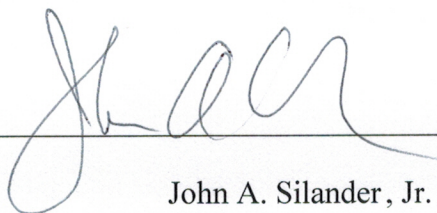
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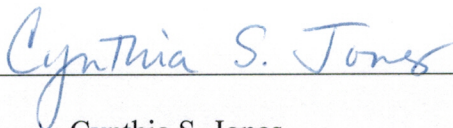
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INTRODUCTION

Tropical landscapes have been severely modified by human activities, including logging, fragmentation, and the conversion of forest into pasture or agriculture (Whitmore and Burselm 1998). Globally, second-growth and degraded forests now comprise over half of the remaining tropical forests (FAO 2010). Whereas old-growth forests have no visible signs of human disturbance, and are relatively stable with regard to structure, species composition and ecosystem properties, second-growth forests are dynamic forest stands that are in the process of recovering from a disturbance (Chazdon 2013, 2014). Second-growth forests not only provide a promising avenue for recuperating biodiversity and ecosystem services (Chazdon et al. 2009), but they also demonstrate community assembly in action, thus providing a natural setting for testing different hypothesis. Complex interactions between environmental factors and regional species pools impact ecosystem processes and species composition during natural regeneration (Brown and Lugo 1990, Chazdon 2003, Chazdon et al. 2007). Thus, advancing sustainable forest restoration and management actions therefore critically relies on our understanding of the factors that influence community assembly during vegetation succession.

Throughout succession, various factors influence changes in species composition and abundance. Stochastic factors that influence community assembly include local site effects (i.e. Norden et al. 2011), colonization history (Kardol et al. 2013), and dispersal limitation (Hubbell 2001). Site level differences in land-use history, such as the type or length of disturbance and the presence of remnant trees, can impact which species are able to successfully establish (Guariguata and Ostertag 2001, Chazdon 2003). Colonization history, or the order of species arrival, can have long-term influences on community structure (Fukami et al. 2005, Kardol et al. 2013). Moreover, when dispersal is limited, the species composition of a successional community is comprised of

species from the regional species pool that are more abundant and closer in proximity to the regenerating stand (Hubbell 2001). As opposed to stochastic processes, under niche-based assembly, the local environment deterministically filters species based on their functional attributes (Weiher and Keddy 1999). In this case, communities are comprised of individuals with the ecological characteristics best suited to survive and grow under the given suite of environmental conditions, and thus changes in abiotic conditions during secondary succession drive species turnover (Weiher and Keddy 1999).

Typically, tropical succession has been viewed as a deterministic process, whereby short- and long-lived pioneers are eventually replaced by shade-tolerant species (Finegan 1996, Chazdon 2013). Yet recent studies have shown that the species composition of tropical second-growth forests often shows limited convergence along successional gradients (Vandermeer et al. 2004; Chazdon et al. 2007; Dent et al. 2013; *but see* Lebrija-Trejos et al. 2010), suggesting a high contribution of historical contingencies and stochastic processes in community assembly. In fact, multiple community assembly mechanisms may simultaneously influence species coexistence (Fukami et al. 2005, Adler et al. 2007, Helsen et al. 2012). To better understand the mechanism of community assembly in tropical successional forests, we must link the ecological strategies of tree species to their abundance along successional gradients.

During the changing environmental conditions during forest regeneration, plant survival and growth are moderated by species-specific morphological and physiological functional traits, which reflect ecological strategies through investment tradeoffs that result in faster growth rates or increased defense (Raaimakers et al. 1995, Poorter and Bongers 2006). The functional trait continuum ranges from fast-resource acquisition (acquisitive) traits to resource-conservation (conservative) traits. Light-demanding early successional pioneer species often have acquisitive

traits, which confer faster growth rates but reduced defensive properties (Raaimakers et al. 1995, Poorter et al. 2004, van Gelder et al. 2006). Shade-tolerant late successional species, on the other hand, often have conservative traits, which promote defense from herbivores and abiotic damage, but at the cost of reduced rates of photosynthesis and growth (Raaimakers et al. 1995, Poorter et al. 2004, van Gelder et al. 2006).

My dissertation research focuses on characterizing the functional traits of dominant tree species in second-growth and old-growth tropical forests to understand the relative influences of stochastic processes and environmental filtering on community assembly during tropical succession. Previous studies that have assessed community level changes in tree functional trait distributions along successional gradients (Lebrija-Trejos et al. 2010, Lohbeck et al. 2013, Dent et al. 2013) have relied on a static chronosequence approach, in which temporal successional trends are inferred by measuring stands of different ages at a single time point. Chronosequence patterns often deviate from true vegetation dynamics because community reassembly patterns are highly idiosyncratic, showing variation with land-use history and landscape factors that influence seed dispersal and establishment (Chazdon et al. 2007, Johnson and Miyanishi 2008). To my knowledge, my dissertation research study is the first to examine patterns of community reassembly during natural regeneration by combining functional trait measurements with rigorous and consistent long-term vegetation dynamics data.

In **Chapter one** I assess community assembly patterns in early stages of pre-montane succession at Las Cruces Field Station in Costa Rica. I combine measurements on leaf functional traits for common species with vegetation dynamics data over the first 11 years of succession in four naturally regenerating plots. I determine the relative roles of deterministic and stochastic processes in community assembly by examining whether species composition and/or functional

trait composition converge among plots over successional time, and by assessing how stand age influences functional trait distributions.

In **Chapters two and three** I apply similar methodology to assess the mechanism of community assembly across a longer-term successional gradient in the wet tropical forest region at La Selva Biological Station in Costa Rica. I link tree and palm functional traits to successional vegetation dynamics in two old-growth and six second-growth forests ranging in age from 10–40 years after the abandonment of pasture. The species composition and diameter at breast height (DBH) have been monitored annually for 7–15 years in these eight 1-hectare study plots—providing the longest second-growth forest time series with annual census data in the world. In Chapter two I assess whether community-level functional traits shift directionally and predictably with stand age. I first compare community-level functional traits for all canopy trees and palms > 5 cm DBH. I then separately consider the patterns for dicot trees and palms. Palms are an important component of tropical forests (Guariguata et al. 1997, Svenning 1998, Marín-Spiotta et al. 2007, ter Steege et al. 2013), but they are often excluded from analyses of community-level functional trait distributions. Using tree size as a proxy for recruitment age, I further compare community-level functional trait patterns among individuals that recruited earlier in the successional process (large trees > 10 cm DBH) and newer recruits that established later in succession and which represent the future of these regenerating forests (small trees, 5 cm \leq DBH \leq 10 cm). In Chapter three I examine patterns of species and functional trait turnover along the successional gradient to determine if functional differences among plots are driven by differences in species composition.

Although natural regeneration can be an effective and low cost means of recovering biodiversity, active restoration approaches are needed to overcome obstacles to natural

regeneration and aid in the recovery of biodiversity and ecosystem services in highly degraded lands (Chazdon 2008). Species selection for these active restoration approaches is often limited to exotic species that are commercially available (Lamb et al. 2005, Chazdon 2008). When native species are used, species selection is limited to those that are known to perform well in a given region, which requires long-term research efforts (Butterfield and Fisher 1994, Piotto 2007). In **Chapter four** I aim to refine ecological restoration techniques in tropical wet forest regions by relating species performances under different environmental conditions to easily measured functional traits. I used an experimental approach to directly test the ability of species with different functional traits to survive and grow under various environmental scenarios. The results of this study benefit restoration efforts by providing guidance in selecting species for restoration.

My dissertation research deepens our mechanistic understanding of successional processes in the tropics by assessing the functional ecology of successional vegetation. My research is among the first to assess how changes in functional trait composition correspond with changes in species abundances along successional gradients in tropical regions, providing central insight into the functioning and demography of trees during natural regeneration. My results inform management strategies for natural regenerating tropical forests, and provide guidance for improving restoration techniques. Due to the large proportion of disturbed tropical forests (Brown & Lugo 1990; Diaz et al. 2004; ITTO 2002), understanding the functional causes and consequences of tropical forest regeneration is vitally important for understanding and protecting tropical biodiversity, and discerning the extent to which we can recover ecosystem processes and services through natural regeneration and ecological restoration.

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CHAPTER ONE

DETERMINISTIC CHANGES IN SPECIES AND LEAF FUNCTIONAL TRAIT COMPOSITION DURING EARLY TROPICAL PRE-MONTANE SUCCESSION

Abstract

Natural regeneration provides an essential avenue to recover biodiversity and ecosystem services in tropical landscapes. Yet, mechanisms of community assembly in tropical successional forests are poorly understood. Changes in species composition may be influenced by deterministic factors, such as environmental filtering and niche partitioning, historical contingencies based on land-use history and seed dispersal, and stochasticity. Here I assess the relative influences of these mechanisms of community assembly during the early stages of succession in four study plots in a tropical pre-montane region. All plots are naturally regenerating following the abandonment of pasture. I combine vegetation dynamics data over the first 11 years of succession with data for six leaf functional traits. I predicted that environmental filtering would drive community assembly, and thus species and functional trait composition would converge among these four plots over time. I also expected that community-level functional trait values would demonstrate directional shifts. Although the initial species composition diverged among these four plots, they became more similar over time, as predicted. However, the species composition of the rare species converged faster than that of the dominant species, suggesting that priority effects also influence community assembly. Functional composition converged over time among plots, as predicted by environmental filtering. Moreover, three of the six traits demonstrated directional shifts with stand age, whereby individuals with resource-conservation traits, such as tougher and denser leaves, became increasingly dominant among stands. Overall, my results provide evidence that environmental filtering is driving force for community assembly during the early stages of succession despite significant site-specific effects of initial species composition.

Introduction

Anthropogenic disturbances are widespread in tropical forests, including logging and land-conversion for pastures or agriculture (Whitmore and Burselm 1998). Currently, regenerating forests cover more area in the tropics than old-growth forests (FAO 2010), and we are only beginning to understand the mechanisms of successional dynamics in tropical regions. The trajectory of plant community assembly during succession may be deterministic or historically contingent, or may include components of both factors. Deterministic factors include niche differentiation and environmental filtering (Weiher and Keddy 1999), whereas historical contingencies are based on priority effects, whereby stochastic variation in the timing and sequence of species arrival has long-term influences on species composition (Law and Morton 1993). The likelihood that deterministic processes or historical contingencies drive community assembly depends on a variety of factors, such as primary productivity, the size of the regional species pool, and rates of seed dispersal and disturbance (Chase 2003). Moreover, various processes may simultaneously influence different aspects of community assembly. For example, recent studies in temperate successional grasslands demonstrate that although a large part of the variation in species composition is driven by priority effects, functional composition is largely deterministic (Fukami et al. 2005, Helsen et al. 2012).

In successional tropical forests, both deterministic factors and priority effects appear to influence community assembly. Stand basal area and species richness often converge with old-growth forests within decades (Aide et al. 2000, Guariguata and Ostertag 2001, Letcher and Chazdon 2009, Lebrija-Trejos et al. 2010a), indicating that changes in forest structure follow a deterministic trajectory. However, a recent analysis across seven Neotropical forest sites demonstrates that individualistic stand-level differences in stem density, basal area and species

density explained more of the variation in forest structure than stand age alone (N. Norden *pers. comm.*), suggesting that priority effects strongly influence successional trajectories. Accordingly, the recovery of species composition is highly dependent on local seed dispersal and site effects, such as soil degradation and land-use history (Brown and Lugo 1990, Chazdon 2003, Chazdon et al. 2007), resulting in limited convergence in species composition among second-growth forests within a region (Vandermeer and Granzow de la Cerda 2004, Chazdon et al. 2007, Norden et al. 2011, Dent et al. 2013; *but see* Lebrija-Trejos et al. 2010a). Observed deviations in community composition, even between forest stands in close proximity to one another (Peterson and Haines 2000, Chazdon et al. 2007), are likely a function of historical contingencies and deterministic processes. Thus understanding the interplay of these two factors provides insight into the process of natural regeneration in tropical forests.

Throughout the changing environmental conditions that occur during forest regrowth, a plant's ability to survive and establish is moderated through species-specific morphological and physiological functional traits (Bazzaz and Pickett 1980, Guariguata and Ostertag 2001, Westoby et al. 2002). These functional traits characterize ecological strategies based on differential resource allocation to leaves, wood and seeds, and influence plant performance and defense (Westoby et al. 2002, Díaz et al. 2004, Garnier et al. 2004, Wright et al. 2004, Poorter and Bongers 2006). At the functional group level, community assembly is generally thought to be deterministic, although the evidence is equivocal (*see* Chapter 2; Chapter 3; Lohbeck et al. 2013, Dent et al. 2013). Following a deterministic view of functional community assembly, early successional species are often fast-growing, light-demanding species with fast resource acquisition traits, such as short-lived leaves with high photosynthetic capacity (Raaimakers et al. 1995, Poorter et al. 2004, van Gelder et al. 2006). Old-growth species, on the other hand, are

generally shade-tolerant and have traits geared towards resource conservation, with tissues that more costly to produce, but are better protected from biotic and abiotic damage (Raaimakers et al. 1995, Poorter et al. 2004, van Gelder et al. 2006). At the community-level, some plant functional traits show directional trends along successional gradients, supporting a niche-based view of community assembly, whereas the trends for other functional traits are either not correlated or only weakly correlated with stand age (Lebrija-Trejos et al. 2010b, Lohbeck et al. 2013, Dent et al. 2013; Chapter 2), suggesting that other factors also influence community assembly. Furthermore, although functional turnover was directional and deterministic during the first 16 years of forest recovery following a hurricane disturbance in Puerto Rico (Swenson et al. 2012), functional turnover was largely stochastic among 10-40 year old forests along a successional gradient in Costa Rica (Chapter 3).

The mechanisms of successional community assembly in the tropics have been difficult to distinguish because most studies rely on a chronosequence approach, which substitutes space for time (Lebrija-Trejos et al. 2010b, Lohbeck et al. 2013, Dent et al. 2013). Chronosequence patterns often deviate from true vegetation dynamics because community reassembly patterns are highly idiosyncratic, showing variation with land-use history and landscape factors that influence seed dispersal and establishment (Chazdon et al. 2007, Johnson and Miyanishi 2008). Few studies have assessed the variation in initial successional dynamics using replicated post-agricultural or post-pastoral sites (Uhl and Serrao 1988, Zahawi and Augspurger 1999, Peterson and Haines 2000, Mesquita et al. 2001, Dosch et al. 2007, Dent et al. 2013), and none of these have explicitly incorporated functional trait measurements to assess functional community assembly.

Here I compare taxonomic and functional composition of four replicate plots during the first 11 years of natural regeneration in a pre-montane forest region of Costa Rica to better characterize the mechanism of community assembly during succession. Species composition of these plots was highly divergent in the first two years of regrowth (Peterson and Haines 2000). Initial colonization patterns among the four plots were influenced by variation in the availability of microsites (*i.e.* rotting logs) that reduce competition with intact graminoid vegetation (Peterson and Haines 2000), as well as dispersal limitation into the abandoned pastures (Dosch et al. 2007). I combine vegetation dynamics data with measurements of six leaf functional traits for the most common species in each plot to determine the influence of deterministic processes and historical contingencies in community assembly. I address three main questions: 1) Do leaf functional traits demonstrate directional trends with stand age at the community-level? 2) Is there a convergence of community-level mean functional trait values and functional distributions? 3) Does species composition or functional trait composition converge among the four plots over time? If environmental filtering drives successional patterns, then I expect to see a convergence in community level functional traits, regardless of differences in species composition. As the forests develop, I also expect to see directional shifts in community-level traits from fast-resource acquisition towards resource conservation.

Methods

Study Sites

This study took place in four abandoned cattle pastures in the vicinity of the Las Cruces Biological Station (run by the Organization for Tropical Studies), in Coto Brus county, southern Costa Rica (8°47'N, 82°57'W). Pre-settlement vegetation in the region is classified as tropical

pre-montane moist forest (Hartshorn 1983). Extensive clearing for cattle pasture in the 1950s and 1960s left a predominantly agricultural landscape with scattered forest remnants (Júarez 1994). The average annual temperature of the region is 20.7°C, with an average annual precipitation of 3820 mm (Jones et al. 2003). The elevation of my study plots ranges from 800 to 1500 meters above sea level.

The four study plots were established in 1996 by fencing off cattle pasture, which had been active for at least 4 years (Peterson and Haines 2000). At the time of initiation, each plot was vegetated by a mixture of grasses, predominantly *Cynodon nlemfuensis*, and contained a few scattered remnant trees (3–7 per plot; Table 1.1) growing inside the pastures or along fencerows (Peterson and Haines 2000). The irregularly shaped plots range in size from 0.304–0.630 ha (Table 1.1). All plots had one relatively straight edge bordering an intact forest patch (3–240 ha; Table 1.1), but were otherwise surrounded by active cattle pasture (Fig. 1.1). All plots were located within 3 km of one another. Woody stems > 1 m tall were inventoried at 1–2 year intervals between 1998 and 2007 (8 censuses total). Remnant trees were excluded from analyses; only colonists were considered as part of the assembling communities. Across all censuses and plots, 122 species were encountered during this study (data not shown).

Functional trait measurements

In July and August 2009, I sampled six leaf functional traits of 280 individuals from 35 species in 18 families (Appendix 1, Table A1.1). These 35 focal species comprised 75.3–96.3% of the abundance of each plot for each censused year (mean \pm standard deviation: $86.3 \pm 0.05\%$). For each individual, I measured six leaf traits that reflect ecological strategies of resource use as well as water and energy balance. Leaf size (LS; cm²) reflects light capturing area, where larger

leaves capture more sunlight but also experience high heat loads and consequently have increased respiration rates (Westoby et al. 2002, Cornelissen et al. 2003). Specific leaf area (SLA; mm^2/mg) measures the amount of light capturing foliar area to biomass investment. The SLA spectrum demonstrates a tradeoff between the rate of return in leaf construction and the duration of return (Westoby et al. 2002). Light demanding species often have higher SLA than shade-tolerant species (Poorter et al. 2004). Leaf dry matter content (LDMC; g/g), leaf thickness (LT; mm), leaf toughness (LTO; N/mm), and leaf density (LD; mg/mm^3) relate to the density of leaf tissue, structural investment, relative growth rate and leaf lifespan (Coley 1983, Wilson et al. 1999, Niinemets 2001, Cornelissen et al. 2003, Vile et al. 2005), and are often higher for shade-tolerant species.

Functional traits were measured using standardized protocols (Cornelissen et al. 2003). For each individual, leaf traits were measured on two sunlit leaves with minimal herbivore damage, and values were averaged prior to analyses. Leaf area was quantified using a digital leaf area meter (LI-3100, LiCor Environmental, Lincoln, Nebraska). I measured fresh and dry leaf mass (after oven-drying for ~72 hours at 60°C) on a digital balance. Leaf thickness was measured with a digital micrometer. Leaf toughness, or punch force, was calculated using a leaf penetrometer (Chatillion 516-1000M push-pull gauge, Chatillion, USA), where the Newtons of punch force were divided by the circumference of the punch (Garnier et al. 2013). Leaf density on a fresh mass basis was calculated as the inverse of $\text{LT} \cdot \text{LDMC} \cdot \text{SLA}$ (Vile et al. 2005). Leaf size, leaf thickness, and leaf toughness were based on lamina measurements only, whereas specific leaf area, leaf dry matter content and leaf density incorporated measurements of both the lamina and the petiole (Cornelissen et al. 2003). Among the six measured traits, leaf thickness and leaf toughness were strongly positively correlated, and both were strongly negatively

correlated with specific leaf area (Appendix 1, Table A1.2). The remaining traits showed negligible to moderate correlations (Appendix 1, Table A1.2).

Compositional Changes

Species mean trait values were calculated as the average of 3–20 individuals per species (Appendix 1, Table A1.1). For each plot in each censused year, I calculated community weighted mean (CWM) values using species mean traits. Community-weighted mean is calculated as the sum of each species' functional trait value weighted by its relative abundance in the community (Garnier et al. 2004), and can be interpreted as the trait value of an average individual in the community. I also compared the functional trait distributions of each plot for the initial, middle, and final censuses (years 1998, 2002 and 2007) using kernel density estimation (Venables and Ripley 2002, Swenson et al. 2012) to examine how the community-wide distribution of functional traits varied across plots.

I further examined changes in functional and taxonomic beta diversity among plots over time. Functional dissimilarity was calculated for each of the eight censuses as the Euclidean distance among CWM values for each pair of plots (6 plot-pair combinations from 4 plots). Univariate functional dissimilarity was calculated for each trait separately, and multivariate functional dissimilarity was calculated for all 6 functional traits combined. For these analyses, CWM was recalculated after standardizing values of each trait to Z-scores (mean=0, variance=1) to control for differences in units and variances among traits. Large values of functional dissimilarity indicate greater differences among plot pairs in CWM trait space.

Similarly, I compared taxonomic beta diversity (compositional change) among the four plots for each sampling year with the density-invariant Morisita-Horn dissimilarity index

(Morisita 1959), which is an abundance-based metric that gives more weight to the dominant species (Jost et al. 2011). I calculated Morisita-Horn dissimilarity index for each pair of plots in each year both for the 35 focal species for which I measured functional traits and for the entire species pool (122 species). I also compared differences in species composition among plots and years for the entire species pool using the abundance-based Chao-Jaccard dissimilarity index (Chao et al. 2005). This estimator assesses the probability that a randomly chosen individual from each community belong to the same species, accounting for the effect of unseen shared species (Chao et al. 2005). The Chao-Jaccard index is less biased by sample size than other estimators, and is sensitive to rare species.

Statistical Analyses

I used linear mixed-effects regressions to assess the trends in community-weighted mean (CWM) trait values, functional beta diversity, and taxonomic beta diversity across the four plots over time. I included data for all sampling years (8 censuses), and included a random intercept and/or slope for plot to account for this lack of independence. Separately for each CWM trait or beta diversity analysis, I first determined the optimal random effect structure (intercept and/or slope for plot) based on the small sample size corrected Akaike's Information Criterion (AIC_c) value (Burnham and Anderson 2002) of models fit with Restricted Maximum Likelihood estimation (REML) (Zuur et al. 2009). The model with the lowest AIC_c score was chosen, unless a simpler (more parsimonious) model was within $\Delta 2 AIC_c$ units of the more complex model (Burnham and Anderson 2002). With the selected random effect term(s) I then compared models with a fixed effect for stand age to simple intercept only models, and again used AIC_c for the model selection. When comparing the fixed effects structures, models were fit with Maximum

Likelihood (ML) (Zuur et al. 2009), but the final best-fit model is presented using REML estimation (Venables and Ripley 2002). Following Nakagawa & Schielzeth (2013), two correlation metrics were calculated for each of the best-fit mixed-effects models. The marginal correlation metric for linear mixed-effects models, $R^2_{\text{LMM(m)}}$, measures the variance described by the fixed effects only. The conditional correlation metric, $R^2_{\text{LMM(c)}}$, expresses the variance explained by both the fixed and random factors. For models that included a random slope term for plot-pair, the correlation metrics were calculated for an equivalent model that only included a random intercept term for plot-pair (Nakagawa and Schielzeth 2013).

In addition to assessing directional trends in CWM values, I also determined whether the four plots converged in functional trait values over time by calculating the variance to mean ratio (VMR) of the CWMs for each census year. This index of dispersion demonstrates the degree of CWM clustering among the four plots. A deterministic model of community assembly would be supported if the plots demonstrated convergence in trait values over time. I used Pearson's correlation to ascertain if VMR significantly increased or decreased with stand age for each trait.

To compare functional trait distributions among the four plots through time, I performed kernel density estimation by applying species mean trait values to each individual (Venables and Ripley 2002, Swenson et al. 2012). For each trait, I used normal reference distribution to select the bandwidth of the kernel density plots (Scott 1992, Venables and Ripley 2002). For each trait in each year I calculated kernel density overlap metric across all four plots (Mouillot et al. 2005).

All statistical analyses were performed in R version 3.0.2 (R Core Team 2013). Community-weighted means were calculated using the 'dbFD' function in the 'FD' package (Laliberté and Legendre 2010, Laliberté and Shipley 2011), and linear mixed-effects models were performed in using the 'lmer' function in the 'lme4' package (Bates et al. 2013).

Results

Successional shifts in community level trait values

Across the four plots, three of the six functional traits demonstrated consistent directional shifts in community-weighted means (CWM) with increasing stand age (Fig. 1.2). Community-weighted mean leaf thickness declined with stand age, while CWM leaf toughness and leaf density increased. The fixed effect, stand age, explained 21–53% of the variation in CWMs for these traits ($R^2_{\text{LMM(m)}}$; Fig. 1.2). The remaining three functional traits—leaf size, specific leaf area, and leaf dry matter content—did not shift directionally with stand age, and instead the intercept-only models were a better fit. Across all traits, the fixed effects (stand age and/or intercept) combined with a random plot effect explained 80–93% of the variation in CWM trait values ($R^2_{\text{LMM(c)}}$; Fig. 1.2).

Although only half of the functional traits changed directionally at the community level with stand age, the variability for all CWM values declined across the four plots over time (Table 1.2). The variance to mean ratio (VMR) among community-weighted mean values of the four plots declined significantly with stand age in five of the six measured traits, but the decline was only marginally significant for leaf density (Table 1.2).

In addition to comparing community-weighted mean values across plots over time, I also assessed shifts in the functional trait distribution in each of the plots over time. The distributions of functional traits demonstrate a convergence across plots over time (Fig. 1.3), suggesting that, across plots, the environment is selecting for species with certain traits. For example, in 1998 plot 1 had a higher proportion of individuals with larger leaves than the other three plots (Fig. 1.2, top left panel). However, as of 2007 the leaf-size distribution in plot 1 shifted towards more

individuals with smaller leaves, in accordance with the other three plots (Fig. 1.3, top right panel).

Taxonomic and functional trait beta diversity

The species composition among plots for the 35 focal species was initially divergent, but demonstrated some convergence with through time (Fig. 1.4a). This pattern was nearly identical when based on the entire species pool (Appendix 1, Fig. A1.1a). Stand age only explained 9% of the variation in Morisita-Horn species beta diversity ($R^2_{\text{LMM(m)}}$), whereas stand age combined with random effects terms for plot explained 89% of the variation ($R^2_{\text{LMM(c)}}$; Fig. 1.4a).

Abundant species are weighted more heavily with the Morisita-Horn index, whereas the Chao-Jaccard index is sensitive to rare species (Jost et al. 2011). Using the Chao-Jaccard index on the entire species pool, species beta diversity also converged among the four plots through time, although most of the convergence occurred very early in succession, between the first and second census (Appendix 1, Fig. A1.1b).

At the functional trait level, plots demonstrated clear convergence in trait similarity over time (Fig. 1.4, b–h). Among plots, multivariate functional beta diversity and dissimilarity for five of the six univariate traits significantly declined with stand age. The fixed effect of stand-age explained 7–41% of the variation in functional composition for these six models ($R^2_{\text{LMM(m)}}$; Fig. 1.4). An intercept-only model was the best-fit for leaf density dissimilarity, which did not significantly converge among the four plots over time. Across all functional beta diversity trait models, the fixed effect(s) (stand age and/or intercept) combined with the random plot effects explained 36–88% of the variation in functional composition ($R^2_{\text{LMM(c)}}$; Fig. 1.4).

Discussion

Species composition and leaf functional traits showed convergent trends among the four study plots during the first 11 years of natural regeneration in this tropical pre-montane region. Community-wide functional traits also changed directionally for three of the six leaf traits. These results provide novel evidence that although historical contingencies influences initial species composition, environmental filtering is a main driver of community assembly during early successional stages.

The species composition of the initial colonizers varied among the study plots. In the first vegetation census, 2 years after cattle exclusion, the mean pairwise Morisita-Horn dissimilarity index among the four plots was 0.63 ± 0.30 (standard deviation). Similarly, the initial mean Chao-Jaccard dissimilarity among the four plots, which is more sensitive to rare species, was 0.57 ± 0.17 (standard deviation). Differences in rotting log microsite availability among plots partially explains the initial variability in species composition (Peterson and Haines 2000). Study plots also experienced variation in seed rain density and species composition, although the seed rain composition did not fully explain differences woody plant establishment (Dosch et al. 2007). For example, there was no influence of the size of the adjacent forest fragments on the total seed input among the four plots (Dosch et al. 2007). Moreover, although the density of regenerating woody seedlings was roughly proportional to the seed rain density, the species composition of the woody plant colonists was rather dissimilar to that of the seed rain (Dosch et al. 2007). Site-specific and species-specific differences in seed removal by predators also help to explain the differences in species composition (Jones et al. 2003). Individualistic species patterns also occurred in an early successional community in Puerto Rico (Myer 2003).

After 11 years of natural regeneration, the species composition of rare species converged faster than the dominant species among plots (Appendix 1, Fig. A1.1). The mean pairwise Morisita-Horn dissimilarity among the four plots was 0.42 ± 0.17 (standard deviation), and the mean Chao-Jaccard dissimilarity was 0.33 ± 0.11 (standard deviation) (Fig. 1.4a; Appendix 1, Fig. A1.1). In fact, much of the convergence in the Chao-Jaccard index occurred between the first and second censuses, when the stands had been naturally regenerating for 2 and 4 years, respectively. Yet the species that dominated the initial colonization period remained dominant over the 11 years of forest regrowth, demonstrating an influence of priority effects on community assembly. For example, in the first census, *Miconia theizans* was common in three of the four plots, particularly so in plot 4 (76% of the total abundance) due to a high abundance of rotting log microsites (Peterson and Haines 2000). This species continued to be the most common species in plot 4 in the final 2007 census (39% of the abundance). Similarly, the species that dominated the other plots in the first census remained common in the final census, suggesting that the species that initially established in each of the plots had a long-term influence on species composition.

At the functional trait level, deterministic processes drove community assembly. Functional beta diversity is clearly converging over time (Fig. 1.4), and the reduced variation among plots in both community weight mean trait values (Table 1.2) and trait distributions (Fig. 1.3) during stand development further supports this conclusion. Similarly, patterns of increasing trait convergence were also found in experimental (Fukami et al. 2005) and natural (Helsen et al. 2012) restored grasslands in Europe. Swenson et al. (2012) also found higher than expected functional turnover based on changes in species composition during the 16 years following a hurricane disturbance in Puerto Rico. Although functional traits appear to be driving early

successional community assembly patterns, when the environmental filter is the strongest, the importance of stochastic processes may become more evident later in succession (Chapters 2 & 3).

In addition to the convergence in functional traits, I also found community-level shifts in three of the six leaf traits. Community-weighted mean (CWM) leaf toughness and leaf density increased with stand age, while leaf thickness decreased. I found similar trends along a 10–40 year successional gradient in the lowland wet tropical forests of Costa Rica, where CWM leaf toughness and leaf density increased among canopy trees and palms, and CWM leaf thickness declined among canopy trees (Chapter 2). Tougher and denser leaves are related to increased construction costs, but also to longer leaf lifespans and increased defense (Coley 1983, Roderick et al. 1999). In this environment, the benefits of having better-defended leaves appear to outweigh the additional construction costs. I found it surprising that CWM leaf toughness increased with stand age, while CWM leaf thickness declined, since species mean values for leaf thickness and leaf toughness were positively correlated (Appendix 1, Table A1.2). However, leaf toughness is primarily driven by vein density, as veins are tougher than lamina matrix (Choong et al. 1992, Choong 1996), and vein density is largely decoupled from leaf thickness. For example, comparing tropical understory and canopy trees, Turner et al. (1993) found that although shade leaves were generally thinner than sun leaves, their fiber content and toughness values were largely similar.

In conclusion, my findings demonstrate that deterministic processes are an important component of community assembly in the early stages of succession. Initially, the species and functional trait composition was highly variable among plots, caused by differences in seed rain, seed removal, and the availability of rotting log microsites (Peterson and Haines 2000, Jones et

al. 2003, Dosch et al. 2007). However, both species and functional trait compositions converged among plots over time. I suggest that similar environmental conditions among plots during these early stages drive the similarity in functional composition. Whereas the presence of rotting logs influenced initial colonization patterns and decreased seedling competition with pasture grasses (Peterson and Haines 2000), I suspect that, over time, benefits of these microsite differences were reduced through crowding effects on the rotting logs coupled with overall reduced competition with grasses during canopy development. Moreover, it is likely that other important environmental conditions that influence community composition, such as light availability and temperature (Lebrija-Trejos et al. 2010b), were largely similar among plots.

These stands represent a ‘best-case’ scenario for natural regeneration. Soil sampling one-year after the plots were established confirmed that the soil chemical properties in the upper 15 cm of these recently abandoned pastures were equivalent to those of the nearby forests (Jin et al. 2000). Moreover, these plots were established on the borders of intact old-growth forest patches, providing nearby seed sources for natural regeneration. Community assembly patterns are likely to be different in regions without viable seed sources nearby, or which have undergone a more intense land-use history (Guariguata and Ostertag 2001, Chazdon 2003). Long-term studies with replicated stand ages, such as this one, provide unique insight into the community assembly process. Similar studies in other regions and across a larger range of stand ages are needed to assess the generality of my results.

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Figure 1.1. Map of study area. Dark areas show remnant forest patches, whereas light areas are human-dominated lands, including agriculture, pasture, or settlement. White lines are roads. The four numbered boxes (1-4) show the locations of the four naturally regenerating study plots (not drawn to scale). Actual plots are not rectangular, and measure 0.373 ha, 0.304 ha, 0.630 ha, and 0.301 ha for plots 1 through 4, respectively. All four plots were fenced off from pasture in 1996.

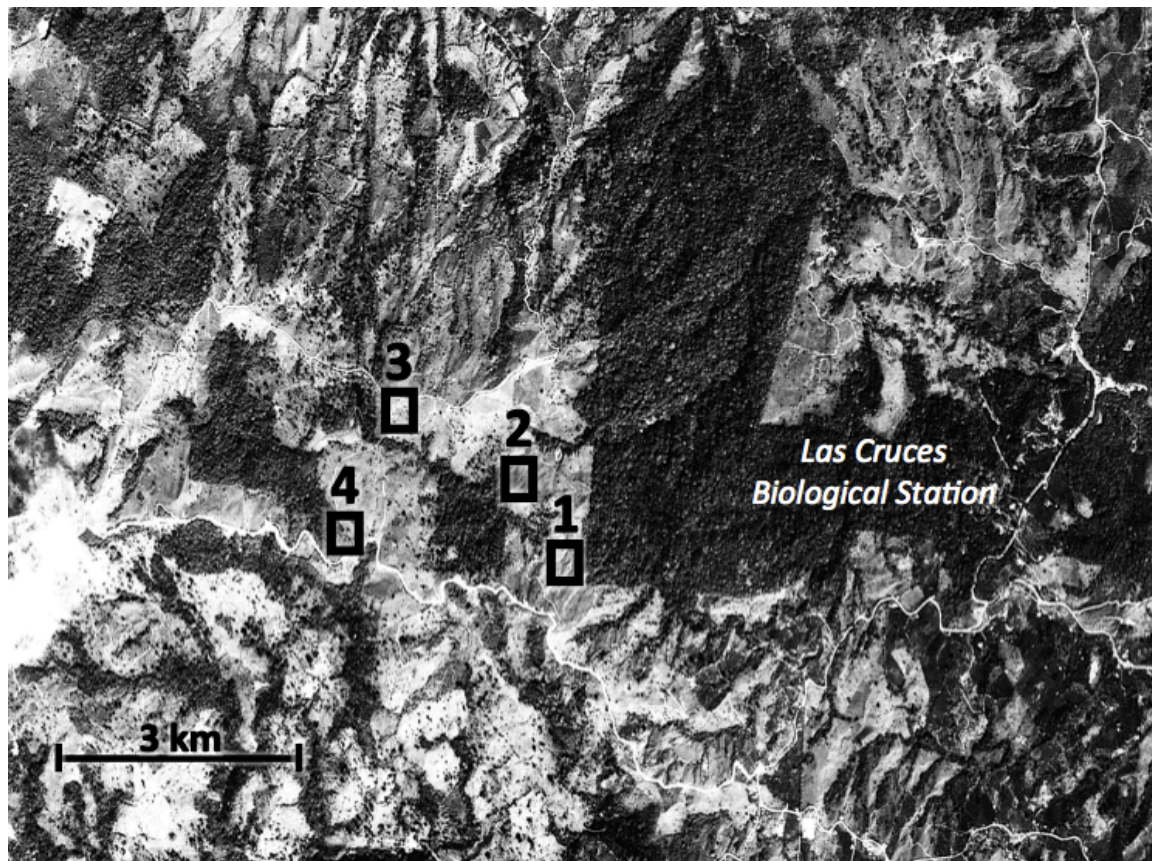


Figure 1.2. Changes in community weighted mean (CWM) trait values with stand age for four naturally regenerating pre-montane old-field plots. Thick lines demonstrate best-fit linear mixed-effects regressions for intercept-only models (dashed lines) or models including a fixed effect for stand age (solid lines). Each mixed-effects model includes plot as a random intercept and/or slope. The marginal correlation coefficient, $R^2_{\text{LMM}(m)}$, demonstrates the proportion of variance in the CWM functional trait value explained by stand age (the fixed effect of the model), whereas the conditional correlation coefficient, $R^2_{\text{LMM}(c)}$, explains the proportion of variance explained by both the fixed and random effects of the model. Key in panel (a) applies to all panels.

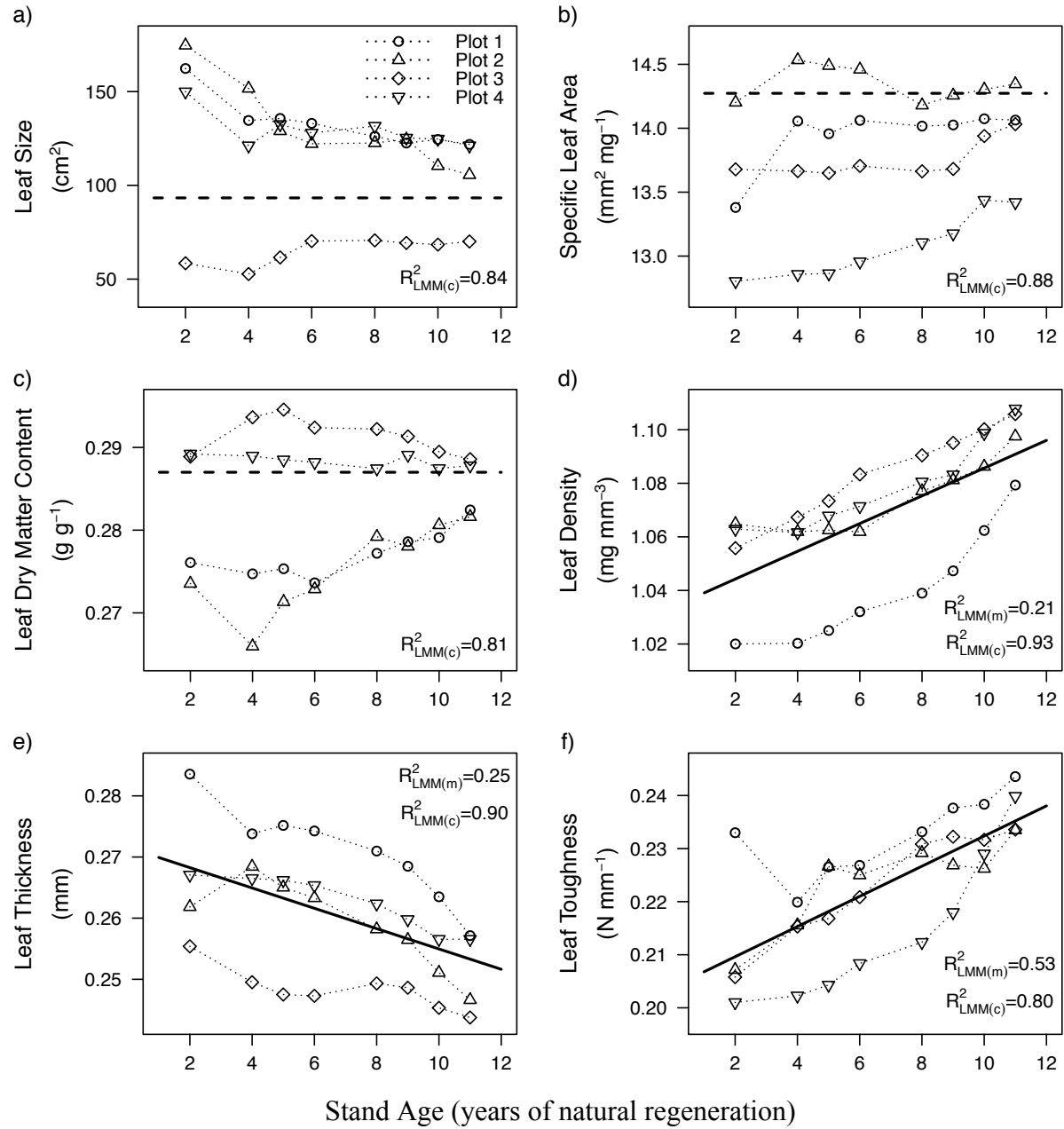


Figure 1.3. Kernel density estimations for each functional trait in each of the four naturally regenerating plots through time, where the density is calculated by assigning species mean trait values to each individual in the plot. Each row is a different trait, and kernel density estimations for three different years (1998, 2002, and 2007) are shown as columns. Trends for each plot are shown as solid or dashed lines in different shades of grey; plot 1 = light grey solid line, plot 2 = dark grey dashed line, plot 3 = dark grey solid line, plot 4 = black dashed line. Kernel density overlap estimates are shown for each panel.

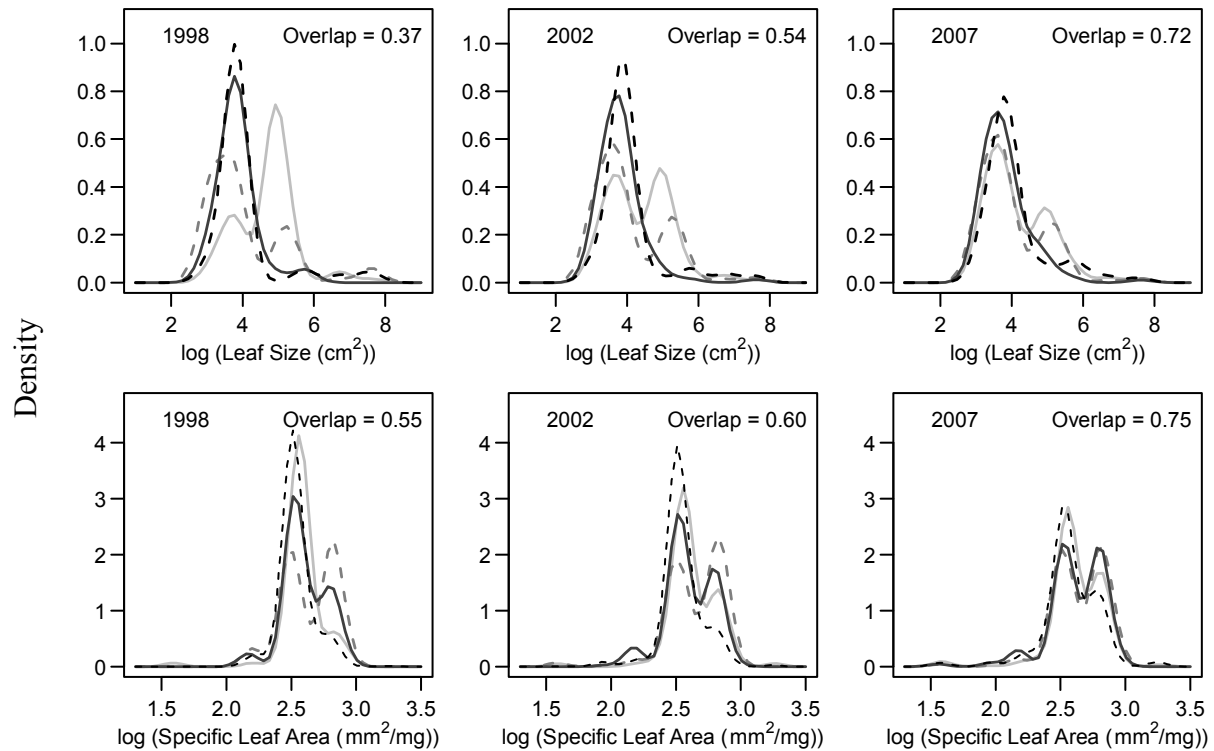


Figure 3 continued

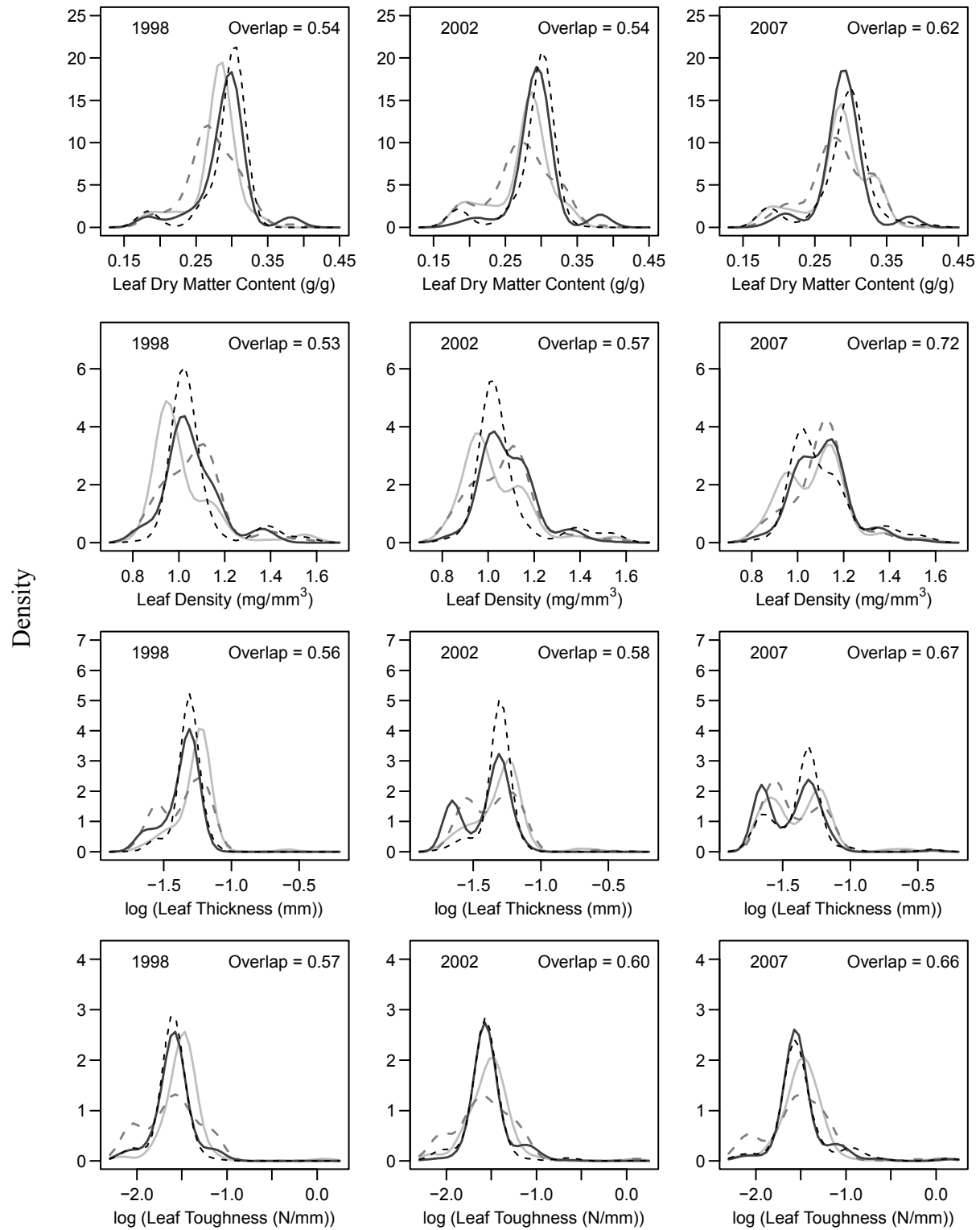


Figure 1.4. Comparison of taxonomic and functional beta diversity among four pre-montane plots during the first 11 years of natural regeneration. Overall mean and standard deviation pairwise dissimilarity among the four plots is given for each census year. Values are based on Morisita-Horn dissimilarity among plot pairs for species composition (a), and community-level Euclidean distance for multivariate functional trait composition (b) and univariate functional trait composition (c-h). Community metrics were calculated from census and functional trait measurements of the 35 most common species among all four plots (Appendix 1, Table A1.1). Dashed and solid lines demonstrate best-fit linear mixed-effects regressions for intercept-only models and models with a fixed effect for stand age, respectively. Each mixed-effects model includes plot as a random intercept and/or slope. The marginal correlation coefficient, $R^2_{\text{LMM(m)}}$, demonstrates the proportion of variance in the dissimilarity metric that is explained by stand age (the fixed effect of the model), whereas the conditional correlation coefficient, $R^2_{\text{LMM(c)}}$, explains the proportion of variance explained by both the fixed and random effects of the model.

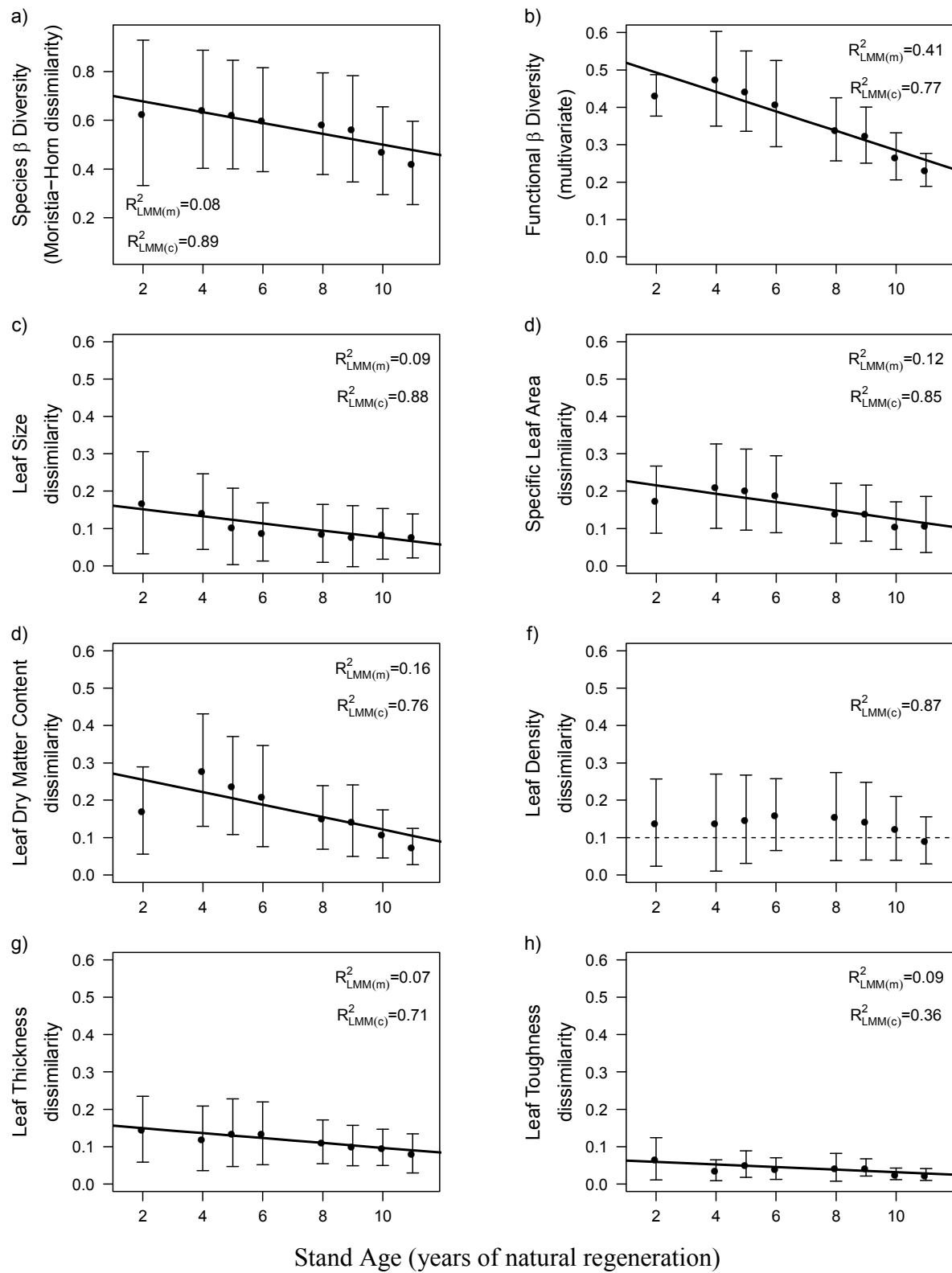


Table 1.1. Characteristics of the four naturally regenerating study plots.

	Plot 1	Plot 2	Plot 3	Plot 4
Plot size (ha)	0.373	0.304	0.630	0.301
Size of adjacent forest patch (ha)	240	10	3	25
Number of remnant trees	7	3	4	4

Table 1.2. Variance to mean ratio (VMR) values of community weighted means calculated in each census year across the four naturally regenerating pre-montane old-field study plots. Pearson's correlation (6 degrees of freedom) of VMR with increasing stand age are shown; with significant correlation coefficients (r) highlighted in bold.

Stand Age	Variance: Mean Ratio					
	Leaf size (cm ²)	Specific Leaf Area (mm ² / mg)	Leaf Dry Matter Content (g / g)	Leaf Density (mg / mm ³)	Leaf Thickness (mm)	Leaf Toughness (N / mm)
2	20.5	0.03	0.00024	0.0004	0.0005	0.001
4	16.4	0.04	0.00058	0.0005	0.0004	0.0003
5	11	0.03	0.00042	0.0005	0.0005	0.0005
6	7.5	0.03	0.00035	0.0005	0.0005	0.0003
8	7.1	0.02	0.00017	0.0005	0.0003	0.0004
9	6.8	0.02	0.00017	0.0004	0.0003	0.0003
10	6.6	0.01	0.00009	0.0003	0.0002	0.0001
11	5.6	0.01	0.00005	0.0002	0.0002	0.0001
r	-0.9	-0.83	-0.74	-0.69	-0.94	-0.8
t	-5.14	-3.65	-2.69	-2.36	-6.57	-3.27
<i>P-value</i>	0.002	0.011	0.036	0.057	<0.001	0.017

APPENDIX 1

Figure A1.1. Comparison of species beta diversity among four pre-montane plots during the first 11 years of natural regeneration, using all species sampled for vegetation dynamics (122 species). Overall mean and standard deviation pairwise dissimilarity among the four plots is given for each census year. Values are based on a) Morisita-Horn dissimilarity index and b) Chao-Jaccard dissimilarity index. Dashed and solid lines demonstrate best-fit linear mixed-effects regressions for intercept-only models and models with a fixed effect for stand age, respectively. Each mixed-effects model includes plot as a random intercept and/or slope. The marginal correlation coefficient, $R^2_{\text{LMM}(m)}$, demonstrates the proportion of variance in the dissimilarity metric that is explained by stand age (the fixed effect of the model), whereas the conditional correlation coefficient, $R^2_{\text{LMM}(c)}$, explains the proportion of variance explained by both the fixed and random effects of the model.

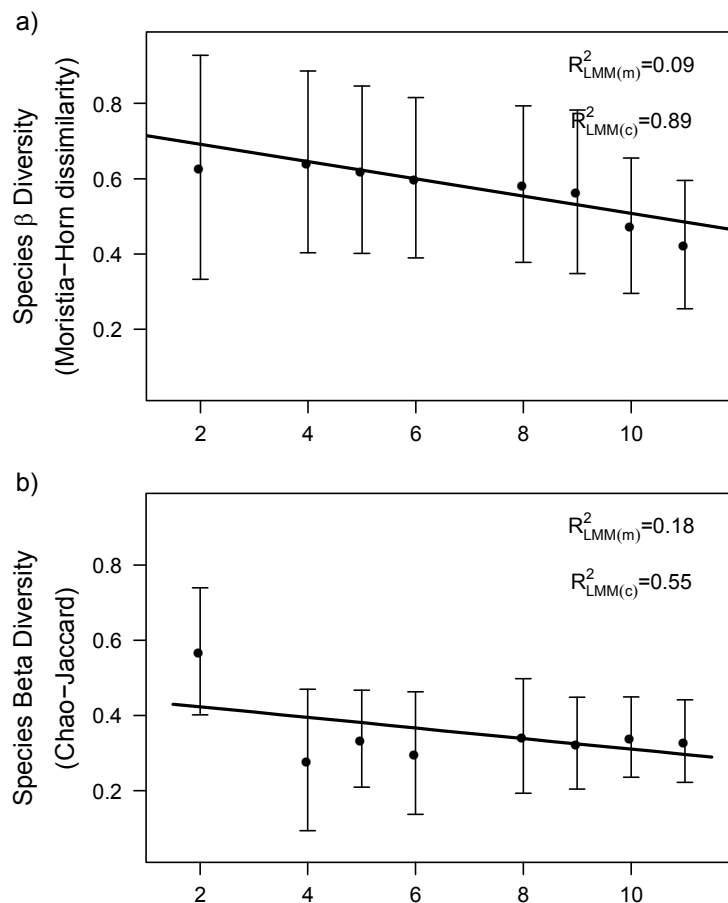


Table A1.1. Species list and number of individuals sampled for functional traits in each of the four naturally regenerating pre-montane moist forest plots.

Species	Family	Plot 1	Plot 2	Plot 3	Plot 4	Total
<i>Calophyllum brasiliense</i>	Calophyllaceae			3		3
<i>Cecropia obtusifolia</i>	Urticaceae	3	4		5	12
<i>Clethra lanata</i>	Clethraceae			5		5
<i>Clusia stenophylla</i>	Clusiaceae			3	5	8
<i>Conostegia rufescens</i>	Melastomataceae	4				4
<i>Conostegia spl</i>	Melastomataceae	5				5
<i>Croton draco</i>	Euphorbiaceae	5		5		10
<i>Elaeagia auriculata</i>	Rubiaceae				5	5
<i>Gonzalagunia rosea</i>	Rubiaceae	5	5	5	5	20
<i>Hampea appendiculata</i>	Malvaceae		5			5
<i>Heliocarpus appendiculatus</i>	Malvaceae		5	4		9
<i>Hyeronima oblonga</i>	Phyllanthaceae				5	5
<i>Lippia oxyphyllaria</i>	Verbenaceae	5	5	5		15
<i>Margaritaria nobilis</i>	Phyllanthaceae			5		5
<i>Miconia theizans</i>	Melastomataceae	5	5	5	5	20
<i>Miconia tonduzii</i>	Melastomataceae		5	3	5	13
<i>Mollinedia viridiflora</i>	Monimiaceae				5	5
<i>Oreopanax costaricensis</i>	Araliaceae	3				3
<i>Palicourea padifolia</i>	Rubiaceae	5	5		5	15
<i>Piper hispidum</i>	Piperaceae				5	5

<i>Piper obliquum</i>	Piperaceae	3			6	9
<i>Psychotria elata</i>	Rubiaceae				5	5
<i>Psychotria stockwellii</i>	Rubiaceae		5	5		10
<i>Rondeletia buddleioides</i>	Rubiaceae		5			5
<i>Saurauia montana</i>	Actinidiaceae		4			4
<i>Saurauia yasicae</i>	Actinidiaceae		5			5
<i>Solanum megalophyllum</i>	Solenaceae			4		4
<i>Topobea multiflora</i>	Melastomataceae			5	5	10
<i>Topobea parasitica</i>	Melastomataceae	3				3
<i>Topobea pittieri</i>	Melastomataceae				5	5
<i>Verbesina tapantiana</i>	Asteraceae				5	5
<i>Verbesina turbacensis</i>	Asteraceae	5	5			10
<i>Vernonia patens</i>	Asteraceae	3	5			8
<i>Viburnum costaricanum</i>	Caprifoliaceae	5	5	5	5	20
<i>Vismia baccifera</i>	Hypericaceae				5	5

Table A1.2. Pearson's correlation among six functional traits measured for 280 individuals (35 species). Significant correlation coefficients are shown in bold type when significant, following Bonferroni-corrected alpha values ($P < 0.0033$).

	Leaf Size	Specific Leaf Area	Leaf Dry Matter Content	Leaf Density	Leaf Thickness	Leaf Toughness
Leaf Size (cm ²)	--	-0.3	-0.29	0.5	0.39	0.22
Specific Leaf Area (mm ² /g)		--	-0.48	-0.31	-0.67	-0.65
Leaf Dry Matter Content (g/g)			--	-0.2	-0.07	0.29
Leaf Density (mg/mm ³)				--	<0.01	0.25
Leaf Thickness (mm)					--	0.56
Leaf Toughness (N/mm)						--

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CHAPTER TWO

CHANGES IN FUNCTIONAL TRAIT COMPOSITION OF CANOPY TREES AND PALMS ALONG A WET TROPICAL FOREST SUCCESSIONAL GRADIENT

Abstract

Second-growth forests provide an important avenue for recuperating biodiversity and ecosystem services in tropical wet forests. To gain a better understanding of the process of community assembly during succession, I assessed the distribution of functional traits along a successional gradient. Under the environmental filtering hypothesis of community assembly, I expected to find strong successional trends in functional trait composition, with community-level increases in fast-resource acquisition traits and declines in resource conservation traits. I monitored successional patterns of vegetation dynamics in eight 1-ha forest stands in northeast Costa Rica annually for 8–16 years. These forest stands include six second-growth forests, ranging in age from 10–40 years after abandonment of pasture, and two old-growth forests. I compared community weighted mean values across the successional gradient using measurements of 10 functional traits for canopy trees and palms > 5 cm diameter at breast height (DBH) and comprising > 80% of the abundance in each stand. Some of the community weighted mean trajectories followed the patterns predicted by environmental filtering, with a decline in fast-resource acquisition traits and an increase in resource conservation traits over successional time. Successional patterns were stronger when community weighted means were weighted by abundance than basal area. However, other traits did not show consistent successional trends and instead demonstrated stochastic variation among plots. Even among the traits that did show successional patterns, many of the trends are weak and demonstrate high plot-to-plot variation, further supporting that importance of stochasticity in community assembly. Many of the successional functional trait patterns were driven by the abundance of palms, which increased during succession. Compared to trees > 10 cm DBH, trees $5\text{ cm} \leq \text{DBH} \leq 10\text{ cm}$ showed a faster convergence with old-growth forests for most functional traits. My results suggest some

convergence in functional composition of second-growth forests with old-growth forests, and provide evidence for both environmental filtering and stochasticity in the community assembly of second-growth tropical wet forests.

Introduction

Secondary forests globally comprise over half of the remaining tropical forests (FAO 2010), providing a promising avenue for recuperating biodiversity and ecosystem services that have largely been lost in human-modified landscapes (Chazdon et al. 2009). The species richness of second-growth forests can reach similar levels to old-growth forests in as few as 30 years (Guariguata and Ostertag 2001, Letcher and Chazdon 2009). Yet, tree species composition varies considerably among similarly aged secondary forests, even in close proximity to one another (Chazdon et al. 2007), and an important subset of old-growth forest species is missing from these young forests (Lamb et al. 2005, Chazdon et al. 2009). The initial species composition is highly dependent on soil degradation, land-use history, and local seed dispersal (Brown and Lugo 1990, Chazdon 2003, Chazdon et al. 2007), which can have long-term effects on the community structure and composition of regenerating forests (Norden et al. 2011). In this study, I compare the distribution of functional traits along a successional gradient to gain a better understanding of community reassembly during wet tropical forest succession.

Succession is a dynamic process, characterized by a constant ebb and flow of species presence and abundance. Species composition is determined in part by the arrival of seeds, but also by changing environmental conditions during forest development. Light availability declines during forests regrowth, and second-growth forests exhibit greater spatial homogeneity of light availability than old-growth forests (Nicotra et al. 1999, Denslow and Guzman G. 2000, Guariguata and Ostertag 2001, Batterman et al. 2013). Lands historically used for pasture or agriculture experience decreased soil fertility (Chazdon 2003), but nutrients in the soil, vegetation, and litter are often restored during regeneration (Lamb 1980, Brown and Lugo 1990, Guariguata and Ostertag 2001). Species' responses to these environmental changes are mediated

by their functional traits, which reveal species-specific patterns of potential resource acquisition and actual resource allocation to leaves, wood, and seeds (Westoby et al. 2002, Díaz et al. 2004, Wright et al. 2004). Under a deterministic model of community assembly, community composition is constrained to species with the appropriate traits to overcome the abiotic and biotic filters necessary to first arrive at a site, and then to establish and grow (Weiher and Keddy 1999). If environmental filtering drives successional changes in species composition, the functional composition will vary in accordance with these changing environmental conditions. Alternatively, if community assembly is driven by dispersal limitation and stochastic events (Hubbell 2001), functional trait distributions will not show a clear directional trend. Another possibility is that successional forests lie somewhere between these two extremes, whereby both environmental filtering and stochasticity influence changes in species composition (Chazdon 2008).

Plant functional traits vary with ecological strategies along a fast-slow continuum, reflecting allocation tradeoffs that result in faster growth rates or increased defense (Westoby et al. 2002, Díaz et al. 2004, Garnier et al. 2004, Wright et al. 2004, Poorter and Bongers 2006). On one end of the functional trait spectrum are species with fast-resource acquisition traits, typified by early successional, short-lived pioneer species. Species with fast-resource acquisition traits invest in cheap, short-lived leaves that provide a quick investment return (Westoby et al. 2002, Poorter and Bongers 2006, Selaya and Anten 2010). They have high specific leaf area, high leaf nitrogen and phosphorous content, and low wood specific gravity (Popma et al. 1992, Ellsworth and Reich 1996, Poorter et al. 2004, van Gelder et al. 2006). Although their tissues provide limited support from abiotic and biotic damage, their traits confer fast photosynthetic rates, and high relative growth rates (Bazzaz and Pickett 1980, Ellsworth and Reich 1996). Late-

successional shade-tolerant species tend to lie on the opposite end of the functional trait spectrum, exhibiting resource-conservation strategies. Species with resource-conservation traits have slow growth rates, but invest in long-lived tissues that are defended against herbivores, pathogens, and breakage (Coley 1983, Augspurger and Kelly 1984, Reich et al. 2003). Shade-tolerant species tend to have tough, dense leaves and high wood specific gravity (van Gelder et al. 2006, Poorter 2009, Poorter et al. 2010). Here I use a multinomial model approach to robustly classify species' habitat affinities, in which species are characterized as second-growth specialists, old-growth specialists, or successional generalists based on their estimated relative abundances in second-growth and old-growth forests (Chazdon et al. 2011). I then examine 10 leaf and stem functional traits (Table 2.1) of the dominant species across a successional gradient to relate functional traits to successional specialists categories and to determine how environmental filtering and stochasticity influence community assembly.

Although various studies have measured functional traits of tree species in a successional context, few have assessed stand-level functional trait dynamics of second-growth wet tropical forests. The few studies that have assessed community level changes in tree functional trait distributions (Lohbeck et al. 2013, Dent et al. 2013) rely on a static chronosequence approach, in which temporal successional trends are inferred by measuring stands of different ages at a single time point. Chronosequence patterns often deviate from true vegetation dynamics because community reassembly patterns are highly idiosyncratic, showing variation with land-use history and landscape factors that influence seed dispersal and establishment (Chazdon et al. 2007, Johnson and Miyanishi 2008). To my knowledge, the present study is the first to combine chronosequence data with long-term vegetation dynamics data and functional trait measurements to examine patterns of community reassembly during natural regeneration.

Tropical forest succession is characterized by four stages: stand initiation, stem exclusion, understory reinitiation, and finally old-growth forest (Chazdon 2008). During the stand initiation phase (0-15 years), short- and long-lived pioneer trees colonize the abandoned land (Finegan 1996, Chazdon 2013). Fast-growing, short-lived pioneers experience high mortality during the stem exclusion phase (15-50 years), although long-lived pioneers continue to dominate into the understory reinitiation phase (30-200 years). Shade-tolerant, old-growth specialists begin to recruit as seedlings, saplings and trees in the stem exclusion phase, and become continuously more abundant and diverse as the forests age (Letcher and Chazdon 2009, Chazdon 2013, 2014). After approximately 200 years the forests transition into old-growth forests, which are characterized by high taxonomic and functional diversity of trees and epiphytes, and are relatively stable with regards to forest structure, species composition and ecosystem properties (Chazdon 2013). Land-use history and landscape characteristics affect the timing and duration of these four phases, and consequently impact the functional composition of the successional community based on variation in the type of species that colonize and persist during these different successional stages. The seedling and sapling layers of second-growth forests converge with old-growth forests in terms of species composition (Norden et al. 2009) and shade-tolerance (Dent et al. 2013). Tree seedlings and saplings represent the future of the second-growth forests, although these individuals must pass through many more filters before they become part of the canopy community. To predict the more immediate future of successional forests we can look at the community of small trees, which have not yet reached the canopy and likely recruited after the current canopy cohort. To my knowledge, this study is the first to explicitly compare the functional trait composition of large and small trees in a successional context.

In this study I use 15 years of tree vegetation dynamics data in eight 1-ha forest monitoring plots to assess changes in functional trait composition during post-pasture succession in the lowland rainforest of Costa Rica. Specifically, my objectives were to:

1. Test whether functional traits vary among successional specialists and generalists. I predict that second-growth specialists will have fast resource acquisition traits, old-growth specialists will have resource conservation traits, and generalist traits will have intermediate traits.
2. Examine patterns of functional trait composition along a successional gradient for canopy trees and palms, using population level mean trait values and weighting trait composition by abundance. I predict that as second-growth forests age, their functional trait distribution will gradually shift from fast resource acquisition traits to resource-conservation traits.
3. Compare the trajectories of functional trait distributions above (objective 2) to trajectories based on the following:
 - a) Using species mean trait values instead of population level means.
 - b) Weighting functional composition by basal area instead of abundance.
 - c) Limiting the community to dicotyledonous trees only, without including palms.
4. Compare the tree and palm functional trait trajectories separately for large individuals (> 10 cm DBH) and small individuals ($5 \text{ cm} \leq \text{DBH} \leq 10 \text{ cm}$). In these second-growth forests, the species composition of younger life stages show increasing similarity to mature forests (Norden et al. 2009), and small individuals developing in the understory experience similar environmental conditions across forest stands. Thus, compared to large trees, I expect faster functional trait convergence among small trees in second-growth and old-growth forests.

Methods

Study Location

The present study took place in eight 1-ha forest plots located in and around La Selva Biological Station, in the province of Heredia, northeastern Costa Rica (Table 2.2). This region is classified as tropical lowland wet forest, with an average annual temperature of 26.5°C and ~3900 mm of rainfall (McDade et al. 1994). The elevation of the study plots ranges from 40 to 200 meters above sea level. The regional landscape is comprised of a mixture of secondary and old-growth forests, pasture, agriculture, and plantations.

Stand characteristics

My study sites include six second-growth and two old-growth forest plots. All second-growth forest plots are naturally regenerating following the abandonment of pasture, whereas the old-growth plots have no recent record of human disturbance. In 2012 the second-growth forest plots ranged in age from 17 to 40 years old. The vegetation dynamics of stems ≥ 5 cm diameter at breast height (DBH) have been monitored annually in all plots for 8–16 years (Table 2.2; Lasky et al. *submitted*, Chazdon et al. 2007, Norden et al. 2012). For my analyses I only included species classified as canopy trees or palms (species with mature adult height ≥ 15 m). I measured functional traits for the most common species, whose cumulative abundance comprised at least 80% of the canopy tree and palm community of each plot for each census year (range: 81.0–97.6%; mean \pm SE: $91.7 \pm 0.005\%$). In total, my dataset comprised 89 tree species and 5 canopy palm species.

Species classifications

I classified my 94 focal species into specialist categories based on their relative abundance in the old-growth and second-growth forest plots between 1997 and 2011. Species were classified as second-growth specialists, old-growth specialists, generalists, or too rare to classify using a multinomial model (Chazdon et al. 2011). Classifications were performed in CLAM (Chao and Lin 2011), using the supermajority rule ($K=2/3$) and an overall $P = 0.01$.

Functional Trait Measurements

Functional trait measurements were conducted over a 4-year period (2008–2012). Following standardized protocols (Cornelissen et al. 2003, Williamson and Wiemann 2010a), I measured 9 leaf traits and two wood traits for each species (Table 2.1). These 11 functional traits are important components of a tree's ecological strategy and demonstrate tradeoffs in resource allocation (Table 2.1). The traits included: leaf size (LS), specific leaf area (SLA), leaf dry matter content (LDMC), leaf thickness (LT), leaf toughness (LTO), and leaf density (LD), leaf nitrogen content (LNC), leaf phosphorus content (LPC), leaf carbon: nitrogen ratio (C:N), wood specific gravity (WSG), and area-weighted wood specific gravity (AWWSG).

Leaf traits were measured on two leaves per individual, and values were averaged prior to analyses. Whenever possible I measured traits on sunlit leaves (79.8% of all leaves measured), with minimal herbivore damage or epiphyll cover (62.0% of all leaves measured). In cases where leaves were collected from individuals found in the shaded understory, I collected leaves with maximal sun exposure from the outer crown. Leaves were transported to the lab in sealed plastic zipper bags, where they were placed in deionized water and stored overnight at 4°C in total darkness prior to trait measurements.

Leaf area was quantified using a digital leaf area meter (LI-3100, LiCor Environmental, Lincoln, Nebraska). I measured fresh and dry leaf mass (after oven-drying for ~72 hours at 60°C) on a digital balance. Leaf thickness was measured with a digital micrometer. Leaf toughness, or punch force, was calculated using a leaf penetrometer (Chatillion 516-1000M push-pull gauge, Chatillion, USA), where the Newtons of punch force were divided by the circumference of the punch (Garnier et al. 2013). Leaf density on a fresh mass basis was calculated as the inverse of $LT \bullet LDMC \bullet SLA$ (Vile et al. 2005). Leaf nitrogen and carbon concentrations were measured on a VarioMax CN Analyzer (Elementar Analysensysteme GmbH, Hanau, Germany), and LPC was measured on a Ciros ICP-OES spectrometer (Spectro Analytical Instruments Inc., Kleve, Germany). For some species, I bulked leaves of 2–6 individuals per plot prior to nutrient analyses (carbon and nitrogen: 49 bulked samples; phosphorus: 84 bulked samples). I assessed leaf size, leaf thickness, leaf toughness and leaf nutrients for laminae only, whereas I included both the laminae and petioles for measurements of specific leaf area, leaf dry matter content and leaf density (Cornelissen et al. 2003). For compound leaves and palms, I measured individual leaflets instead of entire leaves.

Wood specific gravity was measured by coring trees to the pith using a 5.15 mm increment borer (Suunto, Finland). To account for radial variation in wood specific gravity, I separated each wood core into an inner (near pith) section, an outer (near bark) section, and a middle section. The inner and outer sections were each 2–2.5 mm in length, and the remainder of the core was designated as ‘middle’. Wood volume (excluding bark) was measured for each section using water displacement method. Wood cores were oven-dried at 105°C for at least 72 hours prior to measuring dry weight (Williamson and Wiemann 2010a). I calculated standard whole core WSG by summing the three sections together. Many species, particularly second-

growth specialists, show radial variation in WSG (Williamson and Wiemann 2010b, Plourde et al. *submitted*). Thus I also calculated area-weighted wood specific gravity (AWWSG) for each stem by weighting the WSG of each section by its proportional contribution to the stems cross-sectional area (Williamson & Wiemann 2010a, 2010b, Plourde et al. *submitted*).

Twelve species had missing values for 1–4 traits. In those cases, I supplemented my data with data collected near the study sites (WSG for 6 species; LNC and LPC for 3 species: Fernández Méndez, Aquino Yaringaño, Finegan, and Casanoves, *unpublished data*), used a congeneric value (LTO: 1 species), or used the average value of other species in the same genus (C:N, WSG: 1 species) or family (C:N, WSG: 1 species). In once case I used the average value of all species in the dataset (C:N for *Ilex skutchii*). Area-weighted WSG values were not available for the species with missing WSG values (8 species), and so I used standard whole-core WSG values in those cases.

In general, for each species, functional traits were measured in each plot where it was common (*i.e.* one of the species comprising the cumulative > 80% abundance of the plot). I used plot-specific trait values when morphological leaf traits (LS, SLA, LDMC, LT, LTO, LD) were measured on at least 5 individuals, and when leaf nutrients (LNC, LPC, C:N) or wood traits (WSG, AWWSG) were measured on at least 3 individuals in a plot. Otherwise, I used species-mean values calculated from individuals across all plots. Although these plot-specific measurements account for environmental plasticity across study sites, I could not account for year-to-year ontogenetic variation within plots as functional traits were only measured in each plot at one time point. Thus, within site variations in functional trait values solely reflect changes in species relative abundances, whereas among site variations reflect compositional changes in

species relative abundances as well as species level adaptations to local environmental changes (intraspecific variation among plots).

Statistical Analyses

To assess the correlation among functional traits I performed Pearson's correlations on species mean values calculated across all sites. To compare functional traits among specialist categories, I used ANOVA analyses followed by Tukey HSD post-hoc tests. I log-transformed leaf size, specific leaf area and leaf toughness to improve normality.

Using the specialist classifications and abundance data for my 94 focal species, I compared the proportion of second-growth specialists, old-growth specialists, generalists, and species too rare to classify in each plot for each census year. To assess whether the proportion of individuals in each specialist category demonstrated successional trends, I used linear mixed-effects models fit using Restricted Maximum Likelihood (REML) estimation (Venables and Ripley 2002). Old-growth forests were excluded from the models, as their age is unknown. For each trait, I performed a model selection procedure, as described in Zuur et al. (2009). I first optimized the random effects structure by comparing models with a random slope and/or intercept term for plot. The random plot terms account for the repeated measurements in each plot across years. Using the best-fit random effects structure for each successional category, I then compared intercept-only models to models with a fixed effect for stand age. When comparing fixed effect structures, models were fit with maximum likelihood, but the final best-fit model was reassessed with REML estimation (Zuur et al. 2009). At each step of the protocol, the best-fit model was determined from the small sample size corrected Akaike's Information Criterion (AIC_c) value of the models (Venables and Ripley 2002). The model with the lowest

AIC_c score was chosen, unless a simpler (more parsimonious) model was within $\Delta 2$ AIC_c units of the more complex model (Burnham and Anderson 2002).

Canopy palms contributed unequally to the proportion of individuals among sites and years (Appendix 2, Fig. A2.1), and monocots and dicots often show differences in leaf construction and functional traits (Dominy et al. 2008). To understand the extent to which canopy palms influenced successional functional trait patterns, I compared species mean trait values among the 5 canopy palm species and 89 canopy tree species using Welch's t-tests. I used the Holm-Bonferroni method to adjust the *P*-values for multiple comparisons (Holm 1979). Leaf size was log-transformed prior to analysis.

To assess community-level functional changes along the successional gradients, I calculated community weighted mean (CWM) values for each trait in each plot in each census year. Community weighted mean is the sum over all species of the species' trait value weighted by its relative abundance in the community (Garnier et al. 2004), and represents the trait value of an average individual in the community. I used linear mixed-effects models to assess how CWM trait values changed with stand age across the successional gradient, following the same procedure as described for the successional category linear mixed-effects models. I then used linear mixed-effects models to compared successional trends in CWM when calculated in different ways, and among different subsets of data. I compared 1) CWM patterns calculated with species mean values instead of population level values, 2) CWM weighted by relative basal area instead of relative abundance, 3) CWM calculated only for the dicotyledonous tree communities instead of based on the entire canopy community (trees and palms), and 4) CWM calculated separately for the large tree community (DBH > 10 cm) and small tree community (5 cm ≤ DBH ≤ 10 cm). In all cases I excluded old-growth forests.

Following Nakagawa and Schielzeth (2013), two correlation metrics were calculated for each of the best-fit mixed-effects models. The marginal correlation metric for linear mixed-effects models, $R^2_{\text{LMM(m)}}$, measures the variance described by the fixed effects only. The conditional correlation metric, $R^2_{\text{LMM(c)}}$, expresses the variance explained by both the fixed and random factors. For models that included a random slope term for plot, the correlation metrics were calculated for an equivalent model that only included a random intercept term for plot (Nakagawa and Schielzeth 2013).

All statistical analyses were performed in the R statistical program (R Core Team 2013). Community weighted means were calculated in the ‘FD’ package (Laliberté and Legendre 2010, Laliberté and Shipley 2011), and the linear mixed-effects models were analyzed using ‘lme4’ package (Bates et al. 2013).

Results

Functional Traits

The 11 functional traits showed a wide range of values across the 94 species (Appendix 2, Table A2.1). Some of the functional traits were highly correlated (Appendix 2, Table A2.2). In particular, leaf nutrients (leaf nitrogen content, leaf carbon: nitrogen ratio and leaf phosphorus content) were strongly correlated, and specific leaf area was strongly negatively correlated to leaf dry matter content, leaf thickness and leaf toughness. Area-weighted wood specific gravity (AWWSG) and wood specific gravity (WSG) also showed very strong positive correlation (Appendix 2, Table A2.2). As AWWSG is a more appropriate measure of whole-tree wood specific gravity than WSG (Williamson and Wiemann 2010a), and second-growth specialists, in

particular, show radial changes in WSG (Plourde et al. *submitted*), I chose to present AWWSG results instead of WSG for the remainder of the paper.

Each successional category was well represented among the 94 focal species (20, 24, 25, and 25 species for second-growth specialists, generalists, old-growth specialists, and too rare to classify, respectively). Among all individuals ≥ 5 cm DBH, second-growth forests had a high proportion of second-growth specialists (35–62% of individuals) and generalists (22–55% of individuals), and a very low proportion of old-growth specialists (0.6–5% of individuals; Appendix 2, Fig. A2.2). Among the second-growth forests, the proportion of generalists and old-growth specialists increased significantly with stand age (Appendix 2, Fig. A2.2). In most of the second-growth plots, the proportion of second-growth specialists declined with stand age, but the overall trend was not significant (Appendix 2, Fig. A2.2). Old-growth forests contained a low proportion of second-growth specialists (3–10% of individuals), and relatively high proportions of generalists (34–40% of individuals) and old-growth specialists (38–43% of individuals; Appendix 2, Fig. A2.2). Species that were too rare to classify made up less than 12% of the abundance of any plot in any census (Appendix 2, Fig. A2.2).

Only two functional traits differed significantly among specialist categories: second-growth specialists had significantly higher leaf phosphorus content (LPC) and lower area-weighted wood specific gravity (AWWSG) than old-growth specialists (Fig. 2.1). Generalists had intermediate values of these two traits. Species that were too rare to classify also had intermediate values for AWWSG, although their LPC was significantly higher than old-growth specialists.

Successional shifts community level trait values

Community weighted mean (CWM) trait values changed directionally along the successional gradient for half of the functional traits (Fig. 2.2). As predicted, CWMs for three of the resource conservation traits (leaf density, leaf toughness, and carbon: nitrogen ratio) increased with stand age, and CWMs for one of the fast-resource acquisition traits (leaf nitrogen content) declined significantly with stand age. Contrary to predictions CWM leaf size, a fast-resource acquisition trait, increased along the successional gradient. The fixed effect, stand age, explained 10–64% of the variation in CWM functional traits for these five models ($R^2_{\text{LMM(m)}}$; Fig. 2.2). The trends in CWM specific leaf area, leaf dry matter content, leaf thickness, leaf phosphorus content and area-weighted wood specific gravity did not vary consistently along the successional gradient, and intercept-only models were the best-fit for these traits (Fig. 2.2). Across all 10 traits, the best-fit models explained 88–99% of the variation in CWM trait values ($R^2_{\text{LMM(c)}}$), where the random effects for plot identity explained 24–99% of the CWM variation ($R^2_{\text{LMM(c)}} - R^2_{\text{LMM(m)}}$; Fig. 2.2).

Calculating abundance-weighted CWM using species mean trait values instead of population-level means values caused minor but significant changes in the successional patterns for all traits except leaf size (Appendix 2, Fig. A2.3). Specifically, the intercept shifted for three traits (specific leaf area, leaf dry matter content and leaf phosphorus content), while both intercepts and slopes shifted for 6 traits (leaf density, leaf thickness, leaf toughness, leaf nitrogen content, carbon: nitrogen ratio and area-weighted wood specific gravity).

When CWM was weighted by tree basal area instead of abundance, in the importance of stand age in predicting successional patterns changed in five of the 10 successional patterns. When CWM was weighted by abundance, leaf size, leaf density, and leaf toughness varied

consistently along the successional gradient, but stand age was not a significant predictor in these models when CWM was weighted by basal area (Appendix 2, Table A2.3). In contrast, stand age was not an important predictor for abundance-weighted CWM leaf dry matter content and leaf phosphorus content patterns, but stand age improved model-fit for these traits when CWM was weighted by basal area (Appendix 2, Table A2.3).

When directly comparing abundance-weighted and basal area-weighted patterns in the same linear mixed-effects models, the weighting factor significantly influenced successional patterns for all traits (Fig. 2.3). Relative to basal area-weighted patterns, the slopes of the successional patterns were steeper when weighted by abundance for CWM specific leaf area, leaf toughness, leaf nitrogen content, leaf carbon: nitrogen ratio and leaf phosphorus content (Fig. 2.3). Compared to the abundance-weighted successional trends, the intercepts for CWM leaf dry matter content and leaf density were lower when CWM was weighted by basal area. Finally, for three traits the CWM successional patterns were reversed when weighted by abundance vs. basal area. Abundance-weighted CWM leaf size and leaf thickness increased while area-weighted wood specific gravity decreased with succession; the opposite patterns emerged for basal area-weighted CWMs.

Canopy palms and trees

Canopy palms comprised a considerable proportion (>15%) of the individuals in three of the second-growth forests and in both of the old-growth forests (Appendix 2, Fig. A2.1a). I further compared the proportion of individuals that palms comprised for the large (DBH > 10 cm) and small ($5 \text{ cm} \leq \text{DBH} \leq 10 \text{ cm}$) size classes. In the second-growth forests, palms constituted a higher proportion of individuals in the smaller size class compared to the large size

class, whereas the opposite was true in old growth forests (Appendix 2, Fig. A2.1b-c). Across all measured individuals, the palms had significantly larger and tougher leaves, with significantly lower specific leaf area than the dicotyledonous trees (Table 2.3).

The exclusion of palms from the dataset significantly altered the CWM patterns for all traits except leaf phosphorus content. When palms were excluded, many traits showed less striking changes in CWM values across the successional gradient, and in some cases the successional patterns were reversed (Appendix 2, Fig. A2.4). The slopes of the declines in CWM specific leaf area, leaf thickness and leaf nitrogen content were reduced when palms were excluded, as were the increases in CWM leaf density and leaf carbon: nitrogen ratio (Appendix 2, Fig. A2.4). Moreover, although CWM leaf size and leaf toughness increased along the successional gradient when palms were included, excluding palms resulted in slight decreases (Appendix 2, Fig. A2.4). Finally, when palms were included in the analyses, CWM leaf dry matter content increased with stand age and CWM area-weighted wood specific gravity decreased, whereas the reverse was true when palms were excluded (Appendix 2, Fig. A2.4).

Small trees vs. large trees

The species in my dataset comprised 71.1–97.3% (mean: 88.3% \pm 0.008 SE) of the abundance of small trees ($5 \text{ cm} \leq \text{DBH} \leq 10 \text{ cm}$), and 88.4–97.5% (mean: 94.1% \pm 0.002 SE) of the abundance of large trees ($\text{DBH} > 10 \text{ cm}$) in each plot and each census year. The successional patterns in CWM traits varied with tree size class for all 10 functional traits (Fig. 2.4). The CWM trends for trees in the small size class were more pronounced than the trends for trees in the large size class for five functional traits (leaf size, specific leaf area, leaf toughness, leaf nitrogen content and carbon: nitrogen ratio; Fig. 2.4). In contrast, the slope of the CWM leaf density trend

was higher for the large trees than the small trees. Two traits demonstrated intercept shifts with size class; the smaller trees had lower intercepts than large trees for leaf dry matter content and leaf phosphorus content. Neither CWM leaf thickness nor area-weighted wood specific gravity showed successional trends for the entire canopy community (Fig. 2.2), whereas the CWM values for the large and small size class demonstrated opposing trends (Fig. 2.4). For the small tree communities, CWM leaf thickness increased across the successional gradient and area-weighted wood specific gravity declined; large trees showed the opposite trends.

Discussion

This study is the first to combine long-term stand dynamics data with chronosequence patterns to assess changes in functional trait distributions along a tropical wet forest successional gradient, providing a deeper understanding of the role of functional trait variation in community assembly. As predicted by environmental filtering, I observed a directional change in the community weighted mean (CWM) values of some functional traits with stand age (CWM leaf size, leaf density, leaf toughness, leaf nitrogen content and carbon: nitrogen ratio). Apart from leaf density, these directional trends are largely driven by the increasing abundance of palms during forest succession. Other functional traits did not vary consistently with stand age (specific leaf area, leaf dry matter content, leaf thickness, leaf phosphorus content and wood specific gravity), suggesting that stochasticity and land-use history are also important factors in the community assembly of tropical second-growth forests. For most traits, the community-level patterns were stronger for small trees than for large trees, suggesting that the functional composition of second-growth forests is on a convergent trajectory toward old-growth forests.

The functional trends in the large size class suggest that long-lived pioneer species still dominate in the canopies of the second-growth forests.

My predictions that second-growth specialists would have fast resource acquisition traits and old-growth specialists would have resource conservation traits were not universally supported by my data. As expected, second-growth specialists had significantly higher leaf phosphorus content and lower wood specific gravity than old-growth specialists (Fig. 2.1). These two traits are strongly related to growth and survival rates. Old-growth specialists spend most of their lives in shaded understory conditions, where high WSG provides them with structural support and protection from abiotic and biotic damage (Augspurger and Kelly 1984, van Gelder et al. 2006, King et al. 2006). Pathogen activity is reduced in high light environments, and thus high WSG is less critical for second-growth specialists (Augspurger and Kelly 1984). Second-growth specialists are adapted for faster growth rates rather than survival, and generally prioritize short-term gains over long-term costs and risks. Low WSG is correlated with fast growth rates of trees across tropical wet forests (Poorter et al. 2010). Moreover, by producing fatter trunks of lower density wood, second-growth specialists are able to achieve high mechanical strength with low construction costs (Larjavaara and Muller-Landau 2010). The higher concentration of phosphorus in second-growth specialist leaf tissues also imparts higher photosynthetic rates (Raaimakers et al. 1995, Ellsworth and Reich 1996, Wright et al. 2004).

Surprisingly, the other functional traits in this study did not differ among specialist groups. My robust classification scheme was based on each species' relative abundance in second-growth and old-growth forests, and not on their functional characteristics or demographic rates (Chazdon et al. 2011). My results suggest that few species fit precisely into the pioneer and shade-tolerant functional trait dichotomy, and instead fall along a continuum between these two

extremes (Wright et al. 2010). Each of the successional categories demonstrates a large range in functional trait values, suggesting that the functional characteristics I measured are not major factors driving changes in species abundance among second-growth and old-growth forests. Moreover, all of the second-growth stands used for the multinomial classifications were already fairly well developed, with closed canopies. Since my study did not include old-fields, the short-lived pioneer species were already declining or absent from the stands. The low abundance of short-lived pioneers may at least partially explain the lack of significant differences among the successional specialist categories for many of the functional traits. Possibly other functional traits, such as those related to regeneration mode and dispersal (*i.e.* seed size, seedling morphology), would demonstrate more consistent differences among specialist categories (Westoby et al. 2002, Baraloto and Forget 2007).

Although few functional traits varied by specialist category, half of the community-level functional traits showed directional trends with stand age (Fig. 2.2), consistent with the trends predicted by environmental filtering. Light is often the most limiting resource in wet tropical forests (Chazdon and Fetcher 1984). During forest regrowth, light availability declines and becomes spatially more heterogeneous (Nicotra et al. 1999, Denslow and Guzman G. 2000). In accordance with the environmental filtering hypothesis, I predicted a directional trend from acquisitive traits in young second-growth forests towards a predominance of resource conservation traits related to shade-tolerance in older forests. Confirming this trend, I found that as second-growth forests age, CWM leaf nitrogen content declines, whereas CWM leaf density, toughness, and carbon: nitrogen ratio increase (Fig. 2.2). In a successional chronosequence of young second-growth wet tropical forests in Chiapas, Mexico, Lohbeck et al. (2013) also found an increase in CWM leaf density with stand basal area. Surprisingly, I found an increase in

CWM leaf size along the successional gradient. In contrast, Lohbeck et al. (2013) found no correlation of CWM leaf size with stand basal area. The increase in CWM leaf size with succession was largely due to the increasing abundance of the large-leaved palm species with stand age (Appendix 2, Fig. A2.1). When palms were removed from the analyses, CWM leaf size decreases slightly with stand age (Appendix 2, Fig. A2.4). Lohbeck et al. (2013) focused on young second-growth plots (>1-25 yrs) that contained no palms, accounting for the difference in our results.

Contrary to the predictions, I found no pattern in CWM specific leaf area (SLA), leaf thickness (LT), or area-weighted wood specific gravity (AWWSG) with stand age, regardless of whether CWM was weighted by abundance or basal area (Appendix 2, Table A2.3). Similar to my study, Lohbeck et al. (2013) found no successional pattern in CWM wood density. However, Lohbeck et al. (2013) did find an increase in CWM LT with stand age and a decline in CWM SLA with stand basal area. In my study, successional trends for these traits were highly variable among plots, which was largely driven by differences in species composition. Although there was no successional pattern in CWM specific leaf area across all plots, two of the intermediate-aged plots (LSUR and LEPS; Fig. 2.2) showed the expected decline. These are the two second-growth plots located within La Selva Biological Station (Table 2.2), and are surrounded by a higher proportion of old-growth forest compared to the other second-growth plots. In these two plots, palms, which have significantly lower specific leaf area than the trees in the study (Table 2.3), became increasingly more common with stand age (Appendix 2, Fig. A2.1). Thus landscape factors influence the differences in species composition among plots, and, consequently, differences in functional trait composition. Although community weighted mean (CWM) LT was highly variable among young second-growth forests, the older second-growth plots converged

towards old-growth values, such that plots initially comprised of primarily thick-leaved individuals (*i.e.* JE, TIR) demonstrated a decline in CWM LT over time, whereas the opposite was true for plots comprised of primarily thin-leaved individuals (*i.e.* LSUR, LEPS; Fig. 2.2). The trends for CWM AWWSG were variable among second-growth stands. CWM AWWSG increased in one plot (TIR), declined strongly in one plot (LEPS; Fig. 2.2), and demonstrated little change in the other plots (JE, FEB, LSUR, CR). Old-growth specialists had higher AWWSG than second-growth specialists (Fig. 2.1), and the proportion of old-growth specialists increased with stand age (Appendix 2, Fig. A2.2). However, since the proportion of old-growth specialists was low across all second-growth stands, they contributed little to the CWM patterns. Instead, the increase in CWM AWWSG in TIR can be primarily attributed to the decreasing abundance of second-growth specialists (Appendix 2, Fig. A2.2), particularly species with low AWWSG values, such as *Vochysia ferruginea* (AWWSG = 0.34), *Simarouba amara* (AWWSG = 0.36) and *Hampea appendiculata* (AWWSG = 0.27). Similarly, the decline in AWWSG in LEPS was largely influenced by the increasing abundance of palms (Appendix 2, Fig. A2.1) with relatively low AWWSG values, such as *Socratea exorrhiza* (AWWSG = 0.23) and *Iriartea deltoidea* (AWWSG = 0.29). When comparing dicot trees only, AWWSG increased with stand age, while LT decreased (Appendix 2, Fig. A2.4). Similarly, palms were more abundant among the smaller individuals in four of the six second-growth plots, and thus I also observed an increase in LT and a decrease in AWWSG among the small individuals.

The abundance of palms in these forests is clearly an important driver of successional changes in functional composition. Palms are an important component of Neotropical wet forests (Guariguata et al. 1997, Svenning 1998, Marín-Spiotta et al. 2007, ter Steege et al. 2013). Canopy palms were most abundant in the older second-growth forests—particularly in the small

size class—and in the two old-growth forests (Appendix, Fig. A2.1). Although canopy palms and trees only differed significantly in three functional traits (Table 2.3), the inclusion of palms influenced the successional trends for all but one trait (Appendix 2, Fig. A2.4). Compared to trees, the palms in the study had significantly larger and tougher leaves, with lower specific leaf area (Table 2.3). Accordingly, when palms were excluded from the dataset, the CWM trends with stand age for these traits were reversed. The abundance of palms also caused some individualistic trends among sites. The most striking trend was for leaf size in one of the older second-growth plots, LEPS, which had the highest abundance of canopy palms across all plots (Fig. 2.2; Appendix 2, Fig. A2.1).

Comparing the functional distributions of the small and large tree size classes provides insight into the future of these successional forests. The small trees displayed higher rates of functional change than large trees across the successional gradient for half of the measured functional traits. Compared to larger trees, the small tree communities in second-growth forests are more rapidly approaching the functional composition of old-growth forests for leaf size, specific leaf area, leaf toughness, leaf nitrogen content, and carbon: nitrogen ratio (Fig. 2.4). As discussed previously, many of these trends are driven by the higher palm abundance in the small tree size class. Differential palm abundance also led to opposing successional trends for leaf thickness and area-weighted wood specific gravity among the large and small tree communities, producing an overall non-significant pattern with stand age for all trees combined (Fig. 2.2).

The study provides the first evidence that both environmental filtering and stochasticity are important in structuring tree communities over time during tropical forest succession. I found clear trends across a second-growth forest gradient for some functional traits (leaf size, leaf density, leaf toughness, leaf nitrogen content and carbon: nitrogen ratio). However, other

functional traits demonstrated inconsistent successional trends, and I observed some stochastic functional patterns among sites, suggesting that additional factors such as land-use history, landscape patterns, biotic interactions, initial colonization and palm abundance also influence community assembly. The variability in functional composition among sites highlights the importance of applying long-term forest dynamics data to better understand successional patterns.

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Figure 2.1. Functional trait values of 94 canopy trees and palms > 5 cm DBH for four successional classification categories: second-growth specialists (SG), generalists (Gen), old-growth specialists (OG), and too rare to classify (Rare). Groups with different letters indicate significant differences, based on ANOVA analyses with Tukey HSD post-hoc tests. Trait abbreviations: LS = leaf size, SLA = specific leaf area, LDMC = leaf dry matter content, LD = leaf density, LT = leaf thickness, LTO = leaf toughness, LNC = leaf nitrogen content, C:N = leaf carbon: nitrogen, LPC = leaf phosphorus content, AWWSG = area-weighted wood specific gravity.

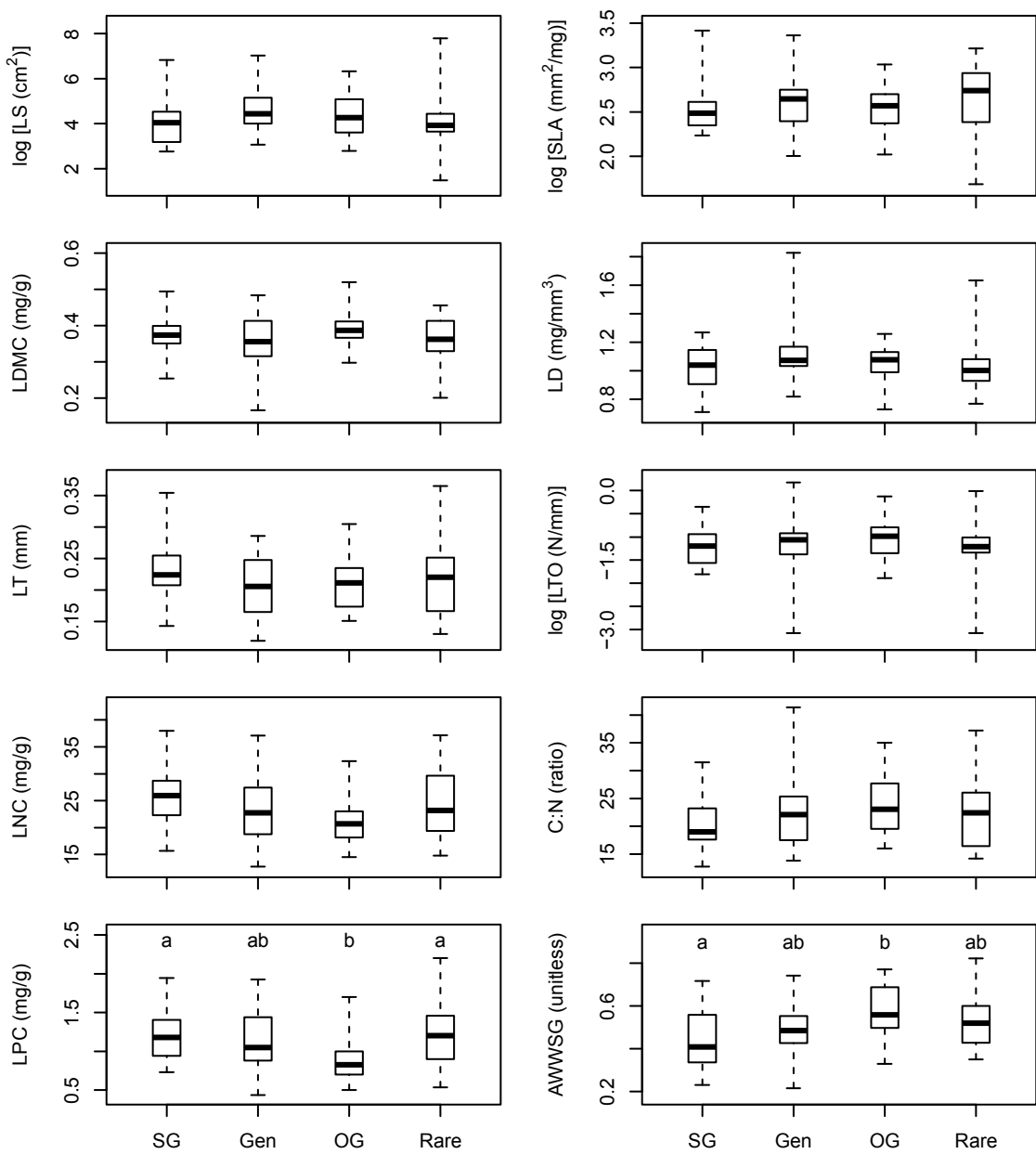


Figure 2.2. Changes in functional trait community weighted means (abundance-weighted) along a successional gradient in wet tropical forests of Costa Rica. The site key in the first panel applies to all panels. Linear mixed-effects model predictions are demonstrated with solid line when stand age was a significant factor in the model (*i.e.* LS, LD, LTO, LNC, C:N), and a dotted grey line when stand age was not significant (*i.e.* SLA, LDMC, LT, LPC, AWWSG). The marginal correlation coefficient, $R^2_{\text{LMM(m)}}$, considers the fit based on fixed effects, while the conditional correlation coefficient, $R^2_{\text{LMM(c)}}$ incorporates the variation explained by both the fixed and random effects. Trait abbreviations as in Figure 2.1.

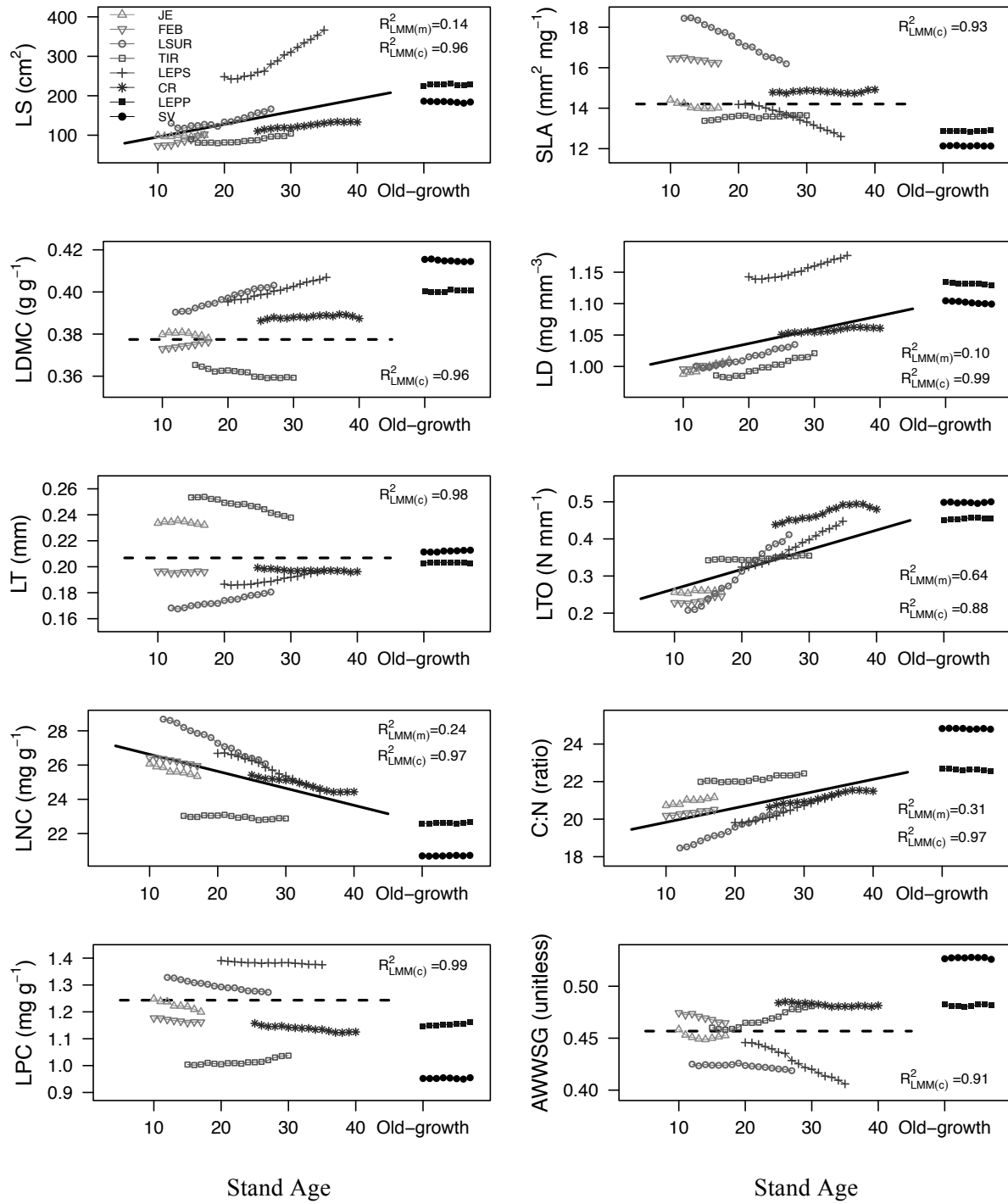


Figure 2.3. Comparison of community weighted mean (CWM) trends along a successional gradient using abundance (abund) or basal area as the weighting factor. All 10 traits show significant differences among abundance-weighted and basal area-weighted trends. Lines are predicted trends based on mixed-effects linear model fits of CWM with stand age. Trait abbreviations and explanation of R^2 values are described in Figures 2.1 and 2.2.

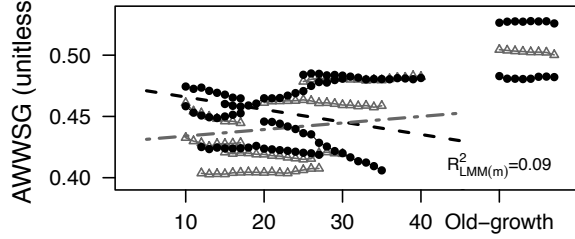
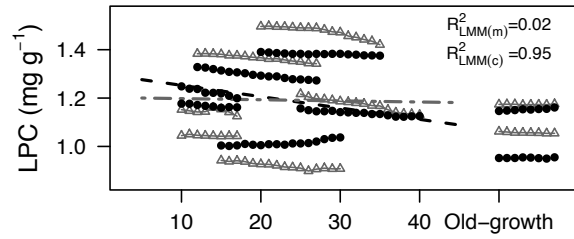
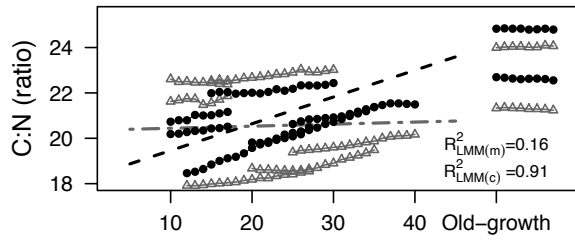
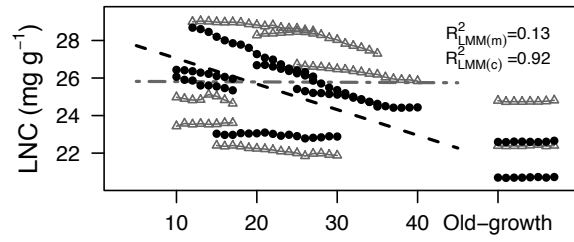
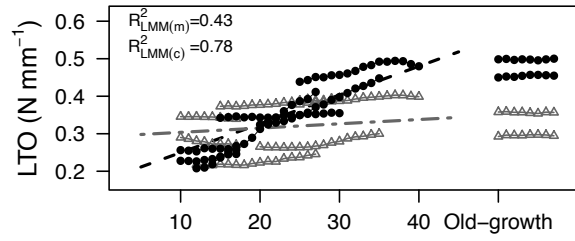
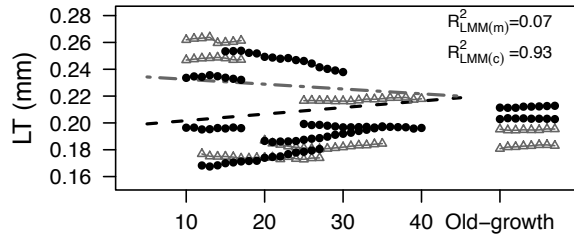
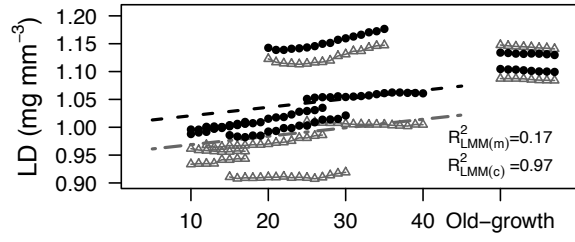
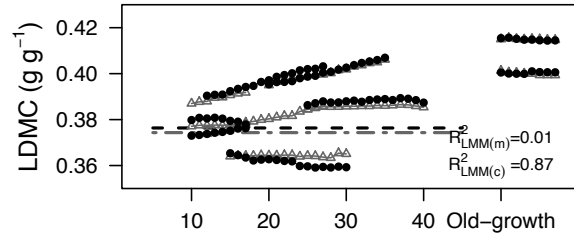
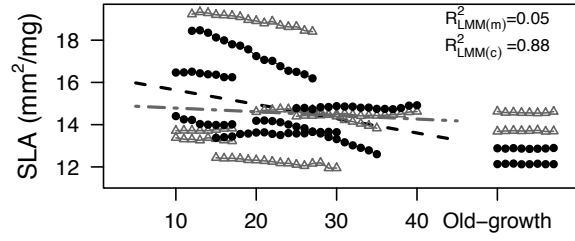
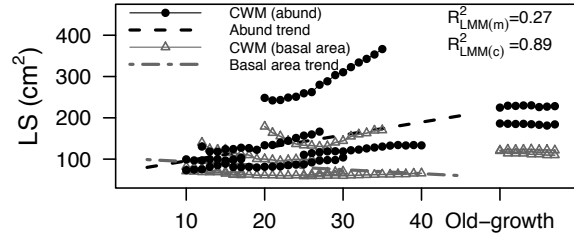


Figure 2.4. Community weighted trait means for small ($5 \text{ cm} \leq \text{DBH} \leq 10 \text{ cm}$) and large ($\text{DBH} > 10 \text{ cm}$) trees along a successional gradient. The site key in the first panel applies to all panels. Stand age, tree size, and the interaction between the two were significant predictors in linear mixed-effects models for all traits except leaf dry matter content (LDMC) and leaf phosphorus content (LPC), for which tree size was the only predictor. Trait abbreviations and explanation of R^2 values are described in Figures 2.1 and 2.2.

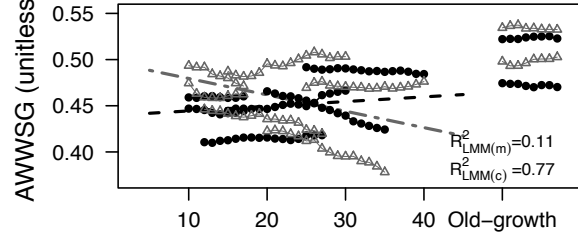
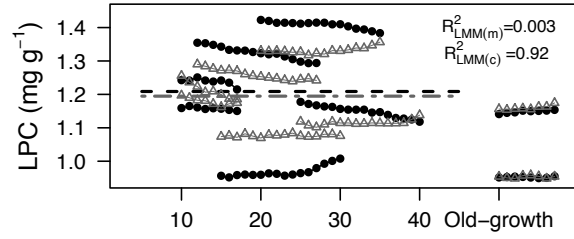
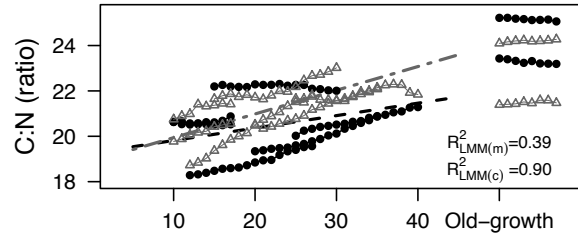
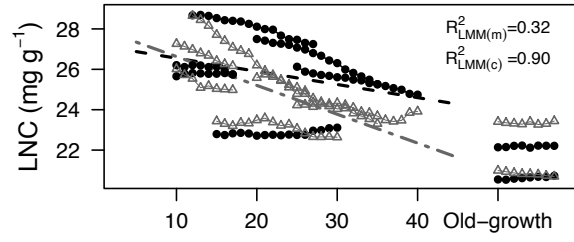
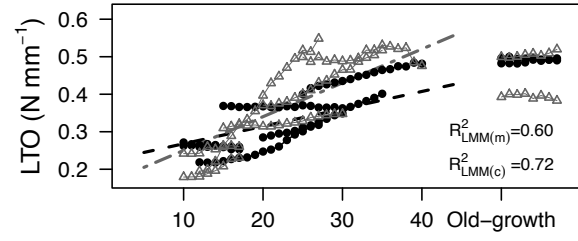
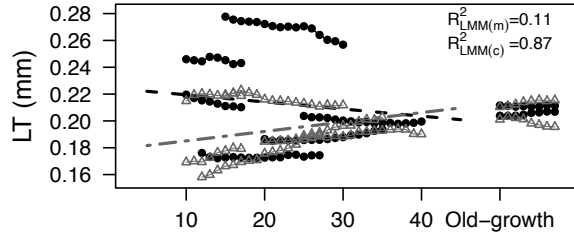
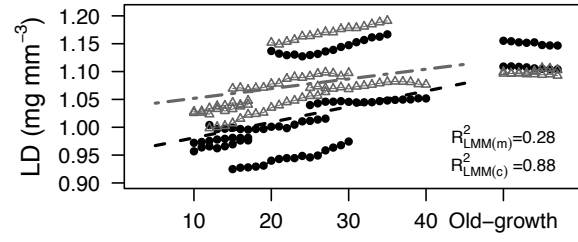
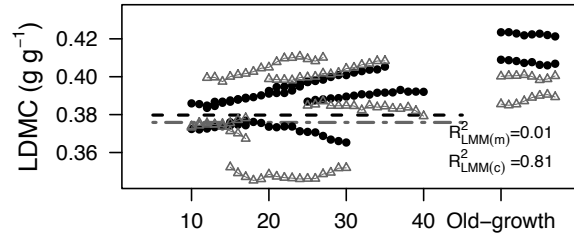
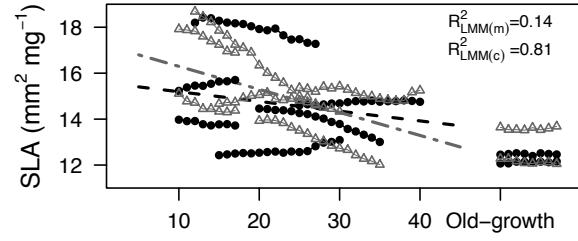
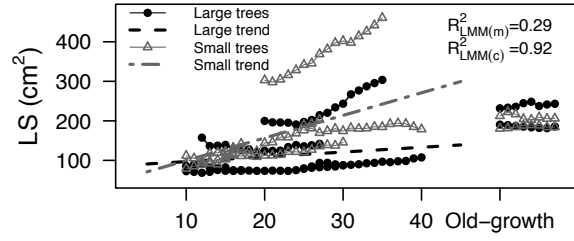


Table 2.1. The ecological significances of the functional traits measured in this study.

Functional Trait (abbreviation)	Units	Ecological significance & correlates	References
Leaf Size (LS)	cm ²	Light capturing area; affects energy and water balance, and chemical and structural characteristics of leaves and support structures.	(Westoby et al. 2002, Cornelissen et al. 2003, Niinemets et al. 2007)
Specific Leaf Area (SLA)	mm ² mg ⁻¹	Light capturing area to biomass investment; dependent on leaf anatomy, chemical or morphological composition. Tradeoff between the potential rate of return per leaf mass and the duration of the return. Linked to energetic cost of leaf construction, photosynthetic capacity, potential relative growth rate, and leaf lifespan. Correlated with leaf thickness, tissue density, and/or vein protrusion.	(Lambers and Poorter 1992, Niinemets 1999, Westoby et al. 2002, Wright et al. 2004)
Leaf Dry Matter Content (LDMC)	g g ⁻¹	Depicts average density of the leaf tissues. Important descriptor of position on resource-use axis. Correlates positively with leaf toughness and leaf life-span, and negatively with potential relative growth rate and specific leaf area.	(Lambers and Poorter 1992, Wilson et al. 1999, Cornelissen et al. 2003)
Leaf Density [fresh] (LD)	mg mm ⁻³	Includes mass and volume of water, intercellular spaces and leaf tissues; demonstrates variation in type and amount of materials to build a leaf.	(Roderick et al. 1999a, 1999b, Niinemets 1999, 2001, Sack et al. 2003, Vile et al. 2005)

		Positively linked with volumetric fraction of dry matter, cell wall thickness, elasticity modulus, and construction cost; negatively linked to photosynthetic rates. Chief driver of specific leaf area.	
Leaf Thickness (LT)	mm	Component of specific leaf area; related to energy balance, light absorption, photosynthetic rates, construction costs, physical strength of leaves, and leaf lifespan.	(Coley 1983, Reich et al. 1991, Agustí et al. 1994, Niinemets 2001, Westoby et al. 2002, Vile et al. 2005)
Leaf Toughness (LTO)	N mm ⁻¹	Relative carbon investment in structural protection of the photosynthetic tissues; provides general-purpose (quantitative) defense. Reduces biotic and abiotic damage. Correlated with leaf lifespan.	(Coley 1983, Reich et al. 1991)
Leaf Nitrogen Content (LNC)	mg g ⁻¹	Constitutes proteins of the photosynthetic machinery and defensive compounds; indicates nutritional quality of leaves. Correlated with carbon assimilation and herbivory rates.	(Coley 1983, Field and Mooney 1986, Raaimakers et al. 1995, Wright et al. 2004)
Leaf Carbon: Nitrogen (C:N)	ratio	Chemical indicator of nutritional value of the leaf, and scales negatively with relative growth rate. Carbon in excess of growth likely allocated to defense.	(Bryant et al. 1983, Lambers and Poorter 1992)
Leaf Phosphorus Content (LPC)	mg g ⁻¹	Key component of photosynthetic machinery; correlated with carbon	(Field and Mooney 1986, Raaimakers et al. 1995,

		assimilation, nutritional quality of leaves, and some defensive compounds.	Wright et al. 2004)
Wood Specific Gravity (WSG)	unitless	Biomass investment per unit wood volume; influences water transport, structural support, and growth rate.	(Augspurger and Kelly 1984, Muller-Landau 2004, van Gelder et al. 2006, King et al. 2006)
Area-weighted Wood Specific Gravity (AWWSG)	unitless	Wood specific gravity values, corrected by proportion of stem diameter each wood section encompasses. Otherwise same ecological significance and correlates as WSG above.	(Williamson & Wiemann 2010a; Plourde et al. <i>submitted</i>)

Table 2.2. Study sites, located in northeastern Costa Rica. Each stand is 1-ha. Vegetation dynamics have been monitored annually for all stems > 5 cm DBH since initial census year. Percent basal area of remnant trees is calculated from total basal area of stems > 5 cm DBH from initial census year. Adapted from Table 1 of Chazdon et al. (2010).

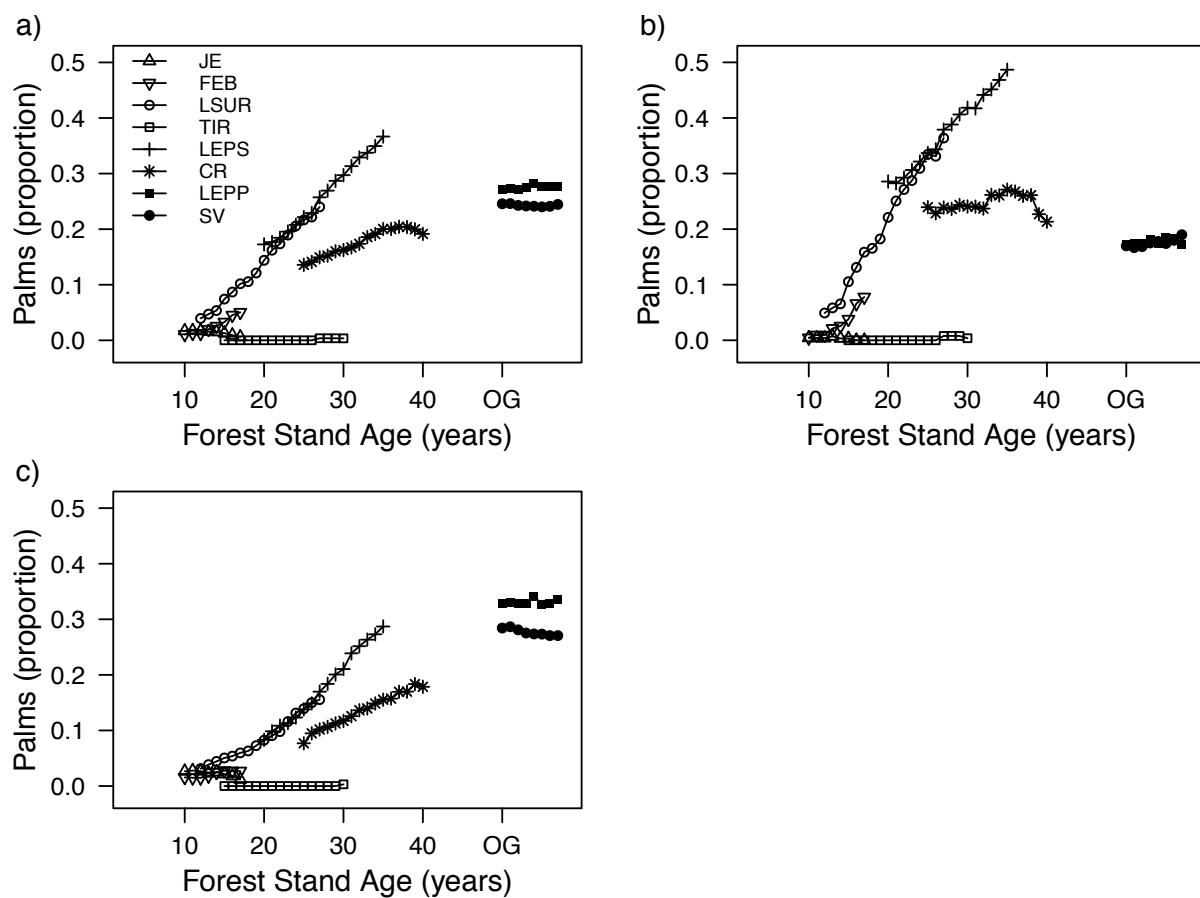
Plot (abbreviation)	Year abandoned	Year census initiated	Forest ages during censuses	% Basal area of remnants (# of individuals)	Location	Latitude, longitude	Surrounding landscape
Finca el Bejuco (FEB)	1995	2005	10-17	26.55 (22)	Chilamate	10.46°N, - 84.06°W	Pasture, old-growth, and second-growth forest
Juan Enriquez (JE)	1995	2005	10-17	0.29 (1)	Chilamate	10.46°N, - 84.07°W	Pasture, old-growth, and second-growth forest
Lindero Sur (LSUR)	1985	1997	12-27	16.93 (10)	La Selva	10.41°N, - 84.03°W	Old-growth and second- growth forest
Tirimbina (TIR)	1982	1997	15-30	11.41 (6)	Tirimbina	10.40°N, - 84.11°W	Pasture, plantations, and second-growth forest
Lindero El Peje Secondary (LEPS)	1977	1997	20-35	3.20 (3)	La Selva	10.43°N, - 84.03°W	Old-growth and second- growth forest
Cuatro Rios (CR)	1972	1997	25-40	2.17 (2)	Tirimbina	10.39°N, - 84.13°W	Pasture, second-growth, and old-growth forest
Lindero El Peje Primary (LEPP)	Old-growth	2005	Old-growth	<i>NA</i>	La Selva	10.42°N, - 84.04°W	Old-growth forest
Selva Verde (SV)	Old-growth	2005	Old-growth	<i>NA</i>	Chilamate	10.44°N, - 84.07°W	Pasture, old-growth, and second-growth forest

Table 2.3. Comparisons of functional trait values for 5 canopy palm species and 89 canopy tree species. Results from Welch’s t-tests, with Holm-Bonferroni adjusted *P*-values for the 11 functional traits. Traits with significant differences between palms and trees are shown in bold.

<i>Functional trait</i>	<i>Palm mean (range)</i>	<i>Tree mean (range)</i>	<i>df</i>	<i>t</i>	<i>P-value</i>
log [Leaf size]	6.03 (5.26–6.82)	4.24 (1.49–7.79)	4.86	5.28	0.032
Specific leaf area	8.58 (7.41–9.71)	14.23 (5.40–30.44)	16.16	-8.21	<0.001
Leaf dry matter content	0.44 (0.40–0.49)	0.37 (0.17–0.52)	5.12	3.81	0.091
Leaf density	1.14 (0.92–1.24)	1.05 (0.71–1.83)	4.80	1.52	0.722
Leaf thickness	0.25 (0.21–0.30)	0.21 (0.12–0.37)	4.71	2.07	0.483
Leaf toughness	0.98 (0.70–1.20)	0.32 (0.05–0.79)	4.22	7.45	0.014
Leaf nitrogen content	19.70 (14.50–29.20)	23.80 (12.72–38.00)	4.51	-1.58	0.722
Leaf carbon: nitrogen ratio	24.72 (16.06–31.22)	22.18 (12.74–41.38)	4.48	0.97	0.763
Leaf phosphorus content	1.23 (0.71–1.60)	1.10 (0.43–2.20)	4.56	0.81	0.763
Area-weighted wood specific gravity	0.35 (0.23–0.46)	0.52 (0.22–0.82)	4.90	-3.94	0.091

APPENDIX 2

Figure A2.1. The proportion of canopy palms among individuals ≥ 5 cm DBH in eight successional vegetation dynamics plots over time. Abundance-based proportions are shown for all canopy species (a), small individuals ($5 \text{ cm} \leq \text{DBH} \leq 10 \text{ cm}$) (b), and large individuals (DBH $> 10 \text{ cm}$) (c). “OG” is old-growth forest (age unknown).



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Figure A2.2. Proportion of trees ≥ 5 cm DBH in each of four specialist categories among eight successional study plots through time. Proportions are shown for the 94 focal species, classified as (a) second-growth specialists (SG), (b) generalists (Gen); (c) old-growth specialists (OG); or (d) too rare to classify (Rare). Linear mixed-effects model results are demonstrated with solid line when forest age was a significant factor in the model (*i.e.* generalists and old-growth specialists), and a dashed line when age was not significant (*i.e.* second-growth specialists and too rare to classify). The marginal correlation coefficient, $R^2_{\text{LMM}(m)}$, considers the fit based on fixed effects, while the conditional correlation coefficient, $R^2_{\text{LMM}(c)}$ incorporates the variation explained by both the fixed and random effects. The key for stand identity in panel (a) applies to all panels; descriptions of each stand can be found in Table 2.2.

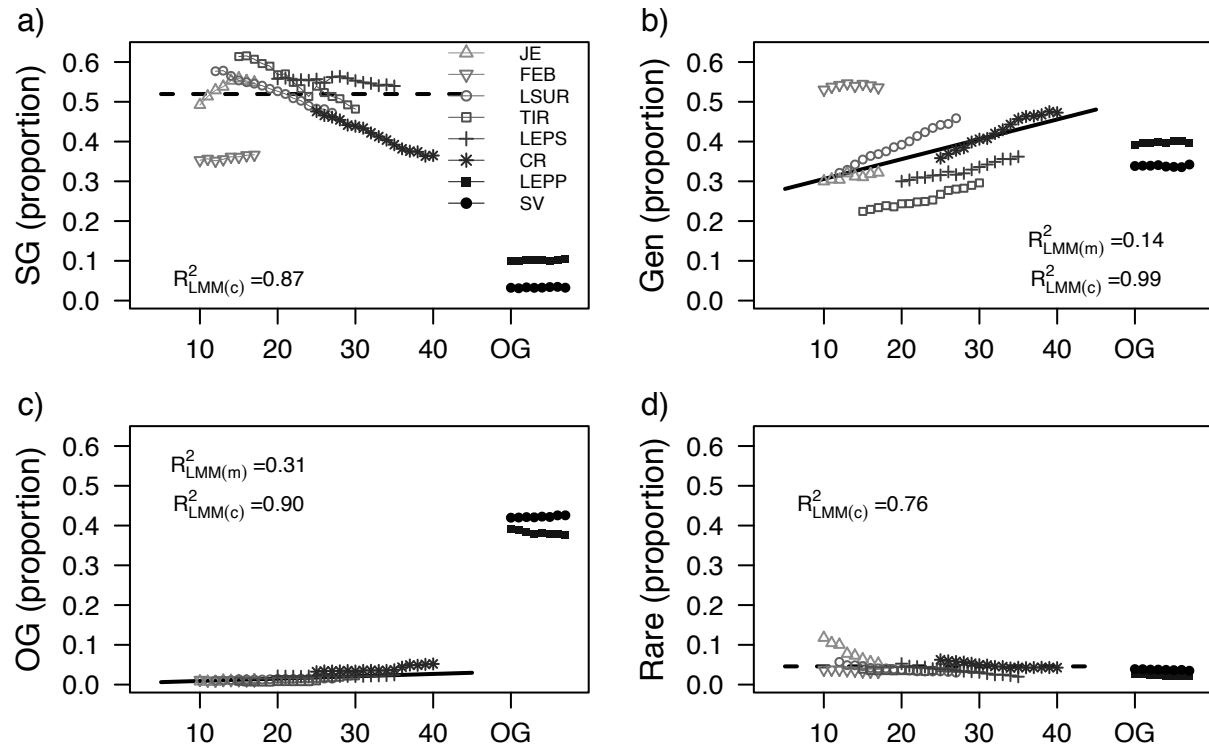


Figure A2.3. Comparison of abundance-weighted community weighted mean trends along a successional gradient using population-level (Pop) means or overall species (Spp) means. Lines are predicted values with stand age based on mixed-effects linear model fits. Nine traits show significant differences among abundance-weighted and basal area-weighted trends: specific leaf area (SLA), leaf dry matter content (LDMC), leaf density (LD), leaf thickness (LT), leaf toughness (LTO), leaf nitrogen content (LNC), leaf carbon: nitrogen ratio (C:N), leaf phosphorus content (LPC), and area-weighted wood specific gravity (AWWSG). Only for leaf size (LS) were the two different trends (species means or population means) equivalent. The marginal correlation coefficient, $R^2_{\text{LMM(m)}}$, considers the fit based on fixed effects, while the conditional correlation coefficient, $R^2_{\text{LMM(c)}}$ incorporates the variation explained by both the fixed and random effects. Key in top left panel applies to all panels.

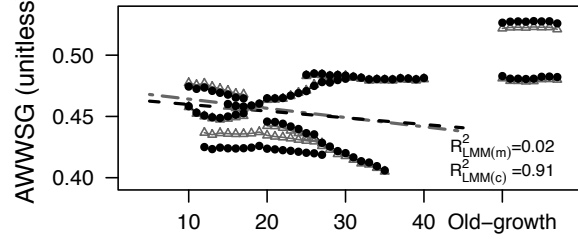
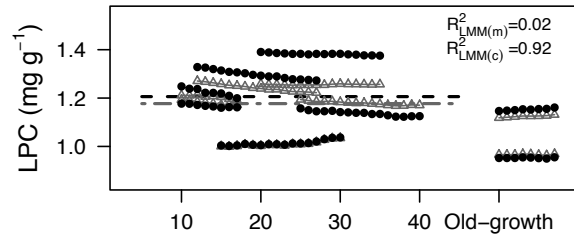
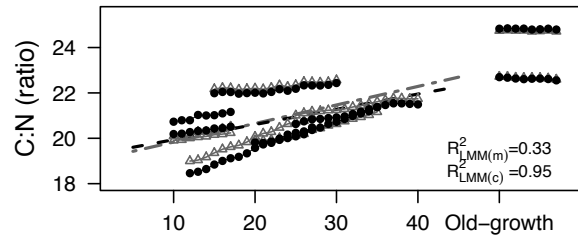
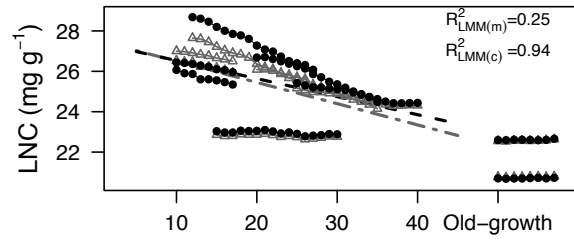
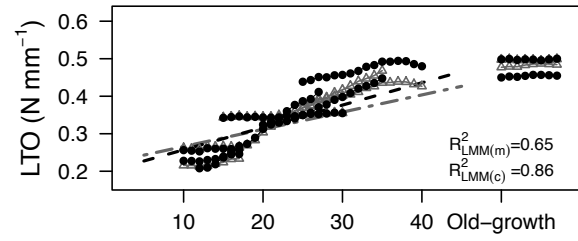
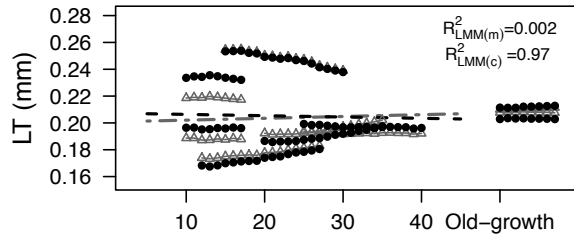
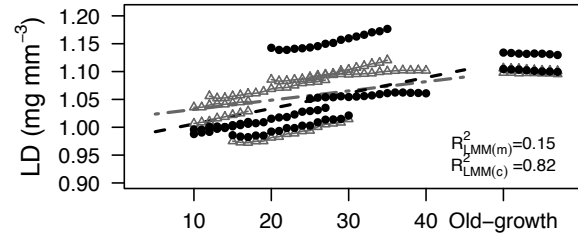
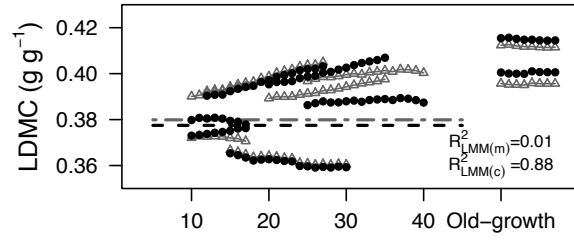
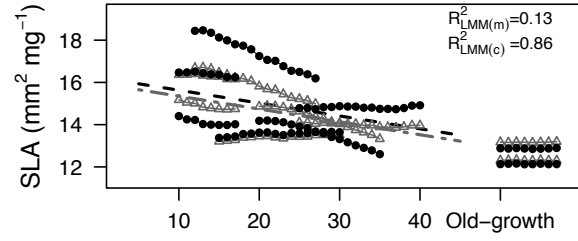
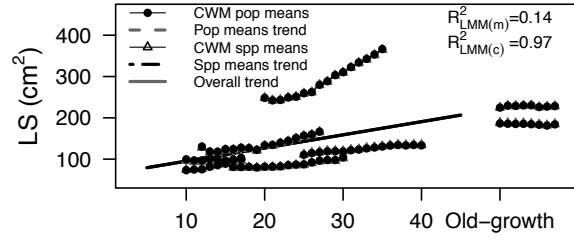


Figure A2.4. Community weighted trait means for all canopy individuals (trees and palms) and canopy trees only (no palms) along a successional gradient. The key in the top left panel applies to all panels. Stand age, palm inclusion, and the interaction between the two were significant predictors in linear mixed-effects models for all traits except leaf phosphorus content (LPC), for which stand age was the only predictor. Trait abbreviations and explanation of R^2 values are described in Figure A2.3.

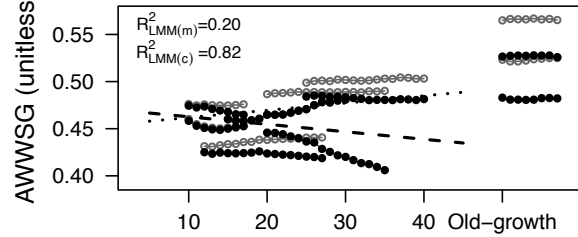
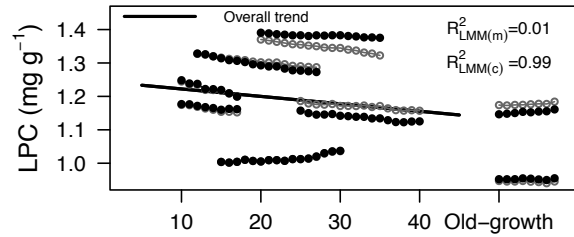
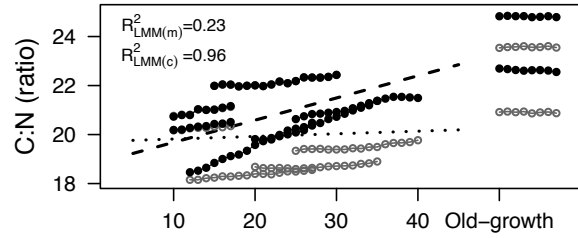
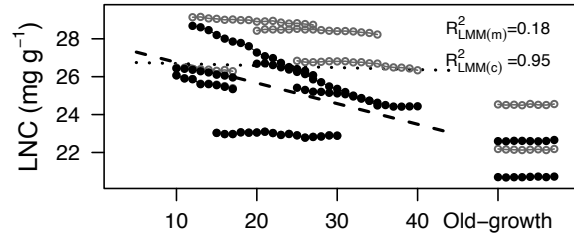
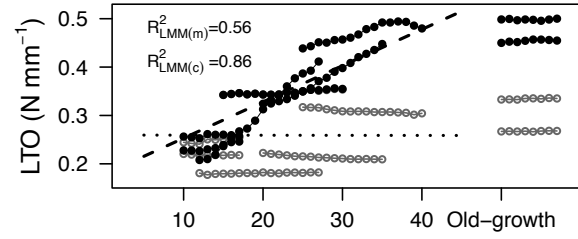
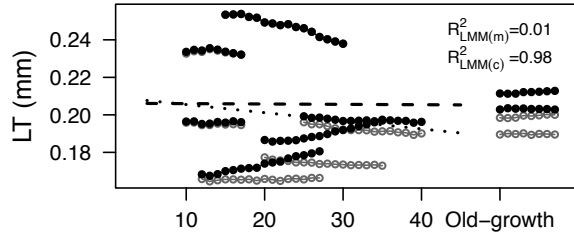
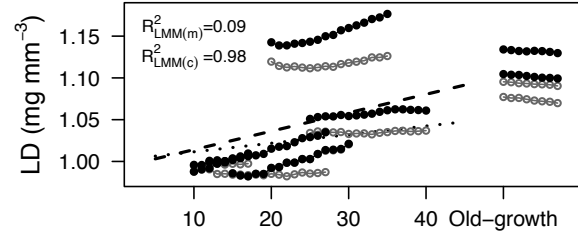
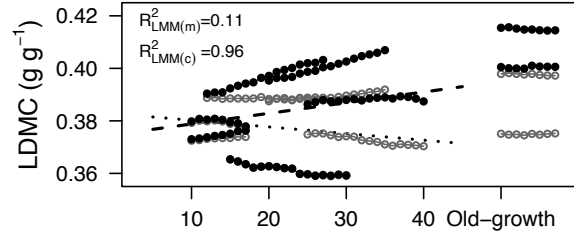
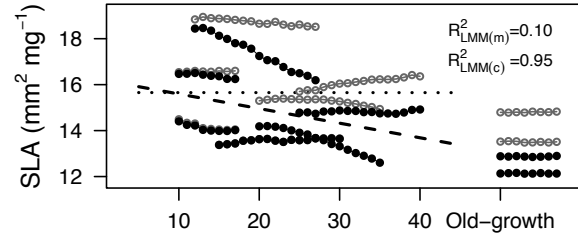
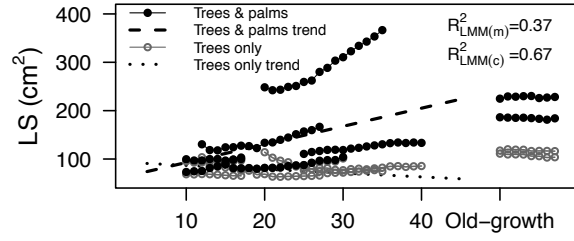


Table A2.1. Information about the 11 functional traits measured in this study. Number of species (N_{spp}) and samples (N_{sample}) measured for each trait, and the mean (\pm standard error), minimum, and maximum values of each trait, calculated across all field-sampled individuals. For most traits, a sample is an individual. However, for leaf nutrients, some of the samples were 2–6 individuals bulked by species and site (49 bulked samples for LNC and C:N; 84 bulked samples for LPC).

Trait (abbreviation)	Units	N_{spp}	N_{sample}	Mean \pm SE	Min	Max
Leaf Size (LS)	cm ²	94	1455	145.87 \pm 7.55	0.78	3564.69
Specific Leaf Area (SLA)	mm ² mg ⁻¹	94	1455	14.08 \pm 0.16	3.95	56.09
Leaf Dry Matter Content (LDMC)	g g ⁻¹	94	1455	0.37 \pm 0.002	0.12	0.62
Leaf Density (LD)	mg mm ⁻³	94	1454	1.05 \pm 0.006	0.61	3.41
Leaf Thickness (LT)	mm	94	1454	0.21 \pm 0.002	0.07	0.49
Leaf Toughness (LTO)	N mm ⁻¹	93	1377	0.37 \pm 0.006	0.012	1.77
Leaf Nitrogen Content (LNC)	mg g ⁻¹	91	425	23.75 \pm 0.30	10.92	43.41
Leaf Carbon: Nitrogen Ratio (C:N)	ratio	91	425	22.12 \pm 0.29	11.41	47.90
Leaf Phosphorus Content (LPC)	mg g ⁻¹	91	358	1.12 \pm 0.02	0.40	2.40
Wood Specific Gravity (WSG)	unitless	86	933	0.48 \pm 0.004	0.15	0.92
Area-weighted Wood Specific Gravity (AWWSG)	unitless	86	933	0.49 \pm 0.004	0.16	0.92

Table A2.2. Pearson correlations among species mean trait values for 94 canopy trees and palms. Strong correlations ($> |0.5|$) are highlighted in bold.

Functional Trait	LS	SLA	LDMC	LD	LT	LTO	LNC	C:N	LPC	WSG	AWWSG
Leaf Size (LS)	--	-0.33	-0.02	0.48	0.37	0.29	-0.17	0.10	0.06	-0.28	-0.28
Specific Leaf Area (SLA)		--	-0.58	-0.35	-0.58	-0.56	0.46	-0.46	0.35	-0.03	-0.04
Leaf Dry Matter Content (LDMC)			--	0.04	-0.08	0.40	-0.25	0.33	-0.24	0.27	0.29
Leaf Density (LD)				--	-0.09	0.12	-0.18	0.24	-0.06	-0.002	-0.008
Leaf Thickness (LT)					--	0.42	-0.28	0.20	-0.20	-0.25	-0.26
Leaf Toughness (LTO)						--	-0.39	0.32	-0.16	-0.05	0.06
Leaf Nitrogen Content (LNC)							--	-0.92	0.64	-0.16	-0.13
Carbon: Nitrogen ratio (C:N)								--	-0.65	0.20	0.18
Leaf Phosphorus Content (LPC)									--	-0.34	-0.34
Wood Specific Gravity (WSG)										--	0.997
Area-weighted Wood Specific Gravity (AWWSG)											--

Table A2.3. Comparison of AIC_c values for mixed-effects models of overall community weighted mean (CWM) functional traits across successional gradient. CWM values were calculated with population level mean trait values, and were weighted by either abundance or basal area. Mixed-effects models were compared with maximum likelihood estimation. All models included a random intercept and/or slope term for plot. Best-supported model for each trait is shown in bold.

<i>CWM Trait</i>	<u>Abundance-weighted</u>		<u>Basal area-weighted</u>	
	<i>Intercept only</i>	<i>Intercept + stand age</i>	<i>Intercept only</i>	<i>Intercept + stand age</i>
Leaf size	575.6	572.5	615.2	616.2
Specific leaf area	-106.3	-107.8	-81.6	-82.4
Leaf dry matter content	-891.6	-890.9	-928.0	-930.8
Leaf density	-650.4	-661.0	-608.2	-608.6
Leaf thickness	-824.1	-821.7	-777.1	-774.9
Leaf toughness	-521.9	-524.1	-595.7	-594.4
Leaf nitrogen content	-110.4	-116.7	-46.7	-50.9
Leaf carbon: nitrogen ratio	-133.3	-140.7	-89.0	-91.7
Leaf phosphorus content	-584.2	-585.3	-495.2	-502.5
Wood specific gravity	-710.9	-709.6	-737.0	-735.9
Area-weighted wood specific gravity	-717.0	-715.9	-738.0	-737.3

CHAPTER THREE

TAXONOMIC AND FUNCTIONAL BETA DIVERSITY OF CANOPY TREES AND PALMS ALONG A WET TROPICAL FOREST SUCCESSIONAL GRADIENT

Abstract

Community assembly during succession may be deterministic, with a clearly defined climax state, or stochastic, whereby distinct communities may arise due to differences in the sequence and timing of species arrival. I compared taxonomic and functional beta diversity along a successional gradient in wet tropical forests to gain a better understanding of the mechanism of community assembly. The successional gradient in northeastern Costa Rica included two old-growth forests and six second-growth forests, ranging in age from 10–40 years after abandonment of pasture. I used 8–16 years of vegetation dynamics data in these eight 1-ha forest stands for trees > 5 cm diameter at breast height, and measured 10 functional traits of species comprising over 80% of the abundance of each stand in each year. I calculated taxonomic beta diversity among plots with the Morisita-Horn dissimilarity index, and functional beta diversity as the Euclidean distance among standardized community-weighted mean trait values. For most traits, functional beta diversity was positively related to taxonomic beta diversity, suggesting that species turnover between plots generally incorporates species with divergent functional traits. Under a deterministic model of community assembly, I predicted that functional beta diversity would be higher than expected based on a null model of random species turnover, particularly among plots with higher differences in basal area. However, only leaf toughness demonstrated significantly higher functional turnover among plots than the null model predictions, and none of the traits demonstrated an increase in functional beta diversity with stand basal area difference. Instead, differences among plot-pairs explained most of the variation in functional beta diversity. These individualistic trends among successional stands support a stochastic model of community assembly, whereby functional differences between stands are not driven by stand age or structure.

Introduction

Theories of tropical plant community assembly during succession fall along a deterministic-stochastic continuum. Under the deterministic view of community assembly, environmental conditions drive sequential replacement of species towards a steady stable state (*i.e.* ‘climax community’) with a single configuration (Clements 1916). On the other hand, the stochastic view of community assembly suggests that community composition and structure are contingent upon historical factors and priority effects (Gleason 1927), whereby stochasticity in the sequence and timing of species arrivals drives community divergence. Although it has been demonstrated that both deterministic and stochastic processes may simultaneously influence different aspects of species coexistence in mature tropical forests (Hubbell 2001, Kraft et al. 2008, Paine et al. 2011, Swenson et al. 2012, Myers et al. 2013), second-growth forests have received less attention. Typically, succession has been viewed as a deterministic process, due to the successional replacement of short- and long-lived pioneers by shade-tolerant species (Finegan 1996, Chazdon 2013). Yet recent studies have shown that the species composition of tropical second-growth forests often shows limited convergence along successional gradients (Vandermeer et al. 2004, Chazdon et al. 2007, Dent et al. 2013; *but see* Lebrija-Trejos et al. 2010), suggesting a high contribution of historical contingencies, path dependence, and stochastic processes in community assembly. Factors such as soil degradation, land-use history and seed dispersal influence the initial species composition during natural regeneration (Brown and Lugo 1990, Chazdon 2003, Chazdon et al. 2007), and these differences can have long-term effects on forest community structure and composition (Norden et al. 2011).

Although species assembly during tropical forest succession has idiosyncratic and stochastic components, the functional aspects of community assembly are expected to be far

more deterministic (Bazzaz and Pickett 1980, Chazdon 2013). Throughout the changing environmental conditions during forest regrowth, species turnover is moderated by species-specific morphological and physiological functional traits (Bazzaz and Pickett 1980, Westoby et al. 2002). Light-demanding early successional species often have fast resource acquisition traits, producing short-lived leaves with high photosynthetic capacity, enabling rapid growth rates (Raaimakers et al. 1995, Poorter et al. 2004, van Gelder et al. 2006). The traits of shade-tolerant old-growth specialists, on the other hand, are generally geared towards resource conservation. The tissues of these species are more costly to produce, but are longer lived and better protected from biotic and abiotic damage (Raaimakers et al. 1995, Poorter et al. 2004, van Gelder et al. 2006). Indeed, at the stand level, such directional trends along successional gradients from fast resource acquisition to resource conservation have been reported in wet tropical forests in Panama (Dent et al. 2013), Mexico (Lohbeck et al. 2013) and Costa Rica (Chapter 2), and in dry forests of Mexico (Lebrija-Trejos et al. 2010, Lohbeck et al. 2013).

Although these patterns of functional trait distributions support a deterministic model of succession, other functional traits show little variation or only weak correlations with stand age or basal area (Lohbeck et al. 2013; Dent et al. 2013; Chapter 2). For these traits, where high levels of site-specific variability cannot be explained by successional age or structure, alternative community assembly mechanisms may be more important than environmental filtering (Spasojevic and Suding 2012). Moreover, community-level variation in functional traits is often driven by differences in species composition, which in turn may be influenced by dispersal limitation, environmental changes, or both (Condit et al. 2002, Swenson et al. 2011, 2012, Myers et al. 2013). Thus, we cannot explicitly identify the mechanisms of community assembly solely by describing temporal changes in the functional composition of plant communities.

Further insights into functional turnover during succession can be gained by directly comparing taxonomic and functional beta diversity, which allows comparison of the functional types of species occurring in various communities (Fig. 3.1). Under the assumption that most of the functional variation among communities results from interspecific rather than intraspecific variation (Cornwell and Ackerly 2009, de Bello et al. 2011), communities with similar species composition should also have similar functional composition. As taxonomic beta diversity increases along a successional gradient, I also expect functional beta diversity to increase in one of two ways. First, a saturating relationship between taxonomic and functional dissimilarity would occur when large differences in species composition have relatively little effect on functional diversity (Petchey et al. 2007) (Fig. 3.1-2). When environmental conditions are similar among communities, environmental filtering would predict such functional redundancy even with high levels of species beta diversity. For instance, since stands of a similar age since abandonment should have similar stand structure and environmental conditions, I would expect limited functional beta diversity among these communities even when species beta diversity is high. Alternatively, if the relationship between taxonomic and functional beta diversity increases indefinitely, this would suggest that communities with divergent species composition also diverge in functional composition (Petchey et al. 2007) (Fig. 3.1-1). Such a trend would occur where sharp environmental gradients are the driving forces for community dissimilarity. For instance, due to the disparate environmental conditions among young second-growth and old-growth forests, I would expect that high species turnover among these different aged stands would be accompanied by high functional dissimilarity. Finally, a lack of relationship between taxonomic and functional beta diversity (Fig. 3.1-3) would suggest that communities are

composed of species with a random subset of functional traits from the regional trait pool, and thus community assembly is neutral with respect to functional trait values.

Functional beta diversity can further be related to species beta diversity by using a null model approach. Swenson et al. (2012) found that, compared to species turnover, functional turnover was lower than expected over time in an old-growth tropical forest in Panama, whereas it was higher than expected in a hurricane-disturbed forest in Puerto Rico. These findings support a deterministic view of community assembly, where the functional composition of each forest type is constrained by environmental conditions, which are relatively stable in the undisturbed forest but change with forest recover in the disturbed forest. To date, this has been the only study to explore functional beta diversity patterns in a successional tropical forest, and it was limited to assessing functional turnover for one plot over the first 16 years following a hurricane disturbance.

Here I assess changes in species and functional beta diversity to explicitly test the mechanisms of functional community assembly along a successional gradient in tropical wet forests of Costa Rica. I combine functional trait data for 94 canopy tree and palm species with 15 years of data on the vegetation dynamics of trees > 5 cm diameter at breast height in eight 1-ha forest monitoring plots. My study plots include two old-growth forests and six naturally regenerating forest stands ranging in age from 10 to 40 years after abandonment of pasture. My specific objectives were to: 1) test for functional redundancy by relating taxonomic beta diversity to functional beta diversity along a successional gradient; 2) determine whether functional beta diversity is greater or less than expected by chance based on the observed differences in species composition among successional plots, using a null model approach (Swenson et al. 2011, Siefert et al. 2013); and 3) relate functional turnover to succession. Using stand basal area as a proxy for

successional stages and environmental conditions, I expected that functional turnover would be highest for plots with disparate stand basal areas under a deterministic model of community assembly.

Methods

Study Area

My study took place in wet tropical lowland rainforests in and around La Selva Biological Station in northeast Costa Rica (Heredia province). This region has an average annual temperature of 26.5°C, and 3900 mm of rainfall (McDade et al. 1994). The landscape is comprised of a mixture of second-growth and old-growth forests, plantations, pastures and cash crops. I conducted this study in eight 1-ha plots, where the species composition and diameter at breast height (DBH) of all stems > 5 cm DBH have been monitored annually for 8–16 years (Appendix 3, Table A3.1) (Chazdon et al. 2007, Norden et al. 2009, Lasky et al. *submitted*). The eight plots include two old-growth forest plots and six second-growth forest plots, which had been regenerating naturally for 10–40 years after the abandonment of pasture. The elevation of the plots ranges from 40 to 200 m above sea level.

I limited my analyses to species classified as canopy trees or palms (species with mature adult height ≥ 15 m), and whose cumulative abundance constituted at least 80% of each plot for each census year (range 80.9–97.6%; mean $91.7 \pm 0.05\%$ standard error). In total, my dataset comprised 89 tree species and 5 canopy palm species.

For each site in each census year, I calculated taxonomic alpha diversity using species equivalents, or Hill numbers (Jost 2006). I compared species equivalents for species richness (q_0), Shannon entropy (q_1), and Simpson concentration (q_2). Whereas q_0 only accounts for the

number of species in each site, q_1 and q_2 also take species evenness into account, with q_2 placing more importance on evenness than abundance. I compared alpha diversity for the entire assemblage of trees > 5 cm DBH (229 species) and separately for the 94 canopy palms and trees for which I measured functional traits.

In my study plots, stand basal area was strongly positively correlated with stand age among second-growth forests ($r = 0.88$; Appendix 3, Fig. A3.1). Stand basal area may be a better descriptor of diversity patterns along a successional gradient than stand age, as it reflects time since abandonment as well as environmental heterogeneity and land-use history (van Breugel et al. 2006, Chazdon et al. 2007, Lohbeck et al. 2012), and directly modifies the local environment (Lebrija-Trejos et al. 2010, 2011, Lohbeck et al. 2012). Moreover, by using stand basal area instead of stand age, I was able to directly compare patterns among second-growth and old-growth forests. Thus I chose to use stand basal area difference among each pair of plots instead of age difference to assess the patterns of functional beta diversity along the successional gradient (see below: *Relating functional dissimilarity to succession*).

Functional Trait Measurements

I determined species mean values of 9 leaf traits and one wood trait for each of the 94 focal species. Functional trait measurements were made between 2008 and 2012. Traits were chosen to characterize species along the fast-slow growth continuum that reflects investment tradeoffs between fast growth rates or increased defense (Dalling et al. 2002, Poorter et al. 2008). Leaf size (LS) affects energy and water balance, where more stressful conditions tends to select for smaller leaves (Cornelissen et al. 2003). Specific leaf area (SLA), leaf nitrogen content (LNC) and leaf phosphorus content (LPC) are three of the key traits of the leaf economics

spectrum (Wright et al. 2004), which primarily relate to photosynthetic capacity. Leaf thickness (LT) and leaf density (LD) are chief determinants of specific leaf area (Vile et al. 2005), and pertain to leaf construction and tissue strength. Leaf dry matter content (LDMC), leaf toughness (LTO), and leaf carbon: nitrogen ratio (C:N) relate to construction costs, defense against generalist herbivores, nutritional quality, and leaf lifespan (Reich et al. 1991, Lambers and Poorter 1992, Wilson et al. 1999). Wood specific gravity (WSG) reflects the biomass investment per unit wood volume, and impacts water transport, structural support and growth rate (Augspurger and Kelly 1984, Muller-Landau 2004, van Gelder et al. 2006). Additional details about these traits are summarized in Chapter 2. Fast resource acquisition (fast-growth) species tend to have high LS, SLA, LNC, LPC, and low LDMC, LT, LTO, LD, C:N, and WSG; species with resource conservation traits (ex. slow-growth species) demonstrate the opposite trends.

Although species mean values were used for all analyses, to account for intraspecific variation in functional trait values the traits of each species were measured for multiple individuals in all or most of the plots where that species was abundant. For each of the 94 focal species, morphological leaf traits were measured on 3–62 individuals (mean number of individuals \pm SE: 15.5 ± 1.3), leaf nutrients were measured on 1–18 individuals (LNC & C:N: 4.5 ± 0.4 ; LPC: 3.9 ± 0.3), and wood specific gravity was measured on 1–52 individuals (10.8 ± 1.1). Twelve species had missing values for 1–4 traits. In those cases I supplemented my data with other data collected near the study sites (WSG for 6 species, LNC and LPC for 3 species: Fernández Méndez, Aquino Yaringaño, Finegan, and Casanoves, *unpublished data*), used a congeneric value (LTO: 1 species), or used the average value of other species in the same genus (C:N, WSG: 1 species) or family (C:N, WSG: 1 species). In once case I used the average value of all species in the dataset (C:N for *Ilex skutchii*).

Functional traits were measured following standardized protocols (Cornelissen et al. 2003, Williamson and Wiemann 2010). Leaf traits were measured on two leaves per individual, and values were averaged prior to analyses. Sun-lit leaves with minimal herbivore damage or epiphyll cover were selected whenever possible. For individuals growing in the shaded understory, leaves with maximal sun exposure from the outer crown were selected. For compound leaved species and palms all measurements were performed on individual leaflets.

After collection, leaves were hydrated in deionized water at 4°C in total darkness for 12–24 hours prior to trait measurements. Fresh and dry leaf mass were measured on a digital balance, where dry weight was measured after ~72 hr in 60°C drying oven. Leaf dry matter content (g g^{-1}) was calculated at the ratio of dry to fresh leaf weight. Leaf size (cm^2) was quantified with a digital leaf area meter (LI-3100, LiCor Environmental, Lincoln, Nebraska). Leaf thickness (mm) was measured with a digital micrometer. I used a leaf penetrometer (Chatillion 516-1000M push-pull gauge, Chatillion, USA) to measure punch force. Leaf toughness (N mm^{-1}) was calculated as punch force divided by the perimeter of the punch. Following Vile et al. (2005), fresh leaf density (mg mm^{-3}) was calculated as the inverse of leaf thickness \times leaf dry matter content \times specific leaf area. Leaf nutrient analyses (LNC, C:N, and LPC) were performed at the University of Connecticut Soil Nutrient Analysis Laboratory. Leaf nitrogen and carbon content (mg g^{-1}) were measured on a VarioMax CN Analyzer (Elementar Analysensysteme GmbH, Hanau, Germany), and leaf phosphorus content (mg g^{-1}) was measured on a CiroS ICP-OES spectrometer (Spectro Analytical Instruments Inc., Kleve, Germany). Specific leaf area (ratio of leaf area to oven-dry mass, $\text{mm}^2 \text{mg}^{-1}$) and leaf dry matter content were calculated for the lamina and petiole combined (Cornelissen et al. 2003); all other leaf traits were based on lamina only. Wood specific gravity (unitless) was measured by coring trees to the

pith using a 5.15 mm increment borer (Suunto, Finland). Wood volume (excluding bark) was measured using water displacement method, and wood cores were oven-dried at 105°C for at least 72 hr prior to measuring dry weight (Williamson and Wiemann 2010).

Compositional changes

I evaluated taxonomic beta diversity (compositional change) among forest stands across all census years using the Morisita-Horn dissimilarity index (Morisita 1959). With this index, values range from 0 (compositionally identical) to 1 (assemblages share no species). As my analysis of species composition among communities was performed on the most abundant species in each plot, the Morisita-Horn index was the most appropriate because it is an abundance-based metric that gives more weight to the dominant species (Jost et al. 2011). I then compared species composition across sites and among years using non-metric multidimensional scaling (NMDS). I also related taxonomic beta diversity to basal area difference among plot-pairs.

For each trait, in each plot and census year, I calculated community-weighted mean trait values (CWM), which is the sum over all species in the community of each species' trait value weighted by its relative abundance (Garnier et al. 2004). Prior to CWM calculation, values of each trait were standardized to Z-scores (mean=0, variance=1) to control for differences in units and variances among traits. Functional dissimilarity was calculated for each census year (1997–2012) as the Euclidean distance among CWM values for each pair of plots. Univariate functional dissimilarity was calculated for each trait separately, and multivariate functional dissimilarity was calculated for all 10 traits combined. Higher values of functional dissimilarity indicate greater differences in CWM values among plot-pairs.

Statistical Analyses

Relationship between species and functional beta diversity

To assess whether species turnover resulted in functional complementarity or redundancy, I used mixed-effects regression analyses to compare the relationship between taxonomic beta diversity (Morisita-Horn dissimilarity) and functional beta diversity (Euclidean distance of CWM values). I included data for all sampling years. For each univariate and multivariate trait, I initially compared generalized least squares linear models with different error structures to account for heteroscedasticity (Zuur et al. 2009). An exponential structure of the variance covariate (taxonomic beta diversity) that varied by strata (plot-pair) was most appropriate in all but three cases. For the univariate leaf size and leaf density analyses, the best variance structure allowed for different variances per stratum (plot-pair), but was not exponential. For specific leaf area, the best variance structure was a power function. To account for the lack of independence among the same pair of plots across years, I then selected a random intercept and/or slope for plot-pair. I determined the best-fit random effect structure by comparing generalized least squares linear models with no random effect to linear mixed-effects models with a random intercept and/or slope term for plot-pair. The best-fit model was selected based on the small sample size corrected Akaike's Information Criterion (AIC_c) value of models fit with maximum likelihood (Venables and Ripley 2002). The model with the lowest AIC_c score was chosen, unless a simpler (more parsimonious) model was within $\Delta 2$ AIC_c units of the more complex model (Burnham and Anderson 2002). With the selected random effect term I then compared models fit with four different fixed-effect structures: intercept only, linear, logarithmic, and quadratic. The models comparing fixed effects structures were fit with Maximum Likelihood (ML) (Zuur et al. 2009), and the most parsimonious best-fit model was

determined using AIC_c. The final best-fit model is presented using Restricted Maximum Likelihood (REML) estimation (Venables and Ripley 2002). Following Nakagawa and Schielzeth (2013), two correlation metrics were calculated for each of the best-fit mixed-effects models. The marginal correlation metric for linear mixed-effects models, $R^2_{\text{LMM(m)}}$, measures the variance described by the fixed effects only. The conditional correlation metric, $R^2_{\text{LMM(c)}}$, expresses the variance explained by both the fixed and random factors. For models that included a random slope term for plot-pair, the correlation metrics were calculated for an equivalent model that only included a random intercept term for plot-pair (Nakagawa and Schielzeth 2013).

Null Model Analysis

I used a null model approach to quantify whether the functional beta diversity differs from a random expectation based on observed levels of taxonomic beta diversity. During each of 999 iterations of the null model, I randomly shuffled the species names within the functional trait dataset and recalculated the Euclidean distance among each pair of plots. This tip-shuffle null model operates under the assumption that compositional change is random with respect to functional traits, while maintaining observed levels of species richness and abundance, taxonomic beta diversity and spatial distribution patterns (Swenson et al. 2011, Siefert et al. 2013).

To assess whether the observed values were more or less extreme than expected by chance for each pair of plots in each year, I calculated the standardized effect size (SES; Gotelli and Graves 1996) as the difference between the observed and mean expected (null) dissimilarity, divided by the standard deviation of the expected values from the 999 iterations of the null model. Values higher than 1.96 or lower than -1.96 indicate significantly higher, or lower,

functional turnover than expected based on species composition, respectively. Significant SES values demonstrate that compositional change is non-random with respect to functional trait values, supporting a deterministic model of community assembly.

Relating functional dissimilarity to succession

I used linear mixed-effects models to assess the relationship of SES functional dissimilarity with basal area difference among site pairs. As in the regression models comparing species and functional beta diversity, I first optimized the random effect structure for plot-pair in each model and then assessed the fixed effects structure. For the multivariate analysis and separately for each trait, I compared a simple intercept model to a model that also included basal area difference. For each analysis, the best-fit model determined by AIC_c comparison is presented using REML estimation (Venables and Ripley 2002), and the marginal ($R^2_{\text{LMM(m)}}$) and conditional ($R^2_{\text{LMM(c)}}$) correlation metrics (Nakagawa and Schielzeth 2013) were calculated.

All statistical analyses were performed in the R statistical program (R Core Team 2013). The NMDS plots were created using the ‘metaMDS’ function in the ‘vegan’ package (Oksanen et al. 2013), which uses several random starts to find a stable solution. Community-weighted means were calculated using the ‘dbFD’ function in the ‘FD’ package (Laliberté and Legendre 2010, Laliberté and Shipley 2011). Linear mixed-effects models were performed using the ‘nlme’ and ‘lme4’ packages (Bates et al. 2013, Pinheiro et al. 2013). Marginal and conditional R^2 values were calculated with the function ‘rsquared.lme’ (Lefcheck 2013).

Results

Stand Characteristics

Species richness (q_0) increased along the successional gradient, with the youngest forest plots showing the lowest species richness and the old-growth forests showing the highest (Appendix 3, Fig A3.2). However, within each plot, species richness showed little change over time. Across all plots, Shannon entropy (q_1) and Simpson concentration (q_2) were lower than species richness. Similar to q_0 , the old-growth forests demonstrated higher q_1 and q_2 values than second-growth forests. However, second-growth forest plots showed little change in q_1 or q_2 values with increasing stand age both within and among plots (Appendix 3, Fig. A3.2). Although the scales differed, the trends within and among plots were similar for Hill numbers calculated from the entire tree assemblage (stems > 5 cm DBH, 229 species) and from the 94 species of canopy trees and palms for which functional traits were measured (Appendix 3, Fig. A3.2).

The NMDS ordination of community composition based on the Morisita-Horn index (2-dimensional stress = 0.13) shows that successional age and plot location influenced species composition (Appendix 3, Fig. A3.3a). The first axis of the 2-dimensional NMDS analysis primarily shows a successional age gradient, with the youngest secondary site on the right, and the old-growth forests on the left (Appendix 3, Fig. A3.3a). The second axis of the NMDS shows an effect of plot location. With the exception of CR, the plots in the lower half of axis 2 are located inside La Selva Biological Station, whereas the upper plots are located in the surrounding region. The species composition within each of the old-growth forest stands showed little change in the 7 years from 2005 to 2012 (Appendix 3, Fig. A3.3a). Within each of the secondary forests, however, species composition gradually became more similar to the old-growth forests over

time. Basal area difference did not explain any of the variation in species composition (Appendix 3, Fig. A3.3b).

Species and Functional Trait Beta Diversity

Functional beta diversity was positively related to taxonomic beta diversity for the multivariate analysis and eight of the ten univariate functional traits (Fig. 3.2). The relationship between species and functional beta diversities was best described by a positive linear regression for the multivariate analysis (Fig. 3.2a), leaf size (Fig. 3.2b), specific leaf area (Fig. 3.2c), leaf density (Fig. 3.2e), leaf nitrogen content (Fig. 3.2h), leaf carbon: nitrogen ratio (Fig. 3.2i), and leaf phosphorus content (Fig. 3.2j). Leaf dry matter content (Fig. 3.2d), leaf thickness (Fig. 3.2f) and leaf toughness (Fig. 3.2g) beta diversities were quadratically related to species beta diversity. The coefficient for the quadratic term was positive for the leaf thickness analysis, resulting in an increase in functional beta diversity with increasing taxonomic diversity. However, the quadratic term coefficients were negative for leaf toughness and leaf dry matter content, resulting in a saturating relationship for leaf toughness beta diversity, and a hump-shaped relationship for leaf dry matter content beta diversity, which initially increased with higher taxonomic beta diversity, but then declined. Wood specific gravity beta diversity (Fig. 3.2k) was logarithmically related to taxonomic diversity, with a negative coefficient for the logarithmic term resulting in declining wood specific gravity beta diversity with increasing taxonomic beta diversity. Across all analyses, taxonomic beta diversity explained <0.1–60% of the variation ($R^2_{\text{LMM(m)}}$) in functional beta diversity. All models also included a random intercept and/or slope for plot-pair to account for the lack of independence across sampling years. When both fixed and random effects were

considered ($R^2_{\text{LMM(c)}}$), the models explained 7–99% of the variation in taxonomic beta diversity (Fig. 3.2).

Functional Beta Diversity

To distinguish whether functional turnover was significantly higher or lower than expected based on species turnover, I related the observed functional beta diversity patterns to the null model results using standardized effect size (SES). For the multivariate analysis across all traits, and separately for each univariate trait, I calculated the SES functional dissimilarity among each pair of plots for each census year. Across all multivariate and univariate analyses, functional turnover was significantly higher than expected based on the null model for 4.8–43.8% of plot-pairs (*i.e.* SES functional dissimilarity > 1.96; Table 3.1). I found no cases where functional beta diversity was significantly lower than expected based on species beta diversity patterns (*i.e.* SES < -1.96).

I further assessed if trends in functional beta diversity were related to differences in stand basal area among plots. Contrary to expectations, wood specific gravity (WSG) demonstrated a negative trend in SES functional dissimilarity with basal area difference among plot-pairs (Fig. 3.3k), indicating that plots with the largest difference in basal area (*i.e.* youngest second-growth vs. old-growth stands) have the most similar standardized community-weighted mean wood specific gravity. Basal area difference only explained 9% of the variation in SES WSG functional diversity ($R^2_{\text{LMM(m)}}$), whereas the fixed and random effects combined ($R^2_{\text{LMM(c)}}$) explained 96% of the variation. Thus for wood specific gravity, the random slope and intercept for plot-pair explained 87% of the variation in SES functional diversity. For the multivariate analysis and the 9 remaining univariate functional traits, the best-fit models were intercept-only

models, demonstrating that stand basal area difference did not influence functional beta diversity patterns (Fig. 3.3a-j). The overall fit of these intercept-only SES functional diversity models was very high, with the proportion of variance explained by the random effects for plot-pair ($R^2_{\text{LMM(c)}}$) ranging from 91 to 99%. Although there was no successional trend for the leaf toughness model, the high estimated intercept value (2.19) indicates that the among-plot dissimilarities in leaf toughness were significantly higher than expected based on differences in species composition. The intercepts for the remaining 9 models (0.08–1.56) were within the bounds of the null model expectation.

Discussion

My results clearly showed that site-specific variation was the prominent factor driving successional changes in functional beta diversity, with little influence of stand age or structure. Deterministic factors rarely explained the variation in either taxonomic or functional composition. These findings contrast with previous studies that suggest that functional composition is strongly influenced by deterministic processes (Fukami et al. 2005, Swenson et al. 2011, 2012, Helsen et al. 2012, Purschke et al. 2013, Siefert et al. 2013). To my knowledge, this study is the first to measure functional beta diversity along a wet tropical forest successional gradient. Successional changes in functional beta diversity appear to be far more stochastic than previously thought.

For the multivariate analysis and most of the univariate traits (*i.e.* leaf size, specific leaf area, leaf density, leaf thickness, leaf nitrogen content, carbon: nitrogen ratio, and leaf phosphorus content), I found a linear or increasing relationship between functional beta diversity and taxonomic beta diversity, suggesting that pairs of plots with high taxonomic dissimilarity are

comprised of species with functionally complimentary strategies. Here, the plots with the most divergent species composition are the young second-growth stands and the old-growth forest stands (Appendix 3, Fig. A3.3a). Thus my results indicate that the species that are present in old-growth forests, but absent from the young second-growth forests, have divergent functional strategies. The saturating relationship between leaf toughness beta diversity and taxonomic beta diversity, as described by a quadratic model fit, suggests that some of the species turnover consisted of functionally redundant species. Communities comprised of functionally redundant species are more resilient to disturbance (Walker 1995). High species turnover has been shown to result in rather stable trait assemblages in other systems (Fukami et al. 2005, de Bello et al. 2009). Functional trait redundancy is common under environmental filtering (de Bello et al. 2009), when similar environmental conditions select for species with similar, well-adapted traits (Weiher and Keddy 1999). Thus the environmental conditions across the plots appear to select for similar leaf toughness strategies. Leaf toughness is positively correlated with defense from generalist herbivores and abiotic damage (Coley 1983), and thus my results suggest that the forests across the successional gradient are relatively resistant to such damage.

Two functional traits showed unexpected results, demonstrating decreasing functional beta diversity with increasing taxonomic diversity. Although leaf dry matter content beta diversity initially increased with taxonomic beta diversity, it later declined among plots with the highest divergence in species composition, and thus the highest functional turnover in leaf dry matter content occurred at intermediate levels of species turnover. Among the second-growth forests in my study area, community-level variation in leaf dry matter content does not show a successional pattern with stand age (Chapter 2). Moreover, the relationship between taxonomic beta diversity and leaf dry matter content beta diversity is the most similar to that expected under

a stochastic model of community assembly (Fig. 3.1-3), suggesting that leaf dry matter content is not an important driver of successional performance. More surprisingly, wood specific gravity turnover was lowest at the highest levels of taxonomic beta diversity, suggesting that the pairs of plots with the highest species turnover (*i.e.* young second-growth stands and old-growth stands) were dominated by species with similar wood specific gravity. Pioneers are known to have low wood specific gravity values, whereas shade-tolerant, late-successional species have high wood specific gravity (Woodcock 2000, van Gelder et al. 2006, Poorter et al. 2010). In my study area, early successional species dominate the young second-growth stands, and the old-growth stands contain a high abundance of canopy palms (Chapter 2). Both of these sets of species have low wood specific gravity values (Chapter 2). Unlike dicotyledonous trees, arborescent palms do not have a vascular cambium, and instead increase their mechanical strength through sustained cell expansion and by increasing the stiffness and strength of their stem tissue with age (Rich 1987). Palms are an important part of Neotropical plant communities (Guariguata et al. 1997, Svenning 1998, Marín-Spiotta et al. 2007, ter Steege et al. 2013), and functionally they seem to deviate from the dichotomous expectations of pioneers and shade-tolerant species.

Contrary to expectations, functional beta diversity was not related to stand basal area difference for any of the analyses except wood specific gravity, for which there was a decline in functional beta diversity with stand basal area difference (Fig. 3.3). Although unexpected, this pattern is consistent with the previous analysis demonstrating a decline in wood specific gravity diversity with increasing species beta diversity.

Across the successional gradient, only one trait, leaf toughness, demonstrated significantly higher functional turnover than expected based on differences in species composition. Using the same datasets here I found that community-level measures of leaf

toughness showed the strongest change along the successional gradient (Chapter 2). The pattern was driven primarily by the increasing abundance of palms in older second-growth forests and in old-growth forests, which have significantly tougher leaves than the other trees measured (Chapter 2). As plants with tougher leaves are better defended against generalist herbivores and physical damage (Coley 1983), the directional turnover observed here suggests that defensive properties are key leaf traits affecting species performance in successional tropical wet forests.

For the remaining functional traits, functional turnover across the successional gradient was no higher than expected based on species turnover, supporting a stochastic model of community assembly (Fig. 3.3). Several factors may explain why I did not see the expected successional patterns. First, all of the plots had closed canopies by the time I began the study (after at least 10 years of forest regrowth), and the environmental conditions may already have been relatively similar among stands. Light is the most limiting resource in wet tropical forests (Chazdon and Fetcher 1984), and light availability declines as second-growth forests develop (Nicotra et al. 1999, Denslow and Guzman G. 2000, Lebrija-Trejos et al. 2011). However, the average light availability of 15–20 year old forests in my study region was similar to old-growth forests (Montgomery and Chazdon 2001). In the relatively homogenous environmental conditions within an old-growth tropical forest, Swenson et al. (2012) also found lower than expected functional turnover. We must keep in mind, however, that the present species composition of the trees in these successional forests depends, in part, on past environmental conditions.

Another possible reason I did not find a successional pattern in functional turnover is because the species composition in my plots was relatively stable, as shown by the low species turnover within each of the study plots (Appendix 3, Fig. A3.3a), making it difficult to attribute

functional changes among forests to stand age or stand basal area (Appendix 3, Fig. A3.3b). Site-specific variability in the initial environmental conditions and/or species establishment patterns appear to have long-term impacts on the species composition in these study sites.

Finally, a high proportion of the species in these plots are common to both second-growth and old-growth forests. Taxonomic and functional beta diversity values are relatively low when there is high abundance of shared species among plots (Condit et al. 2002). When applying a multinomial model that classifies species into habitat classifications based on their relative abundance in second-growth and old-growth forests (Chazdon et al. 2011), I calculate that 22.4–54.6% of the relative abundance of each plot in each year was comprised of generalist species (also see Chapter 2). Many of these generalists are the same species, or at least in the same genus or family, as generalist species found throughout Amazonian forests (Pitman et al. 2001, ter Steege et al. 2013).

Functional beta diversity did show some significant patterns among some of the plots. Over 20% of the plot-pairs in the multivariate analysis and in three of the univariate analyses demonstrated significantly higher functional turnover than expected based on differences in species composition (Table 3.1). Additionally, 87–99% of the variation in functional beta diversity was explained by the random effect of plot-pair ($R^2_{\text{LMM(c)}} - R^2_{\text{LMM(m)}}$, Fig. 3.3), demonstrating that differences in species composition among plots was a strong and consistent driver of the functional beta diversity trends. Similarly, in a recent analysis of successional dynamics in stand structure across seven Neotropical field sites, stand identity explained far more of the variation in forest structure than stand age (Norden et al. *unpublished data*). Clearly, site-specific differences are driven by factors other than differences in stand age or basal area.

Individualistic relationships in functional beta diversity among pairs of plots may in fact demonstrate that both stochastic and deterministic forces influence community assembly. In complex environments such as tropical rainforest, multiple basins of attraction may be driving differences among forest stands (Vandermeer et al. 2004). Multiple stable equilibria are more probable in highly productive environments (Chase 2010), where the regional species pool is large, dispersal is limited, the environmental conditions are relatively benign, and the rates of disturbance are low (Chase 2003). In wet tropical forests, high rates of taxonomic beta diversity at intermediate scales (0.2–50 km) may be explained primarily by dispersal limitation and, to a lesser extent, habitat heterogeneity (Condit et al. 2002, Myers et al. 2013). However, in a study comparing the species composition among all trees > 5 cm DBH in six of my study plots, Norden et al. (2009) found that the dissimilarity among tree assemblages was independent from the spatial distance among plots, suggesting that dispersal limitation is unlikely to be a major factor explaining the variation taxonomic beta diversity in my study. Yet, priority effects are increasingly important in highly productive areas with large regional species pools—such as wet tropical forests—because a large proportion of the species pool can successfully inhabit these environments (Chase 2010). In this case, the species that arrive first can have a significant influence on the future community composition. For example, the timing of species arrival was found to have a large impact on community assembly in experimental plant communities (Kardol et al. 2013), and the effect was stronger with increasing soil fertility. These findings suggest that priority effects are a likely cause of the individualistic patterns in functional beta diversity among my study plots.

Although stochastic processes were the most influential factor of community assembly in my dataset, it is possible that deterministic processes would be more evident with the inclusion

of additional data. My sampling was limited to the most abundant canopy species in each plot, accounting for 81–98% of the abundance, but only 53–78% of the species present in each community in any given year (Appendix 3, Fig. A3.2). Although rare species contribute little to the community-weighted means from which functional beta diversity was calculated, the omission of the rare species from my analyses restricts the species pool and potentially the trait pool from which the null models were calculated. Moreover, although I measured functional traits for each species in each of the forest types where it was abundant, I was unable to explicitly incorporate intraspecific variation into the functional beta diversity analyses. Functional traits can vary as much within a species as among species (Messier et al. 2010). Intraspecific variation may reflect environmental differences (Albert et al. 2010), and can influence functional diversity metrics such as community-weighted means (Albert et al. 2012; Chapter 2). Differences in population-level mean trait values may also further decouple taxonomic and functional beta diversity, whereby functional beta diversity could increase at a faster pace than species beta diversity (Swenson et al. 2011). Thus, it is possible that I would have found a stronger influence of deterministic processes on community assembly if I had incorporated intraspecific variation and rare species into my analyses.

Conclusions

Analyses of functional beta diversity provide a useful metric to assess the mechanisms of community assembly, and they are only recently being applied for this purpose. To my knowledge, I provide the first analysis of functional beta diversity patterns along a long-term successional gradient in wet tropical forests. I show that although deterministic processes influence community assembly to some extent, unexplained variability among forest plots

suggests that stochasticity and uncertainty are the principal drivers of community assembly, at least for the dominant canopy species at this stage of succession (10–40 years of natural regeneration). These results may represent a best-case scenario of successional community assembly, because old-growth forests are still common in the landscape matrix. Future studies should test the generality of these results by applying similar methodology to other successional gradients that include both younger and older forests.

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Figure 3.1. A cartoon depicting the potential relationships between species and functional beta diversity among a set of communities. The gray area shows high functional beta diversity compared to species beta diversity, which would suggest that the species turnover among communities is comprised of species with functional niche divergence. The white area shows low functional beta diversity compared to species beta diversity, which demonstrates that species turnover occurs among species with similar functional traits, *i.e.* species with functional niche convergence. Under scenario 1, high species diversity is accompanied by high functional diversity, which is likely where environmental conditions vary among communities. The saturating relationship depicted in scenario 2 demonstrates limited functional turnover and thus functional redundancy, even among communities with high species turnover. In scenario 3 there is no relationship between taxonomic and functional beta diversity, suggesting that functional turnover is random, and not driven by inherent environmental differences among communities.

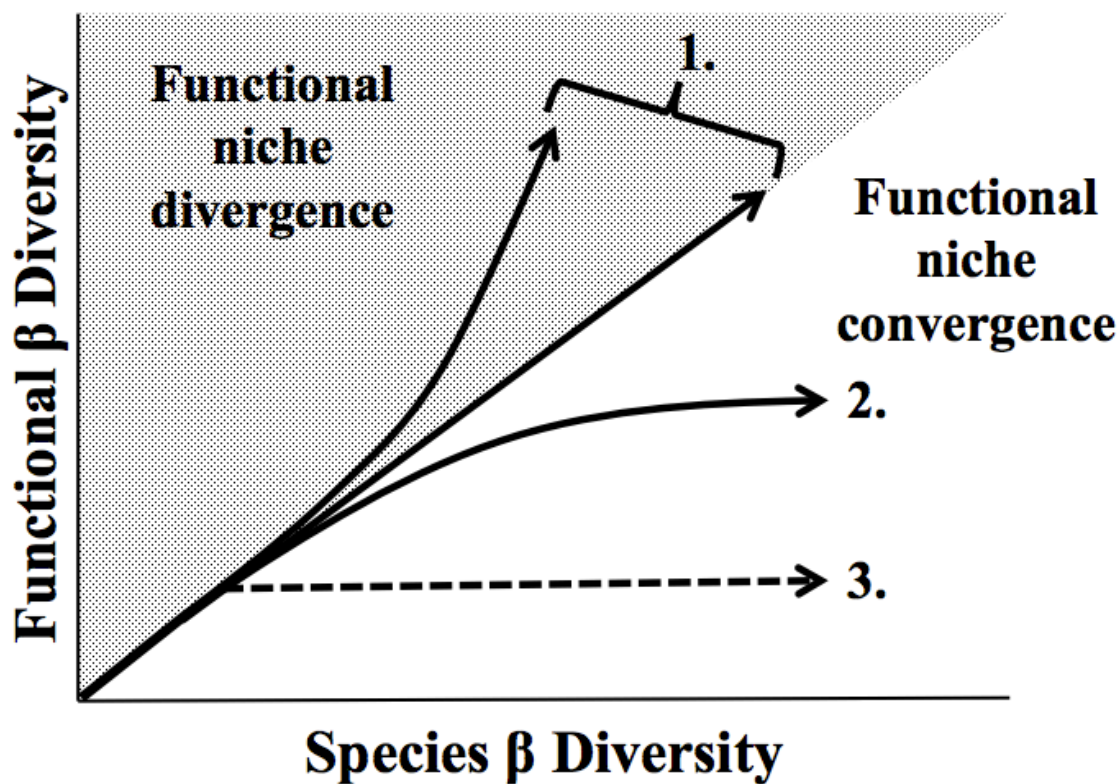
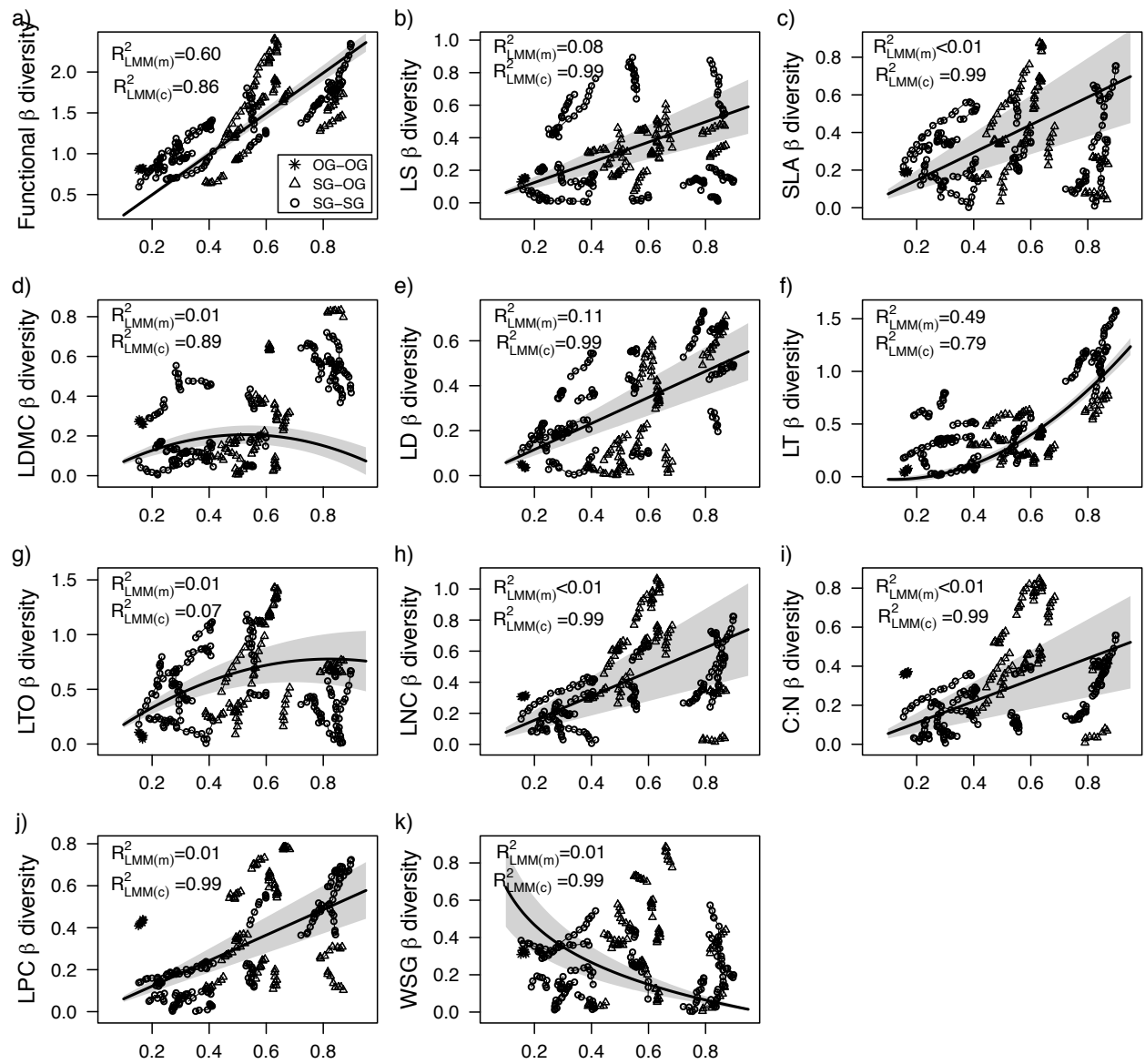


Figure 3.2. Relationship between species beta diversity and functional beta diversity among all plot-pairs for all sample years (1997-2012). Curves display the predicted trend of the best fitting mixed-effects model (linear, logarithmic, quadratic, and intercept only relationships were tested), and grey shading demonstrates 95% confidence intervals for the best-fit curve. The best-fit relationship between taxonomic and functional diversity was linear for the overall multivariate analysis (a), linear for leaf size (b), linear for specific leaf area (c), quadratic for leaf dry matter content (d), linear for leaf density (d), quadratic for leaf thickness (f), quadratic for leaf toughness (g), linear for leaf nitrogen content (h), linear for leaf carbon: nitrogen ratio (i), linear for leaf phosphorus content (j), and logarithmic for wood specific gravity (k). The marginal correlation coefficient, $R^2_{\text{LMM(m)}}$, considers the fit based on fixed effects, while the conditional correlation coefficient, $R^2_{\text{LMM(c)}}$ incorporates the variation explained by both the fixed and random effects. Symbols show relationship between different types of plot-pairs: OG = old-growth, SG = second-growth; key in panel (a) applies to all panels.



Species Beta Diversity (Morisita Horn Dissimilarity)

Figure 3.3. Standardized effect size functional diversity (SES FD) vs. basal area difference among plot-pairs for each sample year (1997-2012). Dashed grey lines indicate significance levels: points higher than 1.96 or lower than -1.96 demonstrate significantly higher or lower functional turnover than expected based on the null expectation. Black lines demonstrate predicted values from the best-fit linear mixed-effects models. Wood specific gravity (k) was the only trait for which basal area difference explained the relationship of SES FD; for the rest of the traits, intercept only models were a better fit. $R^2_{\text{LMM(m)}}$ on wood specific gravity panel demonstrates the proportion of variance in SES FD explained by the fixed effect (basal area difference). On all panels, the $R^2_{\text{LMM(c)}}$ demonstrates the proportion of variance explained by the best-fit mixed-effects model, incorporating the variation explained by both the fixed and random effect terms. Symbol key in panel (a) applies to all panels. Abbreviations as in Figure 3.2.

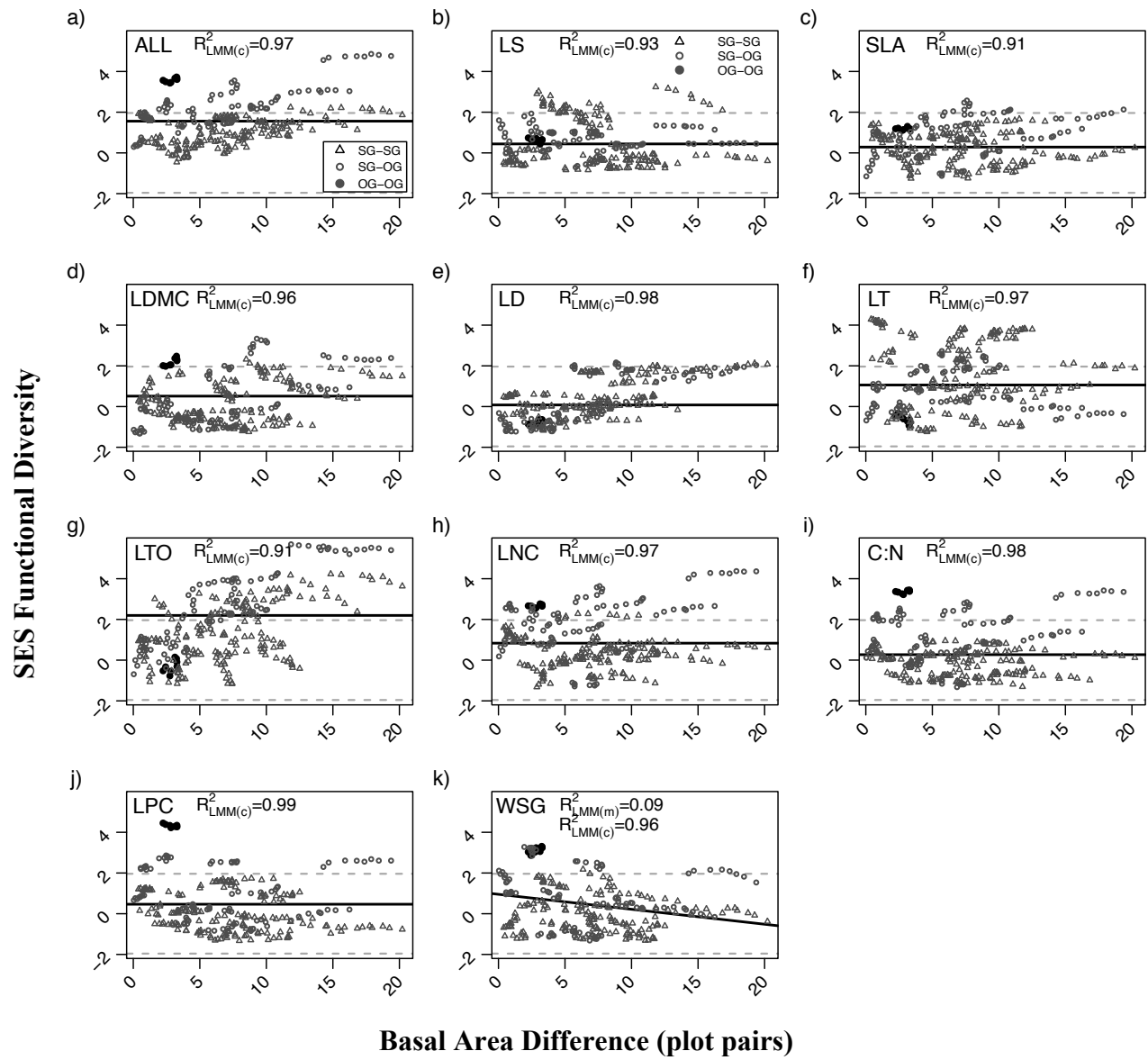
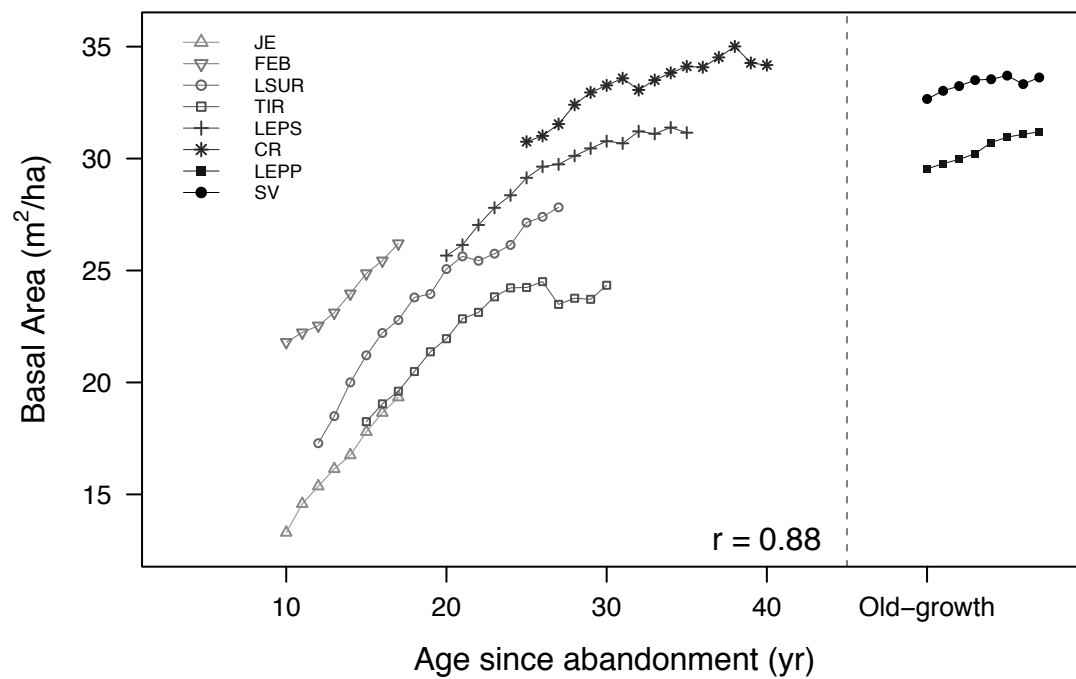


Table 3.1. Overall multivariate and univariate results of standardized effect size functional diversity (SES FD) along a successional gradient in Costa Rica. Percent of plot-pairs with significantly higher functional turnover than expected based on the null model expectations (SES FD > 1.96), and percent of plot-pairs that demonstrated functional turnover within the range of null expectations (-1.96 < SES FD < 1.96). No plot-pairs demonstrated significantly lower functional turnover than expected based on the null model (*i.e.* SES FD < -1.96). For each trait, there were 272 plot-pair combinations across 16 years of sampling.

Functional Trait	SES FD > 1.96	-1.96 < SES FD < 1.96
	(% of plot pairs)	(% of plot pairs)
Multivariate (all traits)	25.0	75.0
Leaf Size (cm ²)	14.0	86.0
Specific Leaf Area (mm ² mg ⁻¹)	4.8	95.2
Leaf Dry Matter Content (mg g ⁻¹)	10.3	89.7
Leaf Density [fresh] (mg mm ⁻³)	4.8	95.2
Leaf Thickness (mm)	33.5	66.5
Leaf Toughness (N mm ⁻¹)	43.8	56.2
Leaf Nitrogen Content (mg g ⁻¹)	23.9	76.1
Leaf Carbon: Nitrogen (ratio)	14.0	86.0
Leaf Phosphorus Content (mg g ⁻¹)	14.7	85.3
Wood Specific Gravity (unitless)	11.8	88.2

APPENDIX 3

Figure A3.1. Relationship of stand age to stand basal area for the eight 1-ha study plots. Pearson correlation coefficient for second-growth forests only is displayed (old-growth forests were not included because their age is unknown).



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Figure A3.2. Three metrics of alpha diversity among stems > 5 cm DBH in six second-growth and two old-growth forest stands in wet tropical forests of Costa Rica, across 16 years of sampling. Alpha diversity is compared among all 229 species sampled (a), and for the 94 canopy tree and palm species subset for which functional traits were measured.

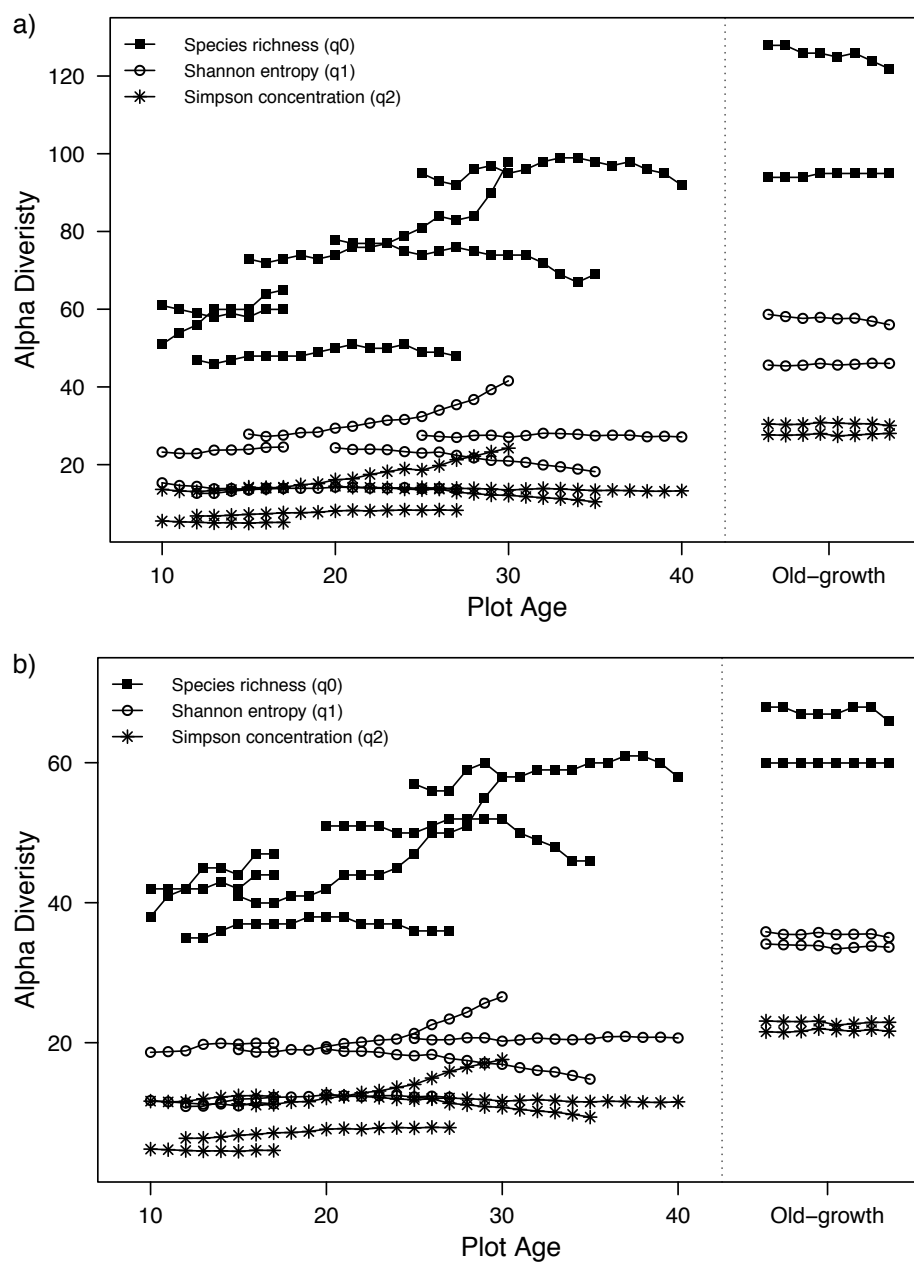


Figure A3.3. Comparisons of taxonomic beta diversity, based on Morisita-Horn dissimilarity, among six second-growth and two old-growth forest stands in wet tropical forests of Costa Rica over 16 years of sampling. Taxonomic beta diversity is calculated from the 94 species for which functional traits were measured, comprising > 80% of the abundance of each plot in each census year. A) NMDS of species composition over time. Circles are second-growth forest plots and squares are old-growth (OG) forest plots. Plot labels and ages ranges are shown near their cluster of points; plot descriptions can be found in Table A3.1. Shades of grey indicate the census year. B) Relationship of species beta diversity to basal area difference for each pair of plots. Dotted line demonstrates best-fit mixed effects model (intercept only). OG = old-growth forest; SG = second-growth forest. Points that are connected with lines demonstrate the same pair of plots over time (across each year of sampling). The conditional correlation coefficient, $R^2_{LMM(c)}$ incorporates the variation explained by both the fixed (intercept) and random (plot-pair) effects.

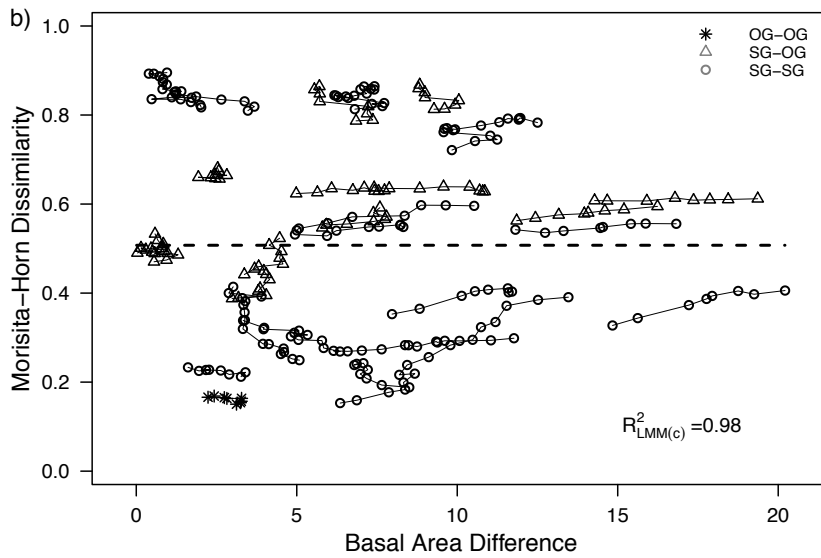
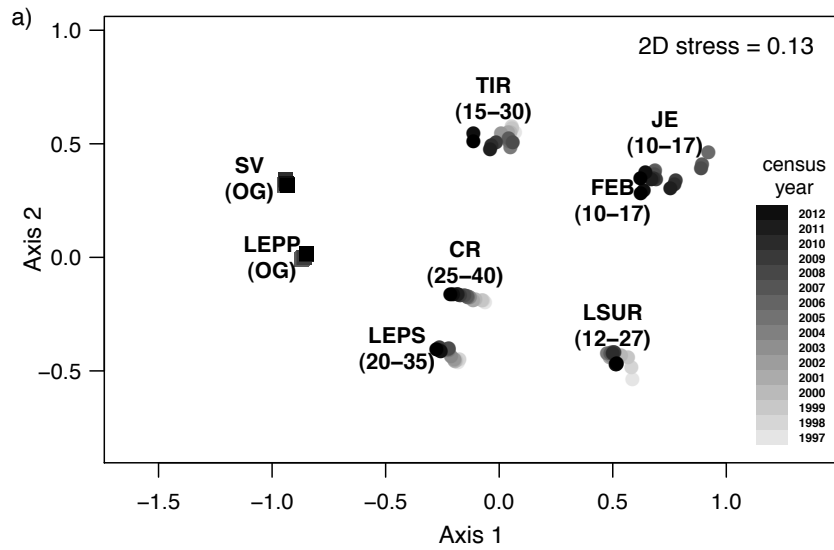


Table A3.1. Study sites, located in northeastern Costa Rica. Each stand is 1-ha. Vegetation dynamics have been monitored annually since initial census year.

Plot (abbreviation)	Year abandoned	Year census initiated	Forest ages for censuses	Location	Latitude, longitude	Surrounding landscape
Finca el Bejuco (FEB)	1995	2005	10-17	Chilamate	10.46°N, - 84.06°W	Pasture, old-growth, and second-growth forest
Juan Enriquez (JE)	1995	2005	10-17	Chilamate	10.46°N, - 84.07°W	Pasture, old-growth, and second-growth forest
Lindero Sur (LSUR)	1985	1997	12-27	La Selva	10.41°N, - 84.03°W	Old-growth and second- growth forest
Tirimbina (TIR)	1982	1997	15-30	Tirimbina	10.40°N, - 84.11°W	Pasture, plantations, and second-growth forest
Lindero El Peje secondary (LEPS)	1977	1997	20-35	La Selva	10.43°N, - 84.03°W	Old-growth and second- growth forest
Cuatro Rios (CR)	1972	1997	25-40	Tirimbina	10.39°N, - 84.13°W	Pasture, second-growth, and old-growth forest
Lindero El Peje primary (LEPP)	Old- growth	2005	Old-growth	La Selva	10.42°N, - 84.04°W	Old-growth forest
Selva Verde (SV)	Old- growth	2005	Old-growth	Chilamate	10.44°N, - 84.07°W	Pasture, old-growth, and second-growth forest

CHAPTER FOUR

USING LEAF FUNCTIONAL TRAITS TO REFINE ECOLOGICAL RESTORATION

TECHNIQUES IN A TROPICAL WET FOREST REGION

Abstract

Enrichment planting and direct planting are commonly used techniques for augmenting species diversity and environmental services during forest regeneration or restoration. My study provides guidance in selecting species for restoration activities, and is among the first to directly link tree species performance across different environmental conditions to easily measured plant functional traits. I used an experimental approach to test whether species' ecological characteristics influence seedling survival in three successional stages. I out-planted seedlings of three second-growth specialist and three old-growth specialist tree species into abandoned pastures, second-growth forests, and old-growth forests at La Selva Biological Station in Costa Rica. I measured seedling growth and survival for 17 months, and compared seedling performance to environmental conditions and plant functional traits. Compared to second-growth specialists, seedlings of old-growth specialists had traits commonly linked with resource-conservation, such as smaller, tougher leaves with lower specific leaf area and higher leaf dry matter content. In contrast, second-growth specialists had functional traits associated with fast rates of resource acquisition. Old-growth specialists had higher survival rates than second-growth specialists in secondary and old-growth forests, and equivalent survival rates in the pastures. Contrary to expectations, growth rates were similar among old-growth and second-growth specialists in all treatments. Differences in survival and growth were often related to leaf size, although other functional traits and light availability were also significant factors in some treatments. Across a suite of environmental conditions and potential restoration settings in wet tropical forest regions, old-growth specialists with resource-conservation traits have higher survival rates than second-growth specialists with fast-resource acquisition traits, and both types of specialists had equivalent growth rates. Selecting old-growth specialists for enrichment

planting and direct planting restoration would lead to more rapidly restored functional diversity, and would also directly benefit landowners due to higher old-growth specialist survival rates.

Introduction

Over half of the world's tropical forests have been degraded or destroyed by human activities, such as logging and conversion of forest to pasture or agricultural land (ITTO 2002). Once the disturbance subsides, forest recovery can occur naturally if viable seed sources are nearby and soil is not heavily damaged (Chazdon 2003, 2013b). Late-successional species, particularly those with large, animal-dispersed seeds, have slow rates of dispersal into early successional habitats (Martínez-Garza et al. 2009), and their establishment can be delayed even after decades of natural regeneration (Finegan 1996). Enrichment planting can accelerate the process of natural regeneration and promote the restoration of species composition, functional diversity, and ecosystem services (Martínez-Garza and Howe 2003, Piotto 2007, Rodrigues et al. 2009). On highly degraded lands, succession often fails to initiate, becomes arrested at early stages, or initiates a pathway to an alternative stable state (Folke et al. 2004, Lamb et al. 2005, Hirota et al. 2011, Chazdon 2013a). When natural regeneration is insufficient for recuperating biodiversity and ecosystem function, active restoration can be used to stimulate forest recovery, recuperate soil nutrients and vegetation structure, and provide habitat for seed dispersers (Hobbs et al. 2007, Chazdon 2008, Cole et al. 2011, Kettle 2012). Here, I performed a seedling enrichment experiment to test whether ecological characteristics of tropical tree species influence growth and survival across three successional stages.

The appropriate design of a reforestation project depends on the initial conditions of the land, the financial resources available, and the ultimate goals of the project. In the tropics, the majority of reforestation projects use exotic species and/or commercially valuable species (ex. *Pinus*, *Eucalyptus*, *Tectona*, or *Acacia*) to create monocultures or low diversity plantations (FAO 2005, Lamb et al. 2005, Chazdon 2008). Yet, the most successful techniques for recuperating

biodiversity and ecosystem services involve mixed forest stands that include a diverse suite of species from a variety of successional guilds, which aids in the recovery of structural complexity and native species composition (de la Peña-Domene et al. 2013). The ecological benefits of using mixed-species stands for restoration have been shown in tropical forests of Costa Rica (Leopold and Salazar 2008), Panama (Potvin and Gotelli 2008, Kunert et al. 2012), eastern Australia (Kanowski et al. 2003), the Atlantic rainforest of Brazil (Wuethrich 2007, Rodrigues et al. 2009), and Southern China (Ren et al. 2007). Planting native tree species in restoration supports local biodiversity of frugivores, pollinators, and herbivores (Kanowski et al. 2005, Grimbacher et al. 2007, Zamora and Montagnini 2007, Catterall et al. 2012). Moreover, native tree species are adapted to local biotic and abiotic conditions, do not become invasive, and eventually provide useful timber and non-timber forest resources that are often preferred by local people (Suárez et al. 2011).

Planting a diverse suite of species can be challenging for various reasons. Species selection for restoration is often limited to nursery-grown seedlings that are readily propagated and have commercial and/or agricultural value (Butterfield and Fisher 1994, Piotto 2007). Using native early successional species provides some initial forest structure, restores microclimatic conditions and encourages animal-mediated seed dispersal, but these native pioneers are often short-lived and have a high likelihood of arriving on their own (Finegan 1996, Martínez-Garza et al. 2009, Meli et al. 2013). Many old-growth forest species are able to colonize and survive in early successional habitats (Loik and Holl 1999, Martinez-Garza and Howe 2003, Martínez-Garza et al. 2005, van Breugel et al. 2007), but their rates of dispersal are often slow. The use of old-growth forest specialists in restoration has been limited because the germination requirements and performance capabilities in different habitats are unknown for most species

(Cole et al. 2011, Kettle 2012). Screening individual species for their ability to establish and survive under various restoration settings is time consuming and expensive. Around the globe, extensive field trials have been used to identify potential species for restoration projects at the site and regional level (*ex.* Carpenter et al. 2004, Shono et al. 2007, Celis and Jose 2011), but the use of these experimental species is limited to areas where they are native and common. Clearly, a more effective way to select native species for restoration projects is needed.

Species functional traits influence their ability to survive and grow in different habitats (Westoby et al. 2002, Díaz et al. 2004, Wright et al. 2004, Violle and Jiang 2009). We can better target appropriate species for restoration by relating easily measured functional traits to species performance in different restoration settings (Loik & Holl 1999; Martínez-Garza et al. 2005; Martínez-Garza, Bongers, & Poorter 2013). The continuum of plant functional traits extends from traits related to fast resource-acquisition to traits related to resource conservation. Trait states reflect investment tradeoffs between fast growth rates (fast-resource acquisition) and increased defense (resource conservation) (Lambers and Poorter 1992, Westoby et al. 2002, Wright et al. 2004). As light is one of the most limiting resources in tropical wet forests (Chazdon and Fetcher 1984), mature forest species tend to be shade-tolerant and consequently have functional traits associated with resource conservation. Although these traits allow mature forest specialists to live in the shaded understory for years, their growth strategy potentially limits their ability to increase photosynthetic and growth rates even when grown in high light conditions (Chazdon et al. 1996). Second-growth specialists, on the other hand, often lie on the fast resource-acquisition end of the functional trait continuum. They are able to grow quickly under high resource conditions, and can reduce their energetic costs under low resource conditions—but not to the same extent as resource-conserving species (Kitajima 1994, Chazdon

et al. 1996). My study is among the first to link functional traits to survival and growth across a range of successional habitats. I aim to provide concrete recommendations for species selection in active restoration and enrichment planting using a novel strategy that can be extended to other areas and habitats under consideration for restoration.

To assess the viability of using plant traits for selecting species in restoration, I related leaf functional traits of six native tree species commonly found in either old-growth or second-growth forests to seedling growth and survival under various environmental conditions in a 17-month field experiment at La Selva Biological Station in Costa Rica. Each species was out-planted into three different habitat treatments (pastures, 25–28 year old second-growth forests, and old-growth forests). I addressed the following questions: (1) Do functional traits differ between seedlings of second-growth and old-growth specialists? (2) How do survival and growth of second-growth and old-growth specialists compare among habitat treatments? (3) Which functional traits best explain growth and survival in each habitat? I expected that functional traits of second-growth specialists would be associated with fast resource-acquisition, conferring high maximum growth rates, whereas traits of old-growth specialists would reflect resource conservation strategies, favoring higher survival and longer leaf life span. Due to the tradeoff between growth in high light environments, and survival in low light conditions (Kitajima 1994), I expected old-growth specialists to survive better than second-growth specialists, especially in the shaded understory of second-growth and old-growth forests. I also predicted that second-growth specialists would show higher growth rates than old-growth specialists, especially within exposed pasture conditions. Finally, I expected that seedlings with resource conservation traits would demonstrate higher survival rates, whereas seedlings with fast resource acquisition traits would show higher growth rates.

Methods

Study Area

My experiment was conducted at La Selva Biological Station, in the Heredia province of Costa Rica. The climate of this region is classified as tropical lowland wet forest, with an annual temperature of 26.5°C and an annual rainfall of approximately 3900 mm (McDade et al. 1994). The vegetation at La Selva Biological Station is predominantly a mixture of old-growth forests and second-growth forests ranging from ~25-45 years old. The more recently acquired Peje Annex consists of several former pasture areas that were abandoned in 1987 and have patchy woody regeneration. Although second-growth forests have naturally regenerated in nearby abandoned pastures (Norden et al. 2009), these pastures are dominated by two fast-growing exotic grass species, *Panicum maximum* Jacq. and *Melinis minutiflora* P. Beauv., which were planted in 1956 (Russell et al. 2007) and appear to be inhibiting forest regrowth.

Experimental Design

To test the influence of environment on seedling performance, I planted seedlings of three second-growth specialists and three old-growth forest specialists into three habitat treatments: pasture, second-growth forest, and old-growth forest. Second-growth forest plots have been naturally regenerating for approximately 25–28 years following the abandonment of pasture. I set up three field plots for each treatment; plots were separated by 200–2300 m. Each plot was 15 m x 23 m and contained 7 rectangular quadrats (4 m x 5 m). Within each quadrat I planted two seedlings from each of the six species, with 1 m x 1 m spacing (total N = 756 seedlings). Individual placement was randomized within each quadrat. To reduce competition by grasses in the pasture plots, I hand cut the grass surrounding each seedling once a month.

Species specialist categories were defined by applying a multinomial model based on the estimated relative abundance of trees ≥ 10 cm diameter in a landscape-scale vegetation inventory dataset of successional and old-growth forests the same study region (Chazdon et al. 2011). I used the simple majority rule ($K = 0.5$; $P = 0.05$), where tree species are classified according to the forest type in which they have higher estimated relative abundance. The second-growth specialists included in this study were: *Cecropia insignis* Liebm. (Urticaceae), *Hampea appendiculata* (Donn. Sm.) Standl. (Malvaceae), and *Simarouba amara* Aubl. (Simaroubaceae); the old-growth specialists were: *Calophyllum brasiliense* Cambess. (Clusiaceae), *Protium panamense* (Rose) I.M. Johnst. (Burseraceae), and *Tetragastris panamensis* (Engler) O. Ktze. (Burseraceae). Hereafter, the species are referred to by their genus names. I selected these particular species because seeds or seedlings were available in the field when the study was initiated (April-May 2010), and because each species has either been used previously in reforestation or provides a provisioning ecosystem service. The three old-growth specialists are considered valuable for timber, and *Calophyllum* has been used in previous reforestation trials. *Cecropia* is often planted to reduce soil erosion, and both *Protium* and *Simarouba* have medicinal uses (Chazdon and Coe 1999). *Protium panamense* is classified as near threatened due to habitat loss (Mitré 2012).

Seedlings were either grown from seeds collected from 5–10 parents at La Selva Biological Station (*Cecropia*, *Simarouba*, *Calophyllum*, *Tetragastris*), or collected from the field as seedlings with seeds or cotyledons still attached (*Hampea*, *Protium*). Pre-germination treatments varied by species. *Cecropia* seeds were germinated on a moist paper towel in a petri dish. *Simarouba* fruits were soaked in water for 1–5 days, and the fruit was removed from the seed prior to germination in soil. *Tetragastris* seeds were separated from their fruit and soaked in

water for 1–2 days. The seeds were then scarified with sand or sandpaper, or nicked with a razor blade, and then soaked in water again for 0–6 hours before planting. No treatment was applied to *Calophyllum* seeds. Successful germination occurred within 1–45 days for all species.

All seedlings of the six species were grown together under shade-house conditions for ~3 months in plastic seedling growth bags containing a 1:1 mixture of sand and homogenized soil from their future home plot. Approximately 2 weeks prior to out-planting, seedlings were transferred to approximate field conditions (full light for pasture seedlings, partial shade for secondary forest seedlings, deep shade for old-growth forest seedlings). In October 2010 seedlings were out-planted into field plots, after removing growth bags but keeping potting soil intact to reduce transplant shock. Any individuals that died within the first week of transplanting were immediately replaced ($N = 39 / 756$). Initial plant height at the time of out-planting ranged from 0.5–38.5 cm (Fig. 4.1).

Plant and Functional Trait Measurements

Three times during the experiment, I measured plant height and stem basal diameter for all seedlings. Following these measurements, I harvested a subset of individuals to measure aboveground biomass (AGB) and functional traits. At the time of planting I harvested three individuals per species per plot ($N = 162$), after 6 months I harvested 6–46 individuals per species, depending on survival rates ($N = 188$), and after 17 months I harvested all remaining survivors ($N = 183$).

For two leaves of each harvested individual, I measured leaf size (cm^2 ; LS), specific leaf area ($\text{mm}^2 \text{mg}^{-1}$; SLA), leaf dry matter content (mg g^{-1} ; LDMC), leaf thickness (mm; LT), leaf toughness (N mm^{-1} ; LTO), and chlorophyll content (index; CCI). Leaf size affects energy and

water balance, where larger leaves have a higher capacity to absorb light, but also experience increased water stress (Cornelissen et al. 2003). Specific leaf area measures the amount of light capturing foliar area to biomass investment, and is often positively related to potential relative growth rate, but negatively related to the energetic cost of leaf construction, structural defense, and leaf lifespan (Coley and Barone 1996, Reich et al. 1999, Westoby et al. 2002, Wright et al. 2004). Specific leaf area is often negatively correlated with leaf dry matter content (LDMC), leaf thickness (LT), and leaf toughness (LTO) (Cornelissen et al. 2003, Díaz et al. 2004).

For the initial and the final harvest, I measured leaf nitrogen content (mg g^{-1} ; LNC), leaf phosphorus content (mg g^{-1} ; LPC), and leaf carbon content (mg g^{-1} ; LCC) for up to three individuals per species per plot, and also calculated leaf carbon: nitrogen ratio (g g^{-1} ; C:N). Leaf nitrogen content (LNC), leaf phosphorus content (LPC), and chlorophyll content are related to the amount of photosynthetic machinery and defensive compounds per unit leaf mass, and are positively correlated with carbon assimilation (Cornelissen et al. 2003, Wright et al. 2004). Wood specific gravity (unitless; WSG) was measured on the basal 2.5 cm section of stem (after removing bark) on up to three individuals per species per plot in the final harvest. Wood specific gravity (WSG) represents the biomass investment per unit wood volume, which influences water transport, structural support, and growth rate (Williamson and Wiemann 2010).

Functional trait measurements were made using standardized protocols (Cornelissen et al. 2003). To ensure equal leaf hydration across treatments and harvests, all leaves were placed in deionized water overnight at 4°C in total darkness prior to measurements. Leaf dry weight was measured after drying at 65°C for at least 72 hours. Leaf traits were measured on entire leaves, including the petiole, and rachis for the compound-leaved *Simarouba*. Petiole measurements were excluded from the leaf traits of *Cecropia* in the final harvest, when petioles comprised 14–

30% of the dry leaf mass, and 2–4% of the leaf area. Saplings of *Protium* and *Tetragastris* have both simple and compound leaves; to retain consistency among harvests, measurements on these species were performed either on entire simple leaves or single leaflets of compound leaves. Leaf toughness, or punch force, was measured using a leaf penetrometer (Chatillion 516-1000M push-pull gauge, Chatillion, USA), and dividing the Newtons of force by the punch perimeter. Leaf density (mg mm^{-3} ; LD) was calculated following Vile et al. (2005), where $\text{LD} = (\text{LT} * \text{LDMC} * \text{SLA})^{-1}$. Chlorophyll content was measured with a Chlorophyll Content Meter (CCM 200, Opti-Sciences Inc., USA). To calculate WSG, fresh wood volume was measured using water displacement method, and stem weight was measured after oven-drying at 105°C for at least 72 hours (Williamson and Wiemann 2010). All leaf nutrients (LNC, LPC, LCC, C:N) were analyzed by the University of Connecticut Soil Nutrient Analysis Laboratory. Nitrogen and carbon concentrations were measured on a VarioMax CN Analyzer (Elementar Analysensysteme GmbH, Hanau, Germany), and phosphorus concentrations were measured on a Ciros ICP-OES spectrometer (Spectro Analytical Instruments Inc., Kleve, Germany).

Plant Performance

I monitored plant survival in the field monthly for 17 months (November 2010 – March 2012). At the end of the experiment, 6 individuals that had green stems but no leaves were counted as dead.

I determined growth rates of individuals that survived until the end of the experiment by relating final plant height and stem basal diameter to initial measurements. Plant height was measured from the base of the stem to the shoot apex, and basal diameter was measured directly above the root-shoot junction. I used natural log transformed growth data for all analyses, and

added small constants to height (8 cm) and basal diameter (2 mm) growth for each individual to remove negative growth rates. Aboveground biomass was also calculated for all individuals that survived to 17 months, after drying all plant material at 65°C for at least 72 hours.

Microenvironmental Measurements

At the onset of the experiment, 5 soil samples per plot (0–20 cm depth) were collected and homogenized through a 2 mm sieve. Soil was analyzed for plant available nutrients (N, P, K, Ca, Mg, Fe, Mn, Cu, Zn, Al, B, pH) at the University of Connecticut Soil Nutrient Analysis Laboratory. Phosphorus results are not reported because all samples were below the detectable limit (<1.1 kg/ha).

In the center of each plot, air temperature and relative humidity were measured at half-hour intervals for approximately one year of the study (Oct 2010 – Oct 2011) using LogTag HAXO-8 Humidity and Temperature Data Loggers (LogTag Recorders Limited, New Zealand). Temperature and relative humidity data were summarized as daily maximum and minimum temperature (°C) and average relative humidity (%). Light availability was assessed at the planting site of each seedling two to three times during the study as the ratio of red to far-red light (R:FR), which most appropriately captures light availability in shaded understory conditions because of its high sensitivity at low diffuse light levels (Capers and Chazdon 2004). Measurements were conducted with a Skye SKR 110 (Skye Instruments Limited, Llandrindod Wells, UK) in overcast conditions. All individuals were measured in Oct 2010 and Apr-May 2011, and most individuals were measured again in Apr-May 2012 (excluding two pasture plots). The R:FR ratio was averaged across the two or three measurements for each individual (N = 756) to assess light availability in each treatment.

Statistical Analyses

Separately for the initial and final harvests, I assessed correlations among functional traits at the individual-level using Pearson correlation. I used ANOVA analyses, followed by post-hoc Tukey HSD, to compare light availability and soil nutrient concentrations among treatments, functional traits among species for the initial harvest, and differences in species functional traits among treatments in final harvest. In cases where there was heterogeneity of variance among treatments, I performed Welch's ANOVA (Welch 1951) followed by Games-Howell post-hoc tests. I used linear mixed-effect models to compare functional traits among species for the final harvest, with habitat treatment as a random effect. Soil nutrients were assessed individually, but I also evaluated multivariate soil nutrient conditions using a principal components analysis on standardized nutrient values (mean = 0, variance = 1). I analyzed the distributions of temperature and relative humidity among treatments using pairwise Kolmogorov-Smirnov two-sample tests, followed by Bonferroni correction. Some variables were log-transformed prior to analyses to improve normality (initial harvest: initial plant height, LS, SLA, LT, CCI, LPC; final harvest: LS, LT, CCI, LNC; soil nutrients: pH, Zn, Ca, K, and Fe).

I compared survival rates among species in each habitat treatment using Kaplan-Meier survival curves (Kaplan and Meier 1958). Individuals that were harvested at 6 months or at 17 months were considered right-censored because I could not account for the timing of natural death. Within each habitat treatment I compared Kaplan-Meier survival curves among species using log-rank tests (Harrington and Fleming 1982).

To determine which covariates influenced mortality risk, I ran Cox proportional-hazards models (Cox and Oakes 1984). For the entire dataset I tested mortality risk among specialist category (old-growth specialist or second-growth specialist), habitat treatment (pasture,

secondary forest, or old-growth forest), and the interaction between specialist category and habitat treatment. The model fit was improved by including random intersect terms for species and plot (ANOVA, $\chi^2=101.89$, $p<0.0001$). Due to the variation in initial plant height among species, I tested the effect of initial plant height on survival within each habitat, and included a random effect for species. Within each habitat treatment I then ran separate Cox proportional hazards models to assess how leaf traits influenced survival in various restoration settings. I compared mortality risk against light availability and all seedling functional traits measured at the time of planting (LS, SLA, LDMC, LT, LTO, LD, CCI, LNC, LPC, LCN). Because leaf traits for the initial harvest were measured only on a subset of individuals, I applied the plot-level species mean trait value to each individual. To account for the variation in initial seedling height, I also included a stratification term for initial plant height category (0.5–10 cm, 10.1–20 cm, or 20.1–38.5 cm), which fits a separate baseline hazard function for each stratum. For the Cox proportional hazards models in second-growth and old-growth forests I included random effects terms for plot, which improved model fit compared to a model with only fixed-effects (ANOVA, secondary forest: $\chi^2=4.97$, $p=0.026$; old-growth forest: $\chi^2=5.20$, $p=0.023$). For the pasture model I used a fixed-effects model because including random effects did not improve model fit (ANOVA, $\chi^2=0.0033$, $p=0.95$).

I used linear mixed-effects models to assess differences in height, basal diameter growth, and final aboveground biomass for the 183 individuals that survived to 17 months. I first compared overall growth among habitat treatments and specialist categories, and the interaction between them. Separately for each habitat treatment, I then assessed the influence of light availability and functional traits on growth. The growth models used leaf trait data from the final harvest (LS, SLA, LDMC, LT, LTO, LD, CCI), but did not include LPC, LNC, LCN, or WSG

because these measurements would have reduced the number of individuals by 97, 64, 64, and 78, respectively. For each of the growth analyses, I built linear mixed-effects models using the Restricted Maximum Likelihood (REML) estimation method (Venables and Ripley 2002), and used likelihood ratio tests to find the optimal random effects structure (Zuur et al. 2009). Leaf size, specific leaf area, leaf thickness, and chlorophyll content index were all right skewed, and thus were log-transformed prior to analysis.

I used model selection comparing all potential variations of each global Cox proportional hazards model and linear mixed-effects model to determine the most parsimonious fixed-effects structures. I based the model selection on the small sample size corrected version of Akaike's Information Criterion (AIC_c), and chose the simplest model within $\Delta 2$ AIC units of the model with the lowest AIC_c score (Burnham and Anderson 2002). For the mixed-effects models, model selection was done with maximum likelihood estimation, but the final model presented was re-run using the REML estimation method (Zuur et al. 2009).

All statistical analyses were performed in R (R Core Team 2013). I used the survival package (Therneau 2012) to conduct the Kaplan-Meier survival curves, log-rank tests, and the Cox proportional-hazards models. I ran the linear mixed-effects models in the lme4 package (Bates et al. 2013). Model selection was performed using the dredge function in the MuMIn package (Bartón 2013).

Results

Microenvironment

The environmental conditions among the three habitat treatments differed significantly (Table 4.1). Light availability and daily maximum temperature were highest in the pasture, and

lowest in the old-growth forests. Pasture plots experienced lower daily minimum temperatures and mean relative humidity compared to the forest plots, and higher daily maximum temperatures. The first axis of the principal component analysis (PC 1), explained 48% of the variation is soil nutrients among habitat treatments, and was significantly different among habitat treatments (Table 4.1). Many of the univariate soil nutrients also showed significant differences among habitat treatments (Table 4.1).

Functional Traits

Functional traits from the initial harvest varied within and across specialist categories, but, as expected, the traits of old-growth (OG) specialist species were generally more aligned with the resource conservation end of the functional trait continuum and the traits of second-growth (SG) specialist species were often aligned with fast-resource acquisition. As these traits were measured when all plants were grown in the same environmental conditions (*i.e.* the shade house), these results demonstrate intrinsic species-specific differences. As expected, OG specialists generally had lower LS, SLA, and LPC than SG specialists, and higher LDMC, and LTO (Fig. 4.1). Contrary to expectations, OG specialists had lower LT and higher CCI than SG specialists. There was no clear trend among specialist categories for LD, LNC, LCC, or C:N. Some of the functional traits from the initial harvest were strongly correlated (Appendix 4, Table A4.1).

Species functional traits from the final harvest varied across habitat treatments, with pasture individuals often exhibiting significantly different trait values than either forest treatment (Appendix 4, Table A4.2). As in the initial harvest, functional traits of the individuals surviving to the final harvest also showed significant differences among

specialist groups, with some distinctions among harvests. In the final harvest, OG specialists generally had lower LT and LNC, but higher LMDC, LTO, C:N, and WSG than SG specialists (Fig. 4.2). However, the traits of SG specialists *Cecropia* tended to be more aligned with the OG specialists. Leaf size, SLA, LD, CCI, LPC and LCC were generally similar among OG and SG specialists (Fig. 4.2). Some of the final harvest functional traits were strongly correlated (Appendix 4, Table A4.3).

Seedling survival

A flooding event in November 2011 caused high mortality in one of the pasture plots (>50% of all seedlings), and thus I excluded data from that plot in the survival analyses. Across all habitat treatments, the experimental seedlings in the remaining 8 plots had a 45.7% probability (± 0.023 SE) of surviving to 17 months. Overall seedling survival did not differ significantly among treatments (Cox proportional hazards model, $P > 0.05$), but survival rates varied both within and among specialist types (Table 4.2). Across all treatments, OG specialists had higher survival than SG specialists (Cox proportional hazards model, log hazard ratio estimate: 1.28 ± 0.57 SE, $P = 0.025$). SG specialists experienced significantly higher mortality risk compared to OG specialists in both the secondary and old-growth habitat treatments, but there was no significant difference among specialist categories in the pasture treatment (Fig. 4.3). Mortality risk decreased significantly with larger initial plant size in the second-growth forests (~10% lower risk per cm height, hazard ratio 0.90, $P = 0.0021$) and old-growth forests (~9% lower risk per cm height, hazard ratio 0.91, $P = 0.0018$), but not in the pasture ($P = 0.91$).

The functional traits that best explained variation in mortality risk differed by habitat (Fig. 4.4). The hazard ratios demonstrate multiplicative effects on hazard risk, where values >1

show increased mortality risk, and values <1 show decreased mortality risk. In most cases, fast resource-acquisition traits increased mortality risk, and resource-conservation traits reduced mortality risk. In the pasture, seedlings with higher leaf toughness (LTO) had a reduced risk of mortality ($\sim 100\%$ lower risk of mortality per Newton increase in LTO), and individuals with higher leaf nitrogen content had lower mortality risk ($\sim 43\%$ lower risk of mortality per mg increase in nitrogen; Fig. 4.4). Seedlings with larger leaves had a higher risk of mortality in the second-growth forests ($\sim 10\%$ higher risk per cm^2), but a reduced mortality risk in the old-growth forests ($\sim 5\%$ lower risk per cm^2 ; Fig. 4.4). Mortality risk was higher for seedlings in the old-growth forests with higher SLA ($\sim 9\%$ higher risk per unit SLA). Higher light availability significantly decreased mortality risk in the second-growth forests ($\sim 100\%$ lower risk per unit increase in R:FR; Fig. 4.4).

Seedling growth

I observed pronounced differences in height growth, basal diameter growth and final aboveground biomass among species and habitat treatments (Table 4.2). For the full mixed-effects model comparing growth among habitat treatments and specialist type, height and basal diameter growth and final aboveground biomass were higher in the pasture than in the secondary and old-growth forest plots ($P < 0.05$ for Tukey contrasts; Fig. 4.5 and Appendix 4, Fig. A4.1). Growth rates were similar between second-growth and old-growth forests for all three growth metrics (all Tukey contrasts $P > 0.05$). Across and within all habitat treatments, specialist categories did not differ significantly in growth (all Tukey contrasts $P > 0.05$). The random effect terms explained a large proportion of the variance of all habitat treatment growth models (Appendix 4, Table A4.4).

In the pasture plots, height growth was positively related to leaf toughness, log chlorophyll content, and log leaf size (Fig. 4.6a). Basal diameter growth and final aboveground biomass were also positively related to log chlorophyll content and log leaf size, as well as light availability (Appendix 4, Fig. A4.2a,b).

In second-growth forest plots, height growth and basal diameter growth were positively related to light availability, and log leaf size (Fig. 4.6b; Appendix 4, Fig. 4.2c). Leaf dry matter content was also included in the best-fit model for height growth, but was only marginally significant. Final aboveground biomass was positively related to leaf density, light availability, leaf toughness, log leaf thickness, and log leaf size (Appendix 4, Fig. A4.2d).

In old-growth forest plots, height growth was positively related to leaf toughness, log chlorophyll content, and log leaf size (Fig. 4.6c). Height growth was negatively related to leaf dry matter content, but the influence was close to zero (linear mixed model regression estimate = -0.004), and likely not ecologically significant. Basal diameter growth and aboveground biomass were both positively related to log leaf thickness and log leaf size (Appendix 4, Fig. A4.2e,f). Increased light availability also increased basal diameter growth (Appendix 4, Fig. A4.2e), and higher log chlorophyll content increased aboveground biomass (Appendix 4, Fig. A4.2f).

Discussion

The results of this study suggest that old-growth specialist tree species can be highly suitable for restoration, in both direct planting and enrichment planting scenarios. I did not observe the expected tradeoff between growth and survival among specialist types. Old-growth specialists survived better than second-growth specialists in secondary and old-growth forests, and equally well in the pasture. Yet growth-rates of both specialist types were equivalent in each

habitat treatment. Growth was higher in the pasture than in the forested habitats for both specialist types. Similarly, Shono et al. (2007) also found that, overall, late-successional species outperformed early-successional species in a reforestation planting trial comparing survival and growth of 45 native tree species in an open habitat in Singapore, and were thus more likely to be good or excellent candidates for restoration. In their study, as in mine, survival and growth varied by species, suggesting further species-specific information is needed to predict which species will perform best.

My results confirm the importance of plant functional traits in determining survival and growth, and suggest that functional traits can provide valuable insight into the species selection process. As expected, second-growth specialist traits were largely associated with the fast resource-acquisition strategy, whereas old-growth specialist traits align with the resource conservation strategy. Also as predicted, many of the traits that increased survival were related to resource conservation. For example, in the pasture plots, individuals with higher leaf toughness were at a reduced risk of mortality. In the second-growth and old-growth forests, individuals with smaller leaves and lower SLA, respectively, had higher survival. Resource conservation traits demonstrate higher structural investment and increased defense, and are positively related to leaf lifespan (Westoby et al. 2002, Wright et al. 2004). At the seedling stage, the ability to protect the few leaves a plant has can determine the difference between life and death. Although I did not directly assess herbivory rates, herbivory has been shown to reduce seedling survival and growth in other studies (Benítez-Malvido et al. 2005, Massad et al. 2011).

Growth, on the other hand, was primarily related to fast resource-acquisition traits, particularly those related to photosynthesis. In some cases fast resource-acquisition traits also increased survival rates. In all environments, individuals with larger leaves grew more, and in

old-growth forests larger-leaved individuals also survived better. In both pasture and old-growth forests, individuals with higher chlorophyll content grew more, and survival was positively related to leaf nitrogen content in the pasture. Leaf size, chlorophyll content, and leaf nitrogen content are related to photosynthetic rates, and higher values of all three traits are related to the fast-resource acquisition strategy. Leaf size controls light capture ability, and chlorophyll content and leaf nitrogen content relate to the amount of photosynthetic machinery in a leaf (Cornelissen et al. 2003, Wright et al. 2004). In closed canopy tropical forests light availability is often less than 2% of full sun (Chazdon and Fetcher 1984, Clark et al. 1996, Nicotra et al. 1999). Individuals with larger leaves, higher chlorophyll content, and/or higher leaf nitrogen content are able to better capitalize on the limiting light resource, can grow faster, and in some cases have higher survival rates.

In fact, the light environment was the most important factor influencing seedling survival and growth in the second-growth forests. Higher light availability also led to increased basal diameter growth and higher final aboveground biomass in the pasture and in the old-growth forests. Seedling survival and growth have been shown to increase with higher light availability for other species my same study region (Kobe 1999, Montgomery and Chazdon 2002, Iriarte and Chazdon 2005) and in the Bolivian Amazon (Peña-Claros et al. 2002).

Contrary to expectations, individuals with tougher leaves grew taller in the pasture and old-growth forests, and demonstrated higher final aboveground biomass in the secondary forests. Tough leaves have high leaf fiber content, which reduces leaf damage by generalist herbivores and increases leaf lifespan (Coley and Barone 1996). With extreme herbivore pressure, leaf toughness could lead to higher growth rates simply by diminishing the amount of leaf tissue lost to herbivores, and thus increasing leaf area at the whole-plant level. In a 4-year reforestation

experiment in the Atlantic rainforest of Brazil, Massad et al. (2011) found that seedlings with high herbivory rates had reduced growth rates. Accordingly, plants with increased defenses, such as tougher leaves with more saponins, experienced reduced herbivory. In my study, two of the second-growth specialists had the lowest leaf toughness at the end of the experiment (*Hampea* and *Simarouba*; Fig. 4.2), and both species experienced relatively low survival (Table 4.2). Furthermore, many of the *Simarouba* individuals in the pasture were attacked by moth larvae from the Yponomeutidae family (*Atteva aurea*) (Boukili, *pers. obs.*). This species-specific herbivory caused significant leaf loss, which influenced mortality and resulted in large variation in growth among the *Simarouba* individuals in the pasture (Table 4.2).

Although *Cecropia* seedlings grew well in the pasture, individuals in the forests experienced complete mortality within 9 months after planting. *Cecropia* is known to be a short-lived, light-demanding pioneer. Although *Cecropia insignis* is able to survive well in canopy gaps (Dalling et al. 2009) my study confirms its inability to survive in the shaded forest understory, and thus should not be used for enrichment planting restoration.

Other research studies comparing seedling performance of early and late successional species have found disparate results. In a recent study in Veracruz, Mexico, Martínez-Garza et al. (2013) compared growth and survival of nine short-lived pioneer and 18 non-pioneer species in pasture plots. In contrast to my results, they found higher growth and survival of pioneers compared to non-pioneers, although several non-pioneers performed nearly as well (Martínez-Garza et al. 2013). Of the second-growth specialists in my study, the only short-lived pioneer species, *Cecropia*, grew significantly more than any other species in the pasture, and was also among the best survivors in the pasture. Had I included more short-lived pioneer species in my study, my findings for the pasture may have changed. Similarly to my study, Martínez-Garza et

al. (2013) found that, among the non-pioneer species, survival in the pasture was positively correlated with leaf dry matter content, a resource-conservation trait. In contrast to my study, Román-Dañobeytia et al. (2012) found that late successional species had very poor survival and growth in the Chiapas region of southern Mexico, whereas early successional species had the highest growth and survival. However, they also found important differences in growth and survival in different sites, suggesting that initial site conditions and land-use history may influence the success of old-growth specialists.

Although my restoration experiment only lasted 17 months, relative species performance in other restoration experiments was constant after 12 months (Martínez-Garza et al. 2013), suggesting that my conclusions would apply to longer time frames. Furthermore, seedlings are particularly susceptible to a wide range of biotic and abiotic mortality risks (Harper 1977). Thus the seedling stage represents one of the most important ecological filters in forest restoration. I have shown that plant traits and environmental conditions influence survival during this vulnerable life stage. My results further suggest that the lack of old-growth specialists in recently abandoned lands and in early secondary forests (Finegan 1996, van Breugel et al. 2007, Martínez-Garza et al. 2009) is due to dispersal limitation or germination characteristics (Holl 1999), and not because these species are unable to survive in those conditions.

In conclusion, my results indicate that successful restoration outcomes may be achieved by planting old-growth specialists in both direct planting and enrichment planting scenarios of wet tropical forest regions. In my study, old-growth specialists showed equivalent growth rates and higher survival rates than second-growth specialists. Because of higher survival rates, planting old-growth specialists would reduce future planting costs to landowners, while also providing an ecological benefit by planting species that are unlikely to arrive on their own

(Finegan 1996). By selecting species based on their functional traits, restoration practitioners can also increase the likelihood of the planted seedlings surviving and growing more quickly. In the wet tropical forests of Costa Rica, focusing species selection on old-growth specialists with large, tough leaves, and high chlorophyll content will have the best results for plant performance. Moreover, increasing the light availability for planted seedlings will lead to higher growth and survival rates. I further recommend planting larger seedlings to increase survival rates, particularly for enrichment planting. My study provides a first step in understanding how plant functional traits can be used to predict seedling survival under a variety of restoration regimes. To assess the generality of these patterns, future experiments should be performed with more species, in other regions, and using additional restoration approaches (ex. direct seeding). Performing these experiments at longer time scales would provide further information about the long-term sustainability of the restored forests.

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Figure 4.1. Species leaf functional traits and plant height from the initial harvest, prior to out-planting. Abbreviations are: leaf size (LS), specific leaf area (SLA), leaf dry matter content (LDMC), leaf density (LD), leaf thickness (LT), leaf toughness (LTO), chlorophyll content index (CCI), leaf nitrogen content (LNC), leaf carbon content (LCC), leaf carbon: nitrogen ratio (C:N), leaf phosphorous content (LPC). *Cecropia*, *Hampea*, and *Simarouba* (white boxes) are second-growth specialists; *Calophyllum*, *Protium*, and *Tetragastris* (grey boxes) are old-growth specialists. For each trait, different letters indicate significant differences among species ($P < 0.05$). Original data are shown, although LS, SLA, LT, CCI, LPC, and height were log-transformed prior to analyses.

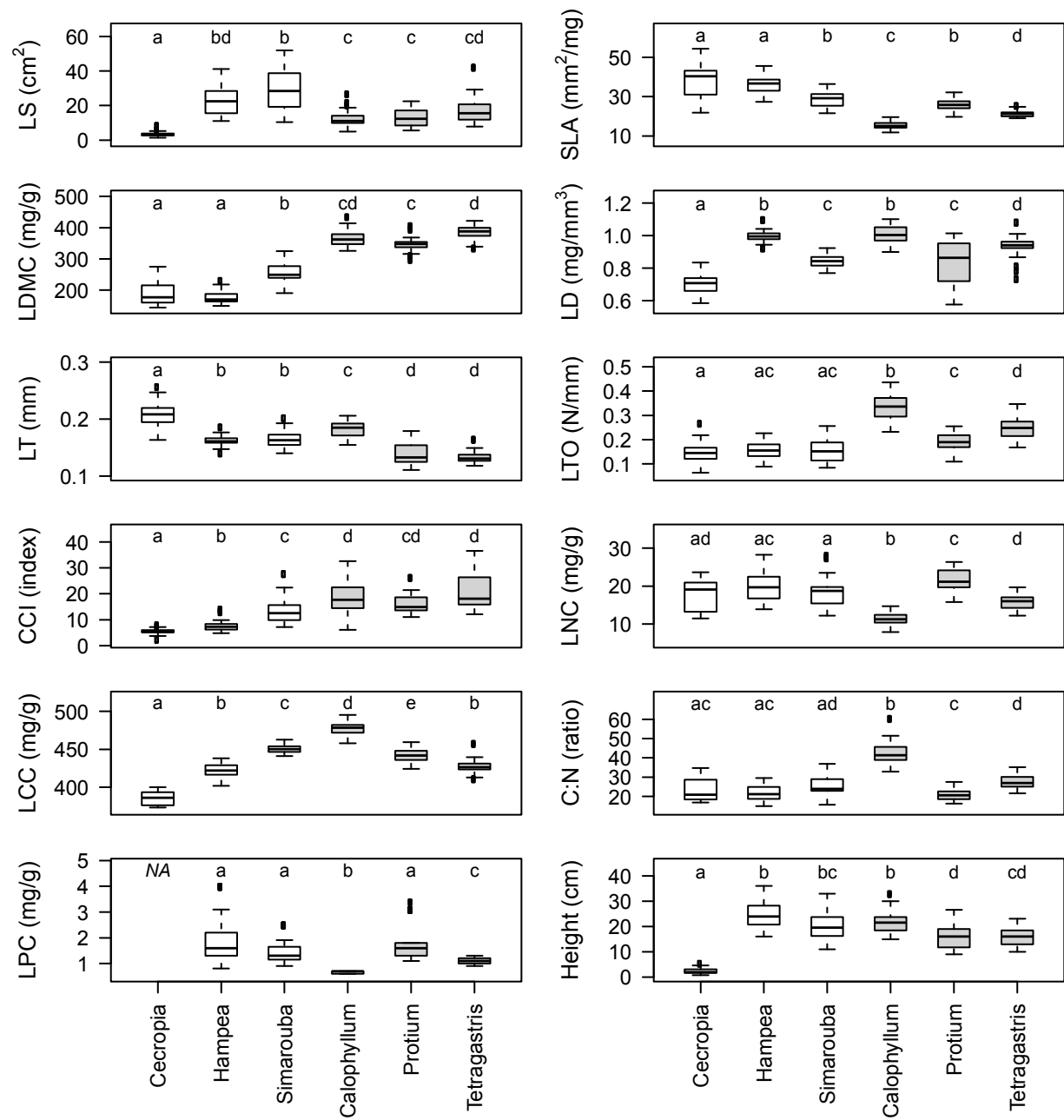


Figure 4.2. Functional traits (mean \pm SE), by species, of all individuals from the final harvest (17 months). *Cecropia*, *Hampea*, and *Simarouba* (white circles) are second-growth specialists; *Calophyllum*, *Protium*, and *Tetragastris* (black circles) are old-growth specialists. For each trait, different letters indicate significant differences among species ($P < 0.05$). WSG = wood specific gravity; all other trait abbreviations are described in Figure 4.1.

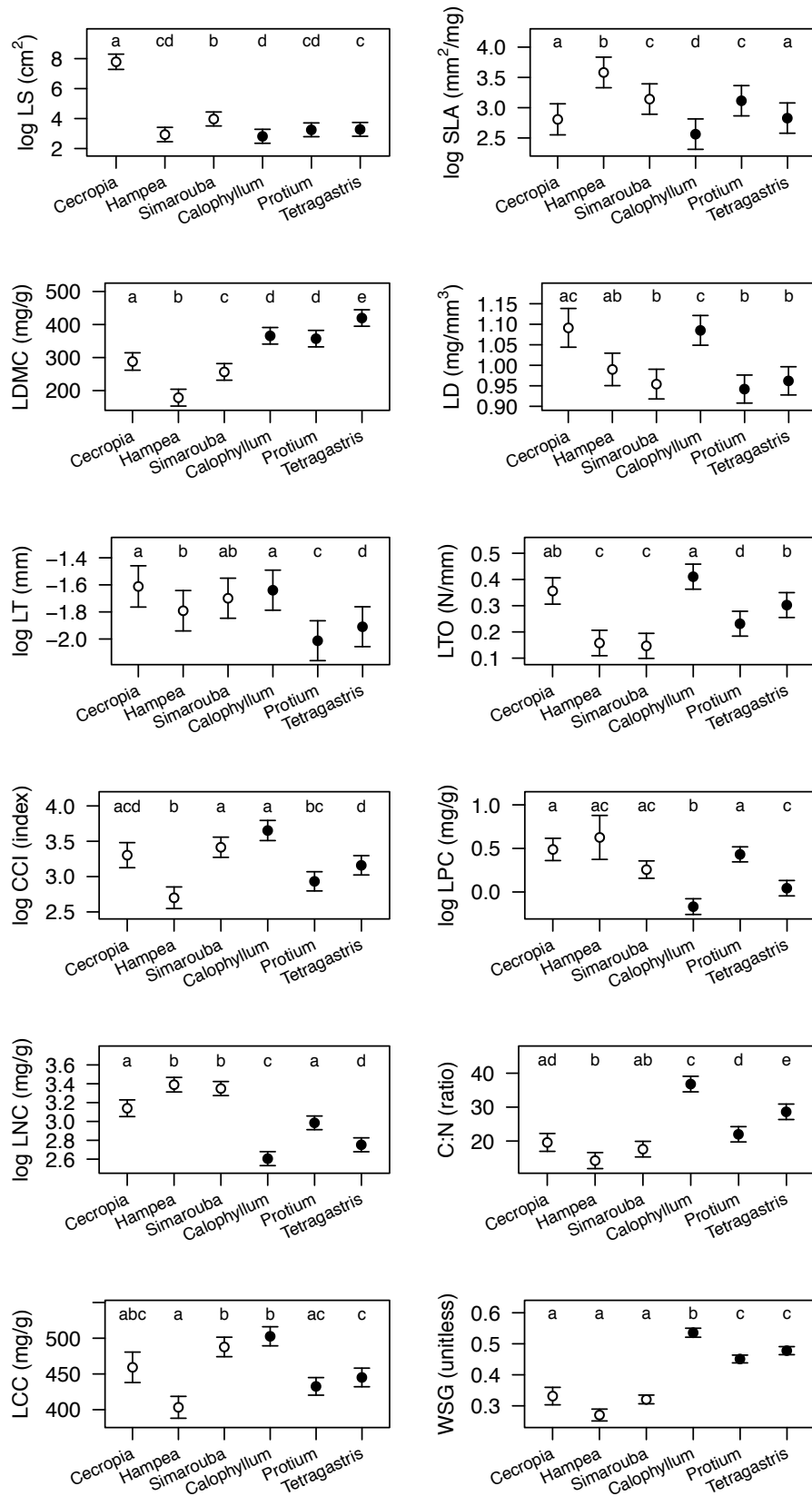


Figure 4.3. Hazard ratio results from Cox proportional hazards model, demonstrating the relative hazard of old-growth (OG) specialists compared to second-growth (SG) specialists in three habitat treatments. Horizontal dotted line shows equivalent hazard among the two specialist categories, and black points indicate significantly reduced mortality risk for OG specialists compared to SG specialists. Vertical lines are $\pm 95\%$ confidence intervals.

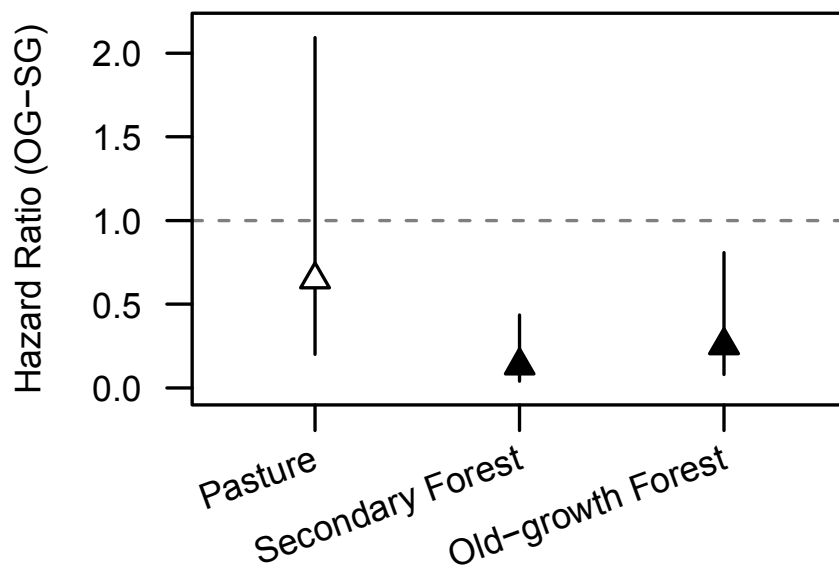
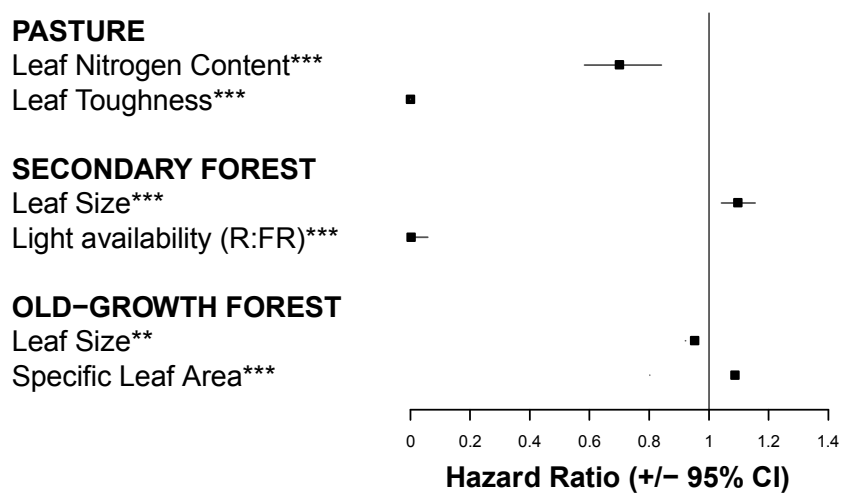


Figure 4.4. Cox proportional hazards models relating survival to traits and environmental conditions in three habitat treatments. Hazards ratios > 1 indicate a higher likelihood of mortality for positive values of the covariate; hazards ratios < 1 indicate higher probability of survival for positive values of the covariate. The increase or decrease in mortality risk for each covariate is proportional to the difference between the hazard ratio and 1. *** $P < 0.001$, ** $P < 0.01$.



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Figure 4.5. Least square mean log height growth of second-growth and old-growth specialists in three habitat treatments. Individuals in the pasture grew significantly more than individuals in either forest type, and there are no significant differences among specialist groups in any habitat treatment. Vertical lines are $\pm 95\%$ confidence intervals.

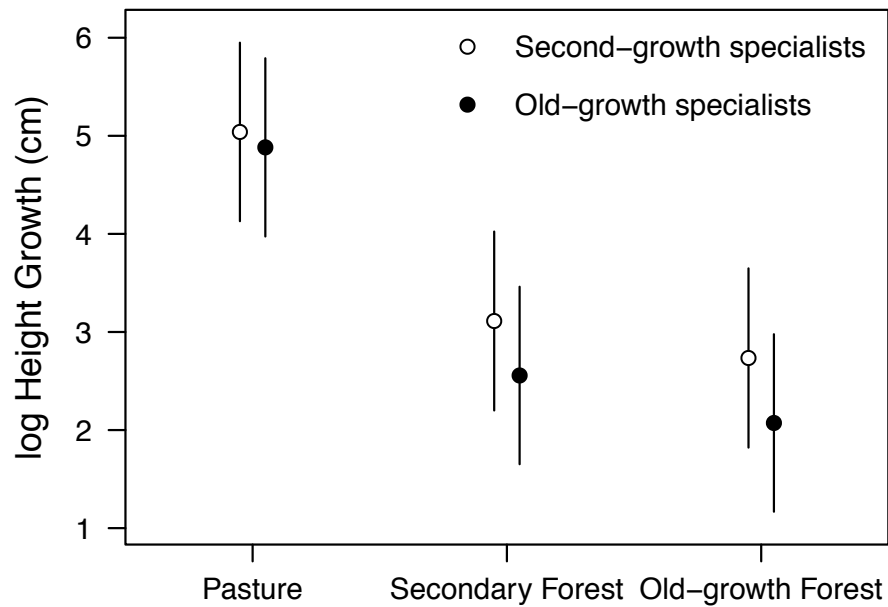


Figure 4.6. Regression estimates for mixed-effects models relating traits to height growth in each of the three habitat treatments. Covariates of the best-fit models are shown for (a) pasture plots, (b) second-growth forest plots and (c) old-growth forest plots. Predictor traits include leaf toughness (LTO), chlorophyll content (CCI), leaf size (LS), light availability (R:FR), and leaf dry matter content (LDMC). Thick vertical bars demonstrate ± 1 standard deviation; thin vertical bars demonstrate 95% confidence intervals. Symbols next to each factor demonstrate Markov chain Monte-Carlo probability estimates, $***P<0.001$, $**P<0.01$, $^{\wedge}P<0.1$.

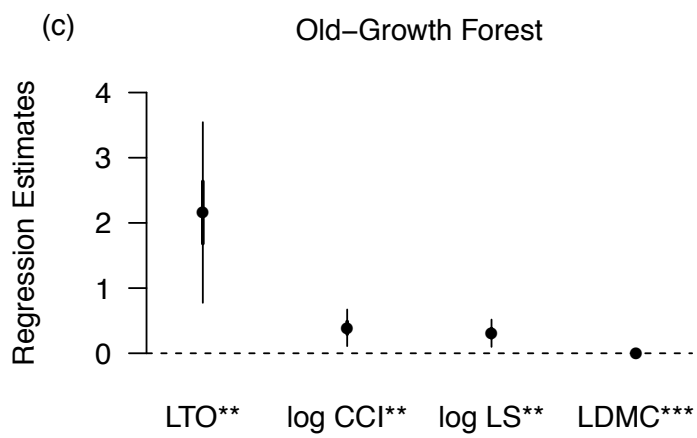
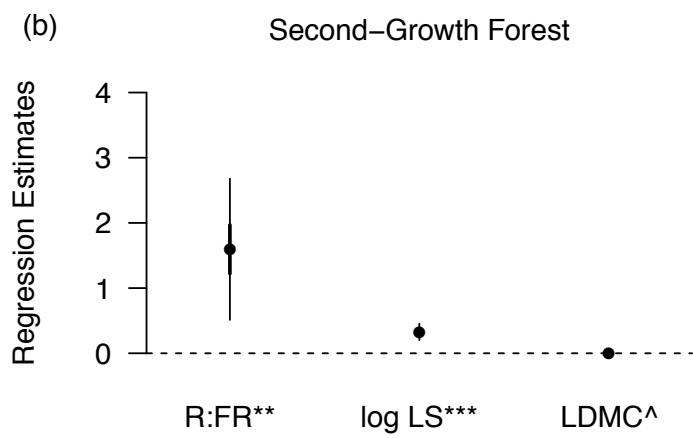
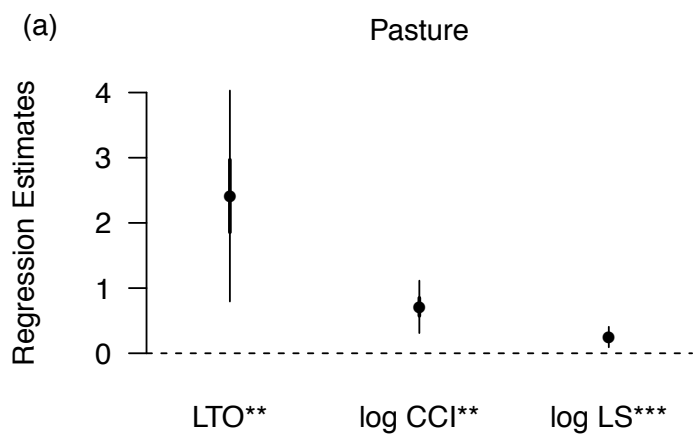


Table 4.1. Environmental differences by habitat treatment, average value \pm SE. Different letters demonstrate significant differences among plot types at the $\alpha=0.05$ level. Original data for all variables are shown, however pH, Zn, Ca, K, and Fe were log-transformed prior to analyses. *P*-values in bold demonstrate significant differences among plots.

ANOVA models

	Pasture	Secondary Forest	Old-growth Forest	F (df)	<i>P</i> -value
Light Availability					
Red: Far Red	1.07 \square 0.003 a	0.38 \pm 0.005 b	0.35 \pm 0.005 c	14710 (2, 753)	<0.0001
Soil Nutrients					
Principal Component 1 (scores) †	-0.16 \square 0.49 a	-2.5 \pm 0.39 b	2.69 \pm 0.20 c	73.2 (2, 24.3)	<0.0001
Nitrogen (%) †	0.56 \square 0.01 a	0.50 \pm 0.02 b	0.54 \pm 0.02 ab	3.9 (2, 27.5)	0.03
Potassium (kg ha ⁻¹) †	217.74 \square 18.37 a	404.10 \pm 51.20 b	163.87 \pm 5.32 c	21.0 (2, 21.5)	<0.0001
Calcium (kg ha ⁻¹) †	335.06 \square 43.37 a	1590.49 \pm 244.06 b	228.13 \pm 7.07 a	56.4 (2, 20.2)	<0.0001
Magnesium (kg ha ⁻¹) †	226.56 \square 31.90 a	387.67 \pm 33.61 b	144.29 \pm 5.11 c	53.6 (2, 21.7)	<0.0001
Iron (mg kg ⁻¹) †	22.98 \square 3.34 a	5.05 \pm 0.77 b	35.56 \pm 0.62 c	78.5 (2, 19.1)	<0.0001
Manganese (mg kg ⁻¹) †	25.35 \square 4.25 a	23.02 \pm 2.76 a	22.00 \pm 0.74 a	0.34 (2, 20.4)	0.71
Copper (mg kg ⁻¹) †	1.01 \square 0.11 a	0.97 \pm 0.12 ab	0.68 \pm 0.02 b	6.5 (2, 20.2)	0.006
Zinc (mg kg ⁻¹)	2.84 \square 1.03 a	2.13 \pm 0.49 a	1.57 \pm 0.22 a	0.6 (2, 42)	0.58
Aluminum (mg kg ⁻¹) †	208.0 \square 6.6 a	157.4 \pm 10.7 b	307.5 \pm 3.5 c	151.6 (2, 23.8)	<0.0001
Boron (mg kg ⁻¹)	0.03 \square 0.02 a	0.12 \pm 0.01 b	0.11 \pm 0.01 b	8.39 (2, 42)	0.0009
pH	4.2 \square 0.04 a	4.8 \pm 0.07 b	3.82 \pm 0.03 c	115.5 (2, 42)	<0.0001

Kolmogorov-Smirnov Models

	Pasture (P)	Secondary (S)	Old-growth (O)	D ₁₀₀₈ P-S	D ₁₀₀₇ P-O	D ₁₀₀₇ S-O
Air Temperature (°C)						
Daily Maximum	39.00 \square 0.18 a	27.67 \pm 0.09 b	26.94 \pm 0.07 c	0.13 (P<0.0001)	0.83 (P<0.0001)	0.68 (P<0.0001)
Daily Minimum	20.40 \square 0.05 a	21.66 \pm 0.04 b	21.69 \pm 0.04 b	0.39 (P<0.0001)	0.38 (P<0.0001)	0.04 (P=0.4108)
Relative Humidity (%)						
Daily Mean	89.71 \square 0.21 a	98.63 \pm 0.07 b	98.88 \pm 0.06 b	0.65 (P<0.0001)	0.69 (P<0.0001)	0.06 (P=0.0808)

† Variables assessed using Welch's ANOVA and Games-Howell post-hoc tests; all other ANOVA analyses used Tukey HSD post-hoc tests

Table 4.2. Survival and mean growth rates by species and plot type 17 months after planting. Number of survivors (n), percent survival (Surv), height growth (HG), basal diameter growth (BDG), and aboveground biomass (AGB) \pm SE are shown for each species in each habitat type. Different letters indicate significant differences ($P < 0.05$) among species in each habitat treatment. Significance tests for survival were based on log-rank tests of Kaplan-Meier survival curves. Significance tests for growth rates (HG, BDG, and AGB) were performed on log-transformed values, although original data are shown.

Species	Pasture					Secondary Forest					Old-Growth Forest				
	n	Surv (%)	HG (cm)	BDG (mm)	AGB (g)	n	Surv (%)	HG (cm)	BDG (mm)	AGB (g)	n	Surv (%)	HG (cm)	BDG (mm)	AGB (g)
<i>Cecropia insignis</i>	10	53.6 ab	502.1 \pm 79.4 a	103.6 \pm 16.7 a	7649.3 \pm 1730.8 a	0	0 c	--	--	--	0	0 c	--	--	--
<i>Hampea appendiculata</i>	2	7.1 c	13.0 \pm 1.5 d	5.1 \pm 2.9 d	4.8 \pm 3.2 c	14	57.1 ab	13.5 \pm 7.9 a	1.1 \pm 0.7 a	1.7 \pm 1.0 b	3	11.8 b	5.5 \pm 2.6 ab	0.6 \pm 0.4 a	0.8 \pm 0.1 ab
<i>Simarouba amara</i>	4 [#]	19.0 bc	147.9 \pm 24.6 bc	36.0 \pm 4.3 b	517.5 \pm 136.7 b	9	37.5 b	7.0 \pm 1.1 a	0.8 \pm 0.3 a	1.3 \pm 0.2 ab	15	63.7 a	4.2 \pm 1.5 a	0.4 \pm 0.3 a	1.3 \pm 0.3 a
<i>Calophyllum brasiliense</i>	4	27.1 b	126.2 \pm 28.6 bc	14.6 \pm 3.4 bcd	136.7 \pm 73.6 bc	14	65.0 a	6.1 \pm 1.0 a	0.4 \pm 0.2 a	1.5 \pm 0.1 a	14	60.3 a	3.2 \pm 0.7 a	-0.03 \pm 0.1 a	1.0 \pm 0.1 a
<i>Protium panamense</i>	14 [#]	83.7 a	185.8 \pm 19.4 b	30.6 \pm 3.0 bc	524.6 \pm 107.4 b	17	81.0 a	5.6 \pm 0.7 a	0.5 \pm 0.1 a	0.7 \pm 0.1 b	14	58.3 a	0.1 \pm 1.0 ab	0.2 \pm 0.2 a	0.6 \pm 0.08 b
<i>Tetragastris panamensis</i>	10	49.4 abc	75.7 \pm 14.3 c	15.9 \pm 2.1 cd	104.4 \pm 31.7 bc	16	68.6 ab	4.2 \pm 0.7 a	0.6 \pm 0.2 a	1.1 \pm 0.2 ab	19	71.4 ab	-1.33 \pm 0.5 b	0.2 \pm 0.1 a	0.6 \pm 0.05 b

[#]Sample size for growth (HG, BDG, and AGB) included 2 additional individuals from 3rd pasture plot, which was not included in survival analyses due to high mortality from a flooding event. The 4 surviving individuals from that plot (2 *Simarouba* and 2 *Protium*) were included in growth analyses.

APPENDIX 4

Figure A4.1. Least square mean log basal diameter growth (a) and log final aboveground biomass (b) of second-growth and old-growth specialists in three habitat treatments. Individuals in the pasture grew significantly more than individuals in either forest type, and there are no significant differences among specialist groups in any habitat treatment. Vertical lines are $\pm 95\%$ confidence intervals.

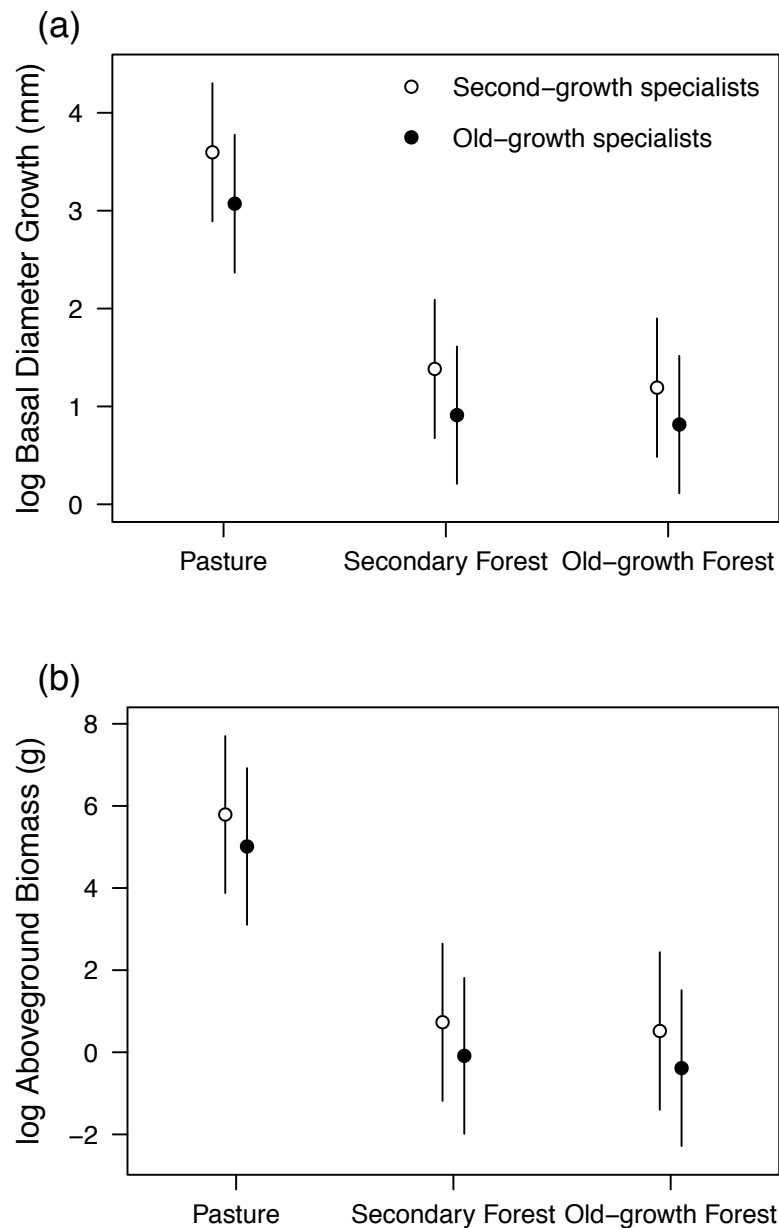


Figure A4.2. Regression estimates for linear models relating traits to basal diameter growth (a, c, e) and final aboveground biomass (b, d, f) in each of the three habitat treatments. All models are mixed-effect models except (d) which is a linear regression. Covariates of the best-fit models are shown for (a, b) pasture plots, (c, d) secondary forest plots, and (e, f) old-growth forest plots. Predictor traits include light availability (R:FR), chlorophyll content (CCI), leaf size (LS), leaf density (LD), leaf toughness (LTO), and leaf thickness (LT). Asterisks show P values (d) or Markov chain Monte-Carlo probability estimates (a-c, e-f) for each factor; *** P <0.001, ** P <0.01, * P <0.05.

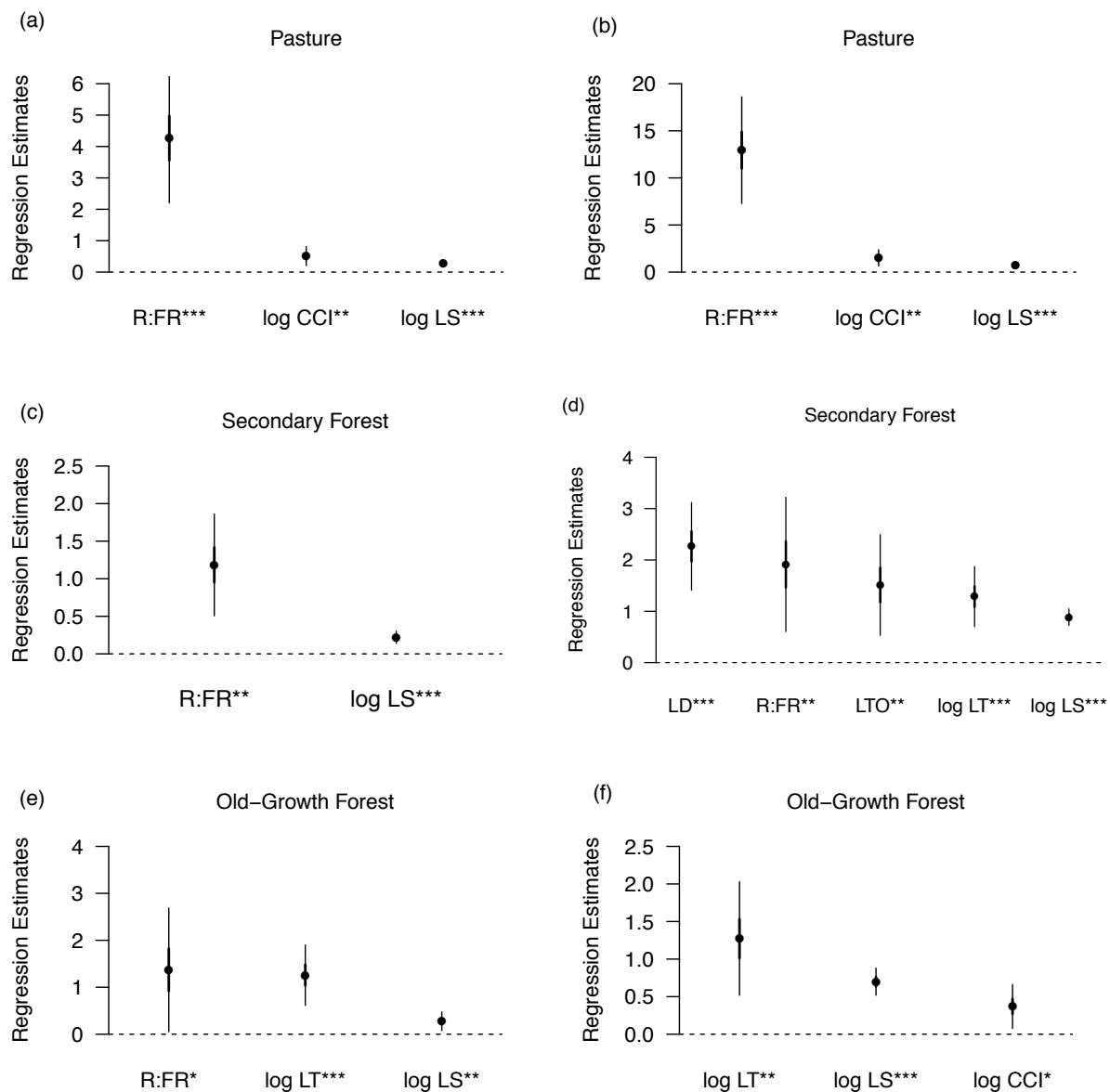


Table A4.1. Pearson correlation among functional trait values for 162 individuals of six tree seedling species in the initial harvest. Strong correlations ($> |0.5|$) are highlighted in bold. Prior to assessing correlations, leaf size, specific leaf area, leaf thickness, chlorophyll content index, leaf phosphorus content and carbon: nitrogen ratio were log-transformed to improve normality.

Functional Trait	LS	SLA	LDMC	LT	LTO	LD	CCI	LNC	LPC	C:N
Leaf Size (LS)	--	0.37	-0.41	-0.02	-0.41	0.05	-0.3	0.07	0.15	-0.13
Specific Leaf Area (SLA)		--	-0.82	-0.21	-0.8	-0.26	-0.55	0.76	0.57	-0.82
Leaf Dry Matter Content (LDMC)			--	-0.28	0.61	-0.04	0.69	-0.48	-0.34	0.5
Leaf Thickness (LT)				--	0.3	-0.01	-0.16	-0.29	-0.32	0.39
Leaf Toughness (LTO)					--	0.27	0.45	-0.54	-0.48	0.63
Leaf Density (LD)						--	-0.15	-0.4	-0.26	0.38
Chlorophyll Content Index (CCI)							--	-0.1	-0.18	0.16
Leaf Nitrogen Content (LNC)								--	0.63	-0.97
Leaf Phosphorus Content (LPC)									--	-0.64
Carbon: Nitrogen ratio (C:N)										--

Table A4.2. Functional traits measured at the final harvest (17 months after out-planting) for six study species grown in three habitat treatments. Mean (SE) are shown for each species and each trait, where different letters indicate significant differences among habitat treatments ($P < 0.05$). *Cecropia*, *Hampea*, and *Simarouba* are second-growth specialists, and *Calophyllum*, *Protium*, and *Tetragastris* are old-growth specialists. Original data are shown, although leaf size, specific leaf area, chlorophyll content, leaf nitrogen content, and leaf phosphorus content were log-transformed prior to analyses. Only pasture individuals of *Cecropia* survived to 17 months, so no comparisons across habitat treatments could be made.

		Pasture	Second-growth Forest	Old-growth Forest
Leaf Size (cm ²)	<i>Cecropia</i>	8318.82 (1680.55)	--	--
	<i>Hampea</i>	11.37 (7.55) a	26.00 (9.52) a	21.22 (4.3) a
	<i>Simarouba</i>	799.05 (188.01) a	27.08 (3.48) b	30.57 (7.73) b
	<i>Calophyllum</i>	26.76 (6.57) a	15.56 (1.26) a	9.85 (1.05) b
	<i>Protium</i>	61.52 (5.5) a	23.62 (2.69) b	16.52 (1.51) b
	<i>Tetragastris</i>	54.08 (5.27) a	24.83 (3.97) b	18.04 (1.16) b
Specific Leaf Area (mm ² /mg)	<i>Cecropia</i>	10.33 (0.82)	--	--
	<i>Hampea</i>	27.20 (4.13) a	46.04 (2.32) b	43.63 (1.06) b
	<i>Simarouba</i>	9.98 (0.56) a	31.36 (1.71) b	34.20 (1.85) b
	<i>Calophyllum</i>	10.46 (0.31) a	17.15 (0.73) b	15.85 (0.90) b
	<i>Protium</i>	14.21 (0.54) a	28.69 (0.79) b	29.25 (0.97) b
	<i>Tetragastris</i>	10.92 (0.27) a	22.17 (0.82) b	21.40 (0.70) b
Leaf Dry Matter Content (mg/g)	<i>Cecropia</i>	336.72 (10.44)	--	--
	<i>Hampea</i>	156.93 (3.14) a	166.6 (5.67) a	154.3 (11.22) a
	<i>Simarouba</i>	329.77 (6.31) a	236.06 (5.41) b	219.53 (7.8) b
	<i>Calophyllum</i>	402.15 (12.26) a	342.57 (7.88) b	344.34 (6.63) b
	<i>Protium</i>	404.35 (5.26) a	336.66 (4.07) b	333.90 (4.26) b
	<i>Tetragastris</i>	479.93 (6.43) a	392.40 (10.63) b	394.20 (6.42) b
Leaf Thickness (mm)	<i>Cecropia</i>	0.27 (0.01)	--	--
	<i>Hampea</i>	0.24 (0.03) a	0.14 (0.003) b	0.16 (0.01) b
	<i>Simarouba</i>	0.33 (0.02) a	0.15 (0.01) b	0.14 (0.004) b
	<i>Calophyllum</i>	0.23 (0.002) a	0.17 (0.01) b	0.17 (0.005) b
	<i>Protium</i>	0.17 (0.004) a	0.12 (0.01) b	0.12 (0.004) b
	<i>Tetragastris</i>	0.19 (0.004) a	0.13 (0.005) b	0.13 (0.002) b

Table A4.2. continued

		Pasture	Second-growth Forest	Old-growth Forest
Leaf	<i>Cecropia</i>	0.45 (0.02)	--	--
Toughness	<i>Hampea</i>	0.10 (0.01) a	0.15 (0.01) a	0.09 (0.04) a
(N/mm)	<i>Simarouba</i>	0.27 (0.01) a	0.10 (0.02) b	0.08 (0.01) b
	<i>Calophyllum</i>	0.55 (0.03) a	0.38 (0.02) b	0.34 (0.02) b
	<i>Protium</i>	0.31 (0.02) a	0.18 (0.01) b	0.20 (0.01) b
	<i>Tetragastris</i>	0.42 (0.02) a	0.27 (0.01) b	0.23 (0.01) b
Leaf Density	<i>Cecropia</i>	1.14 (0.07)	--	--
(mg/mm³)	<i>Hampea</i>	1.00 (0.06) a	0.95 (0.02) a	0.94 (0.04) a
	<i>Simarouba</i>	0.95 (0.05) a	0.91 (0.03) a	0.97 (0.03) a
	<i>Calophyllum</i>	1.04 (0.01) ab	1.02 (0.02) a	1.12 (0.03) b
	<i>Protium</i>	1.04 (0.01) a	0.89 (0.03) b	0.89 (0.02) b
	<i>Tetragastris</i>	1.02 (0.01) a	0.89 (0.03) b	0.98 (0.02) a
Chlorophyll	<i>Cecropia</i>	22.15 (1.76)	--	--
Content	<i>Hampea</i>	7.39 (0.84) a	18.68 (1.93) a	22.39 (1.11) a
(index)	<i>Simarouba</i>	44.10 (8.15) a	34.42 (2) a	28.96 (2.76) a
	<i>Calophyllum</i>	16.60 (2.16) a	54.93 (3.7) b	42.30 (2.99) c
	<i>Protium</i>	17.44 (0.98) a	22.28 (2.85) a	20.19 (1.47) a
	<i>Tetragastris</i>	14.56 (1.8) a	30.45 (2.99) b	30.14 (1.64) b
Leaf	<i>Cecropia</i>	1.88 (0.14)	--	--
Phosphorus	<i>Hampea</i>	--	1.80 (NA)	--
Content	<i>Simarouba</i>	1.23 (0.03) a	1.45 (0.05) a	1.45 (0.13) a
(mg/g)	<i>Calophyllum</i>	0.93 (0.09) a	0.87 (0.05) a	0.75 (0.03) a
	<i>Protium</i>	1.80 (0.16) a	1.53 (0.13) a	1.46 (0.11) a
	<i>Tetragastris</i>	1.67 (0.18) a	0.91 (0.06) b	0.85 (0.04) b
Leaf	<i>Cecropia</i>	20.43 (1.41)	--	--
Nitrogen	<i>Hampea</i>	28.26 (NA) a	30.15 (0.95) a	35.79 (5.83) a
Content	<i>Simarouba</i>	21.68 (0.76) a	32.81 (1.95) b	32.48 (0.84) b
(mg/g)	<i>Calophyllum</i>	12.56 (0.19) a	15.02 (0.48) b	13.77 (0.3) b
	<i>Protium</i>	18.14 (0.57) a	20.68 (0.69) b	21.02 (0.86) b
	<i>Tetragastris</i>	13.47 (0.60) a	17.12 (1.25) b	17.13 (0.42) b

Table A4.2. continued

		Pasture	Second-growth Forest	Old-growth Forest
Leaf Carbon	<i>Cecropia</i>	475.66 (3.63)	--	--
Content	<i>Hampea</i>	450.66 (NA) a	385.67 (18.62) a	412.6 (41.57) a
(mg/g)	<i>Simarouba</i>	497.14 (3.7) a	481.00 (4.81) b	481.43 (2.86) b
	<i>Calophyllum</i>	503.03 (9.8) ab	501.80 (1.19) a	507.90 (1.27) b
	<i>Protium</i>	466.37 (10.3) a	440.79 (18.58) ab	384.54 (21.40) b
	<i>Tetragastris</i>	476.64 (4.78) a	439.26 (13.64) a	424.80 (19.07) a
Leaf	<i>Cecropia</i>	23.85 (1.66)	--	--
Carbon:	<i>Hampea</i>	15.95 (NA) a	12.96 (0.89) a	11.92 (1.73) a
Nitrogen	<i>Simarouba</i>	23.06 (0.77) a	14.86 (0.85) b	14.90 (0.38) b
(ratio)	<i>Calophyllum</i>	40.06 (0.82) a	33.75 (1.32) b	37.01 (0.79) ab
	<i>Protium</i>	26.05 (1.18) a	21.5 (1.09) b	18.29 (0.63) b
	<i>Tetragastris</i>	35.71 (1.52) a	26.45 (1.53) b	24.78 (0.93) b
Wood	<i>Cecropia</i>	0.33 (0.04)	--	--
Specific	<i>Hampea</i>	0.24 (0.03) a	0.26 (0.02) a	0.31 (0.04) a
Gravity	<i>Simarouba</i>	0.29 (0.01) a	0.34 (0.01) b	0.33 (0.01) b
(unitless)	<i>Calophyllum</i>	0.48 (0.01) a	0.56 (0.02) a	0.55 (0.03) a
	<i>Protium</i>	0.48 (0.02) a	0.45 (0.02) a	0.42 (0.02) a
	<i>Tetragastris</i>	0.54 (0.02) a	0.47 (0.02) ab	0.43 (0.03) b

Table A4.3. Pearson correlation among functional trait values for 183 individuals of six tree seedling species in the final harvest (after 17 months in the field). Strong correlations ($> |0.5|$) are highlighted in bold. Prior to assessing correlations, leaf size, specific leaf area, leaf thickness, chlorophyll content index, leaf phosphorus content, leaf nitrogen content and leaf carbon content were log-transformed to improve normality.

Functional Trait	LS	SLA	LDMC	LD	LT	LTO	CCI	LPC	LNC	C:N	LCC	WSG
Leaf Size (LS)	--	-0.51	-0.09	0.05	0.68	0.18	-0.08	0.47	0.35	-0.35	0.06	-0.67
Specific Leaf Area (SLA)		--	-0.53	-0.45	-0.8	-0.69	0.16	-0.09	0.44	-0.45	-0.31	0.11
Leaf Dry Matter Content (LDMC)			--	0.25	0	0.51	-0.39	0.03	-0.63	0.52	-0.07	0.45
Leaf Density (LD)				--	0.08	0.42	-0.04	0.01	-0.28	0.3	0.18	0.06
Leaf Thickness (LT)					--	0.42	0.03	0.11	-0.08	0.15	0.37	-0.44
Leaf Toughness (LTO)						--	-0.28	-0.06	-0.68	0.68	0.25	0.28
Chlorophyll Content Index (CCI)							--	-0.52	0.26	-0.17	0.26	-0.14
Leaf Phosphorus Content (LPC)								--	0.38	-0.46	-0.41	-0.34
Leaf Nitrogen Content (LNC)									--	-0.96	-0.2	-0.7
Leaf Carbon : Nitrogen ratio (C:N)										--	0.41	0.67
Leaf Carbon Content (LCC)											--	0.14
Wood Specific Gravity (WSG)												--

Table A4.4. Proportion of variance explained by random effects terms for the mixed-effects growth models. “*NA*” indicates that the term was not included in the most supported model. Note that the best-supported aboveground biomass model in the second-growth forest was a linear regression, and thus did not include any random effects terms.

Model	Growth Type	<u>Random effect terms</u>	
		Species (%)	Plot (%)
Overall	Height (cm)	52.6	13.8
	Basal Diameter (mm)	54.1	16.2
	Aboveground Biomass (g)	52.9	18.0
Pasture	Height (cm)	<i>NA</i>	64.3
	Basal Diameter (mm)	<i>NA</i>	52.0
	Aboveground Biomass (g)	<i>NA</i>	60.8
Second-growth forest	Height (cm)	17.2	<i>NA</i>
	Basal Diameter (mm)	<i>NA</i>	8.7
	Aboveground Biomass (g)	<i>NA</i>	<i>NA</i>
Old-growth forest	Height (cm)	16.0	<i>NA</i>
	Basal Diameter (mm)	13.1	<i>NA</i>
	Aboveground Biomass (g)	<i>NA</i>	26.6