

A FUNCTIONAL TRAIT BASED APPROACH TO UNDERSTAND TROPICAL FOREST
COMPOSITION AND FUNCTION IN A COSTA RICAN LANDSCAPE

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Abstract

Quantifying the factors driving tropical forest composition, structure and function is a continuous area of ecological research. Recently, novel approaches have enabled research questions on this topic to be addressed not only using a taxonomic approach (species identity and abundance), but through the characterization of the collection of species functional traits present within plant communities. This functional trait approach is powerful because traits are directly linked to the performance of species in their environment, determining how they use limiting resources, limiting their geographic range and areas of distribution, and determining ecosystem processes and services delivered to humans.

The research reported here follows this functional approach. Located within the San Juan La Selva Region in northern Costa Rica, the study landscape encompasses 6,166 km² across edaphic, climatic and elevation gradients. Using species abundance and six functional traits from more than 250 species of dominant canopy trees and palms in 127 old-growth forest plots, we sought to (i) better understand the underlying factors determining the assembly processes of old-growth forest communities, (ii) assess current and future spatial distributions of community functional properties, and (iii) quantify relationships between forest canopy functional characteristics and hydrologic processes.

This work highlights the value of using functional traits to assess community assembly. In particular, we demonstrate through the use of functional traits the role that niche assembly mechanisms play in the community composition of old-growth forest communities along edaphic and climatic gradients. Moreover, by building response models of community traits values to climate variables, we predict community functional properties under current and future scenarios of climate change, discussing the consequences that the observed reduction in functional area occupied by these forest communities could have on ecosystem function. Finally this research demonstrated that particular functional elements of lowland forest canopies influence the spatial redistribution of rainfall. Therefore, future shifts in species and functional group composition could potentially change the hydrological cycle in these ecosystems. Our ability to accurately assess vegetation responses to environment and predict composition changes in tropical landscapes undergoing continuous transformation derived by human activities is relevant to finding appropriate conservation approaches of remnant forest fragments.

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Dedication

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Chapter 1: A Functional Approach to Understand Tropical Forest Composition and Function in a Costa Rican Landscape, an Introduction

Plant functional traits include any morphological, physiological or phenological feature measurable at the individual level that influence plant species growth, reproduction and survival (Violle et al., 2007). As a consequence, plant functional traits define the range of environments in which species can grow and survive. A shift in the approach to assess community composition and vegetation distribution along environmental gradients has occurred whereby functional trait mediated vegetation responses are considered either independently or in combination with species taxonomic identity (Boulangéat et al., 2012; Cornwell & Ackerly, 2009; Douma et al., 2012; Keddy, 1992; Shipley, Vile, & Garnier, 2006; Siefert, Ravenscroft, Weiser, & Swenson, 2013; Swenson, Anglada-Cordero, & Barone, 2011; Van Bodegom et al., 2012). It is now recognized that ecologists need to resolve the extent to which the structure and dynamics of ecological communities can be predicted from species functional traits (Sutherland et al., 2013).

Identifying the underlying drivers of community diversity and composition continues to present some of the most challenging questions in ecological research (Sutherland et al., 2013). Studies that disentangle which deterministic and stochastic processes control community assembly have traditionally been conducted from a taxonomic perspective (Chain-Guadarrama, Finegan, Vilchez, & Casanoves, 2012; Condit et al., 2002; Pyke, Condit, Aguilar, & Lao, 2001; Sesnie, Finegan, Gessler, Ramos, & Rica, 2009; Tuomisto, Ruokolainen, & Yli-halla, 2003). However, given the advantages of evaluating functional traits to assess species relationship with the environment and reveal those principles explaining the assembly of communities (Cornwell & Ackerly, 2009; Götzenberger et al., 2012; Kraft, Valencia, & Ackerly, 2008; Siefert et al., 2013; Swenson et al., 2011; Swenson, 2013), a large amount of plant species functional traits data is being collected across the globe (Chave et al., 2009; Kattge et al., 2011; I. J. Wright et al., 2004). In the same sense that plant communities respond to environmental and spatial variability as mediated through the functional traits of their component species, community diversity and composition influence ecosystem processes and the resistance and resilience of ecosystems to environmental change (Chapin et al., 2000; de Bello et al., 2010; Díaz et al., 2007, 2011; D U Hooper et al., 2005; S Lavorel & Garnier, 2002). Studies focusing on the interaction between community properties

and ecosystem functioning must thus include assessment of the relative contribution of community functional properties to ecosystem functioning to then be able to predict the responses of ecosystems to environmental change based on species functional traits (Sutherland et al., 2013).

Owing to the high biodiversity and rapid rates of species turnover found in Neotropical forests, assessing community and ecosystem function is a great challenge. While recent studies have assessed the functional beta diversity of plant communities along environmental and disturbance gradients (Swenson et al., 2012, 2011), research in the tropics has only recently begun particularly because databases including species, functional traits and environmental data across large geographic areas are incomplete. Previous research conducted in the San Juan La Selva region (Aquino, 2009; Fernández Méndez, 2007; Sesnie et al., 2009), combined with new trait measurements conducted within this dissertation, allowed me to compile a large data set including tree and palm species abundances, functional traits, and environmental variables across more than 100 forest sites, to answer the following research questions: (1) what factors control plant community assembly in highly diverse Neotropical forests? (2) What are the potential changes in functional composition under a future climate change scenario? (3) Are functional properties of forest canopies related to the process of rainfall redistribution?

This dissertation includes three chapters related to three main disciplinary research questions described above. All of them are formatted as manuscripts to be submitted for publication. In Chapter 2, *Disentangling plant community assembly mechanisms in highly diverse Neotropical forests through the assessment of functional beta diversity*, I sought to identify the roles of environmental deterministic and dispersal assembly mechanisms in originating and maintaining community turnover of old-growth forests in northern Costa Rica. I analyzed patterns of taxonomic and functional turnover using existing vegetation data and by measuring a set of six foliar and stem traits of dominant species, and compared the functional approach to the taxonomic approach in which vegetation response to environment is assessed based only in species abundances. Using multivariate statistical methods such as variation partitioning and Mantel correlation tests and Mantel correlograms, I demonstrate in this chapter that functional traits better respond to spatial and environmental variables of forest sites, and that environmental heterogeneity better explains the high beta diversity

characterizing these old-growth forests. Overall, my findings indicate that functional traits hold great potential for estimating community assembly mechanisms in these Neotropical forests. Chapter 2 was submitted to the journal *Ecography*, with Bryan Finegan, Lee Vierling, Steven Sesnie and Zayra Ramos as co-authors.

In Chapter 3, *Trajectories of old-growth Neotropical forest plant functional composition under climate change*, I explored the relationships between community weighted mean trait values and current and future climate, seeking to examine potential changes in functional composition of old-growth forest communities. Through generalized additive modeling, I assessed the response of CWM traits to climate predictors, and used the modeled relationships to predict and map current and future values of community traits. Lowland forest communities showed a similar direction and magnitude of change towards the functional space currently occupied by most distant foothills forest communities, indicating a change from communities characterized by community traits values associated with more conservative species, to communities characterized by CWM trait values associated to more exploitative species. The observed reduction of the functional space occupied by old-growth forest communities may have further effects on ecosystem functioning and ecosystem services currently delivered by these tropical rainforests. Chapter 3 will be submitted to the *Journal of Vegetation Science* with Pablo Imbach, Sergio Vilchez, Lee Vierling and Bryan Finegan as co-authors.

In Chapter 4, *The functional and structural characteristics of forest canopies drive distinctive throughfall patterns between old-growth and second-growth Neotropical rain forests*, I assessed the influence of vegetation properties on the temporal and spatial variation of canopy throughfall. By measuring throughfall, vegetation structure, and averaged trait values in more than 300 locations under secondary and old-growth forest canopies, I found that old-growth forests showed higher spatial variability in throughfall, especially under lower rainfall amounts, than secondary forests. This result is likely associated with the abundance of canopy palms characterized by a particular suite of functional traits such as large and hard leaves. Results of this chapter indicated what traits may be most valuable for the purpose of understanding the relationship between tropical forest functional diversity and partitioning of rainfall, and how the functional approach may complement measures of forest structure and canopy cover for this purpose. In addition, this work highlights the need to understand how

potential changes in the hydrological cycle in these ecosystems may occur with future shifts in species and functional group composition, as occurs during forest succession. Chapter 4 was submitted to the journal *Functional Ecology* with Zion Klos, Bryan Finegan, Lee Vierling, Fernando Casanoves, Robin Chazdon and Tim Link as co-authors.

Finally, in Chapter 5, I provide perspectives on my combined body of work and thoughts on future research in this realm of ecology.

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Chapter 2: Understanding Plant Community Assembly Mechanisms in Highly Diverse Neotropical Forests through the Assessment of Functional Beta Diversity

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Abstract

The mechanisms controlling tree species assembly in Neotropical forests are still debated. A taxonomic approach has traditionally been used to assess vegetation response to environmental and spatial predictors, but the information held in species functional traits should further elucidate the factors determining community turnover in these diverse forests. To test hypotheses related to environmental deterministic and dispersal assembly of Neotropical forest communities, we assessed patterns of taxonomic and functional turnover, or beta diversity, across broad geographic and environmental gradients. Using abundance and functional trait data for dominant trees and palms distributed in 127 forest plots across a northern Costa Rican landscape, we quantified the influence of environmental and spatial predictors on taxonomic and functional composition variation (variation partitioning) and assessed patterns of taxonomic and functional turnover with increasing geographic and environmental distances (Mantel correlation tests and Mantel correlograms). Environmental predictors explained greater proportion of taxonomic and functional composition variation than spatial predictors. Functional and taxonomic turnover increased with increasing geographic and environmental differences between plots, but once controlling for environmental change spatial patterns in taxonomic and functional composition were no longer observed. However, spatial structure in residual taxonomic and functional turnover was observed when examining individual distance lags. This, together with the pure effect of spatial predictors, suggests that community turnover is also explained by geographic proximity between plots alone. Our results indicated the existence of a scale-dependent interaction between deterministic and stochastic community assembly, showing that community turnover results from species recruitment along regional spatially structured environmental gradients, and from species limited dispersal at local scales. As such the

assessment of functional turnover hold great potential for estimating community assembly mechanisms in this biome.

Introduction

Community assembly mechanisms have been traditionally studied using a taxonomic approach by quantifying patterns of species turnover or beta-diversity with geographic distance (Pyke et al. 2001, Condit et al. 2002, Tuomisto et al. 2003, Sesnie et al. 2009, Chain-Guadarrama et al. 2012). However, community assessment based solely in taxonomic information is a limited approach for understanding mechanisms responsible for species turnover (Swenson et al. 2011, Siefert et al. 2013). The taxonomic approach does not allow the environmental deterministic assembly hypothesis to be directly tested simply because the environment filters species by their differing ecological strategies indicated by particular functional traits and not by their taxonomic identity (Keddy 1992). Functional traits hold information about the physiology, morphology and behavior of individuals (Violle et al. 2007) and indicate ecological strategies which are related to the response of species to environment (Wright et al. 2004, 2005, Chave et al. 2009). Given the advantages of evaluating functional traits to assess species relationship with the environment and reveal those principles explaining the assembly of communities (Kraft et al. 2008, Cornwell and Ackerly 2009, Swenson et al. 2011, Götzenberger et al. 2012, Swenson 2013, Siefert et al. 2013), a large amount of plant species functional traits data is being collected across the globe (Wright et al. 2004, Chave et al. 2009, Kattge et al. 2011). In particular these efforts have allowed a shift in the approach to study plant community turnover and assembly, assessing not only taxonomic but as well as functional beta diversity (Swenson et al. 2011, Siefert et al. 2013), and offering new insights on the degree to which individuals are sorted from regional pools according to their functional traits (or niche based or environmental deterministic recruitment) or following dispersal limitation (Legendre et al. 2005, Tuomisto and Ruokolainen 2006, Götzenberger et al. 2012, Swenson 2013).

In a trait-based ecology, hypotheses about assembly in plant communities can then be framed by assessing functional turnover jointly with taxonomic turnover. Under niche community assembly species are selected by the environment on the basis of their functional traits and spatial structure of community turnover results from dependence on spatially

structured or autocorrelated environmental variables (Legendre et al. 2005, Tuomisto and Ruokolainen 2006). Under this scenario both variation in taxonomic and functional composition among plots are expected to simultaneously occur due to variation in environmental variables. Under this deterministic assembly rule an increase in taxonomic and functional beta diversity with increasing geographic (i.e. distance decay in community similarity) and environmental distances is expected. However, because spatial structure of community turnover is determined by dependence on underlying spatially structured environmental variables, increasing community turnover with geographic distance is not expected when controlling for the effect of environmental differences. Under a dispersal assembly rule, as predicted by Hubbell's neutral theory (Hubbell 2001), species sorting at local communities occurs randomly, but species composition fluctuations are spatially autocorrelated due to spatially limited dispersal (Legendre et al. 2005, Tuomisto and Ruokolainen 2006). Because under this second assembly hypothesis spatial structure of community turnover is due to geographic proximity between plots (i.e. entirely due to autocorrelation) and not the result of dependence on spatially structured environmental variables, an increase in community turnover with geographic distances is expected to occur even when the effect of environmental has been removed.

Owing to the high biodiversity and rapid rates of species turnover found in Neotropical forests, assessing community assembly rules from a functional perspective represents a great challenge (Swenson 2013). Work in Amazonia has demonstrated that variation in forest dynamics, structure and function is related to soil fertility and climate gradients across the basin (ter Steege et al. 2006, Fyllas et al. 2009, Patiño et al. 2012, Quesada et al. 2012), showing that vegetation responds functionally to environment but without explicitly testing community assembly hypotheses. Such tests in the Neotropics were done by Swenson et al. (2011) in Puerto Rico by assessing beta functional diversity along altitude. They suggested the presence of environmental control of community beta diversity, but without explicitly measuring the environmental variables driving such turnover. In the present study, by analyzing patterns of taxonomic and functional turnover, we sought to identify the roles of environmental deterministic and dispersal assembly mechanisms in originating and maintaining community turnover of old-growth forests in northern Costa Rica. Using taxonomic data of 260 canopy tree and palm dominant species distributed in 127 forest plots

over a >250,000 ha landscape, in combination with information of six functional traits. plot-level soil samples and broader-scale climatic data, our specific objectives were to: i) quantify the amount of taxonomic and functional turnover explained by spatial and environmental predictors, ii) determine whether patterns of taxonomic and functional turnover increase with increasing geographic and environmental differences between plots, iii) differentiate patterns of spatial autocorrelation from environmental spatial dependence in taxonomical and functional turnover. Results from raw and distance based multivariate analysis were used to answer the associated questions: i) are taxonomic turnover and functional turnover positively related, suggesting that species are selected by the environment on the basis of their functional properties? Or, ii) does change in taxonomic composition occur independently from change in functional composition, suggesting that dispersal limitation plays a key role in determining species assemblages?

Methods

Study Area

The study was carried out in the landscape within the limits of the San Juan La Selva Biological Corridor of northern Costa Rica (Fig. 1). The landscape is characterized by relatively steep spatially structured environmental gradients of soil chemical and physical properties, climate and elevation (Sesnie et al. 2009). Cooler environments with higher soil organic matter and sand content are observed towards the foothills of the Central Volcanic Range, which differ from heavy clay dominated soils in the lowlands (Lieberman et al. 1996, Sesnie et al. 2009). Precipitation decreases from east to west with distance from the Caribbean Coast across all the landscape, so the western lowlands are characterized by seasonally lower precipitation (Sesnie et al. 2009; Fig 1).

Species composition data

Species data were available from a previous study (Sesnie et al. 2009) where in 127 0.25 ha plots all trees (≥ 30 cm DBH) and palms (≥ 10 cm DBH) individuals were recorded, identified and diameter measured at breast height (DBH). Plots were distributed along elevation from 30 to 1200 m asl. Methods for measurement and plot establishment can be found in Sesnie et al. (2009). In this study, a total of 4,808 individuals were used for statistical analysis, which

corresponded to 260 species and morphospecies— species identified at genus level but differentiated in the field as different species by an expert parataxonomist using morphological characteristics. This set of ≥ 30 cm DBH canopy trees comprise 70-80% of the total estimated above-ground standing biomass relative to the community ≥ 10 cm DBH (unpublished data). Canopy palms represent a lower proportion of total biomass per plot, however, they are considered important elements in Neotropical forests (Sesnie et al. 2009, Chain-Guadarrama et al. 2012) and due to particular foliar and stem traits values palms are recognized as an a priori functional group within plant communities (Chazdon et al. 2010).

Functional trait data

Traits choice in highly diverse systems like these Neotropical forests favors relatively easily measured functional traits that reflect important plant ecological strategies (Kraft et al. 2008, Siefert et al. 2013). All 260 species registered in vegetation plots were selected for trait measurement. Trait measurements complemented an existing trait database for dominant tree and palm species in the region partially published in Kattge et al. (2011). We measured six functional traits that summarize species leaf and wood plant economic spectra and vary across environmental gradients (Wright et al. 2004, 2005, Cornwell and Ackerly 2009, Ordoñez et al. 2009, Chave et al. 2009): specific leaf area (SLA), leaf area (LA), leaf dry matter content (LDMC), foliar nitrogen and phosphorous content (N and P), and wood specific gravity (WSG) (Supplementary material Appendix 1, Table A1). We followed known methodologies for the sampling and measurement of foliar traits (Garnier et al. 2001, Pérez-Harguindeguy et al. 2013) and WSG (Chave et al. 2006, Williamson and Wiemann 2010), respectively made on five and three individuals per species all collected within the study region. Under the assumption that at genus and family level a relevant percentage of the species-level trait variation is held (Chave et al. 2006, Fyllas et al. 2009, Patiño et al. 2012), genus-mean or family-mean trait values were calculated from species occurring in the studied forests and assigned to individuals identified as different morphospecies. The complete set of traits was finally obtained for 257 species. More detailed information on trait measurement is found in Appendix 1.

Soil, terrain and climate data

To assess the relationships between functional and taxonomic data with environment we used the same soil and climate variables described in Sesnie et al. (2009), corresponding to on-site measured values of soil chemical and texture properties for each plot, and six annual and seasonal temperature and precipitation variables obtained from the Worldclim bioclimate dataset (Hijmans et al. 2005). Different from Sesnie et al. (2009), we used a higher resolution 10 m digital elevation model developed in the Climate Change and Watershed Program at CATIE to obtain elevation and slope data for each plot.

Analysis of taxonomic and functional composition

Taxonomic composition was represented by a table of species abundance per plot. Functional composition was represented by a table of community weighted means (CWM) traits per plot (Violle et al. 2007). For each plot the abundance-weighted mean trait values were calculated with the `functcomp` function implemented in the `FD` package (Laliberte and Shipley 2011) in R (R Development Core Team). To visualize the distribution of forest plots in trait space, CWM trait values per plot were used to run a principal component analysis (PCA) in InfoStat software (Di Rienzo et al. 2012). Information of plot membership of floristic groups recognized by Sesnie et al. (2009) was overlapped in the biplot to also visualize differences in species composition along axes related to functional traits. PCA was run separately for communities represented by canopy tree and palm species combined (from here on “tree-palm communities”) and canopy tree species only.

To quantify the amount of taxonomic and functional turnover explained by spatial and environmental variables, we performed a variation partitioning analysis (Borcard et al. 1992, Legendre 2008) at the two levels of community analysis, i.e., tree-palm communities and tree communities separately. Adjusted coefficients of determination (R^2_{adj}) were reported (Peres-Neto et al. 2006). Our response matrices were either the Hellinger transformed species abundances data (Legendre and Gallagher 2001) or z-standardized (mean = 0, SD = 1) CWM traits per plot. Our first predictor component corresponded to the set of log-transformed soil, climate and terrain variables. Our second predictor component was represented by a set of positive vectors describing spatial relationships obtained from a geographic Euclidean matrix through a principal coordinates of neighbor matrices (PCNM) analysis (Borcard and Legendre

2002). To prevent overestimating the explained variance, prior to the variation partitioning analysis, a two-step forward selection analysis was run on the sets of environment and space variables (Blanchet et al. 2008). Variation partitioning and significance tests were conducted using `var.part` and `anova.cca` functions in `vegan` package (Oksanen et al. 2013) in R. PCNMs were generated with the PCNM package (Legendre et al. 2012) and forward selection using functions `rda`, `RsquareAdj` and `forward.sel`, of `packfor` (Dray et al. 2011) and `vegan` R packages.

Analysis of taxonomic and functional turnover

We analyzed patterns of taxonomic and functional turnover increase with increasing geographic and environmental differences through simple and Mantel correlation tests. Correlations between taxonomic, functional and environmental distance matrices with a geographic distance matrix were performed to assess the spatial structure in the taxonomic, functional and environmental data. The correlations between functional and taxonomic turnover with environmental change were also assessed. To assess if functional composition changes between forest plots occur along with taxonomic composition changes we also assessed the correlation between taxonomic and functional turnover. Because spatial patterns in functional and taxonomic turnover may occur due to spatial autocorrelation or due to their dependence on autocorrelated environmental variables we performed partial Mantel tests to assess if the correlation between taxonomic and functional turnover with geographic distance still occur when controlling for environmental differences between plots. The functions `mantel` and `partial.mantel` in the `vegan` R package were used.

To further examine the spatial structure of species assemblages we computed Mantel correlograms. In comparison to a Mantel correlation test between ecological and geographic distances that results in a global measure of spatial structure, Mantel correlograms partition the analysis into a series of distance classes that allows to assess the spatial patterns at different scales and reveal non-linear patterns (Dray et al. 2012, Borcard and Legendre 2012). In a Mantel correlogram Mantel correlation statistics (r_M) are plotted against distance classes, where positive and negative autocorrelation are respectively expressed by positive and negative values of r_M . Correlograms were performed for taxonomic, functional and environmental turnover. In line with partial Mantel tests, we computed Mantel correlograms

for the taxonomic turnover data after accounting for its correlation with environmental distances. For this, the residuals of a linear regression of taxonomic turnover against environmental change were used. Spatial structure of residual functional turnover independent of variation associated with environmental variables was also assessed. Following the Sturge's rule (Legendre and Legendre 1998) geographic distances were divided into 14 classes, the first spaced at 1 km, the second at 2km, and the rest at 5 km intervals. Maximum distance between two plots was 63.5 km. At each spatial lag rM were tested for significance through 999 permutations and corrected p-values were obtained by progressive Bonferroni corrections (Legendre and Legendre 1998). The function `mantel.correlog` in the `vegan` library in R was used.

Both Mantel test and Mantel correlograms were performed by means of ecological and geographic distance matrices among plots. We calculated a Euclidean distance matrix using plot's Universal Transverse Mercator (UTM) coordinates. Geographic distances were then transformed to natural logarithms following the idea that floristic similarity decreases linearly with increasing logarithm of geographic distance. A Euclidean distance matrix was calculated for the set of log-transformed environmental predictors including soil, climate and elevation variables. The Euclidean distance measure was also used to calculate a functional composition distance matrix from previously z-standardized CWM traits per plot. Species abundances were Hellinger transformed prior to calculating a Euclidean dissimilarity matrix for taxonomic composition. As previous analysis, these distance-based tests were run for the tree-palm community and canopy trees separately.

Results

Ordination of forest plots in the trait space

Forest plots were differentially distributed in the CWM trait space (Fig. 2, Supplementary material Appendix 2, Fig. A1). PCA axes 1, 2 and 3 explained 93% of the observed functional variability among forest sites for tree-palm communities, and 87% for canopy trees only (Supplementary material Appendix 2, Table, A2, A3). Functional distance between plots also reflected differences in plots membership to the different broad floristic groups defined by Sesnie et al. (2009), indicating that both taxonomic and functional turnover occurs among plots. Along Axis 1, plots belonging to the foothill floristic group, with lower palm densities,

were characterized by higher values of CWM SLA, N and P, in contrast, lowland forest plots, with higher palm densities, showed higher CWM LDMC and LA (Fig. 2a; Supplementary material Appendix 2, Table, A2). Forest plots were further differentiated along axis 2 in relation to CWM WSG and LDMC positively correlated with this axis, and CWM P and LA on the opposite direction (Fig. 2a). Plots belonging to lowland forest dominated by *Pentaclethra maculosa* were more widely distributed in the trait space than those in the other two forest types. The tree-palm community biplot (Figure 2a) suggests a trend from more conservative trait values in lowland forest to more acquisitive trait values in foothills forests. When only assessing the tree community this trend became more evident (Fig. 2b; Supplementary material Appendix 2, Fig. A1b). Along axis 1 and 2 plots belonging to foothill forests were associated with higher values of CWM LA, SLA, P and N, and were well differentiated from those of lowland forests, with higher values of CWM LDMC and WSG (Fig. 2b). When only tree species were taken into account the former higher CWM LA trend towards the lowlands, probably drove by high LA values of abundant palm species, was now representative of the foothills forests with tree species with larger and more acquisitive leaves. Without palms, *P. maculosa* forests are more clearly differentiated from the other two forest types along axis 2, by their higher CWM LDMC and N.

Variation in community composition: explaining overall community turnover

Different space and environmental predictor variables were retained by forward selection among taxonomic and functional composition data, and tree-palm and tree communities (Supplementary material Appendix 2, Table A4). When assessing taxonomic composition a higher total amount of variance was explained for the tree-palm community in comparison to the tree community alone (Fig. 3). At the two levels of community analysis environmental predictors slightly better explained taxonomic composition than spatial predictors. However, both the pure effect of environmental gradients and spatial predictors on taxonomic turnover was considerable lower than the effect of the interaction between environment and space (Fig. 3). A higher total amount of variance in functional composition was explained in comparison to taxonomic composition, at both levels of community analysis (Fig. 3). Similarly with taxonomic composition, in both community level analyses a considerable percentage of total variance explained by the environment and the space corresponded to the fraction explained

by the intersection of both factors. However, the pure effect of environmental predictors on functional turnover was considerably higher than the pure effect of space, indicating that environmental predictors and its interaction with measured spatial factors together better explain the variation in functional composition.

Variation in community turnover and spatial structure

Mantel test showed that taxonomic, functional and environmental dissimilarity matrices were positively correlated with the geographic distance matrix (Table 1), revealing a spatial structure in both taxonomic and functional turnover. Moreover, taxonomic and functional dissimilarity matrices were strongly positively related between them, and each one strongly positively correlated with the matrix of environmental distances between plots (Table 1). When controlling for environmental differences among plots, the correlation between taxonomic differences and geographic distances was no longer significant. Finally, the correlation between functional dissimilarities and geographic distance was no longer significant when controlling for environmental differences in the case of tree communities, and still significant but very low in the case of tree-palm communities (Table 1).

Positive autocorrelation values at short distances and negative autocorrelation values at long distances in the Mantel correlograms indicated a spatial gradient in environmental change (Fig. 4) and taxonomic (Fig. 5a) and functional (Fig. 5c) turnover, which took similar values among points closer in geographic distance, and very different values at plots located far apart. When assessing the taxonomic composition of the tree-palm community, forest sites located at distances up to 13 km showed positive spatial autocorrelation. Tree communities showed a more spatial patchiness, with patterns of significant and no significant r_M up to 28 km. Significant negative values were first observed at the >38-43 km distance class at both community level analysis, indicating that differences in community taxonomic composition between pair of sites located at these distances were in average greater than expected than those located at any other distance class. Negative r_M were observed up to 53 km. The same spatial structure observed in the tree-palm community taxonomic turnover was observed when assessing functional turnover; positive spatial autocorrelation was observed up to 13 km, while negative autocorrelation was observed among plots separated between >38 to up to 53 km. When assessing the tree community separately no spatial patchiness was observed,

positive autocorrelation was observed up to 8 km and negative autocorrelation from >43 km up to the largest distance class (58-63.5 km). Significant positive and negative r_M at different distance classes were still observed when assessing residual taxonomic (Fig. 5b) and functional (Fig. 5d) turnover controlling for environment, indicating that spatial structure still exists when the effect of environmental dissimilarities is removed.

Discussion

Explaining the mechanisms that govern community assembly and generate the high species turnover of tropical forests remains a major challenge for ecology. In this study we complemented the taxonomic approach with the power of traits-based ecology to test assembly hypotheses of tree and palm communities in Northeastern Costa Rica. Results from our multivariate analysis under both the raw and distance approaches suggest that taxonomic and functional turnover patterns in this Neotropical landscape are organized by spatially structured regional environmental gradients. However, a small proportion of variation in community composition was explained by spatial gradients per se, and spatially structured residual taxonomic and functional composition was observed, possible due to species limited dispersal. We now discuss our findings in detail.

Relationship between taxonomic and functional composition

The assessment of community composition relying on functional characteristics of dominant species allowed us to ordinate forest plots in the multivariate space of CWM of six relevant functional traits (Fig.2). Results showed that forest plots not only strongly differed by their CWM traits, but as well that ordination axes summarizing this functional information reflect differences in taxonomic composition among plots, in this case by plots association to broad floristic groups previously recognized in the region (Sesnie et al. 2009). The high correlation found between taxonomic and functional dissimilarities between plots (Table 1) supported PCA results, indicating that when taxonomic turnover occurs functional turnover also does. Plots' CWM trait values are indeed dependent on the species composing the community, however, a change in trait values with taxonomic change is not necessarily expected, since taxonomic turnover can occur between two homogenous functional communities (Sokol et al. 2011). The change of functional change with taxonomic change between forest lots is a first

evidence of environmental sorting of species at local communities from the regional species pool.

Contribution of environmental and spatial predictors to overall community turnover

To test hypotheses about the origin of community turnover between forest sites using a raw data analysis approach, we partitioned the variation of taxonomic and functional composition data among environmental and spatial components. The influence of the spatially autocorrelated environmental gradients on taxonomic composition variation was evidenced by the larger amount of variance explained by the intersection between the environmental and spatial predictors (Fig. 3) (Legendre et al. 2005). A very small and similar proportion of taxonomic composition variance explained by environmental and spatial predictors on their own, jointly with the larger proportion explained by their interaction, makes difficult to separate environmental determinism from other mechanisms that would also generate spatial structure, such is the case of species limited dispersal (Legendre et al. 2005, Legendre 2008, Meynard et al. 2011). The assessment of functional composition allowed to better disentangle the effects of environment and space. Not only a greater amount of variation of functional composition was explained in comparison to taxonomic composition, but as well the effect of the pure effect of environmental predictors was clearly larger than that of the pure effect of space (Fig. 3), indicating that more variation in functional composition is associated to environmental predictors independent of their spatial structure. Overall, our variation partitioning results give more support for an environmental deterministic assembly hypothesis in line with recent work on functional beta diversity patterns across local and continental scales in temperate (Siefert et al. 2013) and tropical systems (Swenson et al. 2011). However, as demonstrated by the lower but significant proportion of variance explained by the pure effect of spatial predictors, spatial patterns in functional and taxonomic composition may also be partially attributed to spatial autocorrelation resulting from dispersal limitation and not only to spatial dependence on autocorrelated environmental variables (Meynard et al. 2011, Siefert et al. 2013). As discussed by Legendre et al. (2005), Siefert et al. (2013) and Meynard et al. (2011), this additional spatial structure in the taxonomic and functional composition not related to the environment could also reflect the effect of unmeasured spatially structure environmental variables and thus not interpreted as evidence of dispersal limitation. However,

it can also be discussed that if this missing environmental gradients were spatially auto correlated a larger role of spatial structure per se and a smaller role for the environment-space interaction would be expected (Meynard et al. 2011).

Maintenance of variation in community turnover

Through distance based approach analysis we also found evidence to support the main effect of environment over other mechanisms in maintaining community turnover (Table 1). The existence of spatially structured environmental gradients, the increase in taxonomic and functional turnover with increasing geographic distance (i.e. distance decay of community similarity), the existence of an even stronger positive relation between functional and taxonomic turnover with environmental distances and the strong relationship between taxonomic and functional turnover suggest that the spatial structure in community composition follows the spatial structure of environment. Moreover, no significant correlation between taxonomic and functional differences with geographic distances was longer observed when controlling for environmental differences between plots, indicating that the spatial structure in community turnover arises from dependence on spatially autocorrelated environmental gradients, in line with an environmental assembly hypothesis (Tuomisto and Ruokolainen 2006).

Spatial structure of old-growth forest communities

Mantel correlograms indicated that functional and taxonomic similarities between sites occurring at short lag distances are higher than expected by chance, and are more different than expected by chance between sites occurring at long lag distances (Borcard and Legendre 2012). Examining the spatial structure of environmental variables (Fig. 4) allows to conclude that closer forest plots tend to show similar communities because the environmental conditions are rather similar, and that any pair of sites located far apart falling in contrasting environmental conditions differ in their functional and taxonomic composition. Under environmental deterministic assembly lack of spatial structure in taxonomic and functional turnover is expected once controlling for environmental differences between plots, however, significant r_M were still observed at different distance classes (Fig. 5b, d). In contrast to partial Mantel correlation tests which indicated the lack of spatial structure in taxonomic and

functional turnover once the effect of environment was removed, observed spatial structure of residual taxonomic and functional turnover in Mantel correlograms suggests nonlinear relationships between these community composition distance matrices and geographic distances (Lichstein 2007).

Positive r_M at small geographic distances in these residual correlograms indicated the stronger homogenizing effect of dispersal between close sites (Tuomisto and Ruokolainen 2006), thus indicating that autocorrelation in taxonomic and functional exist independently of the spatial structure of environmental change, in response not only to environmental variables but also to geographic distance itself, potentially because of dispersal limitation (Sokol et al. 2011, Meynard et al. 2011, Chain-Guadarrama et al. 2012, Siefert et al. 2013). This suggests the importance of spatial constraints at small geographic distances for among-site species variation. Lower than expected (negative r_M) and higher than expected (positive r_M) similarity values at larger distance classes observed in the correlograms of the residual taxonomic turnover, may be attributed to unmeasured autocorrelated environmental variables related to species turnover between sites (Legendre et al. 2005, Legendre 2008, Meynard et al. 2011). In particular it is known that edaphic conditions are likely to change at smaller scales than climatic variables, which could result in observed patterns of very different communities in terms of taxonomic composition at shorter distances and similar forest plots again at larger distance classes as observed in residual taxonomic turnover correlograms. Negative spatial autocorrelation values at the larger distance classes, as observed in the correlograms of the residual functional turnover, may result of unmeasured climatic conditions, as well as differences in biogeographic origins of species that exist in these highly diverse forests, as discussed in further detail below.

Tree-palm communities vs. tree communities

Greater amount of variance explained when including palm species is probably related to differences in palm species abundances among plots, which are attributed to soil texture and drainage conditions in this region (Clark et al. 1995, Sesnie et al. 2009). In fact while in some plots palm species are not present ($n = 10$), in some others palm individuals are highly abundant and represent more than 50% ($n = 36$) or even 70% ($n = 1$) of the total number of individuals within the plot. Added to this, foliar functional trait of palms with very particular

set of values increases differences in CWM traits between pair of forest plots, allowing a greater variance of functional composition to be explained. By observing the PCA biplots the influence of palm species can also be observed, in particular on patterns of CWM LA and SWG.

Plant community assembly of old-growth forests in northern Costa Rica

Our discussion of the mechanisms underlying old-growth forest floristic and functional composition are summarized in a conceptual figure that describes the shaping of local communities and the resulting observed broad functional and floristic groups (Fig. 6). First, deterministic recruitment takes place along the spatially structured edaphic, climatic and elevation gradients giving place to two major functional forest types towards opposite ends of the environmental gradient. In one extreme, in the resource richer soils and less seasonal climate of the foothills, we find a forest characterized by higher values of CWM SLA and N and P, and low values of CWM WSG and LDMC— potentially a forest with high process rates and stem turnover. At the other extreme, in the clay soils and more seasonal climate environments of the lowlands, is a forest characterized by high values of CWM WSG and LDMC, but lower values of CWM N and P and SLA— from which it can be inferred that process rates are slower than in the foothills. In Amazonia trends in forest structure and function following climate and soil gradients have also been described and summarized as “slow forests” with poor nutrient soils, higher wood density, smaller foliar area and larger seed mass in the northeastern region, and “faster forests” with lower wood density, larger foliar area and smaller seed mass, on more fertile soils in the southwestern region basin (ter Steege et al. 2006, Fyllas et al. 2009, Malhado et al. 2009, Patiño et al. 2012, Quesada et al. 2012). Along environmental gradients taxonomic identity thus changes, finding a group of species characteristic of higher elevations such as those belonging to genera *Guarea*, *Weinmannia*, *Tovomita*, *Quetzalia*, *Annona*, *Dystovomita*, *Andira*, *Nectandra* and *Garcinia*, and another conformed by lowland species such as *P. macroloba*, *Q. polychroma*, *Vochysia ferruginea*, *V. alleni*, and canopy palms *Welfia regia*, *Socratea exorrhiza* and *Euterpe precatoria*. In lowland environments particular species are good examples of functional traits characteristics of these environments such as *Dipteryx panamensis*, *Chrysophyllum colombianum*, *Tabebuia chrysantha* and *Dialium guianensis* with high WSG, and

Podocarpus guatemalensis with the lowest SLA values among species (Zamora et al. 2004, Sesnie et al. 2009). Second, species turnover among local communities within these major functional provinces is maintained through the mechanism of dispersal limitation related to geographic distance between forest sites. Finally, our landscape presents a unique situation in which the tree flora is made up of species with different biogeographic origins: trans-Andean (northwestern) South America, South America Atlantic slope, and North America or Northern Central American affinities (Hammel 1990, Hartshorn and Hammel 1994). This interesting biogeographic aspect of our landscape could potentially contribute to the spatial effect identified through the variation partitioning and correlogram analyses, and explain among sites taxonomic differentiation. In line with these ideas, our Mantel correlograms (Figs. 5a) can also be interpreted in relation to above floristic and functional differences along geographic distance; significant positive r_M at short distances classes and significant negative r_M at long distance classes demonstrate two well differentiated forest groups, while sites located at intermediate lag distances with no significant r_M could describe forests located in the transition zone between this two. This grouping of forest plots coincided with broadly defined floristic groups named by Sesnie et al. (2009) who observed differential distribution of species composition in forest sites in the landscape associated to soil and climate gradients. In this case plots belonging to the *P. macroleba* forest type identified by Sesnie et al. (2009) represent an intermedium in the functional and taxonomic gradient being distributed more widely in the trait space and with species from both above described forest groups.

Future research

In this study we did not take into account intraspecific trait variability which can account for a large proportion of trait variation (Albert et al. 2010, Lepš et al. 2011), and has been proved to play a strong role in assessing non-random community assembly mechanisms (Cornwell and Ackerly 2009, Jung et al. 2010, Paine et al. 2011). Because we probably underestimated functional composition response to environment, our results can be considered conservative. However, we still got a significant signal of the environment and we expect that using intraspecific trait data will result in similar but stronger trends. In our large study area, however, questions are raised regarding the potential importance of intraspecific variation, first because its effect is expected to decrease as geographic scale increases (Albert et al.

2011), and second, because the measurement of trait intraspecific variability in studies with large geographic areas and long environmental gradients makes sense only if at least some species occur along a considerable part of the environmental gradients (Lepš et al. 2011). In our study, none of the 260 recorded species was present in all 127 sampled plots, 65.5% of the species were present in 5 plots or less, and 32.2% were present in only one plot. In a study like ours where area extent and high species diversity are major constraints to obtain intraspecific trait values, fixed trait values measured for different forest types or altitudinal ranges could be used that reduce the underestimation of the functional response to environment (Lepš et al. 2011).

Traits in this study were selected as reflecting species position in leaf and wood economic spectrum, however the inclusion of other traits related to species response to environmental change, such as height, seed mass, leaf N:P, leaf life span (Wright et al. 2004, Cornwell and Ackerly 2009, Ordoñez et al. 2009, Swenson et al. 2011, Siefert et al. 2013), would allow to assess if similar functional turnover patterns and interactions with taxonomic turnover are obtained. Because species capacities of dispersal determine species' response to landscape structure at different scales (Metzger 2000), incorporating traits related to dispersal ability of species would be of interest to better assess the importance of among forest sites geographic distance and the effect environment on taxonomic and functional turnover and community assembly (Vellend 2010, Weiher et al. 2011). Finally, the inclusion of other species and life forms found in smaller diameter classes within subcanopy and understory plant species in these Neotropical forests (Guariguata et al. 1997) could be considered. The inclusion of such species would allow us to better detect the effect of environmental and spatial predictors on community composition given that these species differently respond to climatic and edaphic gradients.

Conclusions

To our knowledge this study conducted in an area over 250, 000 ha represents the first analysis of functional turnover across broad regional- scale geographic, edaphic and climatic gradients in the Neotropics. Our raw and distance-based multivariate analyses of functional turnover are novel and robust tests of community assembly hypothesis that demonstrate that functional traits in combination with taxonomic identity hold great potential for estimating

community assembly rules that might not be evident when studying patterns of taxonomic turnover alone. In particular, incorporating functional aspects into ecological patterns allowed us to capture important signals of niche-base assembly mechanisms. Our initial research questions represented a dichotomy where plant community composition could be related to either environmental deterministic mechanisms or limited dispersal. However, our results indicate the existence of an interaction between environmental deterministic and limited dispersal community assembly mechanisms, where high species turnover and diversity is maintained through species sorting along regional environmental gradients, and dispersal limitation in relation to geographic distance between forest sites.

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Tables

Table 1. Simple and partial Mantel correlation test results between taxonomic (TAXO) and functional (CWM) composition distance matrices and geographic (XY) and environmental (ENV) distance matrices. In partial correlations distance matrix following symbol | was controlled. Tests were performed for the tree-palm community and the tree community separately. Significant correlations were determined from 999 permutations, *** $p \leq 0.001$, ** $p \leq 0.01$, * $p \leq 0.05$.

		Tree-palm	Trees
Simple	ENV*XY	0.53***	0.53***
	TAXO*XY	0.24 ***	0.22 ***
	CWM*XY	0.24 ***	0.17 ***
	TAXO*ENV	0.53***	0.40***
	CWM*ENV	0.38***	0.29***
	TAXO*CWM	0.63***	0.53***
Partial	TAXO*XY ENV	-0.04	0.02
	CWM*XY ENV	0.06*	0.03

Figures

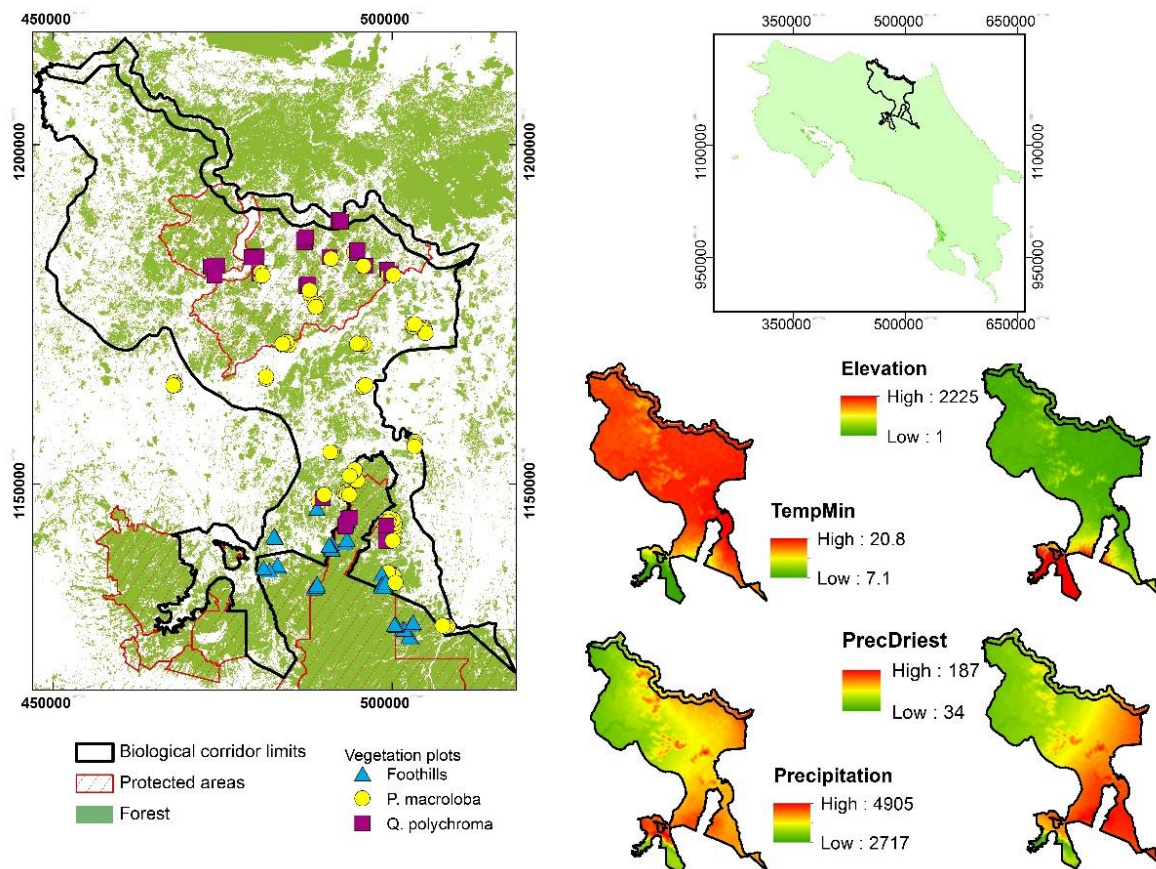


Figure 1. Location of forest plots (0.25 ha) and elevation and climatic gradients distributed across the area of the San Juan La Selva Biological Corridor landscape, northeastern Costa Rica.

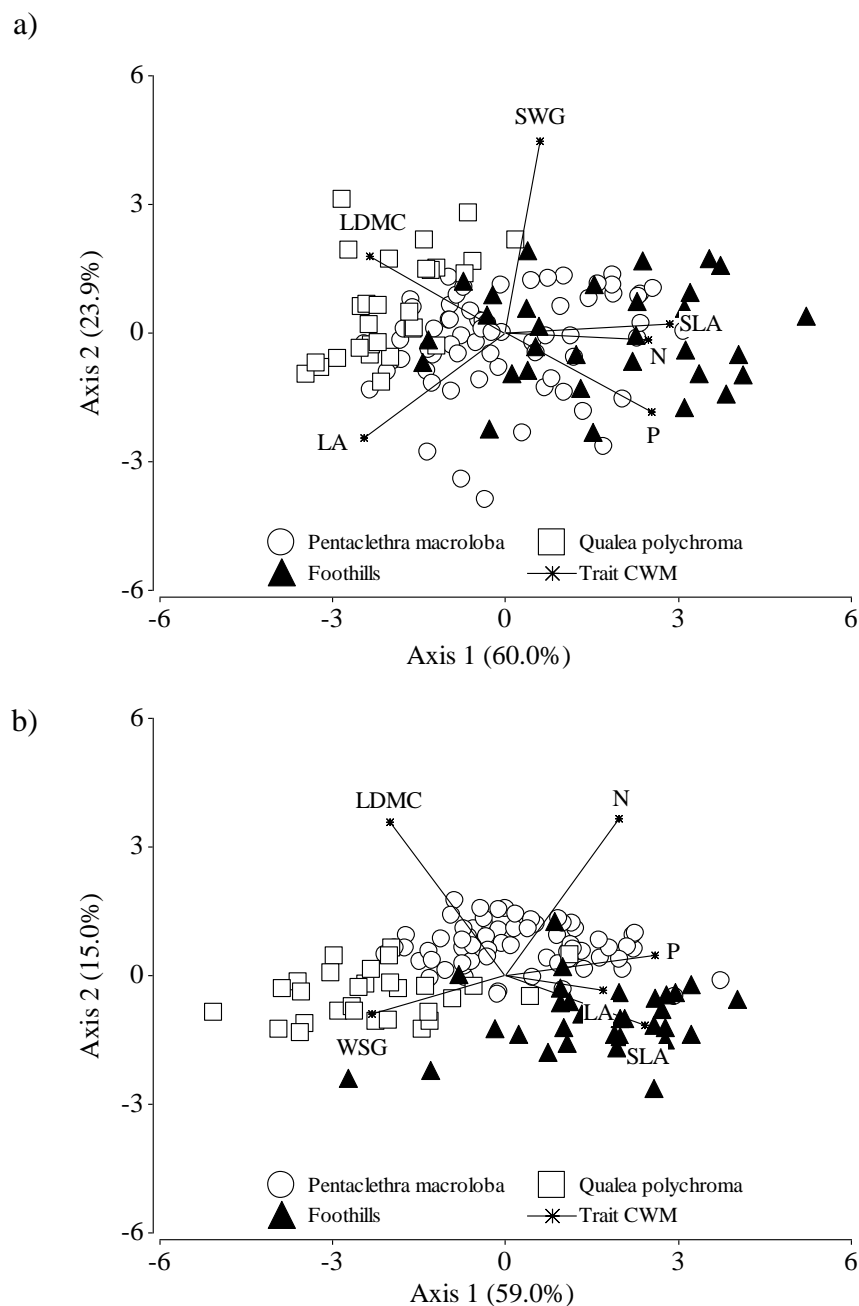


Figure 2. Ordination of vegetation plots ($N = 127$) along PCA axes one and two summarizing the functional trait space from six community weighted mean traits calculated using relative abundance of both plant and tree species (a) and only tree species (b). Plots are differentiated by their membership to three forest types previously delimited in the study region by Sesnie et al. (2009). Traits are wood specific gravity (WSG), leaf dry matter content (LDMC), leaf area (LA), specific leaf area (SLA), and Nitrogen (N) and Phosphorus (P) leaf content.

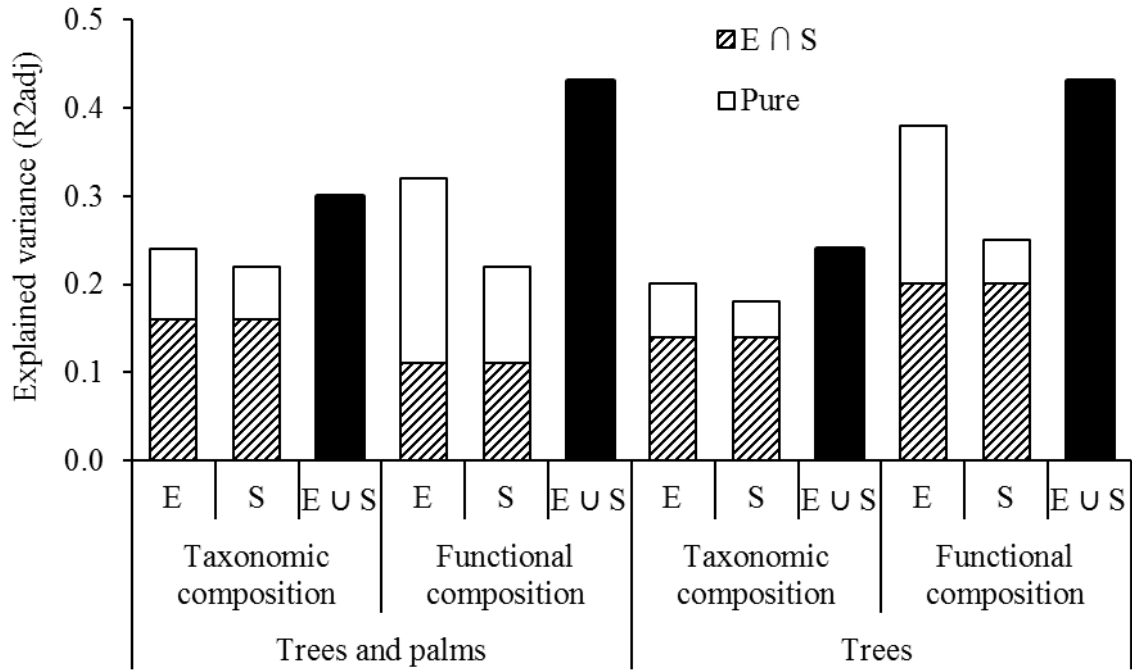


Figure 3. Variation partitioning results for taxonomic and functional composition. Adjusted coefficients of determination (R^2_{adj}) for each fraction are reported. Fractions are: E: environment; S: space; $E \cap S$: intersection of E and, i.e. the fraction of total variation explained by E and S that cannot be separated from each other (hatched bar); and $E \cup S$: union of E and S, i.e. total explained variance (black bar).

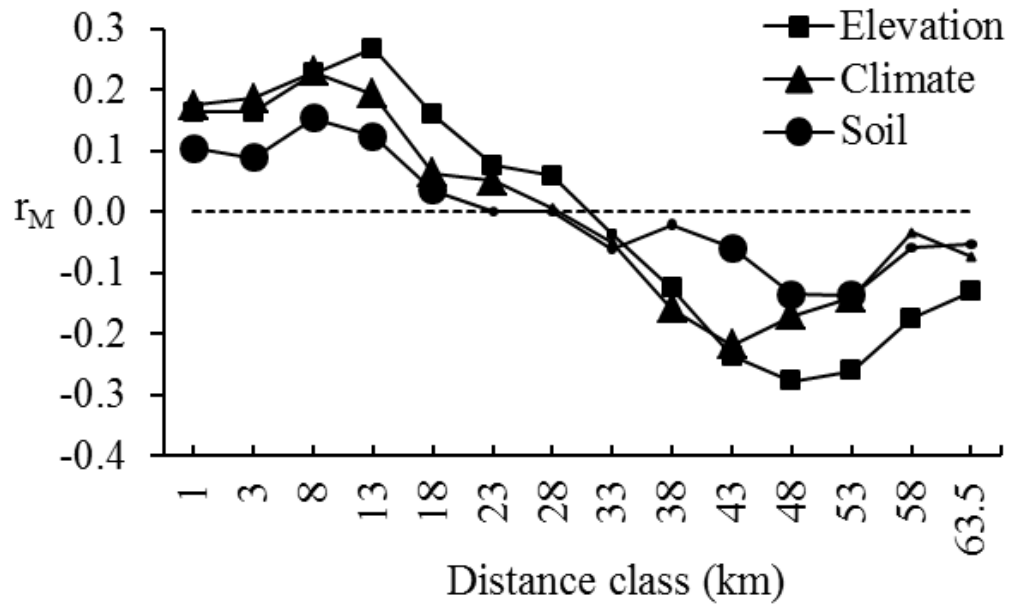


Figure 4. Mantel correlograms illustrating distance decay in environmental similarity. Large symbols indicate a significant (progressive Bonferroni corrected $p \leq 0.05$, 10000 permutations). The maximum geographic distance in each class is showed.

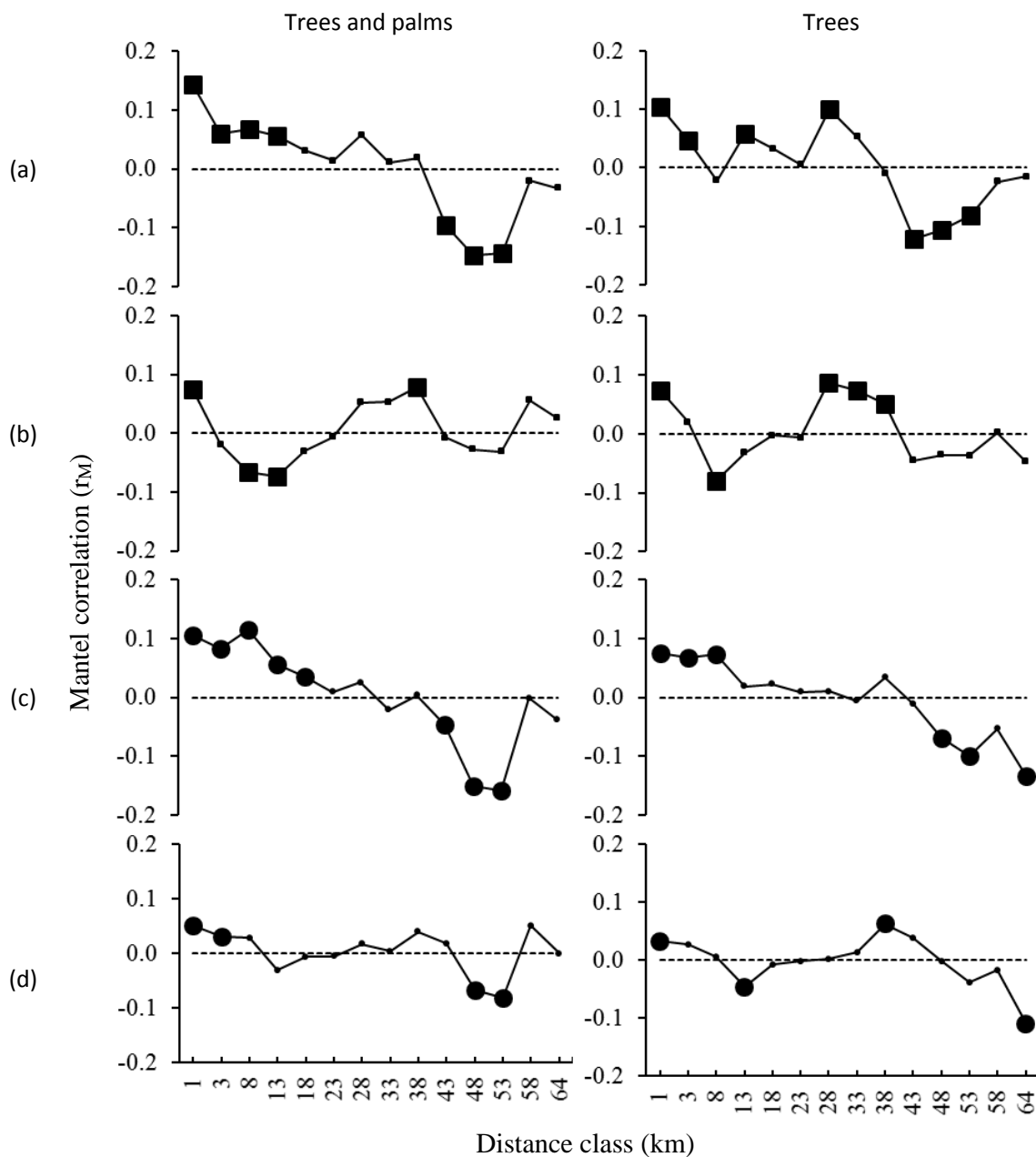
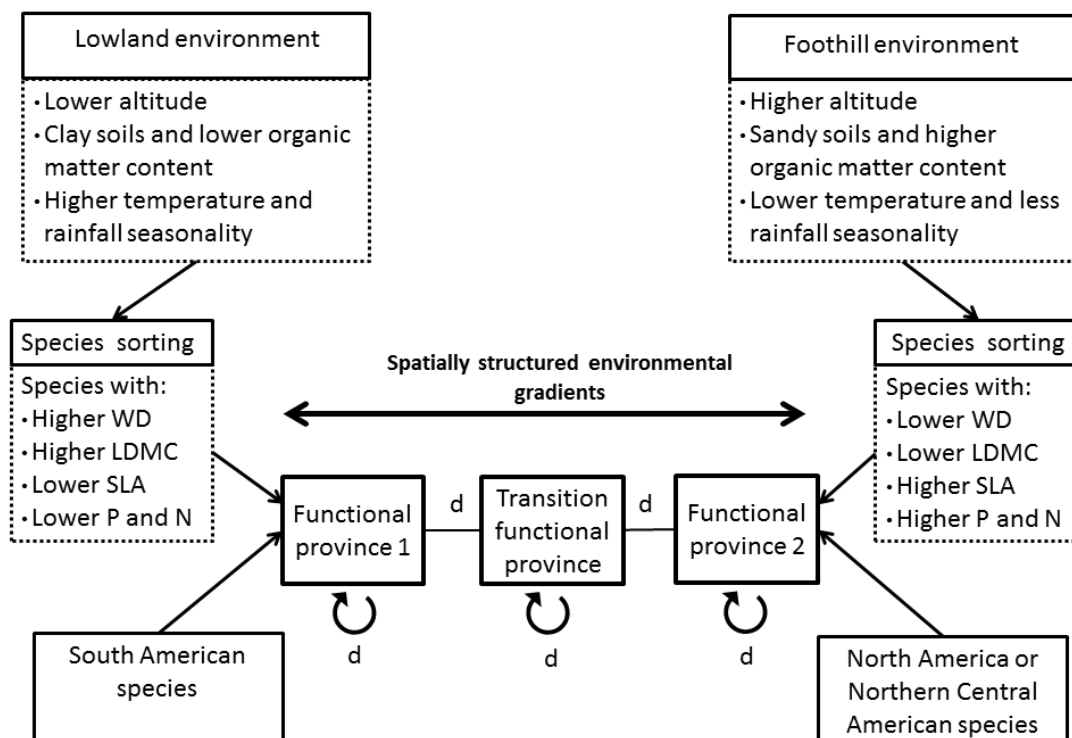


Figure 5. Mantel correlograms illustrating distance decay in taxonomic and functional similarity of plant communities, with (right column) and without (left column) canopy palms. (a) Distance decay in taxonomic similarity across distance classes. (b) Distance decay in residual taxonomic similarity, controlling for the effect of environment. (c) Distance decay in functional similarity across distance classes. (d) Distance decay in residual functional similarity, controlling for the effect of environment. Large symbols indicate a significant (progressive Bonferroni corrected $p \leq 0.05$, 999 permutations). The maximum geographic distance in each class is showed.



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Figure 6. Conceptual figure summarizing environmental and spatial mechanisms related to plant community assembly in the forests of the San Juan La Selva landscape, Costa Rica. Lowland and foothill environments represent the extremes of the spatially structured environmental gradients. In each extreme of these gradients two different functional provinces result from species sorting by the environment in accordance to their functional traits (WSG: wood specific gravity, SLA: specific leaf area, LDMC: leaf dry matter content). Dispersal spatial mechanisms (d) among local communities within functional provinces maintain taxonomic turnover and diversity. Different biogeographical origins of species contribute to the spatial structure of taxonomic composition and the differentiation of different forest types across the landscape. An intermediate forest type results from a combination of lowland and foothills species recruited given certain environmental conditions and dispersed from close local communities given species dispersal capacities.

Supplementary material

Apendix 1

Table A1. Short description and summary statistics of functional traits measured for canopy tree and palm species in the San Juan La Selva landscape, Costa Rica.

Trait (Abbreviation, Units)	Description	Mean \pm S.E.	Range
Specific leaf area (SLA, mm ² g ⁻¹)	Fresh leaf area divided by dry leaf mass.	14.04 \pm 0.29	5.69 - 46.75
Leaf area (LA, mm ²)	One-sided projected surface area of a single or an average leaf or leaf lamina.	71448.77 \pm 21917.23	485.88 - 3553833.17
Leaf Nitrogen content (N, mg g ⁻¹)	Total amount of N per unit of dry leaf mass.	24.46 \pm 0.38	2.3 - 40.9
Leaf Phosphorous content (P, mg g ⁻¹)	Total amount of P per unit of dry leaf mass.	1.09 \pm 0.02	0.4 - 2.3
Leaf dry matter content (LDMC, mg g ⁻¹)	Oven-dry mass of a leaf divided by its water-saturated fresh mass, related to the average density of the leaf tissues.	403.31 \pm 4.63	190 - 645.35
Wood specific gravity (WSG, g cm ⁻³)	Oven-dry mass of a section of a plant's main stem divided by the volume of the same section when still fresh.	0.57 \pm 0.01	0.07 - 0.87

Notes: Descriptions are based on Pérez-Harguindeguy et al. (2013).

Sampling and measurement of functional traits

For foliar trait measurements we collected five individuals per species, and measured 5 leaves per individual. Following Garnier et al. (2001) and Pérez-Harguindeguy et al. (2013) we collected foliar material including young, totally developed and expanded leaves, without no apparent damage by herbivorous or pathogens. Collected material was kept in plastic bags under a cool environment and rehydrated in the laboratory before foliar measurements. Leaf area in compound leaved species was the sum of individual leaflets without the petiole. In the case of palms LA area was calculated only for eleven randomly selected leaflets, and the mean leaflet area multiplied by the total number of leaflets to calculate total LA. LA measurements were made with a LI-3100C Area Meter with a 1mm resolution. For the measurement of SLA and LDMC leaves were oven dry at a 65°C during 48 hours. For specific wood gravity wood cores were taken for three individuals per species. Wood samples were oven dried at 101-105 °C for 24 hours or until constant weight (Williamson & Wiemann, 2010) and volume calculated following the water displacement method (Chave, 2006; Williamson & Wiemann, 2010). From field sampling and lab measurements we measured foliar trait values for 171 species (94% of all the individuals), and assigned genus and family level foliar trait values to 73 and 16 species in that order (respectively 4.2% and 1.7% of all individuals). In the case of WSG, we measured trait values for 159 species (93.3% of all individuals) and assigned genus and family mean level trait values to 80 species and 18 species (in that order, 4.7% and 1.8% of all individuals).

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Appendix 2

Table A2. Eigenvalues, cumulative percent variation, eigenvectors and correlation coefficients (within parenthesis) of the first three principal components for the six community weighted mean traits of canopy tree and palm species that best predicted forest plots functional composition. Eigenvectors are in order by their r value of the Axis 1.

Variables	Axis 1	Axis 2	Axis 3
Eigenvalue	3.6	1.43	0.55
Cumulative percent variation	60	84	93
Eigenvectors			
SLA CWM	0.50 (r = 0.95)	0.04 (r = 0.04)	-0.12 (r = -0.09)
P CWM	0.44 (r = 0.84)	-0.32 (r = -0.39)	0.02 (r = 0.01)
N CWM	0.43 (r = 0.82)	-0.03 (r = -0.03)	0.74 (r = 0.55)
WSG CWM	0.10 (r = 0.20)	0.78 (r = 0.94)	-0.22 (r = -0.17)
LA CWM	-0.43 (r = -0.81)	-0.43 (r = -0.51)	-0.02 (r = -0.02)
LDMC CWM	-0.41 (r = -0.78)	0.31 (r = 0.38)	0.62 (r = 0.46)

Notes: Community weighted means for six functional traits. LA: leaf area, SLA: specific leaf area, LDMC: leaf dry matter content, WSG: wood specific gravity, N: Nitrogen foliar content, P: Phosphorous foliar content. Correlation coefficients in bold denote significant correlations ($p \leq 0.05$).

Table A3. Eigenvalues, cumulative percent variation, eigenvectors and correlation coefficients (within parenthesis) of the first three principal components for the six trait community weighted means of canopy tree species that best predicted forest plots functional composition. Eigenvectors are in order by their r value of the Axis 1.

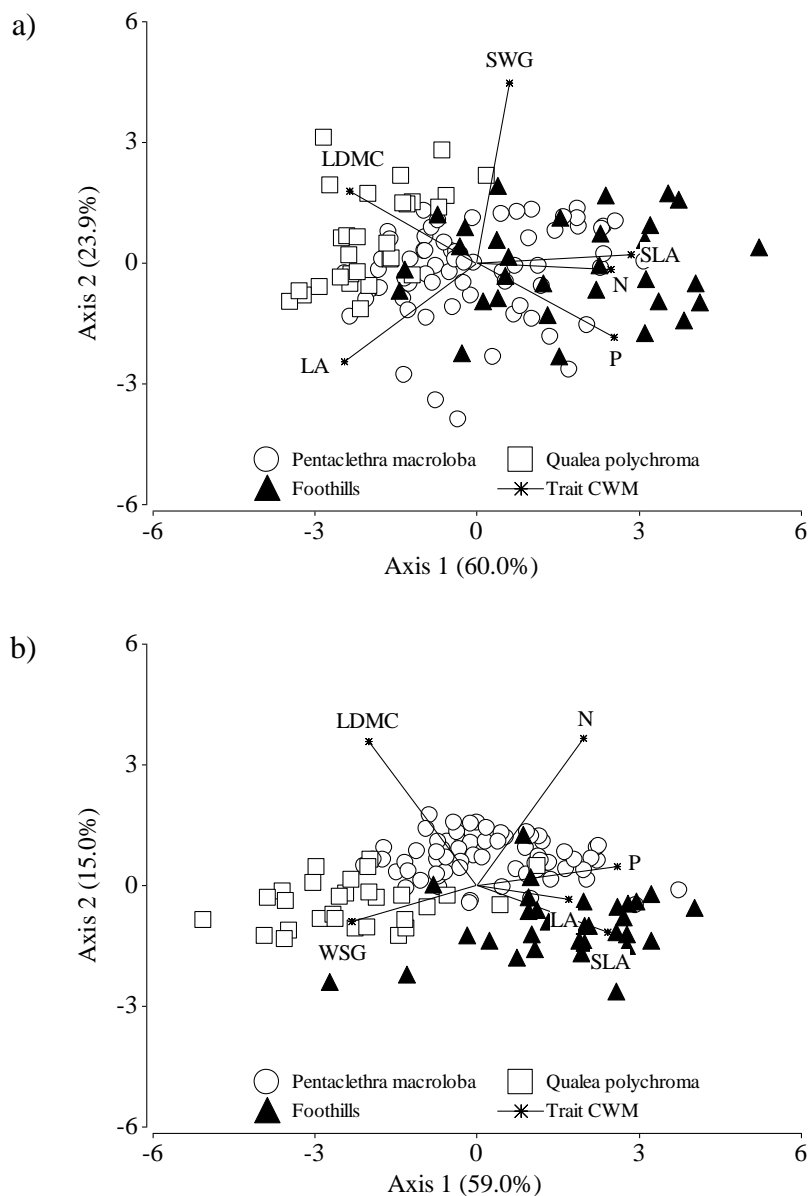
Variables	Axis 1	Axis 2	Axis 3
Eigenvalue	3.54	0.90	0.78
Cumulative percent variation	59	74	87
Eigenvectors			
P CWM	0.48 (r = 0.91)	0.09 (r = 0.08)	-0.11 (r = -0.09)
SLA CWM	0.45 (r = 0.85)	-0.22 (r = -0.20)	-0.27 (r = -0.24)
N CWM	0.37 (r = 0.69)	0.68 (r = 0.65)	-0.25 (r = -0.22)
LA CWM	0.32 (r = 0.59)	-0.06 (r = -0.06)	0.88 (r = 0.78)
LDMC CWM	-0.38 (r = -0.71)	0.67 (r = 0.63)	0.22 (r = 0.20)
WSG CWM	-0.43 (r = -0.82)	-0.17 (r = -0.16)	-0.16 (r = -0.14)

Notes: Trait community weighted means (CWM) of six functional traits. LA: leaf area, SLA: specific leaf area, LDMC: leaf dry matter content, WSG: wood specific gravity, N: Nitrogen foliar content, P: Phosphorous foliar content. Correlation coefficients in bold denote significant correlations ($p \leq 0.05$).

Table A4. List of spatial vectors (PCNM) and environmental variables selected through a forward selection procedure used in the variation partitioning analysis on taxonomic and functional composition of old-growth forest in the San Juan La Selva landscape.

	Species composition		Functional composition	
Variation explained by:	Trees and palms	Trees	Trees and palms	Trees
Environment	Soil: Clay, silt, OM, Ca Climate: TempSd, TempMin, Prec, PrecCV, PrecDriest Elevation	Soil: Clay, Silt, OM, Ca, pH Climate: TempSd, Tempmin, Prec, PrecCV, PrecDriest Elevation	Soil:Ca, P Climate: Temp, TempSd, PrecDriest Elevation	Soil: Clay, Silt, OM, Ca, pH Climate: TempSd, Tempmin, Prec, PrecCV, PrecDriest
Space	12 PCNMs	14 PCNMs	7 Pcnms	7 PCNMs

Notes: Abbreviations correspond to OM: Organic matter, Temp: Annual mean temperature, TempSD: Temperature seasonality (SD), TempMin: Minimum temperature of coldest month, Prec: Annual precipitation, PrecDriest: Precipitation of driest month, PrecCV: Precipitation seasonality (CV).



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Figure A1. Ordination of vegetation plots (N = 127) along PCA axes one and three summarizing the functional trait space from six traits community weighted means (CWM) calculated using relative abundance of both plant and tree species (a) and only tree species (b). Plots are differentiated by their membership to three forest types previously delimited in the study region by Sesnie et al. (2009). Traits are wood specific gravity (WSG), leaf dry matter content (LDMC), leaf area (LA), specific leaf area (SLA), and Nitrogen (N) and Phosphorus (P) leaf content.

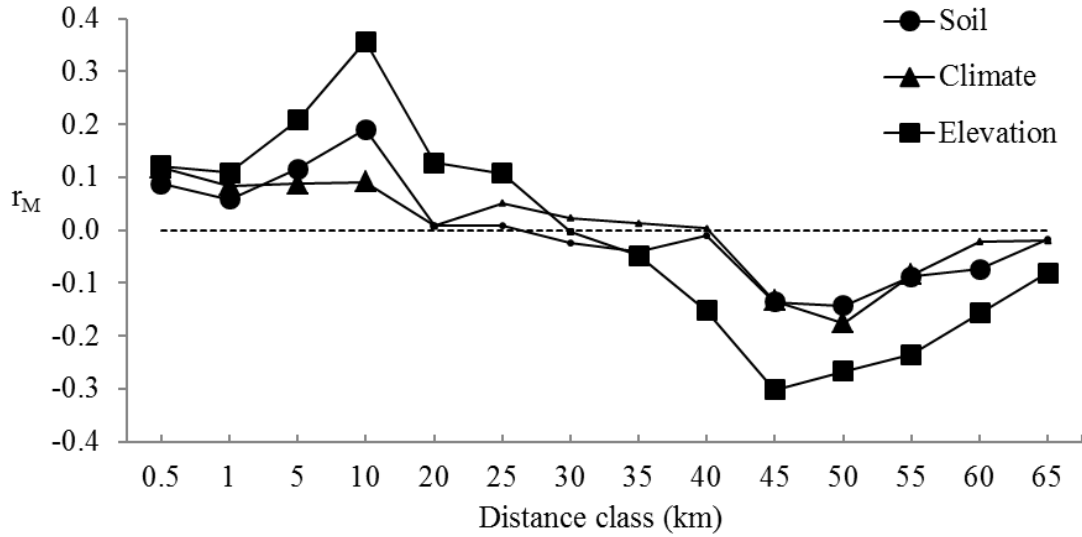


Figure A2. Mantel correlogram illustrating distance decay in taxonomic similarity soil, climate and elevation variables characterizing studied forest plots in the San Juan La Selva landscape in northern Costa Rica. Large symbols indicate a significant (progressive Bonferroni corrected $p \leq 0.05$, 10000 permutations) Mantel statistic (r_M) for each distance class. The x-axis shows the maximum geographic distance in km in each class

Chapter 3: Potential Trajectories of Old-Growth Neotropical Forest Plant Functional Composition under Climate Change

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Abstract

Question: We modeled community weighted mean (CWM) trait values of tropical forests under current climate and quantified potential changes in functional composition due to global warming.

Location: San Juan La Selva region, northern Costa Rica.

Methods: We used the abundance of trees and palms species together with values of six functional traits (leaf area: LA, specific leaf area: SLA, leaf dry matter content: LDMC, leaf nitrogen: N and phosphorus content: P) for 257 species distributed across 127 (0.25 ha) forest plots to calculate per-plot community weighted mean (CWM) trait values. We summarized variation in eight temperature and precipitation variables along two main climatic gradients through a kernel principal component analysis. We quantified the response of CWM traits to current climate gradients using generalized additive modeling. Modeled relationships were then used to predict and map CWM traits under current and future (RCP 8.5, year 2050) climate, and quantify changes in these functional properties. 17 general circulation models were assessed to calculate uncertainty in predictions. Using kernel functions we calculated the probability density of forest plots within a bidimensional trait space both under current and future climate conditions, and quantified the potential changes in functional area.

Results: Precipitation variables were more important predictors than temperature in modelling CWM traits. With projected climate change, we observed increases in CWM SLA, N and P, while CWM LDMC decreased in most of forest plots. No consistent trends were found for

CWM LA and WSG. Uncertainty in predicted changes under the future scenario varied across the study area and among traits. Lowland forest communities converged on a single direction of CWM traits change, while foothills forest communities showed divergent future trends. Area of current functional space occupied by forest plots was reduced by 50% under future climate. More than 65% of current functional space was lost and given new combinations of CWM traits forest communities occupied new areas of functional space.

Conclusions: Our results for a high emission scenario indicated a change from communities with “conservative” CWM trait values to communities characterized by more “acquisitive” CWM trait values. The observed reduction of functional area among old-growth forest communities under future climate may have further effects on ecosystem functions and services currently delivered by these tropical rainforests.

Introduction

Understanding relationships between vegetation patterns and environmental characteristics is a central theme dating to the earliest studies of plant community ecology (see Egerton 2013). A shift in the approach to model vegetation and community composition along environmental gradients has occurred in recent decades, in which vegetation-environment relationships are studied using plant functional traits, instead of using species taxonomic identity alone (Keddy 1992; Shipley et al. 2006; Cornwell & Ackerly 2009; Swenson et al. 2011; Douma et al. 2012; Van Bodegom et al. 2012; Boulangeat et al. 2012; Siefert et al. 2013). Plant functional traits are defined as any morphological, physiological or phenological feature measurable at the individual level and influencing species performance (Violle et al. 2007). As a result, functional traits limit the range of environments in which plant species can grow and survive, thus constraining their geographic ranges. Because functional traits are also related to ecosystem functioning (de Bello et al. 2010), conceptual frameworks have been developed where traits are considered key components of ecosystem processes and services (Chapin et al. 2000; Lavorel & Garnier 2002; Hooper et al. 2005; Díaz et al. 2007; Díaz et al. 2011).

Functional properties of plant communities can be summarized by different metrics related to the diversity or central tendency of functional traits values (Mason et al. 2005; Mouchet et al. 2010). In particular, the community weighted mean (CWM) trait value (i.e. the

average trait value calculated as the sum of species trait values weighted by their relative abundance in the community; Garnier et al. 2004; Díaz et al. 2007), is a promising approach to summarize community functional properties in ways that are useful for quantifying ecosystem functioning (Garnier et al. 2004; Ruiz-Jaen & Potvin 2011; Dias et al. 2013; Lavorel 2013) and plant community relationships to environmental variables (Shipley et al. 2006; Swenson & Weiser 2010; Kleyer et al. 2012; Dubuis, Rossier, et al. 2013; de Bello et al. 2013; Siefert et al. 2013; Fortunel et al. 2014).

Functional traits may therefore hold great utility in forecasting the response of plant communities to climate change, however, how tropical forest functional characteristics will change as a result of climate change remains unknown. Evidence for climate change is unequivocal, with projected impacts on all global ecosystems (IPCC 2013). Precipitation over tropical areas has increased over the last decade, with concomitant increases in the number of heavy precipitation events, however precipitation trends reported vary depending on location (IPCC 2013). In Central America and northern South America, evidence show a general warming trend over the 1961–2003 period, with rainfall events intensifying due to a larger contribution of wet and very wet days to total annual rainfall (Aguilar et al. 2005). Central America is also one of the regions showing a consistent drying signal in future climate scenarios (Neelin et al. 2006), and the magnitude of change in climate in this region is expected to be larger than any other tropical region (Giorgi 2006) moving ecosystems out of their historical climate range relatively sooner (Hawkins & Sutton 2011). In Costa Rica it has been shown that tree growth is affected by dry-season conditions and variation in mean annual nighttime temperatures (Clark et al. 2010), and preliminary models for tropical lowlands suggest that these forests will experience a net loss of plant species richness due to climate moving out of their current range of heat tolerance (Colwell et al. 2008).

Climate change will cause major changes in ecosystem, structure and function as a consequence of alteration in plants group dominance, ecological interactions among species, and shifts in species geographical ranges, with predominantly negative consequences for biodiversity and ecosystem goods and services (IPCC 2013). Because tropical tree species richness is high and species exhibit differential sensitivity to changes in climate, modelling changes in plant community functional composition represents an appropriate mechanistic approach to assess how tropical forest will respond to global change. In spite of this, few

attempts to build spatially explicit models of functional traits have been made (Swenson & Weiser 2010; Dubuis, Rossier, et al. 2013), none of which are for tropical areas, and only Dubuis et al. (2013) assess climate change impacts. Here, we explore the relationship between old-growth rain forest CWM trait values and climatic gradients under current and future conditions, to examine potential changes in community functional composition. Using abundance data of tree and palm species in concert with values of six functional traits for 257 species distributed across 127 forest plots across a 6,166 km² landscape in northern Costa Rica, our specific objectives were to (i) model the response of CWM traits to current climate predictors, (ii) use the modeled relationships to predict and map current and future values of CWM traits, and (iii) quantify potential changes in CWM trait values and bidimensional functional area occupied by the plots under a range of models within a future climate change scenario. These objectives are part of a larger study grounded in the finding that niche assembly processes predominate in the determination of community assembly in these forest communities, indicating that both climatic and edaphic variables control forest functional beta diversity (Chapter 1).

Methods

Study area

Located in northeastern Costa Rica, the study area covers 6,166 km² and extends from the highlands of the Central mountain range of Costa Rica to the lowlands of the San Juan River, which forms the Nicaraguan border (Figure 1). Elevation in the area ranges from near sea level to 2,881 m a.s.l. The study area includes the San Juan-La Selva Biological Corridor (SJLS-BC), an important ecological conservation initiative that provides habitat connectivity for many forest species along the Mesoamerican Biological Corridor. Gridded data sets for the region (Hijmans et al. 2005) indicate a mean annual temperature range from 26.2°C to 10.8° following elevation, and a mean annual precipitation range from 2,134 mm to 4,932 mm. Temperature and precipitation vary with elevation and distance from the Caribbean coast (Figure 1). While having high human settlement, the landscape still contains more than 50% of its original forest cover (Morse et al. 2009; Fagan et al. 2013), including two Holdridge life zones (Lieberman et al. 1996). Old-growth forests are well differentiated by species

composition and climatic and edaphic characteristics to form three main vegetation types: two lowland forest types and one foothill forest type at higher elevations (Sesnie et al. 2009).

Species and functional trait data

Abundance data of canopy tree (≥ 30 cm dbh) and palm (≥ 10 cm dbh) species were retrieved from a data set of 127 0.25 ha old-growth forest plots established by Sesnie et al. (2009) across the SJLS-BC area (40 - 1200m a.s.l; Figure 1). Detailed information on plot establishment, measurement of individuals and species identification can be found in Sesnie et al. (2009). All tree and palm species registered in vegetation plots and identified to the level of species or genus ($n = 257$) were selected for trait measurement. Trait measurements carried in this study complemented an existing tree and palm species trait database collected as part of the Diversus Collaborative Research Network (IAI CRN 2015) project and partially published in Kattge et al. (2011). Following standardized protocols (Garnier et al. 2001; Williamson & Wiemann 2010; Pérez-Harguindeguy et al. 2013), we measured six functional traits known to covary with climate (Wright et al. 2004; Wright et al. 2005; Ordoñez et al. 2009; Chave et al. 2009), including leaf area (LA, mm²), specific leaf area (SLA, mm² mg⁻¹), leaf dry matter content (LDCM, mg g⁻¹), leaf nitrogen (N mg g⁻¹) and phosphorus (P mg g⁻¹) content, and wood specific gravity (WSG, g cm⁻³). Foliar traits and WSG were respectively measured in five and three individuals per species collected within the study area. Detailed information on trait sampling and measurement is found in Chapter 1. The average trait value per species was combined with species relative abundance per plot to calculate CWM values of each trait per plot. CWMs were computed with the 'FD' library (Laliberté & Legendre 2010) in the statistical software R (R Development Core Team 2014).

Climate data

Climatic predictors variables corresponded to eight bioclimatic variables from interpolated weather station data representing mean climate conditions for the 1950-2000 period (Hijmans et al. 2005) and downscaled to ~1 km resolution grids (data available at <http://www.worldclim.org>). We selected annual mean temperature, minimum temperature of the coldest month, maximum temperature of the warmest month and standard deviation of temperature as a measure of seasonality. Precipitation variables included mean annual

precipitation, precipitation of the driest month, precipitation of the wettest month and coefficient of variation of precipitation.

Future climate data (for the 2041-2060 period) were derived from 17 general circulation models (GCMs) outputs under a high radiative forcing scenario of 8.5 Wm⁻² (RCP 8.5, corresponding to ~1370 ppm CO₂ by the year 2100; van Vuuren et al. 2011), from the Coupled Model Intercomparison Project, Phase 5 (CMIP5), and used on the Fifth Assessment IPCC report (AR5) (IPCC 2013). Coarse GCM outputs were downscaled (to 0.30 seconds, ~1km) using the delta method that relies on adding future climate anomalies to a high resolution historical climatology (WorldClim 1.4, Hijmans et al. 2005, available at <http://www.worldclim.org>). All GCMs under the selected scenario showed an increase in mean annual temperature between 1.4 - 2.9 °C over the study area. In contrast, precipitation increased or decreased depending on the location and model. We found an increase in mean annual precipitation ranging from 3 - 836 mm, with 12 of all 17 assessed models showing a positive anomaly. Precipitation of the wettest month is also predicted to increase (13 of 17 models showed positive anomalies), showing an opposite trend to decreasing anomalies for the driest month, in overall indicating increased seasonality in precipitation under the future scenario. Summary statistics for current and future eight climatic variables are given in Table S1.

Data analysis

Assessing the response of CWM traits to climate

The response of individual CWM traits to climate predictors was assessed through generalized additive models (GAMs). Function ‘*gamm*’ in the ‘*mgcv*’ library (Wood 2011) was used in the R statistical environment. The Gaussian distribution and the P-splines smoothing function were used as GAM parameters. GAMs included a correlation structure to take into account the lack of independence of residuals. Before performing GAMs, we used a kernel principal components analysis (KPCA), a nonlinear form of PCA, to reduce the multidimensional climate variability and to extract orthogonal axes of climatic variation for use in the GAM modeling, as well as to avoid problems related to having collinearity among climatic predictors. The function ‘*kpca*’ in the ‘*kernlab*’ library (Karatzoglou et al. 2004) in R was used to run KPCAs. Universal Transverse Mercator (UTM) latitude and longitude

coordinates were also added to the models as predictors to assess any spatial trends in CWM traits and as covariates of climatic predictor variables.

Predicting current and future CWM traits

To obtain CWM trait values for each plot under current climatic constraints, we extracted the fitted values from the GAMs described above. We first used the KPCA fitted model for current climatic data to predict axes of future climatic variation. We then used the above-described fitted GAMs to predict trait CWMs under future climate conditions for each plot under each of the 17 GCMs. Using continuous climate grids, we followed the same procedure to predict current and future values of each CWM trait across the entire landscape and to assess their spatial distribution. Continuous forest cover was assumed even when forest cover correspond to ~50% of the total study area. CWM trait values were assumed to change under future climate conditions when the mean future value from across all 17 GCMs projections was below (indicating a decrease) or above (increase) the 95% confidence interval around fitted values from GAMs. Proportion of change was calculated both at the plot level and at landscape level, respectively as the number of plots or pixels showing significant increase or decrease in their CWM trait values. At landscape level the likelihood of change was estimated as the percentage of scenarios showing a significant decrease, increase or no change in CWM traits, relative to the 95% confidence intervals around current fitted CWM traits from GAMs.

Assessing changes in multi-trait community functional composition

Using a PCA, plots were ordinated in the multivariate space of the six CWM traits predicted under current climatic conditions. Function 'prcomp' in 'stats' R library (R Core Team 2012) was used to perform PCA. Using the same fitted function in this PCA, plots were ordinated in the functional space given their future average CWM trait values (from 17 assessed GCMs). The direction and magnitude of plots functional changes from present to future conditions was then assessed. Through bivariate kernel functions we calculated the probability density of forest plots within the functional space of the two first PCA axes both under current and future climate conditions. Functions 'kernelUD' in the 'adehabitat' library (Calenge 2006) in R were used to perform the two-dimensional kernel density estimations. The area no longer occupied by the future functional space ('lost' functional space), the new area occupied by the

future functional space ('gained' functional space), and the area shared by current and functional space (unchanged functional space) were calculated. Functions 'kernel.area' and 'kerneloverlap' in the 'adehabitat' library (Calenge 2006) in R were respectively used to calculate above described areas of functional space.

Results

Response of CWM traits to climatic variables

Kernel PCA axes depict the climate variation of plots across two major climatic gradients (Figure 2). PCA Axis 1 represented a precipitation gradient, being positively correlated with precipitation seasonality and negatively correlated with mean annual precipitation and precipitation of the wettest and driest months (Table S2). Along PCA Axis 2 vegetation plots were better differentiated in relation to temperature variables, all negatively correlated with this axis (Table S2), but both precipitation of the wettest month and coefficient of variation of precipitation were positively associated with this axis.

GAMs assessing the response of individual CWM traits to climate predictors indicated that the percentage of explained deviance in the six CWM traits ranged from 54.4% (LA) to 18.2% (WSG) (Figure 3). LA, SLA, LDMC and N CMWs were relatively well predicted ($R^2_{adj} > 30\%$), while P and WSG showed lower adjusted R squared values ($R^2_{adj} < 0.24$). Either PCA Axis 1 or PCA Axis 2 explained most of the trait variation and showed a prevalent non-linear relationship with all CWM traits (Figure 3; Table S3; Figure S1). PCA Axis 1 was a significant factor in all CWM traits except LDMC, which was the only trait that significantly responded to PCA Axis 2. UTM X coordinates were a significant factor for LA, SLA, N and P (Table S3).

Community traits projection under current and future climatic constraints

Future climate models indicated a general increase in plot CWM SLA, N and P (Figure 4, Table S4). Although no plots showed a decrease in CWM N, nearly 55% of plots showed no future change in CWM values of this trait. Trends for community LDMC indicated a general decrease, however nearly 40% of plots showed no significant change in this CMW trait (Figure 4). Predicted future trends for currently low LDCM values varied widely among assessed future GCMs. No clear tendency was observed for LA and WSG CWMs, with

similar proportion of plots showing increase and decrease in community values, particularly in the case of WSG (Figure 4). CWM WSG showed an increase in plots where it is currently low, and a decrease where it is currently high, with the latter plots also showing higher uncertainty in future predictions due to larger standard errors (Figure 4).

Changes in community functional composition

The first two axes of the PCA using current plot CWM traits explained 76% and 13% of total variance among vegetation plots (Figure 5). CWM SLA, P, N and WSG were positively correlated with PCA Axis 1, and CWM LA and LDMC negatively correlated with this Axis (Table S5). CWM LDMC and N were positively correlated with PCA Axis 2, while CWM LA was negatively correlated with this same axis (Table S5). The observed increase in CWM N, SLA, P and WSG values, and the decrease of CWM LA and LDMC values from current to future climate conditions resulted in the aggregation of plots and a consequent reduction of the functional space (Figure 5a). Functional space area was reduced by 50.4% percent, from 42.61 square units under current conditions to 21.59 square units under future climate. Of total functional space occupied by forest plots under current climate 67% percent was lost following future climate CWM trait predictions, while remaining 33% was still shared with future functional space, indicating that 35% of future functional space corresponds to values of multidimensional space not previously occupied by forest plots under current climate conditions.

Under the future climate scenario, forest plots currently classified as lowland forest types with higher LA and LDMC CWMs moved along PCA Axis 1, showing increased community values of WSG, N, SLA and P (Figure 5c,d). These lowland forest plots also moved towards negative values of PCA Axis 2, indicating a slighter decrease in community LDMC. No general trend was observed for those plots within the foothills forest type (Figure 5b). However, foothills forest plots that are currently more similar to current lowland forest plots followed similar trends observed in lowland forests moving towards positive values of Axis 1 and negative values of Axis 2.

Landscape patterns of CWM traits along climatic gradients

According to patterns observed for the 127 old-growth forest plots (Figure 4) CWM SLA, LA and P either increased or showed no change across the entire study region under the future climate scenario (Figure 6). Increases in these CWM traits were mainly observed in the eastern portion of the study region, towards the Caribbean coast. Similar proportions of increase and decrease for both LA and WSG CWMs were observed across the study area, however large zones showed no change in these traits. CWM LA values also increased in the eastern portion of the study region, while increases in CWM WSG were observed in the north center portion, showing a range reduction in CWM WSG values in this portion of the study region. CWM LDMC decreased showing a strong range reduction in most of the study area, with the exception of the area corresponding to the foothills towards the higher altitudes of the Central Mountain Range. Higher certainty values in future predicted values were observed for N, P and SLA CWMs with 56%, 47% and 46% of total landscape area showing likely probabilities of change ($\geq 66\%$). Future trends in LA, WSG, and specially LDMC CWMs showed less convergence among climate models, showing small proportions of total landscape area with likely probabilities of change (Figure 6).

Discussion

Understanding the effects of climate change on vegetation remains a major challenge in ecology, particularly for highly diverse tropical forests. In our study we were able to successfully build models of CWM trait response to climatic gradients to predict and spatially project current and future community weighted mean values for six functional traits related to the stem and leaf economic spectrum of plant species. We found that the main east-west precipitation gradient (from the Caribbean coast) was a more important predictor of CWM traits than the temperature gradient towards the Central Mountain Range. By carrying out current and future predictions of the functional properties of lowland and foothills plant communities we assessed the direction and magnitude of the potential climate-induced change, which resulted in higher values of CWM SLA, P and N, and lower values of CWM LDMC, and the reduction of the bidimensional functional space occupied by 127 old-growth forest plots.

Climatic gradients underlying community trait patterns

CWM trait values responded clearly to the current precipitation gradient, which is characterized by greater rainfall seasonality to the west and in higher altitude areas within the Central Mountain Range. In accordance with future precipitation projections previously described for Central America (Aguilar et al. 2005), there was a large variation in future precipitation patterns among the 17 assessed climate GCMs (RCP 8.5, year 2050), however we found likely changes (with varying magnitudes) in future traits values over 50% of the study area. Although patterns across altitudinal gradients have been used to highlight the impact of temperature change on biological communities (Malhi et al. 2010), we demonstrate that future precipitation patterns in tropical regions may be of great importance for lowland and premontane forests. The assessment of vegetation plots in higher altitudes, however, must be considered in future research in the study area, since their inclusion in our models of functional response to climate will allow to better predict future CWM traits in higher altitudinal areas towards the Central Mountain Range with climates differing from the climatic range found among assessed forest plots. Finally, due to the lack of detailed continuous edaphic data our CWM trait response models did not take into account edaphic variables known to greatly influence functional trait values (ter Steege et al. 2006; Fyllas et al. 2009; Quesada et al. 2012; Fujita et al. 2013; Fortunel et al. 2014) and improve models of species distributions (Dubuis, Giovanettina, et al. 2013). Our spatial projections of CWM traits should improve when including soil predictors (Swenson & Weiser 2010; Dubuis, Rossier, et al. 2013). It must be considered, though, that soil variables in our study area covary with climate and elevation (Lieberman et al. 1996; Sennie et al. 2009), and thus our models may indirectly account for soil variability. Finally, under the future scenario we used, less than two percent of total area showed no-analogous climate when assessing values of climate PCA 1, and less than one percent when assessing climate PCA axis 2. Even when projected climate does not predict great areas of no-analog climate in this region, these new climatic conditions may arise under other climatic scenarios, imposing new questions on the possibility of new species arrival with new functional strategies completely changing the CWM traits (Dubuis, Rossier, et al. 2013).

Future changes in functional composition of old-growth forest communities

Our results suggest that lowland plant communities characterized under current climate conditions by high values of CWM LA and LDMC, will undergo changes in their functional composition towards higher values of CWM N, LA, P and WSG, and lower values of CWM LDMC and LA, i.e. similar to community trait values currently associated to forest communities in the foothills forests. These future CWM trait values suggest a shift in lowland plant communities with more conservative plant species with denser, nutrient poor leaves and slower growth, to communities with more exploitative plant species with fast nutrient acquisition and turnover, associated with thinner, nitrogen-rich leaves and fast growth (Wright et al. 2004; Poorter et al. 2009; Wright et al. 2010; Lavorel 2013; Adler et al. 2014). Such changes in forest functional composition resulting both in the reduction of current functional space and new combination of CWM trait values within new functional space may have repercussions in ecosystem functioning, since leaf and stem traits and different plant functional groups are known to affect ecosystem processes such as above-ground biomass storage (Ruiz-Jaen & Potvin 2011; Conti & Díaz 2013), litter decomposition (Cornwell et al. 2008; Brovkin et al. 2012; Freschet et al. 2012), soil N and P pools and primary productivity (Hooper & Vitousek 1997; Brovkin et al. 2012). In this sense, functional diversity metrics taking into account functional richness, evenness and divergence of trait values should also be assessed to better understand the possible consequences of the observed functional change (Clavel et al. 2011), as evidence exists that not only dominant species drive ecosystem functioning but also non additive effects among species with different trait values may occur (Lavorel 2013).

Models such as the Community Assembly by Trait Selection (CATS) proposed by Shipley et al. (2006) suggest that CWM trait values allow to predict the potential current and future occurrence of species within plant communities. Although such an approach has been successfully applied in low diversity system like arid steppes (Frenette-Dussault et al. 2013) and temperate vegetation communities (Shipley et al. 2011; Laughlin et al. 2011), in Neotropical forests with high taxonomic turnover, as in the case of the old-growth forest here studied (see chapter 1), the abundance prediction levels for rare (low abundance) species under this approach should be low (Sonnier et al. 2010; Merow et al. 2011; Shipley et al. 2012). Rare species within communities may still have great effects on functional

composition and ecosystem functioning, and thus assessing the multidimensional functional composition of plant communities and their response to climatic variation allows to better assess vegetation changes under environmental change. Few species level assessments provide limited understanding of ecosystems functioning, and coarse scale modeling approaches focused on plant functional types (Krinner et al. 2005; Thuiller et al. 2006; Küster et al. 2011) do not allow for an understanding on the plant community level response to changes in structure and function. In this sense, the use of continuous functional trait data can help improve vegetation models widely used to assess potential impact on ecosystems and functions (Van Bodegom et al. 2012; Boulangéat et al. 2012).

Conclusions

Our study represents the first attempt to project CWM traits under future climatic conditions in the Neotropics as part of the greater challenge of understand impacts of climate change on different component of biodiversity. We report shifts in community functional composition in old-growth Costa Rican forests, where changes in precipitation and temperature gradients predict denser leaf, richer nutrient leaves in future lowland communities currently distributed in poor soil environments. Our results indicated a change from communities characterized by CWM traits values associated with more conservative species to communities characterized by CWM trait values associated to more acquisitive species. The observed reduction of the current multi trait functional space among old-growth forest communities as well as new trait combinations observed under future climate may have further effects on ecosystem functioning and ecosystem services currently delivered by these tropical rainforests. More studies on the drivers of change of tropical vegetation must be conducted to better project possible effects community assembly and ecosystem functioning.

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Figures

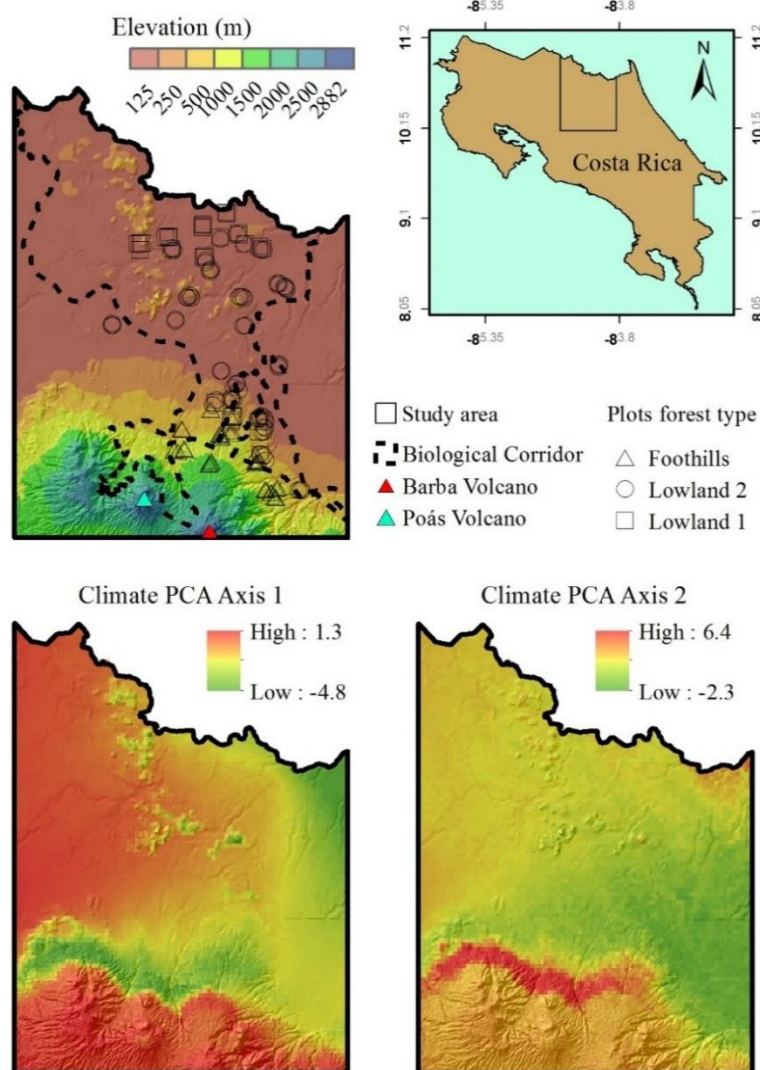


Figure 1. Study area location in northern Costa Rica. Sampled vegetation plots were established from north to south within the limits of the San Juan La Selva Biological Corridor. Plots are classified into one foothills forest type and two lowland forest type following Sesnie et al. (2009). Eight temperature and precipitation variables were summarized in two principal component analysis (PCA) axes of variation (see Figure 2). PCA axis 1 represents a precipitation gradient (with higher values related to higher precipitation seasonality and lower values to higher total annual precipitation). Axis 2 represents both a temperature and precipitation gradient (with higher values associated with higher seasonal precipitation and higher precipitation during the wettest month, and lower values related to higher temperatures across the year and higher temperature seasonality).

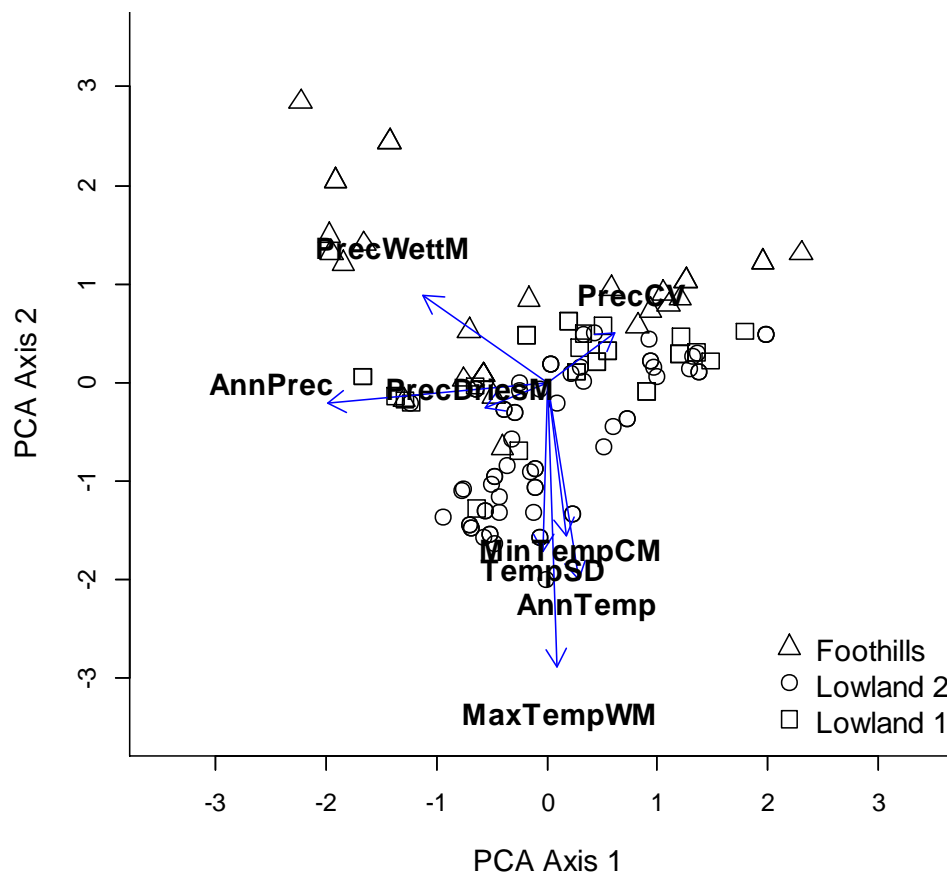


Figure 2. Results from a kernel principal component analysis to ordinate 127 vegetation plots in the multivariate space of eight temperature and precipitation variables. AnnTemp: annual mean temperature; MinTempCM: minimum temperature of the coldest month; MaxTempWM: maximum temperature of the warmest month; TempSD: standard deviation of temperature; AnnPrec: mean annual precipitation; PrecDriesM: precipitation of the driest month; PrecWettM: precipitation of the wettest month; PrecCV: coefficient of variation of precipitation.

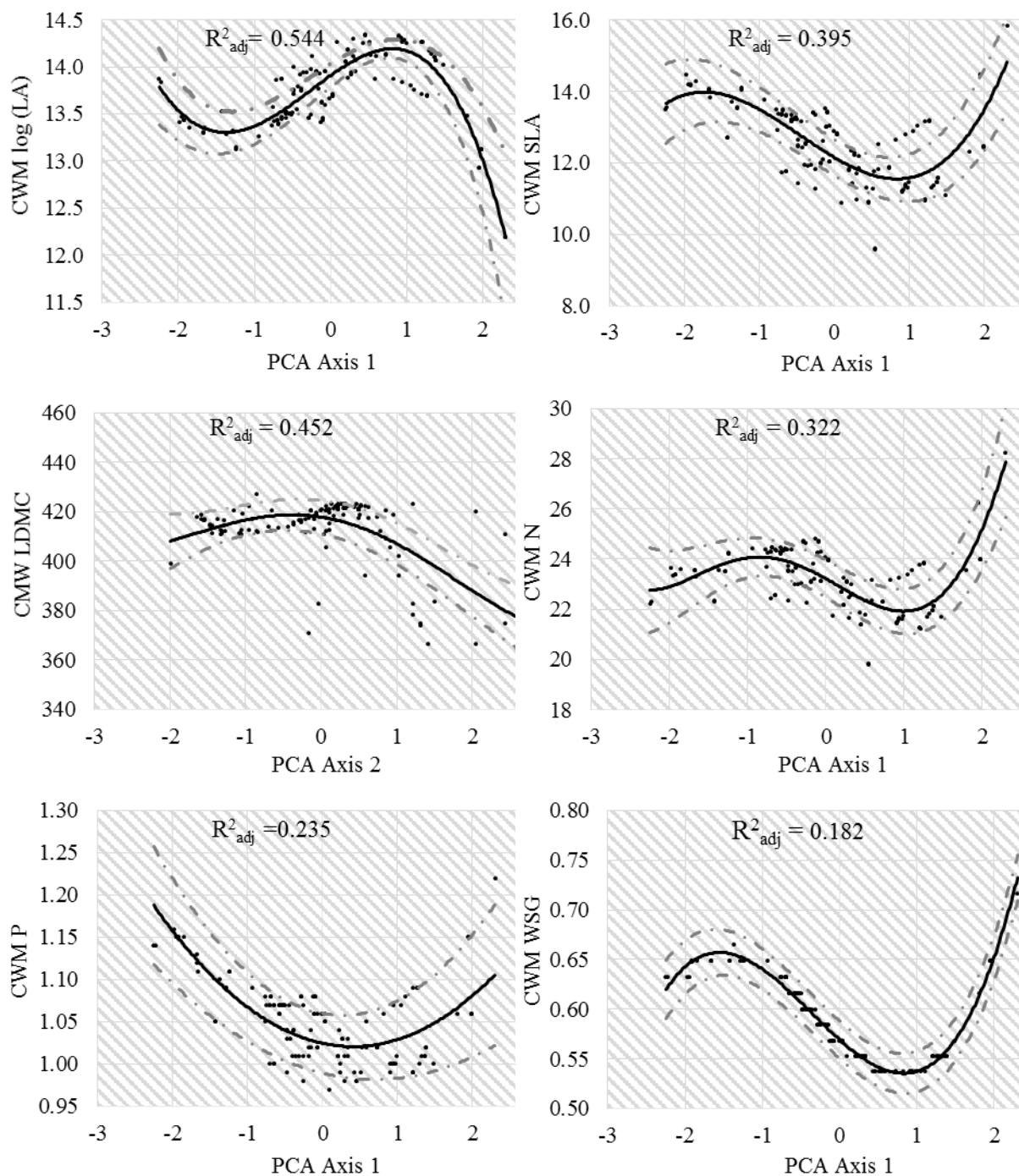


Figure 3. Generalized additive regression models (GAMs) illustrating the relationship between CWM traits and the most significant climate PCA axes of variation. Dashed lines represent the 95% confidence interval. Explained deviance (R^2_{adj}) represents a significant model ($P < 0.001$)

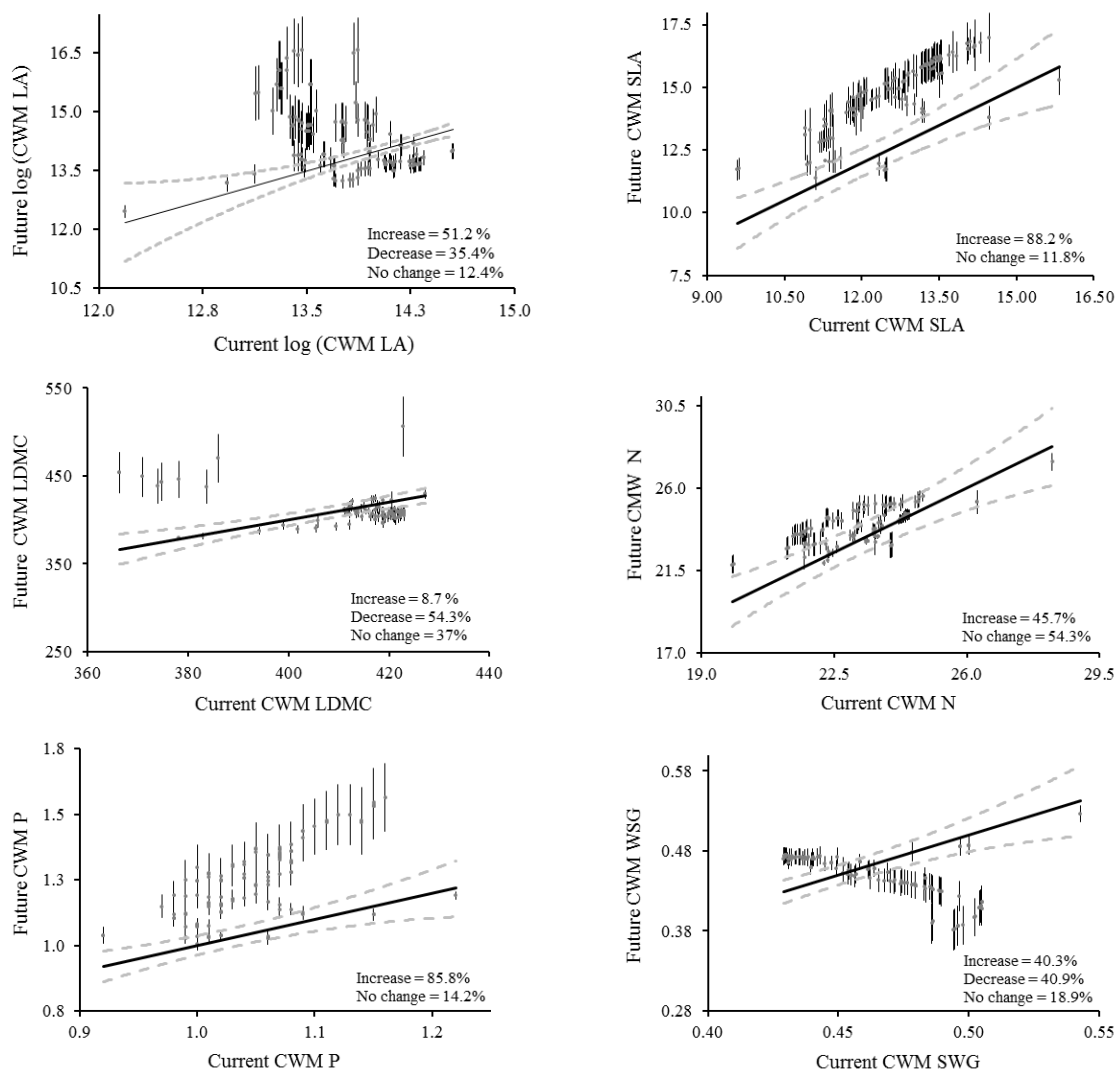


Figure 4. Comparison of predicted community weighted mean values of six functional traits for 127 forest plots under current and future climate. Black squares indicate the average predicted CWM trait values under future climatic models (2050, RCP 8.5) and vertical black lines \pm standard error from 17 general circulation models. Black solid lines represents a model where no changes in CWM trait values would occur. Future average predicted CWM trait values laying within model prediction boundaries under current climate (95% prediction interval, dashed grey lines) indicate lack of predictive capacity to conclude on trait changes. The proportion of increase, decrease, and no change under future climate shown in the lower right box were determined as average predicted future CWM trait being above, below, or within the confidence intervals.

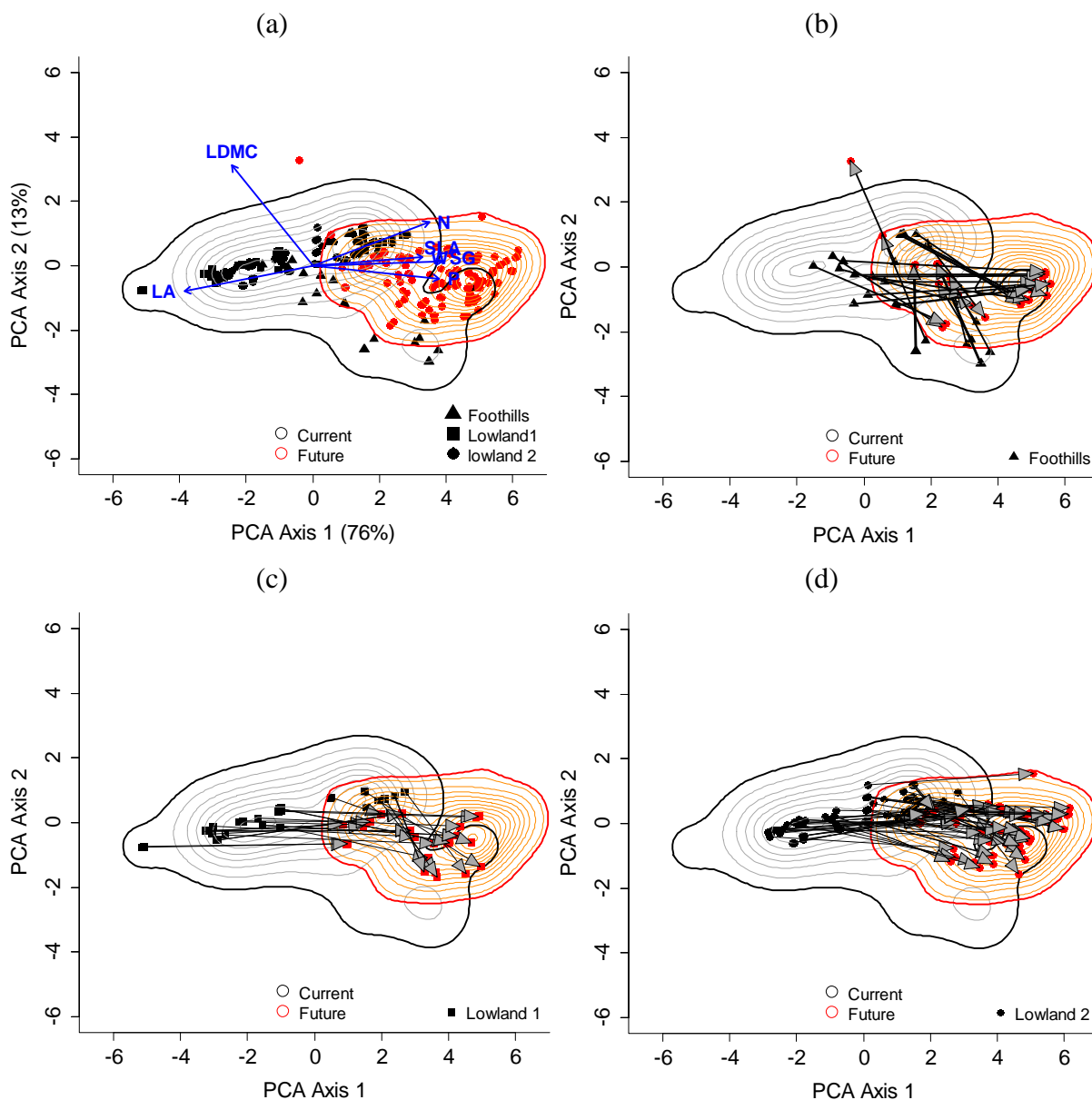
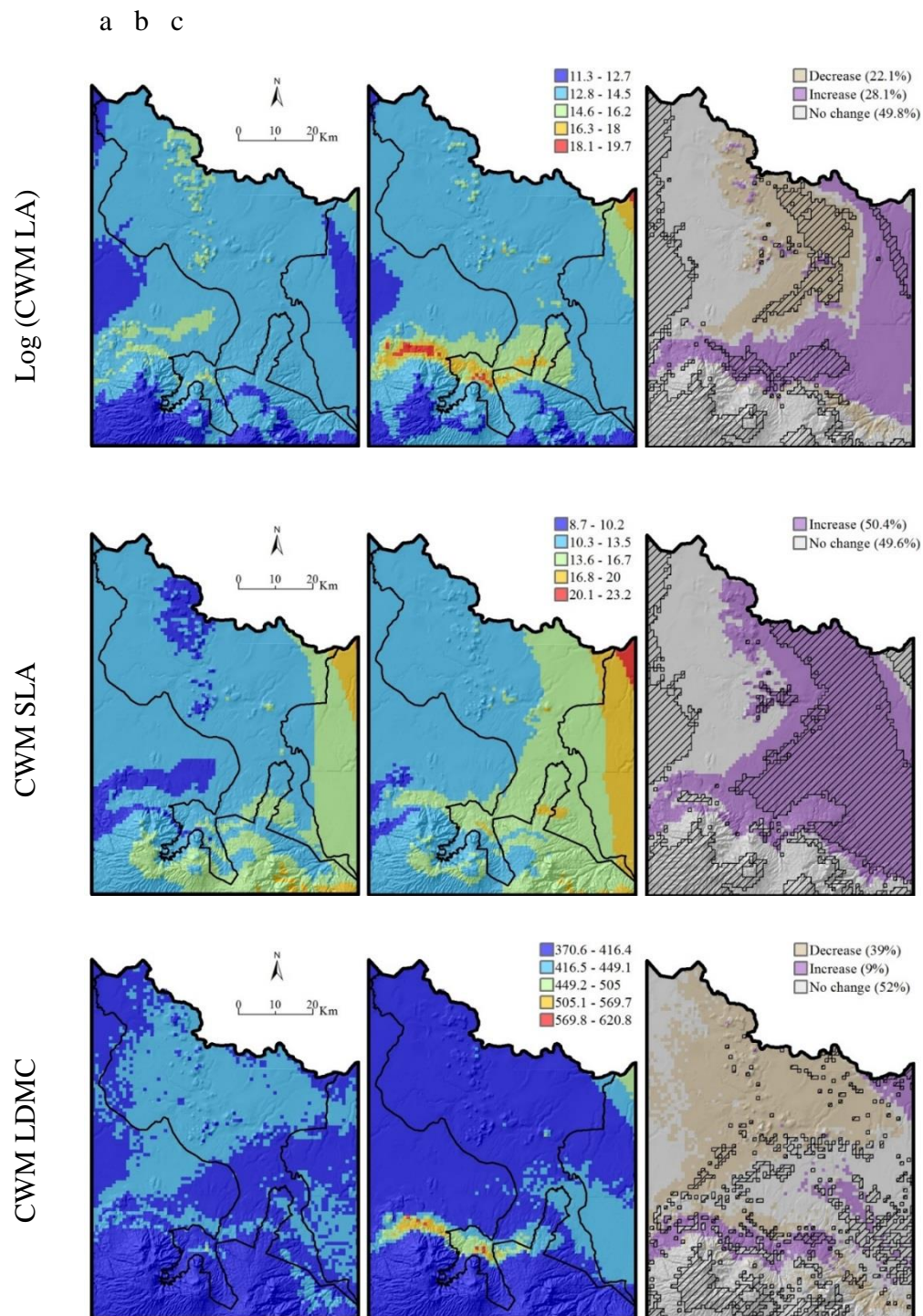


Figure 5. Vegetation plots distribution in functional space under current and future climate. Blue arrows indicate the association of each CWM trait with functional PCA axes of variation. Black points in (a) represent 127 vegetation plots ordinated in the functional space given their six CWM functional trait values under current climate conditions. Red points in (a) represent vegetation plots ordinated in the functional space given their six CWM functional trait values predicted under future climate. Contours represent the probability density of forest plots in the bivariate space of functional PC Axes 1 and 2. Arrows indicate the direction and magnitude of climate-induced shift for foothills (c,d) and lowland (b) forest plots.



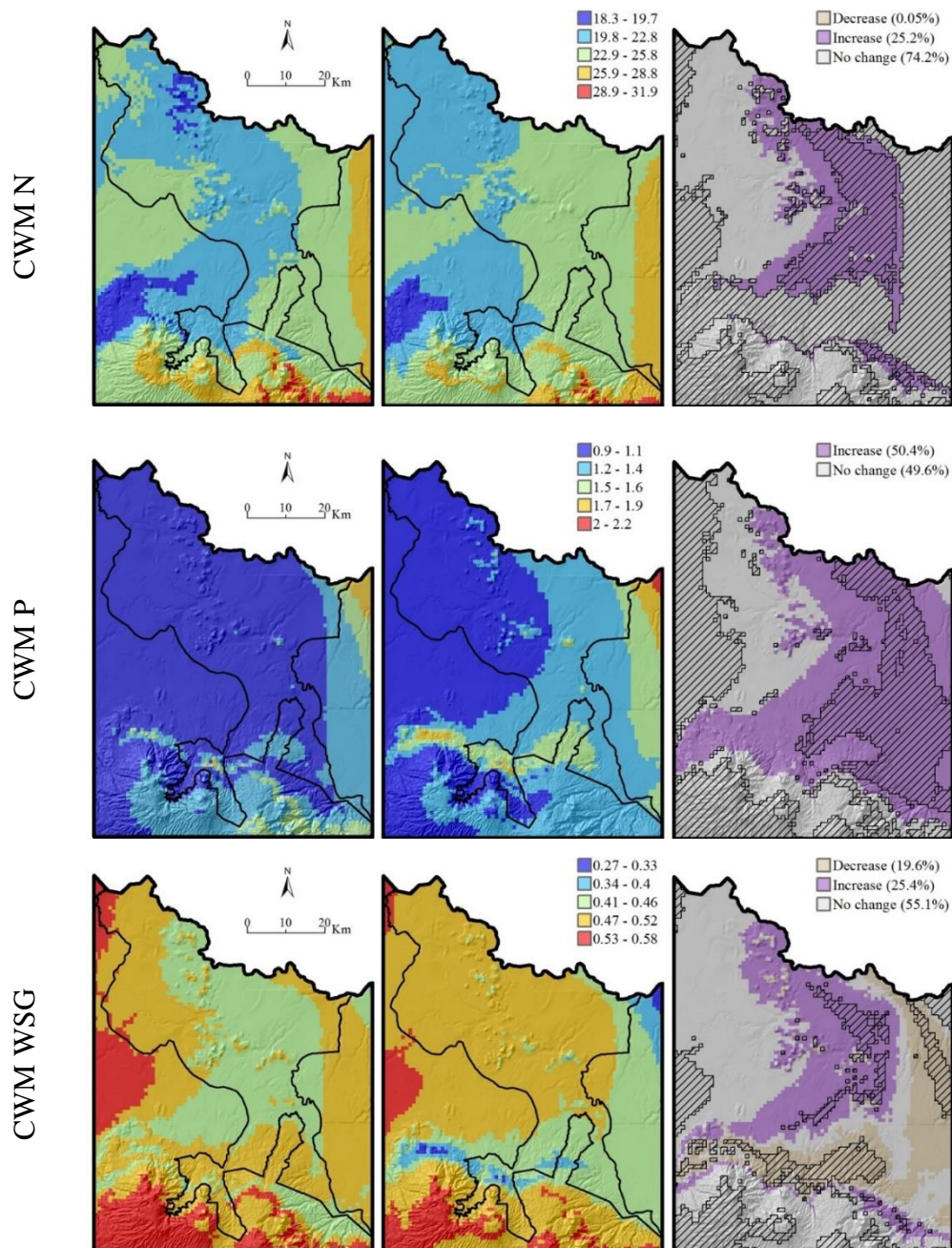


Figure 6. Predicted CWM traits for (a) current and (b) future climatic conditions (year 2050) under the RCP 8.5 for the San Juan La Selva region of northeast Costa Rica. In (b) the mean value from 17 global climatic models is shown. Future areas of increase, decrease or no change in CWM traits (c) indicate that mean future predicted values are above, below or within 95% confidence intervals of current predictions from generalized additive mixed models (GAMs). Dashed areas indicate that projected changes are likely to occur (a change is found in $\geq 66\%$ of future climate models).

Supporting informationl

Table S1. Summary statistics of current and future (year 2050) climate in the San Juan La Selva Region. Future climate data correspond to average values from 17 general circulation models (GCMs) under a high radiative scenario (RCP 8.5).

Variable (Units)	Current		Future	
	Mean \pm SE	Range	Mean \pm SE	Range
AnnTemp ($^{\circ}$ C)	24.1 \pm 0.04	10.8 - 26.2	26.2 \pm 0.04	12.9 - 28.3
MaxTempWM ($^{\circ}$ C)	30.2 \pm 0.04	15.7 - 32.8	32.2 \pm 0.04	17.7 - 34.9
MinTempCM ($^{\circ}$ C)	18.6 \pm 0.04	5.8 - 20.8	20.7 \pm 0.04	7.9 - 22.9
TempSD ($^{\circ}$ C)	6.6 \pm 0.01	4.9 - 8.0	6.6 \pm 0.01	5.0 - 7.8
AnnPrec (mm)	3607.8 \pm 6.6	2134 - 4932	3687.3 \pm 7.0	2215.2 - 5007.4
PrecWettM (mm)	460.1 \pm 0.69	223 - 648	561.7 \pm 1.1	296.7 - 817.1
PrecDriesM (mm)	108.6 \pm 0.55	8 - 188	105.9 \pm 0.52	7.9 - 182.5
PrecCV (%)	39.4 \pm 0.12	20 - 80	45.4 \pm 0.09	30.9 - 82.2

AnnTemp: annual mean temperature; MinTempCM: minimum temperature of the coldest month; MaxTempWM: maximum temperature of the warmest month; TempSD: standard deviation of temperature; AnnPrec: mean annual precipitation; PrecDriesM: precipitation of the driest month; PrecWettM: precipitation of the wettest month; PrecCV: coefficient of variation of precipitation.

Table S2. Pearson correlation coefficients between eight climatic predictors characterizing 127 vegetation plots and first two axes of variation summarizing this climatic information from a kernel principal component analysis. Only significant correlated variables are shown (p value < 0.001).

Bioclimatic predictor	PCA Axis 1	PCA Axis 2
AnnTemp		-0.57
TempSD		-0.94
MaxTempWM		-0.64
MinTempCM		-0.59
AnnPrec	-0.97	
PrecWettM	-0.43	0.34
PrecDriesM	-0.83	-0.37
PrecCV	0.66	0.54

AnnTemp: annual mean temperature; MinTempCM: minimum temperature of the coldest month; MaxTempWM: maximum temperature of the warmest month; TempSD: standard deviation of temperature; AnnPrec: mean annual precipitation; PrecDriesM: precipitation of the driest month; PrecWettM: precipitation of the wettest month; PrecCV: coefficient of variation of precipitation.

Table S3. Summary of generalized additive models on the relationship between community-weighted mean traits and climatic PCA axes and UTM coordinates. Degrees of freedom for smoothed terms PCA axis and UTM coordinated correspond to the effective degrees of freedom used to fit the curves. Parametric coefficients are presented for UTM coordinates when linear relationship was found between them and response CWM traits.

Trait Factors	Model R^2_{adj}	Degrees of freedom	<i>F</i> -ratio	<i>P</i> -value	Parametric estimate
Leaf Area (LA)	0.544				
Climate PCA 1		4.44	14.41	< 0.0001	
UTM X Coordinates		1.63	19.17	< 0.0001	
Specific Leaf Area (SLA)	0.395				
Climate PCA 1		4.17	11.42	< 0.0001	
UTM X Coordinates		1	25.35	< 0.0001	0.0001009
Leaf Dry Matter Content (LDMC)	0.452				
Climate PCA 2		5.75	17.35	< 0.0001	
Wood Specific Gravity (WSG)	0.182				
Climate PCA 1		3.97	6.75	< 0.0001	
Leaf Nitrogen content (N)	0.322				
Climate PCA 1		4.60	7.36	< 0.0001	
UTM X Coordinates		1	18.70	< 0.0001	0.0001157
Leaf Phosphorous content (P)	0.235				
Climate PCA 1		3.62	7.40	< 0.0001	0.0000044
UTM X Coordinates		1	11.23	< 0.01	

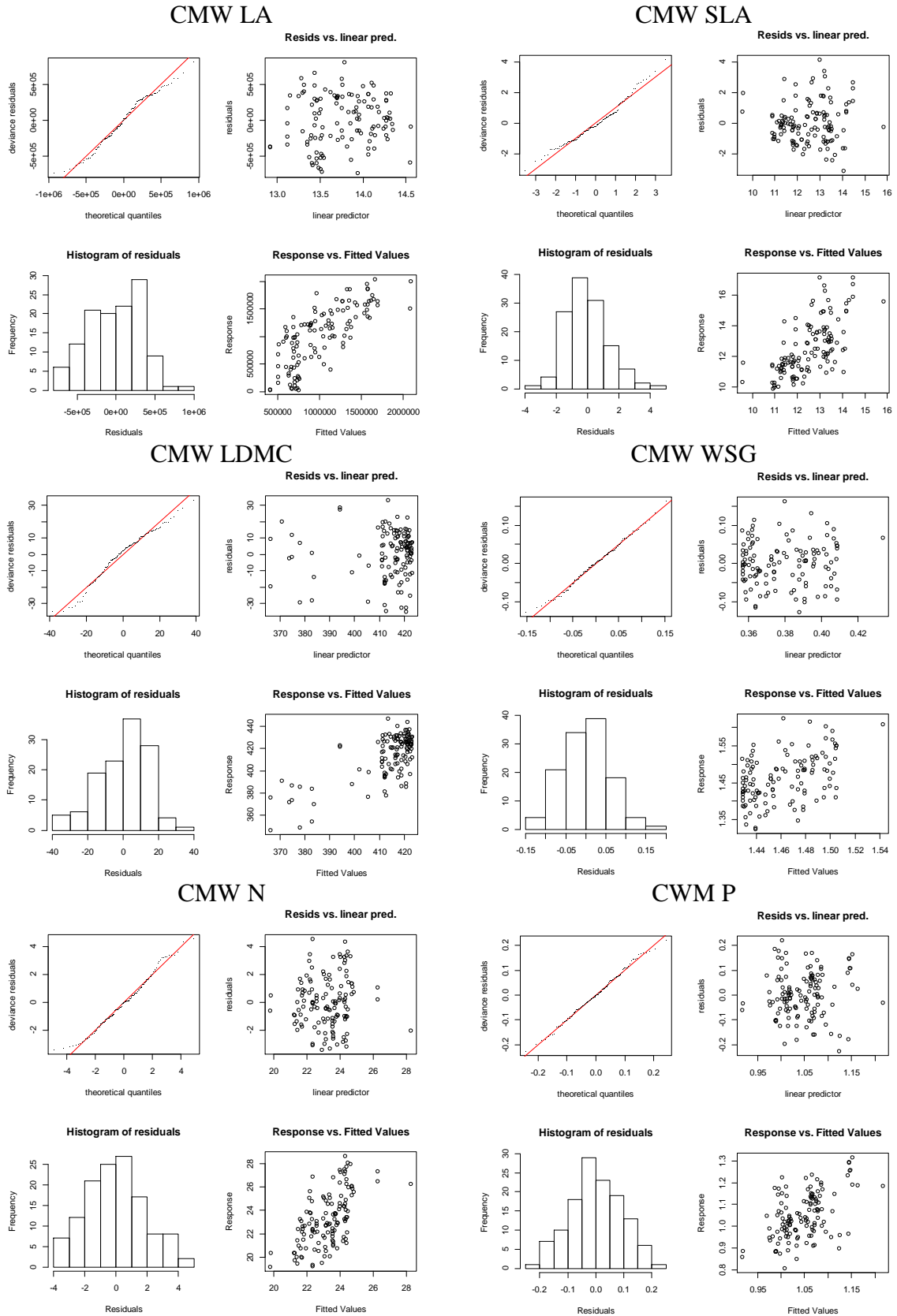


Figure S1. Diagnostic information of fitted GAMs on six CWM functional traits.

Table S4. Summary statistics of current and future (year 2050) community weighted mean (CWM) trait values in 127 old-growth forest plots in the San Juan La Selva Region. Future CWM trait data correspond to plot's average values from 17 general circulation models (GCMs) under a high radiative scenario (RCP 8.5).

Variable (Units)	Current		Future	
	Mean \pm SE	Range	Mean \pm SE	Range
LA	13.8 \pm 0.03	12.2 - 14.6	14.3 \pm 0.08	12.5 - 16.8
SLA	12.5 \pm 0.10	9.6 - 15.8	14.6 \pm 0.13	11.4 - 16.9
LDMC	413.3 \pm 1.17	366.4 - 427.2	411.3 \pm 1.4	379.0 - 505.8
WSG	0.46 \pm 0.002	0.43 - 0.54	0.45 \pm 0.002	0.38 - 0.53
N	23.2 \pm 0.11	19.8 - 28.3	23.9 \pm 0.09	21.8 - 27.4
P	1.1 \pm 0.004	0.92 - 1.2	1.2 \pm 0.01	1.0 - 1.6

Table S5. Pearson correlation coefficients between five CWM traits characterizing 127 vegetation plots and first two axes of variation summarizing this functional information from a principal component analysis. Only significant correlated variables are shown (p value < 0.05).

CWM traits	PCA Axis 1	PCA Axis 2
WSG	0.83	
LA	-0.96	-0.20
SLA	0.97	
LDMC	-0.61	0.78
N	0.87	0.34
P	0.95	

Chapter 4: The Functional and Structural Characteristics of Forest Canopies Drive Distinctive Throughfall Patterns between Old-Growth and Second-Growth Neotropical Rain Forests

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Summary

1. Relationships among forest plant diversity, canopy structure, and forest hydrology have long been recognized. However, there is a great need to study how metrics of forest biodiversity may be linked to hydrologically-based ecosystem service provisioning.
2. In this study we quantified the relationship between two key components of this link: the functional and structural characteristics of tropical moist forest canopies and rainfall redistribution.
3. We measured forest structural and functional characteristics and throughfall under old-growth and second-growth forest canopies (n=14) of northern Costa Rica to understand how key vegetation properties correlate with the mean and variance of throughfall over time and space.
4. Throughfall was directly affected by rainfall amount (ANCOVA, $F = 1164.1$, $p < 0.0001$). While mean throughfall did not differ between old-growth and second-growth forests, we observed an effect of forest type on the spatial variation of throughfall (ANCOVA, $F = 16$, $p = 0.0001$). Higher throughfall heterogeneity was observed in old-growth forests under low rainfall in comparison to second-growth forests, whereas the latter showed no change in throughfall heterogeneity with changes in rainfall magnitude. Spatial differences were related mainly to the differential abundance of palms, with greater number of these individuals in old-growth forests. In particular, palm occurrence was found to be a fundamental driver of relationships found between structural metrics (i.e. canopy cover), functional metrics (i.e. specific leaf area weighed mean), and throughfall ($R^2_{\text{adj}} = 0.15$, deviance explained 18%).

5. These findings confirm the role of palms as an a priori functional group in Neotropical forests and support the stated relationship between biodiversity and forest hydrological processes. Our results also indicate what traits may be most valuable for the purpose of understanding the relationship between tropical forest functional diversity and partitioning of rainfall, and how the functional approach may complement measures of forest structure and canopy cover for this purpose. In addition, this work highlights the need to understand how potential changes in the hydrological cycle in these ecosystems may occur with future shifts in species and functional group composition, as occurs due to forest succession.

Introduction

The role of the canopy interception in the hydrologic cycle of forested systems has long been recognized (Bruijnzeel 1988, 1990, 2004; Ataroff & Rada 2000; Bryant, Bhat & Jacobs 2005). Vegetation is a main factor affecting the quantity, quality, location, and timing of water flowing through an ecosystem, and thus can either improve or degrade the supply of hydrological services (Brauman et al. 2007). In particular, forest vegetation affects watershed and landscape scale hydrology by modulating transpiration and evaporative losses, which subsequently modifies infiltration, deep percolation, runoff, and ultimately the amount of streamflow leaving forested watersheds and sustaining downstream water uses (Bonell 1998; Ataroff & Rada 2000; Bruijnzeel 2004; Brauman et al. 2007).

Rainfall partitioning is of particular interest for understanding links between forest characteristics and hydrological outcomes. Through the process of rainfall partitioning, precipitation that is intercepted by the canopy may be evaporated to the atmosphere (interception), stored on the canopy (storage), channeled downward along branches and stems (stemflow), or dripped and/or passed directly to the ground (throughfall) (Crockford & Richardson 2000). Redistribution of rainwater by the forest canopy is thus a key process controlling hydrologic ecosystem services derived from forest systems. The relationship between forest structural and functional diversity and water supply for the needs of people is a prime example of human dependence on ecosystems (Millennium Ecosystem Assessment 2005; Díaz et al. 2011).

At the plot scale, water reallocation by vegetation is traditionally studied by measuring or estimating incident precipitation and relative throughfall, stemflow, and interception loss (Cavelier et al. 1997; Crockford & Richardson 2000). The shape and distribution of the canopy cover and strata (i.e. the forest structure) affects the rates and magnitudes of water fluxes during and following precipitation due to different storage and transport capacities within the vegetation strata that influence the amount and rate of water reaching the ground (Crockford & Richardson 2000; Ataroff & Rada 2000). The relationship between forest structure and rainfall redistribution in tropical and temperate forests has been highlighted as a topic of increased research interest over the past decade (e.g. Crockford and Richardson, 2000; Levia and Frost, 2006), with a particular recent focus on how individual species (and their functional traits) affect the total amount and spatial distribution of water reaching the soil (Park & Cameron 2008; Barbier, Balandier & Gosselin 2009; Pérez-Harguindeguy et al. 2013).

In the tropics, studies have assessed the association and spatial variability of interception, throughfall, and stemflow with variables such as stand basal area (Ponette-González, Weathers & Curran 2010), leaf area index (Cavelier et al. 1997; Hölscher et al. 2004; Fleischbein et al. 2005; Dietz, Hölscher & Leuschner 2006; Ponette-González et al. 2010; Holwerda et al. 2010), tree height (Dietz et al. 2006; Ponette-González et al. 2010), and tree crown size (Dietz et al. 2006). In addition, the presence of certain plant functional types in the canopy is thought to exert strong controls on hydrological function. For example, epiphytes and related plants may play a crucial role with respect to spatial patterns of throughfall because of their high capacity for water storage (Ataroff & Rada 2000; Hölscher et al. 2004; Zimmermann, Wilcke & Elsenbeer 2007; Ponette-González et al. 2010; Holwerda et al. 2010), while palms may potentially regulate throughfall and stemflow through accumulation and redistribution of water as it moves down through the canopy (Schroth et al. 1999; Tobón Marin, Bouten & Sevink 2000; Germer, Elsenbeer & Moraes 2006; Holwerda, Scatena & Bruijnzeel 2006). Other tree functional traits have been suggested to be relevant for estimating stemflow and throughfall such as leaf shape and orientation, branch angle and bark thickness and type (Crockford & Richardson 2000; Levia, Delphis & Frost 2003; Holder 2012; Pérez-Harguindeguy et al. 2013), and traits such as leaf tensile strength and foliar

rigidity have been related to specific water storage capacity (Carlyle-Moses, Laureano & Price 2004).

Despite the focus of previous studies on how different features of vegetation structure affect rainfall redistribution, the ecological concepts of functional traits, functional groups or functional diversity are seldom utilized to understand forest hydrology, and few studies have sought to identify the hydrological role of vegetation at the species or community level from a functional perspective (Nadkarni & Sumera 2004; Park & Cameron 2008; Fu et al. 2009; Barbier et al. 2009). When focusing on ecosystem processes such as rainfall redistribution, the effects of biodiversity should be assessed beyond species by taking into account functional traits of plants (Millenium Ecosystem Assessment 2005; Díaz et al. 2011). These vegetation characteristics are correlated with species' growth rates, lifespan, and the decomposability of their litter and as a consequence, the kind, range, and relative abundance of functional traits will affect ecosystem functioning (Chapin et al. 2000; Millenium Ecosystem Assessment 2005; Díaz et al. 2007). According to De Bello et al. (2010) the assessment of water regulation ecosystem services via plant functional traits has mainly focused on processes such as evapotranspiration and surface and soil water fluxes, and little work has been conducted in tropical forests. In particular, rapid anthropogenic ecological changes in tropical forests underscore the importance of characterizing the influence of forest disturbance and management on hydrological processes (Giambelluca 2002), including deforestation and subsequent regrowth through secondary succession (Harvey et al. 2008; Chazdon et al. 2009a, Chazdon et al. 2009b). Empirical studies that examine relationships between biodiversity and ecosystem functions in human-modified landscapes are therefore vitally important and can potentially provide incentives for protecting disturbed and regenerating forest because of the ecosystems services they provide (Finegan 1992; Chazdon et al. 2009a, Chazdon et al. 2009b).

In this study we quantified the relationship between two key components of the link between biodiversity and downstream ecosystem services: the functional and structural characteristics of tropical forest canopies and rainfall redistribution. We measured throughfall under old-growth and second-growth forest canopies to i) compare stand-level means and variability of throughfall between these two forest types and ii) determine the key microsite-level vegetation structural and functional properties correlating with throughfall. Our analyses

at both individual collection sites and at the larger stand level allowed us to assess throughfall pattern differences in second-growth relative to old-growth forests, and to elucidate the extent to which functional traits of dominant tree species account for these differences.

Material and methods

Study area and site selection

Our study was conducted in the Sarapiquí Region of northeastern Costa Rica, within the limits of the San Juan La Selva Biological Corridor (Fig. 1). In this human-modified landscape, more than 50% of the total area is old-growth and second-growth forests preserved within a matrix of silvopastoral and agricultural lands, including both small scale and extensive banana and pineapple plantations (Morse et al. 2009; Fagan et al. 2013). The old-growth forest in which we worked has been characterized as *Pentaclethra*-palms forest (Sesnie et al. 2009). A total of fourteen 1 ha permanent forest plots were selected to perform throughfall experiments (Fig. 1, Table 1). Plots included old-growth or second-growth forests, that varied in species richness and structure (Table S1). Seven plots were in regenerating forests on former agricultural land and pastures abandoned between 16 and 49 years before the study (Finegan 1992, Chazdon et al., 2010). The other seven plots were from long-term studies of logging and silviculture in old-growth forests (Quirós 1998; Finegan & Camacho 1999). All plots occurred within privately owned farms (Fig. 1).

Measurement of throughfall and total rainfall

The throughfall data were obtained using 15.24 cm (182.4 cm²) diameter collectors. Collectors consisted of 3.8 l (1 gallon) plastic bottles, placed upside down at 1.3 m above the ground and attached to mounting rods. To account for the spatial variability of throughfall (Loescher, Powers & Oberbauer 2002; Carlyle-Moses et al. 2004) within each plot, 25 fixed collectors were systematically spaced every 20 m in a grid pattern. A buffer of 10 m was considered from the plot edges to avoid vegetation outside the plot directly affecting throughfall measurements. We did not measure stemflow, as it typically represents a very small fraction of the total water reaching the ground in Neotropical forests (Cavelier et al. 1997; Tobón Marin et al. 2000; Chappell, Bidin & Tych 2001; Hölscher et al. 2004; Fleischbein et al. 2005; Holwerda et al. 2006; Cuartas et al. 2007; Hofhansl et al. 2012). Eight

reference rainfall collectors were placed in open areas next to groups of adjacent plots to measure unobstructed rainfall. In this case, collectors included a funnel lid with a surface area of 102.6 cm² attached to the 3.8 l bottles; a floating ball was used as a stopper valve to reduce evaporation. Evaporation in the below-canopy collectors was assumed to be minimal since relative humidity remained near saturation all day (Table 2) and little shortwave radiation penetrated to the land surface under the dense canopy cover (Table S1, Figure 2).

Measurements of throughfall and rainfall were made on a weekly basis during the rainy season for a period of 64 days between July 4th and September 6th 2011, and conducted manually by decanting to a graduated cylinder. After each measurement, collectors were cleaned of debris. Distance between sites and remoteness made it difficult to perform measurements on the same days. Measurement dates were therefore staggered from Monday to Friday, such that collection in a given group of close plots was made on the same day each week. The Tirimbina Reserve's meteorological station was used as a representative sample to describe overall temporal rainfall patterns during the study period (Table 2).

Vegetation composition and structure

We utilized detailed vegetation censuses and monitoring data within all plots (see Chazdon et al., 2010; Finegan and Camacho, 1999; Quirós, 1998) to characterize vegetation composition and structure. All individuals ≥ 10 cm diameter at breast height (dbh) have been recorded, labeled, diameter measured, and identified to the species level. We recorded all individuals whose foliage crossed the vertical above each individual collector's catchment surface and they were identified in the field by an expert parataxonomist. For labeled individuals > 10 cm dbh, species names and dbh were retrieved from the existing database. A total of 1246 individuals were recorded above 351 throughfall collectors, which corresponded to 215 species and morphospecies (unique species identified at genus level but differentiated in the field as different species by the parataxonomist using morphological characteristics). Of the total number of recorded individuals, 698 (56%) were ≥ 10 cm dbh and 545 (44%) were < 10 cm dbh; 3 individuals lacked dbh information.

We recorded the vertical position of each individual above the collector, from the lowest (number 1) to the highest. To assess canopy openness we acquired a 3872×2592 pixel digital photograph of the canopy above each collector using a single-lens-reflex digital

camera. Narrow field-of-view digital cover photography aimed at the zenith is a single view-angle method that has been shown to accurately assess canopy cover (Pekin & Macfarlane 2009). Focal distance (18 mm) and maximum aperture (3.6) were maintained equal, changing the ISO to correct for day light differences. Photographs were processed with ENVI 4.8 software (Exelis, Inc.) through the Region Of Interest (ROI) tool, manually assigning threshold brightness values to separate sky pixels from canopy pixels in the blue band of the RGB images (Fig. 2). From these data we calculated the percentage of both canopy and sky above each collector over an approximately 102° angular view towards vertical.

Measurement of plant functional traits

The 698 individuals > 10 cm dbh that occurred above the collectors (corresponding to 143 different species) were selected for trait measurement. Measuring all the species in this diameter range follows the idea that dominant species are more important for ecological functioning than those that occur more sparsely (Grime 1998; Götzenberger et al. 2012; Pérez-Harguindeguy et al. 2013). We selected a set of foliar and whole plant traits potentially related to throughfall but whose value in this context does not seem to have been tested, including: leaf area (LA), specific leaf area (SLA), leaf dry matter content (LDMC), leaf texture (LTx), stem texture (STx), branch insertion angle (BIA), epiphyte carrying capacity (ECC), crown density (CD) and strata (ES). We propose that these easily measured traits are related to water redistribution processes in forests. Trait descriptions, categories and postulated relationships to throughfall are described in Table S2.

Five individuals per species were collected in the study region for trait measurement. Sample handling and measurement procedures followed Garnier et al. (2001) and Pérez-Harguindeguy et al. (2013). Genus- or family-mean trait values were assigned to those individuals identified as different morphospecies (cf. Chave et al. 2006, Fyllas et al. 2009, Patiño et al. 2012). For traits LTx, STx, BIA, ECC, CD, ES, on-site observations were complemented with data retrieved from secondary sources including floras describing species from the study region (Flora Mesoamericana and Flora de Nicaragua available online through the Missouri Botanical Garden <http://www.tropicos.org/>, and La Selva florula Digital <http://sura.ots.ac.cr/local/florula4/index.php>), herbarium specimens (CATIE micro-herbarium) and unpublished local databases.

We assigned complete sets of trait values to 126 species (corresponding to 97.4% of all dominant > 10 cm dbh individuals recorded above throughfall collectors). From field sampling and lab measurement we assigned LA values to 124 species (96.8% of dominant individuals). Genus mean and family mean of LA were assigned to two species (0.4% and 0.1%, respectively, of all dominant individuals). We assigned species level SLA and LDMC values to 114 species (94.3% of dominant individuals). Genus and family means of SLA and LDMC were assigned respectively to 8 (2.6%) and 4 (0.6%) species. LA and SLA values for 72 species were retrieved from an unpublished trait database created by F. Fernandez, B. Finegan, B. Salgado-Negret and F. Casanoves, also held in the TRY database (Kattge et al. 2011), for which the same sampling design and measurement methodology was followed. From field observations we assigned categorical traits LTx, STx, FP, BIA, ECC, CD and ES to 104 species (91% of dominant individuals). From both secondary sources and genus and family level means we assigned information to 22 species (6% of dominant individuals). Trait values varied widely among the species recorded (Table S3). Variation was particularly large for leaf area, due to the presence of dominant canopy palms in these forests.

Weighted functional traits

To describe forest functional properties, we calculated community weighted means (CWM) at the plot level, selecting species summing 80% of each plot's total basal area (considered as the sum of all individuals ≥ 10 cm dbh). Species relative basal area per plot was used as the weighting variable.

To assess the relationship between canopy functional characteristics and throughfall at the microsite scale, we adapted approaches to the measurement of community functional properties and proposed a new fine-scale measure of forest canopy functional characteristics, the collector-weighted mean (COWM). For the calculation of COWM traits, collectors with complete sets of trait values for all recorded individuals ≥ 10 cm dbh were selected and used for further statistical analysis (n=308). We propose different approaches to calculate trait COWMs that take into account either the size of individuals (absolute or relative basal area) or the position of individuals above the collector. COWMs that take into account basal area are the sum of the products of an individual's absolute or relative basal area and the value of a given trait. Stem diameter has been shown to be related to crown diameter and depth in these

Neotropical forests (King 1996; King & Clark 2011), so under the absolute basal area weighting scheme this relationship is maintained and expressed in the resultant functional value. COWMs taking into account the vertical position of the individuals above the collector, assign weights to individuals in direct proportion to their height above the collector. For this weighting scheme, the absolute number of the position of the individual above the collector was multiplied by the individual's trait value.

Data analysis

Throughfall patterns in old-growth and second-growth forest

We calculated the weekly mean and coefficient of variation of throughfall per plot using data from all twenty five collectors per plot. Under the mixed effects modelling approach and using the statistical software InfoStat (Di Rienzo et al. 2013), we conducted analyses of covariance (ANCOVA) to assess the effect of forest type, total rainfall and their interaction on the mean and coefficient of variation (CV) of throughfall per plot. A first-order autoregressive correlation structure was assumed to take into account repeated measurements of throughfall over the 8 week sample period. Heterogeneous variances were also assumed for each week. Given that we found a significant effect of the interaction between forest type and total rainfall on throughfall we compared mean and CV of throughfall between forest types under low (≤ 40 mm), intermediate (> 40 mm - < 140 mm) and high values (≥ 140 mm) of total rainfall amounts. These rainfall categories corresponded to data corresponding to the <25th, 25th to 75th, and >75th percentiles, respectively.

Canopy characteristics and their relationship with water redistribution

We performed a principal components analysis (PCA) to visualize variation in the canopy properties among old-growth and second-growth forests. The resultant distribution of plots in the multivariate space is created by canopy structural and functional characteristics, the latter summarized by trait CWM calculated at the plot level from those species summing to 80% of plot's basal area as described in section 2.5.

The relationship between throughfall and structural and functional characteristics of the forest canopy was assessed at the collector scale as follows. Throughfall percentage was calculated per collector by dividing accumulated throughfall by accumulated rainfall in the

eight weeks of measurements. We used generalized additive models (GAMs) to develop predictive models of throughfall percentage as a nonlinear function of canopy structural characteristics and traits COWMs using the `gam` function in the `mgcv` library in R (R Development Core Team 2011). Different models including different COWM schemes and correlation structures were assessed. The best model was selected using the Akaike Information Criterion (AIC). The smoothing parameter estimation method was Restricted Maximum Likelihood (REML). Finally, due to our interest in throughfall patterns related to canopy palms as individuals bearing unique values of functional traits, at the plot level we assessed the correlation between palm abundance and throughfall CV. Because palm abundance tends to increase with secondary forest age in this landscape, we also tested for the correlation between plot throughfall CV and plot age under different rainfall amounts. This analysis was only conducted using secondary forest plots since it is not possible to assign an age value to old-growth forests.

Results

Temporal variations in the local climate during the sample period are described using the Tirimbina Private Reserve's meteorological station data (Table 2). La Tirimbina Reserve is in a central location among the study plots, excluding the Corinto sites (Fig. 1). Rain events occurred during 89% of the days within the study period, with an average magnitude of 6.4 mm. Average daily temperature (25°C) and relative humidity (88.5%) were high and relatively constant during the study period (Table 2). Data from collectors of unobstructed rainfall in open areas close to forest patches showed that the first week of measurements presented the highest average amount of total rainfall across plots (Fig. 3). Due to collector overflow, the first week of data from Corinto plots was removed from the analysis. On average, the lowest amount of rain was observed during week five. Corinto sites, located towards the foothills of the Central Mountain Range (Fig. 1), tended to always differ from the rest of the plots distributed in the Sarapiquí area by showing higher weekly rainfall amounts (Fig. 3).

On average, 94% of the total 351 established collectors could be measured each week, with the remainder exhibiting overflow, leakage, or damage. Across all weeks and all collectors, throughfall on average corresponded to 68.6% of total rainfall, ranging from 0 to

232.9%. Throughfall at individual collectors exceeded total rainfall in 46 of 351 collectors on average per week; these collectors with amounts of throughfall higher than measured unobstructed rainfall (“negative interception”) represented between 7.4 % and 18.9 % of total measured collectors among all weeks. This suggests that a portion of intercepted precipitation is funneled by leaves, branches or stems, creating focused throughfall points.

PCA biplots summarized differences in structural and functional canopy properties among forest plots (Fig. 4). Functional properties refer to CWM calculated from traits of species composing 80% of basal area per plot. Old-growth and second-growth plots were clearly separated by this analysis in the space determined by functional and structural characteristics linked to the hydrological cycle. Axis 1, 2 and 3 explained 82% of observed variance (Table 3). Old-growth forest plots had positive values on Axis 1 associated with higher values of CD, ECC, LDMC, LA CWM, and palm abundance, while second-growth forest plots had negative values on the same axis associated with higher values of LTx, BIA, and SLA CWM. Axes 2 and 3 highlighted a gradient within second-growth forest plots in relation to structural and functional properties such as palm and tree abundance and LA, ES, and STx CWM values.

Total rainfall had a significant effect on throughfall (ANCOVA, $F = 1164.1$, $p < 0.0001$), and mean throughfall below forest canopies increased linearly with increasing total rainfall (Fig. 5a). No differences were found in mean throughfall between forest types, indicating that the average amount of water reaching the ground by the throughfall process increases in a similar way in second-growth and old-growth forest canopies as rainfall increases (Fig. 5a). On the other hand, a significant effect of the interaction of forest type and total rainfall amount was observed on plot throughfall CV ($F = 16$, $p = 0.0001$), indicating that variability of throughfall within a plot differed between old-growth and second-growth forests, depending on the magnitude of rainfall. Comparisons of throughfall CV between forest types indicated that differences existed under low (≤ 40 mm) and high (≥ 140 mm) rainfall amounts, with respectively higher and lower throughfall CV in old-growth than second-growth canopies (Fig. 5b). As total rainfall amount per week increased, throughfall CV decreased only in the old-growth forest plots.

The analysis of the relationship between canopy properties and total interception at the collector scale showed that throughfall values above individual collectors changed in a

nonlinear fashion with canopy cover percentage, abundance of palms, and SLA COWM (relative basal area as weighting factor), which together were significant predictors of the amount of rainfall reaching the forest floor ($R^2_{adj} = 0.15$, deviance explained 18%; Fig. 6). Throughfall was affected by the interaction between canopy cover, SLA COWM, and palm abundance ($F = 2.5$, $p = 0.0006$) indicating that the effects of each of these canopy properties on throughfall are not independent from one another. Higher abundance of palms indicated lower amounts of throughfall (Fig. 6a, b). Moreover, palm presence affected the relationship of canopy cover and SLA with throughfall. Higher canopy cover percentage resulted in less throughfall, with a continuous steep decrease in throughfall as canopy cover increased where palm abundance was high, and a less steep decrease above collectors with no palms (Fig. 6a). The least throughfall was observed where palm abundance was highest and SLA COWM lowest. The non-linear relationship between throughfall and SLA can be explained by the interaction with the amount of canopy cover above collectors. None of the other weighting schemes used to calculate COWMs showed significant relationships with throughfall.

Palm abundance and basal area per plot was greater in old-growth forest compared to second-growth forests (Fig. 4, Table S1). The role of palms on rainfall redistribution under the forest canopy, considering them as an a priori functional group with specific values of leaf traits (Fig. S1), was further assessed at the plot scale through Pearson correlations between plot throughfall CV and total number of palms registered above collectors in the plot (Table 4). Palm abundance was significantly positively correlated with throughfall CV only under low rainfall amounts (≤ 120 mm). The number of palms above a single collector ranged from 0 to 5, corresponding to 0-75% of total individuals above collectors, except for three collectors in which palms were the only individuals registered; canopy cover percentage ranged from 69.9% to 99.9%. Palm abundance was highly correlated with plot age ($r = 0.75$), so correlation between plot throughfall CV and plot age was also assessed under low and high rainfall amounts (Table 4). In accordance with patterns observed in Fig. 5, under low rainfall amounts plot age was positively correlated to CV of throughfall, indicating that when weekly rainfall events are ≤ 100 mm spatial variation in throughfall increases with forest succession in these ecosystems. Under high rainfall amounts, a negative correlation was observed, indicating the lower spatial variability of throughfall under old-growth canopies also observed in Figure 5b.

Discussion

To understand the relationship between rainfall redistribution and canopy properties in old-growth and second-growth forest stands, we measured weekly throughfall and quantified its relationship to canopy structural and functional properties. Specifically, our main findings indicated that i) throughfall amount was directly determined by total unobstructed rainfall, with no differences in mean throughfall between old-growth and second-growth forest types; ii) in contrast, spatial variability of throughfall under old-growth canopies was higher than under second-growth forest canopies; iii) canopy cover was directly related to the amount of water reaching the ground, while species traits summarized in COWM showed nonlinear relationships with throughfall; and iv) the presence of palm individuals in the canopy seems to drive the observed relationships between canopy properties and throughfall spatial variation. Several studies have previously assessed rainfall redistribution under forest canopies in the tropics, however the effect of functional traits has not been directly assessed. Here, we discuss our main results in the context of these previous studies.

Dependence of throughfall amount (Elsenbeer, Cassel & Zuniga 1994; Cavelier et al. 1997; Schroth et al. 1999; Crockford & Richardson 2000; Ataroff 2002; Loescher et al. 2002; Carlyle-Moses et al. 2004; Levia & Frost 2006; Park & Cameron 2008; Huitao et al. 2012) and spatial variability (Loescher et al. 2002; Carlyle-Moses et al. 2004; Levia & Frost 2006; Holwerda et al. 2006; Zimmermann et al. 2007; Huitao et al. 2012) on the magnitude and intensity of rainfall is well recognized. It is expected from this previous work that higher precipitation volume will result in higher throughfall volume and lower spatial variability of throughfall. In accordance with this expectation, total weekly rainfall in our study affected weekly measurements of mean and CV of throughfall. Despite similar positive relationships between total rainfall and throughfall among forest types (Fig. 5a), the effect of total rainfall on plot throughfall CV differed between old- and second-growth stands (Fig. 5b). Throughfall spatial heterogeneity in the old-growth forest stands decreased as expected with increasing rainfall amounts, but no such relationship was observed in second-growth stands. These differences may be explained by differences in canopy functional and structural characteristics between these two forest types, as observed in the PCA biplot, that lead to differential redistribution of incoming homogeneous rainfall by creating focused throughfall points.

Observed mean throughfall percentage in our study (68.6%) fell within the range (58% - 91%) reported in previous research in tropical lowland and montane rainforests (Scatena 1990; Elsenbeer et al. 1994; Cavelier et al. 1997; Crockford & Richardson 2000; Tobón Marin et al. 2000; Chappell et al. 2001; Nepstad 2002; Fleischbein et al. 2005; Dietz et al. 2006; Cuartas et al. 2007). From digital cover photography we estimated that mean canopy cover was 97.4% with no significant difference between forest types (Table S1), which may contribute to high value of observed water interception by the canopy. Canopy cover in combination with palm abundance and SLA COWM best explained the amount of throughfall. Canopy cover or similar measures such as LAI are expected to influence throughfall (Crockford & Richardson 2000; Levia & Frost 2006), and their positive effect on rainfall interception have been previously assessed by other studies (Loescher et al. 2002; Fleischbein et al. 2005; Dietz et al. 2006).

SLA COWM calculated from species level trait data and relative basal area of individuals above collectors has not been reported in previous throughfall studies. SLA COWM was the only significant weighted mean trait related to the process of rainfall redistribution in these tropical forests. SLA is inversely associated with leaf structural resistance (Onoda et al. 2011), and thus its association with rainfall redistribution is expected, in particular by the role that different leaf structural resistances may play in splitting rain drops. Because evaporation from splash droplets is thought to drive interception losses (Murakami 2006), future work should explore the relationships to throughfall of other traits linked to leaf structural resistance, such as lamina thickness, tissue density and toughness per unit tissue density (Onoda et al. 2011), though the large amount of SLA data current available un traits databases have great potential for further use in studies like ours.

None of the other COWM traits we measured showed significant relationships with throughfall. It may be that for traits like stem texture, branch insertion angle, crown density and epiphytes, their direct measurement on individuals found above collectors is more closely related to water redistribution within the stand than species-level trait values. This could especially be the case for a trait like epiphyte carrying capacity, because actual epiphyte load (Zotz & Schultz 2008) and diversity (Köster, Nieder & Barthlott 2011) is strongly related to tree size. This approach would greatly increase research effort, however, and a major goal of functional ecology is to understand ecological processes with the reduced effort and

intermediate resolution of species-level trait values (Pérez-Harguindeguy et al. 2013). It is especially interesting that COWM SLA was related to throughfall when COWM LDMC and LA were not. LDMC, for example, is positively related to leaf stiffness (Markesteyn et al. 2011) which could potentially influence throughfall. In general however, the relationships of leaf traits to throughfall are much less well-understood than are their relationships to photosynthetic capacity, longevity and other components of the leaf economics spectrum (Wright et al. 2004), and more work for the validation of traits is recommendable.

Palm abundance was both related to throughfall amount at the collector scale (Fig. 6), and to throughfall plot spatial variability under low-intermediate rainfall amounts (Table 4). Although total basal area and stem density did not vary between second-growth and old-growth forest, basal area of adult canopy palms was substantially higher in our old-growth plots (Table S1), as reported by Guariguata et al. (1997) and Montgomery and Chazdon (2001) for forests in the same region. Palms are distinctive canopy features of studied old-growth forests (Sesnie et al. 2009) and can represent more than 20% of total LAI (Clark et al. 2008). This structural difference also results in a major functional difference affecting redistribution of rainfall; palms are a well-defined a priori functional group on the basis of traits such as very high leaf area, high leaf tensile strength and relative low specific leaf area (Fig. S1). Our study suggests that palm presence in forest canopies may play a very important role in relation to rainfall redistribution, influencing the amount of rainfall reaching the ground as well as the spatial distribution and magnitude of these rainfall inputs. Under conditions of low amount of precipitation palms function as an umbrella redirecting water to their stems and conducting it directly to the ground, creating greater differences in throughfall between locations with and without palm presence. If the large and dissected leaves of palms take longer to wet-up and bend as weight of water increases over them, under higher rainfall palms may stop acting as interceptors and start acting as drippers, conducting water to the ground off of their leaves and thus homogenizing water amounts that pass through the canopy and reach the ground (Fig. 7). The role of palms as interceptors and drippers has been previously discussed by Schroth et al. (1999) and Germer et al. (2006). This “interceptor” or “drinker” status seems to be related to leaf and other three-dimensional traits of palms in comparison to other plant species, such as palm leaf curvature and the channel-type morphology of palm petioles that are also related to palms age and size.

Overall, canopy structural differences between second-growth and old-growth Neotropical forests are well known (Guariguata & Ostertag 2001; Montgomery & Chazdon 2001; Drake et al. 2002). In particular, the presence of larger and higher stature trees in old-growth forests in comparison to second-growth vegetation, as well as differences in allometric patterns and damage and mortality rates of dominant species in intermediate diameter classes of the canopy and subcanopy layers, result in different clearing dynamics within these two forest types (Guariguata & Ostertag 2001; Montgomery & Chazdon 2001) related to canopy gaps and spatial variation in the forest canopy. Whereas canopy-to-forest-floor-gaps occur in old-growth forests, large treefall gaps are generally absent in second-growth stands since most individuals in the intermediate diameter class (10-25 cm) do not have the volume or size to create them (Montgomery & Chazdon 2001). While these structural differences have been interpreted in relation to increased spatial heterogeneity of diffuse light transmittance within the understory of old-growth forest plots compared to second-growth plots (Guariguata & Ostertag 2001; Montgomery & Chazdon 2001), we suggest that they can also explain the observed higher spatial variability of throughfall in old-growth forests (Fig. 5b).

Focused throughfall inputs observed as measurements of throughfall values over 100% of total rainfall demonstrated the existing heterogeneity in the spatial distribution of water reaching the soil. The phenomenon of focused throughfall points resulting in negative interception values has previously been reported (Lloyd & Marques 1988; Germer et al. 2006; Holwerda et al. 2006). Results from related research on deep percolation pathways in the same set of forest plots by Klos et al. (unpublished data) suggests that the focusing of homogeneous rainfall into heterogeneous throughfall via the forest canopy results in the creation of focused deep percolation that more rapidly transports water beyond the root zone and into deep drainage than homogenous throughfall. The higher spatial heterogeneity of throughfall observed in old-growth forests with particular structural and functional characteristics thus highlights the role that old-growth forests may play in subsurface flow regulation, promoting the formation of rapid deep percolation pathways and therefore increasing groundwater recharge and sustaining dry season flow. This is highly relevant in the context of future climate scenarios for the region that project decreases in precipitation and runoff, increases in temperature and evaporation, and less certain trends in leaf area index (Imbach et al. 2012).

The role of palms, as an a priori functional group and as relevant components of Neotropical forest supports the stated relationship between biodiversity and ecosystem processes, and spurs new research questions about the hydrological cycle in these forest ecosystems. Palms high stemflow capacity (related to high leaf area, steep fronds growing from central stems, and relatively smooth bark; Holwerda et al. 2006) and growth synchronicity with the rainy season (Germer et al. 2010, 2006) highlight other not yet assessed roles that palms may have on the hydrological cycle of forests by influencing temporal patterns of throughfall and hydrologic processes such as infiltration capacity, saturation-excess overland flow and/or groundwater recharge via deep percolation. We suggest that additional research on the influence of palms on the hydrologic cycle should be completed, especially under scenarios that reduce palm abundance such as second-growth forests and at edges in forest fragments as demonstrated by Schedlbauer et al. (2007) and Bouroncle and Finegan (2011) in the same landscape. Given the rapid changes currently occurring in tropical regions (Giambelluca 2002), studies assessing recovery of hydrological processes and ecosystem services across forests following succession are needed, especially when concomitant changes in relative composition of both individual species and plant-life forms (e.g. palms) also occurs, with potential implications for ecosystem functioning (Guariguata & Ostertag 2001).

Expected relationships between leaf area and rainfall interception has proved difficult to estimate (Loescher et al. 2002; Fleischbein et al. 2005; Dietz et al. 2006; Park & Cameron 2008; Ziegler et al. 2009). Our additive model included canopy cover as a significant variable explaining throughfall, however a percentage of variation in throughfall remained unexplained. As discussed by other authors, identifying the obvious influence of canopy cover on throughfall at the individual collector level may become difficult because methods for estimating LAI do not operate at the same spatial resolution as the collector catchment area, so estimated canopy closure or LAI may not represent the actual canopy area affecting throughfall at any given point (Fleischbein et al. 2005; Levia & Frost 2006; Ziegler et al. 2009). Canopy photos such as those taken during this study can be analyzed across different fields of view, which may help to understand such relationships in the future. However, such a detailed and angle-specific accounting for canopy gap fraction was beyond the scope of this study, particularly because we were unable to characterize the angle of incoming rainfall,

which is affected by wind speed and direction, and may influence the relationship between canopy gap fraction and throughfall (Crockford & Richardson 2000; Levia & Frost 2006).

The same logic can be followed regarding our measured COWM traits. The effect of the functional properties of canopy species may be better found at a different scale considering not only those individuals right above the collector but those within a larger area surrounding points of measured throughfall (Nadkarni & Sumera 2004; Ponette-González et al. 2010). A complex interaction could exist where vertical overlaps of species present in a larger radius above collectors have nonlinear influences on throughfall measured at particular points on the ground. It is also possible that features related to branch and crown properties, tree height, and basal area may be better described at the individual tree level and not at the species-level (Park & Cameron 2008; Ponette-González et al. 2010), however the measurement of many more individuals per plot would result in high-cost measurement of traits for hundreds of species using standard protocols.

A study like ours may be complemented by the assessment of individual event data in comparison to weekly accumulated rainfall data. If the canopy does not completely dry between rainfall events, different amounts of potential canopy water storage within the stands may occur with each new rainfall event, which can confound relationships between throughfall and measured canopy properties (Carlyle-Moses et al. 2004; Dietz et al. 2006). The measurement of individual rainfall events would allow to separately assess high and low rainfall magnitudes and intensities, as well as control canopy water storage potential, helping to find stronger relationships between throughfall patterns and structural and functional properties of the canopy (Carlyle-Moses et al. 2004; Park & Cameron 2008).

Overall, our findings indicate a major functional effect of the forest canopy on the ecosystem processes of rainfall redistribution, and support the hypothesis that a relationship exists between biodiversity and ecosystem functions in these highly diverse forests. Validation of functional properties relationships to ecosystem processes is the key step in the conceptual framework proposed by Díaz et al. (2007), and the first step to further demonstrate the links between biodiversity and ecosystem services needed to show the complete value of biodiversity (Millenium Ecosystem Assessment 2005).

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Tables

Table 1. Selected old-growth and second-growth forest plots in which rainfall experiments were established in 2011. See Finegan and Camacho (1999), and Quirós (1998) for plot establishment, logging and silvicultural treatments details in La Tirimbina and Corinto sites. See Chazdon et al. (2010) for the remaining sites.

Forest type	Plot	Coordinates	Years since abandonment* or timber extraction**	Plot size (m)
Second-growth	Tirimbina		29*	50 × 200
Second-growth	Cuatro Rios		39*	50 × 200
Second-growth	El Bejuco		16*	50 × 200
Second-growth	Juan Enriquez		16*	50 × 200
Second-growth	Aceituno		39*	100×100
Second-growth	Manú		49*	100×100
Second-growth	Botarrama		49*	100×100
Old-growth	Selva Verde		None	50 × 200
Old-growth	Tirimbina 2		22**	100×100
Old-growth	Tirimbina 4		22**	100×100
Old-growth	Tirimbina 8		22**	100×100
Old-growth	Corinto 2		None	100×100
Old-growth	Corinto 4		19**	100×100
Old-growth	Corinto 8		None	100×100

Table 2. Rainfall, temperature and relative humidity patterns during the study period from July 4, 2011 to September 6, 2011. Data collected from La Tirimbina Reserve's meteorological station, located in the Sarapiquí region in northern Costa Rica. Mean values of temperature and relative humidity are followed by coefficient of variation and maximum – minimum values.

Number of days observed	64		
Total rainfall (mm)	612.4		
Number of days with rain events	57 (89.1 %)		
Number of days with total rainfall > 0.2 mm	53 (82.8%)		
Number of rain events	96		
Number of rain events > 0.2 mm	73 (76%)		
	Mean	CV	Range
Average rain event size (mm)	6.4	156.2	0.2-55
Average rain event duration (hrs)	2.6	82.5	1 - 12
Average rainfall intensity (mm/hr)	2.1	144.7	0.2 - 18
Daily temperature (°C)	25	12.9	20 - 33.3
Daily relative humidity (%)	88.6	8.4	59 -95

Table 3. Summary statistics and significant correlation coefficients ($p < 0.05$ within parentheses) of the first three principal components in relation to measured vegetation variables and mean throughfall.

Variables	Axis 1	Axis 2	Axis 3
Eigenvalue	5.28	2.96	1.58
Cumulative explained variation (%)	44	69	82
Eigenvectors			
FOLIAGE %	0.15	-0.12	0.39
# PALMS	0.23 (r = 0.53)	-0.46 (r = -0.79)	0.16
# TREES	-0.18	0.001	0.66 (r = 0.83)
ES CWM	0.08	0.54 (r = 0.93)	-0.08
LTx CWM	-0.38 (r = -0.88)	-0.01	-0.24
STx CWM	0.16	0.52 (r = 0.89)	0.02
BIA CWM	-0.31 (r = -0.72)	-0.22	-0.39
ECC CWM	0.41 (r = 0.94)	0.12	-0.11
CD CWM	0.42 (r = 0.97)	-0.03	-0.03
LA CWM	0.27 (r = 0.62)	-0.36 (r = -0.63)	-0.004
SLA CWM	-0.29 (r = -0.67)	-0.04	0.40
LDMC CWM	0.33 (r = 0.75)	-0.10	-0.06

Notes: CANOPY: canopy cover percentage, # PALMS: Palm density, # TREES: tree density, ES: strata, LTx: Leaf texture, STx: Stem texture, BIA: Branch insertion angle, ECC: epiphytes carrying capacity, CD: crown density, LA: leaf area, SLA: specific leaf area, LDMC: leaf dry matter content.

Table 4. Pearson correlation coefficients between plot-level throughfall CV and palm abundance and plot age under two categories of rainfall amount.

Rainfall category (mm)	Palms	Plot age
≤ 100	0.46 (< 0.0001)	0.30 (0.004)
$> 100 \leq 162$	0.04 (0.86)	-0.54 (0.01)

Figures

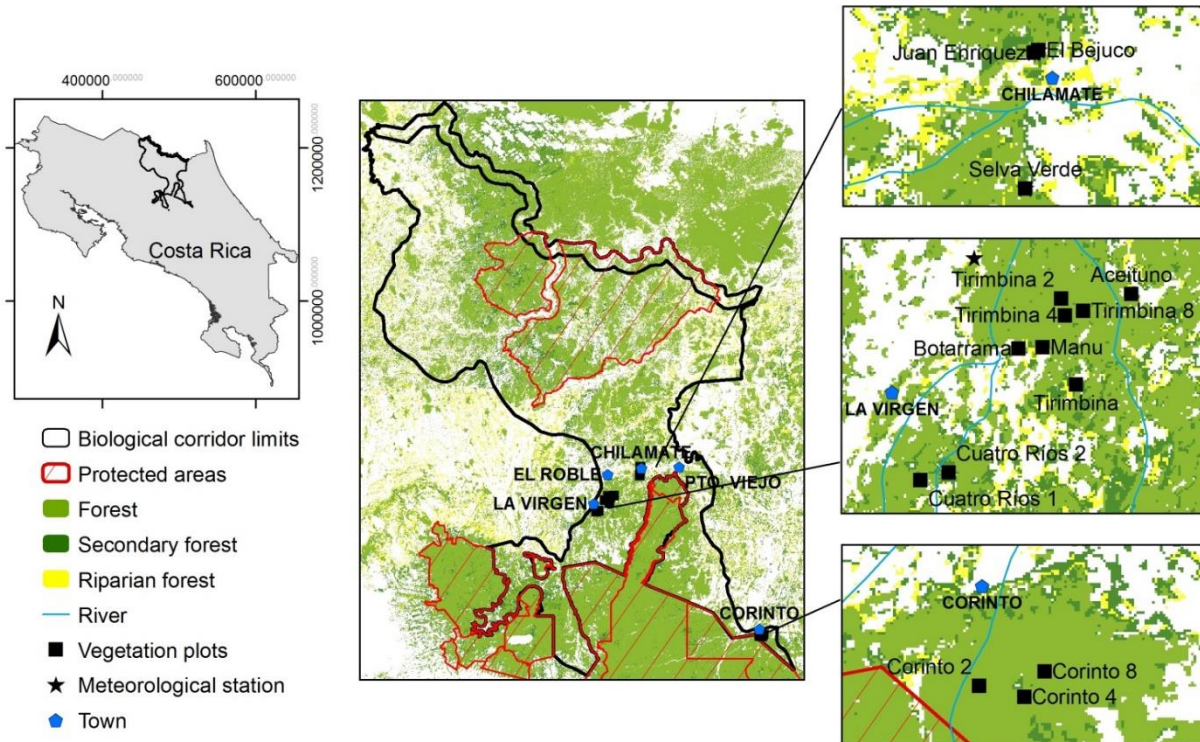


Fig. 1. Permanent sample plots in the Sarapiquí region of Costa Rica selected for the assessment of the relationships between structural and functional properties of plant communities and throughfall.

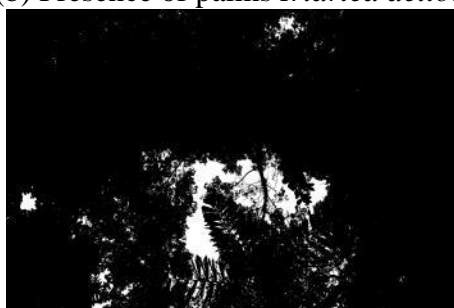
(a) Presence of forest clearings



Old-growth. Selva Verde # 24.
Canopy cover = 74.2 %.



Second-growth. Tiribimina # 16.
Canopy cover = 81.59 %.

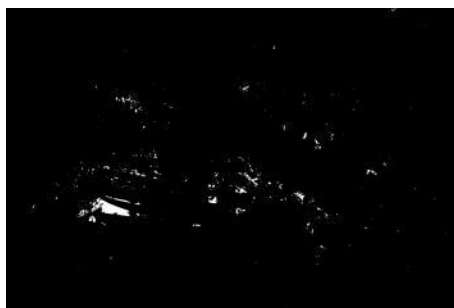
(b) Presence of palms *Iriartea deltoidea* and *Welfia regia* above throughfall collectors

Old-growth. Corinto 4 # 01.
Canopy cover = 94.4 %.

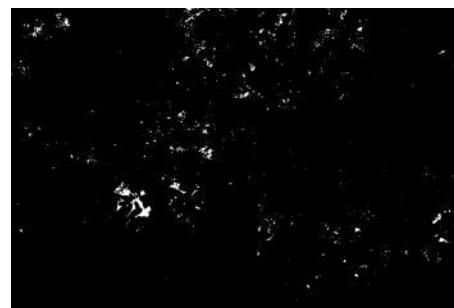


Second-growth. Aceituno # 2.
Canopy cover = 97.2 %.

(c) High canopy cover above throughfall collectors.



Old-growth. Selva Verde # 8.
Canopy cover = 99.3 %



Second-growth. Cuatro Ríos # 12.
Canopy cover = 99.0%

Fig. 2. Digital cover photography above throughfall collectors in old-growth and second-growth forests. Examples include forest clearings (a), presence of canopy palms (b) and high canopy cover (c).

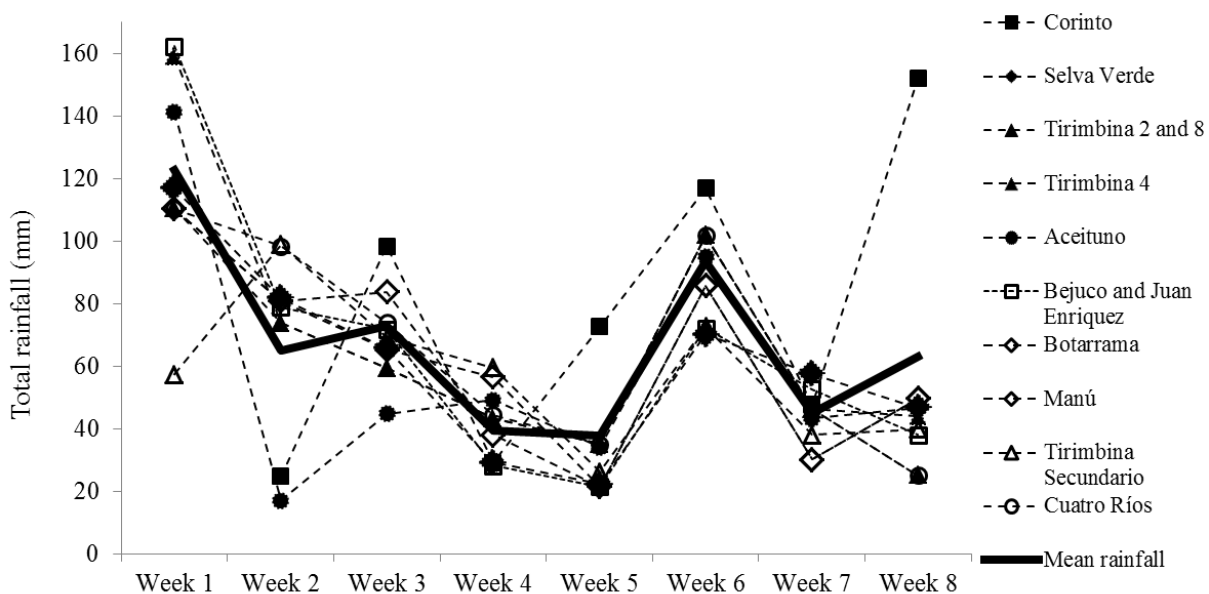


Fig. 3. Patterns of weekly rainfall during the study period. Mean rainfall (solid black line) per week is the average of total rainfall measured in eight reference collectors outside 14 selected old-growth and second-growth forest plots. Measurement dates were staggered along the week, such that collection on a given group of close plots was made on the same day each week.

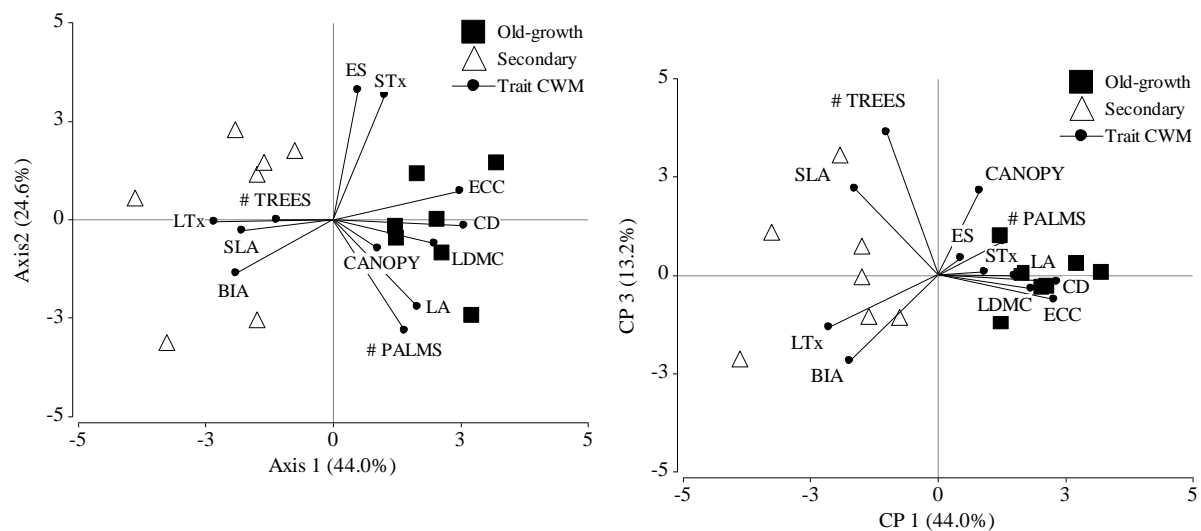


Fig. 4. PCA of functional and structural characteristics of fourteen rainforest plots. Variables are tree abundance (# TREES), palm abundance (# PALMS) and canopy cover (CANOPY), and community weighted means of leaf area (LA), leaf dry matter content (LDMC), specific leaf area (SLA), leaf texture (LTx), stem texture (STx), strata (ES), epiphytes carrying capacity (ECC), branch insertion angle (BIA), and crown density (CD). White triangles are second-growth forest plots, black squares are old-growth forest plots.

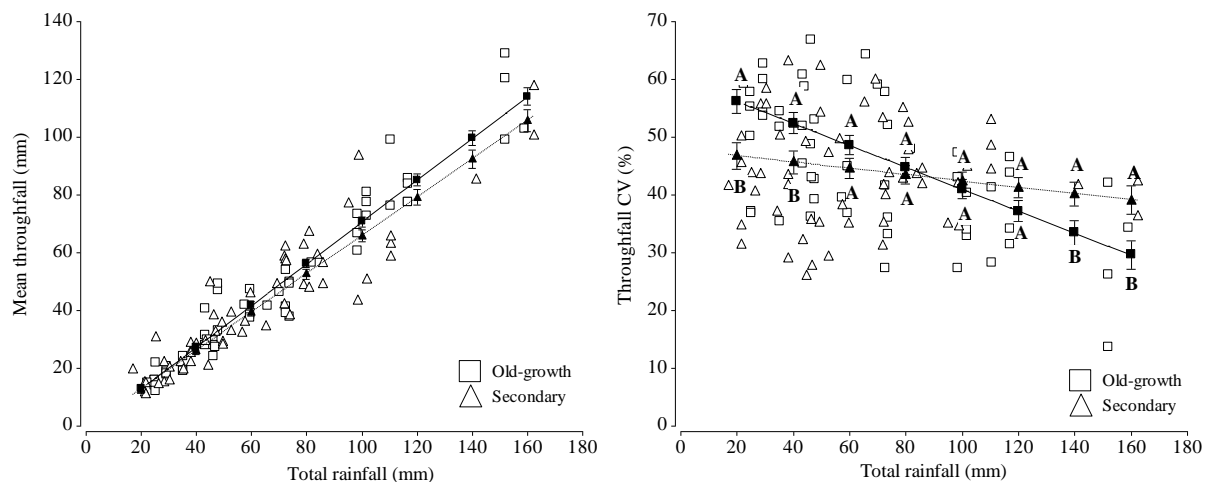


Fig. 5. Mean (a) and coefficient of variation (b) of weekly throughfall (mm) per plot against total weekly rainfall (mm) in permanent sample plots in old-growth (black squares, solid line) and second-growth (white triangles, dotted line) lowland rainforest communities. Different letters from covariance analysis denote significant differences ($p = 0.05$) in throughfall CV under low, intermediate and high rainfall amounts.

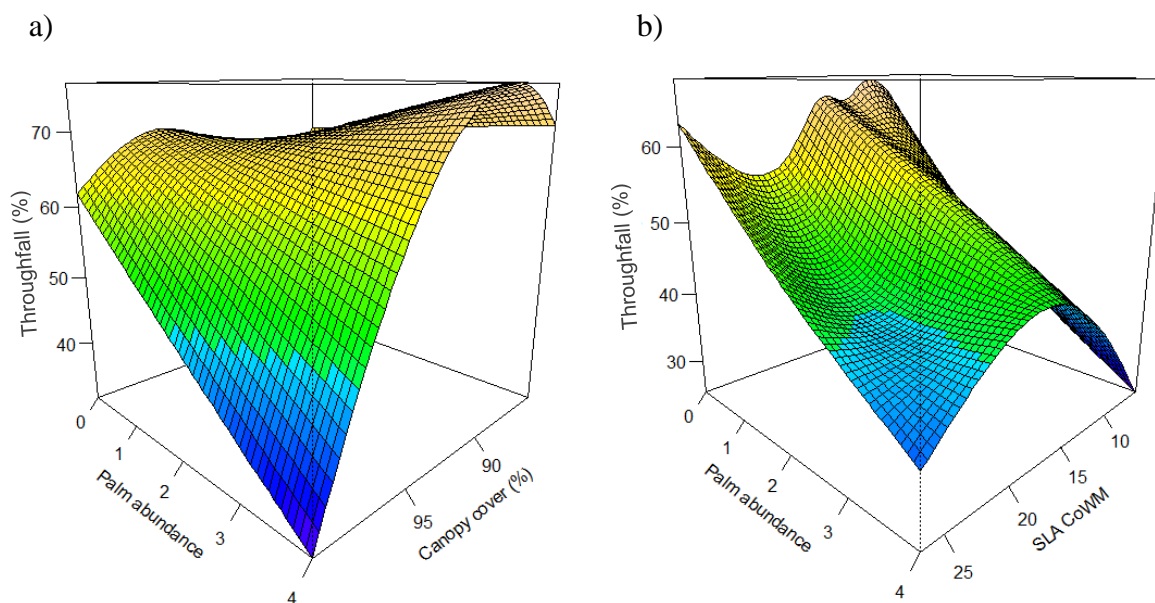
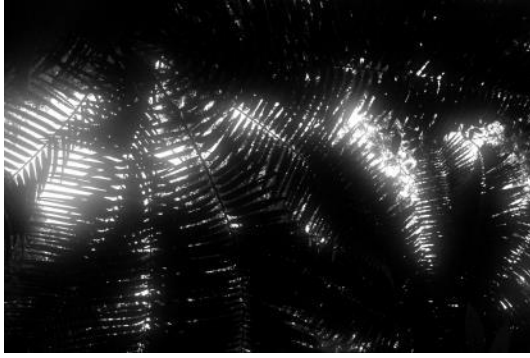


Fig. 6. Generalized additive models to illustrate the relationships between throughfall and canopy features. Data correspond to 308 collectors distributed in 14 old-growth and second-growth forest plots. The interaction between palm abundance, percentage of canopy cover and specific leaf area (SLA) weighted mean above collectors (C_{oWM}) significantly affected percentage of throughfall. a) Shows throughfall percentage as a function of palm abundance and canopy cover percentage. b) Shows throughfall percentage as a function of palm abundance and specific SLA C_{oWM} .



a)



b)



c)

Fig. 7. Palms can either intercept water and conduct it away from collectors (a, c) or funnel it towards them via their drip tips (c).

Supporting information

Table S1. Differences in species richness, structural and functional properties of canopy between old-growth and second-growth forests resulting from an analysis of variance (ANOVA). Mean and standard errors are given.

Variables	Old-growth	Second-growth	F	P value
Palm abundance	72.86 ± 11.45	32.86 ± 13.17	5.26	0.041
Palm basal area	1.29 ± 0.23	0.47 ± 0.18	8.05	0.015
Palm species richness	4.57 ± 0.20	3.71 ± 0.68	1.46	0.250
Tree abundance	442.29 ± 28.36	570.71 ± 80.09	2.29	0.167
Tree basal area	26.63 ± 0.81	29.79 ± 4.20	0.55	0.473
Tree species richness	105.43 ± 4.00	78.29 ± 9.83	6.06	0.030
Dap 10-20				
Tree abundance	258.71 ± 22.81	332 ± 46.78	1.98	0.185
Tree basal area	4.06 ± 0.39	5.88 ± 0.87	3.69	0.079
Dap 20-30				
Tree abundance	81.71 ± 6.10	124.43 ± 21.97	3.51	0.086
Tree basal area	3.96 ± 0.29	6.46 ± 1.10	4.86	0.048
Dap 30-60				
Tree abundance	86.86 ± 7.95	101.43 ± 19.26	0.49	0.498
Tree basal area	12.01 ± 1.04	13.85 ± 2.68	0.41	0.534
Dap > 60				
Tree abundance	15 ± 3.35	9.29 ± 2.49	1.87	0.197
Tree basal area	6.59 ± 1.69	3.6 ± 0.89	2.46	0.143
Foliage cover	97.58 ± 0.40	97.26 ± 0.47	0.27	0.614
ES CWM	2.87 ± 0.04	2.87 ± 0.07	0.0003	0.986
LTx CWM	1.14 ± 0.03	1.63 ± 0.06	45.92	< 0.0001
STx CWM	3.62 ± 0.08	3.44 ± 0.19	0.73	0.410
BIA CWM	1.21 ± 0.01	1.28 ± 0.02	7.19	0.02
ECC CWM	1.09 ± 0.02	0.96 ± 0.02	31.40	0.0001
CD CWM	1.85 ± 0.01	1.53 ± 0.03	104.04	< 0.0001
LA CWM	145039.41 ± 30380.50	41718.27 ± 15015.75	9.30	0.010
SLA CWM	11.03 ± 0.11	12.2 ± 0.46	6.10	0.030
LDMC CWM	323.33 ± 1.96	311.16 ± 3.56	8.98	0.011

Table S2. Description of functional traits to be evaluated in tree and palm species in fourteen old-growth and second-growth forests in the Sarapiquí region, northeastern Costa Rica, and the expected relationship with throughfall. Last two columns indicate if traits were measured directly from field samples or if other sources of information were used to locate species within functional traits categories. Trait descriptions are based on the protocol by Pérez-Harguindeguy (2013). Otherwise references are cited.

Traits	Units	Description	Field sample	Literature / Herbarium
Foliar				
Specific leaf area (SLA)	mm ² g ⁻¹	Fresh leaf area divided by dry leaf mass. Leaf with higher SLW values are related to higher throughfall.	X	
Leaf area (LA)	mm ²	Is the one-sided projected surface area of a single or an average leaf or leaf lamina. Larger leaves are related to lower throughfall.	X	
Leaf texture (LTx)		The following five categories are considered according to the texture of both adaxial and abaxial sides of the leaf: glabrous / glabrous = 1, glabrous / rugose = 2, glabrous / trichome = 3, rugose / rugose = 4 and trichome / trichome = 5. Rugose and bearing trichome leaves are related to lower throughfall.	X	X
Whole plant traits				
Stem texture (STx)		Relevant for the estimation of stemflow and throughfall (Crockford & Richardson 2000b, Levia & Frost 2003, Barbier et al. 2009, Bäse et al. 2012). Categories assigned according to the presence of fissures, lenticels and scales.	X	X

	Smooth = 1, with slight amount of lenticels = 2, scales like paper = 3, lenticels-blister-like = 4, scales in plates or slightly fissured = 5, and fissured or cracked= 6. Higher stem rugosity, related to the presence of lenticels, scales and fissures, is related to lower throughfall.	
Branch insertion angle (BIA)	Relevant for the estimation of stemflow and throughfall (Crockford & Richardson 2000b, Levia & Frost 2003). Three categories: $> 60^\circ = 1$, between 30° and $60^\circ = 2$, $< 30^\circ = 3$. As the angle becomes more perpendicular to the main stem, throughfall values will decrease.	X
Epiphytes carrying capacity (ECC)	Related to canopy water storage capacity (Hölscher et al. 2004, Nadkarni & Sumera 2004). Three categories (Aquino 2009): High = 3, medium = 2 and low = 1, corresponding respectively to $> 60\%$, $30\%-60\%$, and $< 30\%$ of trunk and primary branches covered by vascular epiphytes. Higher amount of epiphytes is related to lower throughfall.	X
Canopy density (CD)	Three categories: low dense= 1, dense = 2, and very dense = 3. Category 1 correspond to the situation when looking at the canopy the area enclosed by the circle of a binocular is empty in more than 60%; category 2 will be the case where the area is empty between 30-60%, while very dense canopy, category 3, the area is empty in less than 30%. Higher crown density is related to higher throughfall.	X

Table S3. Descriptive statistics for measured functional traits of dominant tree and palm species above throughfall collectors.

Trait	Mean	SE	CV	Min	Max
LA (mm ²)	136,097.4	49,009.5	404.2	1,828.0	3,553,833.2
SLA (mm ² mg ⁻¹)	15.1	0.5	37.0	5.7	46.8
LDMC (Mg g ⁻¹)	388.6	6.2	18.0	190.0	530.0
BIA	1.7	0.0	23.3	1.0	3.0
ECC	1.3	0.0	18.7	1.0	2.2
CD	2.3	0.0	17.2	1.2	3.0
ES	3	-	-	1	4
LTx	1	-	-	1	5
STx	3	-	-	1	6

Median values in bold are given for categorical traits.

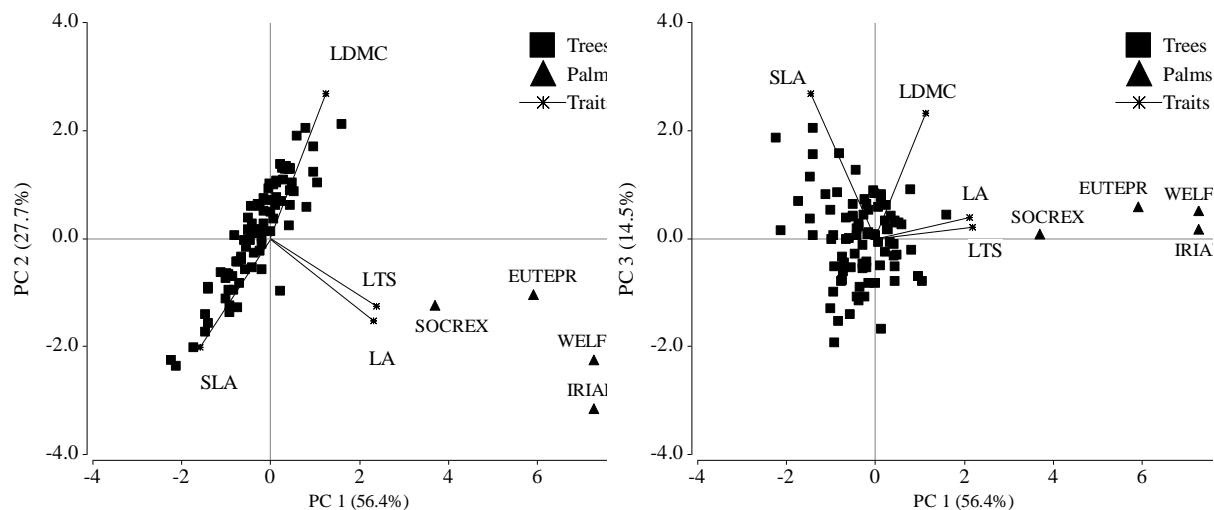


Fig. S1. Biplot from PCA showing species distribution in the foliar trait space built by specific leaf area (SLA), leaf area (LA), leaf tensile strength (LTS), and leaf dry matter content (LDMC). Palm species symbolized in triangles and tree in squares. Data corresponds to 122 tree and four palm dominant species in forests of the Sarapiquí region in Northern Costa Rica. Palm species are *Welfia regia* (WELFRE), *Socratea exorrhiza* (SOCREX), *Iriartea deltoidea* (IRIADE) and *Euterpe precatoria* (EUTEPR). Non published data was collected by F. Fernández, S. Aquino. Three principal components explained a total of 99% of variation. LTS (0.61), LA (0.59) and LDMC (0.32) were positively correlated with axis one. SLA (-0.41) was negatively associated to axis one. LDMC (0.69) was positively correlated to axis two, while SLA (-0.52), LA (-0.39) and LTS (-0.32). SLA (0.75), LDMC (0.65), LA (0.11) and LTS (0.06) were correlated to axis three (weights of each variable are within parenthesis).

Chapter 5: Conclusions and Future Work

In this dissertation, I evaluated the use of functional trait information of the species composing highly diverse Neotropical forest communities to better understand mechanisms underlying community assembly. By employing this functional approach, I also assessed potential responses of forest communities to climate change, and then determined the effects of forest canopy functional properties on hydrological processes at the plot scale. My main findings included:

1) Functional traits in combination with taxonomic species identity hold great potential for determining community assembly rules that might not be evident when studying patterns of taxonomic turnover alone. A higher amount of explained variance was obtained when assessing functional composition in comparison to taxonomic composition. In particular, incorporating functional aspects into ecological patterns allowed us to capture important signals of niche-base assembly mechanisms. However, an interaction exists between environmental deterministic and limited dispersal community assembly mechanisms. Specifically, the analyses reveal that high species turnover and diversity are not only maintained through species sorting along regional environmental gradients, but also by the limited dispersal distance of species relative to the geographic distance between forest sites.

2) It is possible to build models of traits response to climate, and to project functional properties of plant communities under current and future climatic conditions. This finding contributes to our understanding of how climate change may affect biodiversity. Shifts in functional composition of old-growth forest communities from conservative to more acquisitive community trait values is expected to occur under a high radiative forcing scenario by 2050, which results in a general reduction of the multivariate functional properties characterizing old-growth forests.

3) An effect of the forest canopy on the processes of rainfall redistribution exists involving the functional characteristics of dominant plant species. Canopy palm species, highly abundant in old-growth forests and bearing a particular set of trait values, were associated with the higher spatial variability of throughfall observed in mature forests relative to secondary forests. In particular, palm occurrence was found to be a fundamental driver of the relationships found between structural metrics (i.e. canopy cover), functional metrics (i.e. specific leaf area weighed mean), and throughfall.

Based on these findings, my prospectus of future work in this line of research should include the following. First, our ability to model vegetation responses to environmental variables would improve by including intraspecific trait measurements. Future research should assess of intraspecific trait variability, which can account for a large proportion of trait variation and has been shown to play a strong role in assessing non-random community assembly mechanisms. Second, including a greater set of traits within the stem and leaf economic spectrum of plant species would also likely improve multidimensional analyses of functional composition across axes of environmental variation. Functional trait data gathered in this work adds to the global initiative currently underway to compile a wide range of plant traits data with which to conduct community and evolutionary ecology and biogeography research. As functional trait data related to the different aspects of plant life cycles become more available across the tropics, models that include a continuous response of vegetation to environmental change will likely assist our understanding of plant community dynamics within these highly diverse forest ecosystems. Third, more detailed information on underlying functional trait drivers that describe patterns across scales of time and space is also necessary to improve analyses of vegetation data. In this study, assessment of the spatial distribution of traits across the entire landscape would have improved had continuous edaphic variables been available, which have been shown to explain both taxonomic and functional composition variation among forest sites. Fourth, to improve assessments of the relationship between the functional properties of forest canopies and rainfall redistribution, it may be necessary to explore traits related to leaf stiffness and other fine scale traits measurements at the individual level, as well as the measurement of individual rain events while controlling for external factors such as wind, angle of incoming rainfall, and evaporation from splash droplets, known to affect models of rainfall redistribution. Overall, further effects of functional composition variation on ecosystem functioning will require direct measurement of other processes of interest occurring at different spatiotemporal scales and related to different ecosystem services that benefit human communities living in this Neotropical landscape. A complete validation of the relationship between functional properties of ecological communities and ecosystem functioning would allow improved assessments of the consequences of species and functional composition change predicted to occur in human dominated landscapes.