

**FUNCTIONAL DISTRIBUTION PATTERNS OF PLANTS IN A TROPICAL DRY
FOREST OF LA GUAJIRA, COLOMBIA**

*Patrones de distribución funcional de plantas en un bosque seco tropical de La Guajira
colombiana.*

Maestría en Manejo, Uso y Conservación del Bosque

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Thesis:

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Manejo, Uso y Conservación del Bosque

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Abstract

Studies on community assembly mechanisms driving plant species in tropical forests have shown contrasting positions between the predominance of biotic and abiotic selection forces at local scales. We determined the influence of local topography variations and the effects of functional density dependence on the functional distribution patterns in a tropical dry forest (TDF). To do this, we measured leaves and wood traits for 87 species in a 10-ha permanent plot and used the topographic information to define local environmental variations. To evaluate the effects of density dependence, we use the effective distance of the nearest neighbor, and we use the functional dissimilarity and richness index to determine the proportion of the biotic and abiotic factors influencing the community assembly. We found that at the local scale, both topography and functional density dependence differentially affect the functional distribution of plant species in TDF, where, 1) the topography gradient affects the availability of resources at local scale, where at the extremes of this gradient were found a low functional richness and a high functional dissimilarity, and 2) the few density of individuals and species determine low values of functional richness and high functional dissimilarity, but it is subrogated for the effect of local topography. Thus, we conclude that local topography determines the community assembly in TDF, while the functional density dependence have no important effects on this ecosystem. Our results give guidelines for design novel tools for conservation and restoration actions in this threatened degraded ecosystem in Colombia.

Keywords: biotic and abiotic factors, community assembly, dependence, functional density, functional traits, topography.

Introduction

Understanding the factors that influence the community assembly of plant species in tropical forests allows us to be certain about the mechanisms that promote the diversity of these forests (Kraft, Valencia & Ackerly, 2008; Swenson & Enquist, 2009). Historically, the study of spatial distribution patterns of plant species has been approached from various theories based on stochastic processes as a consequence of the neutrality of intraspecific characteristics and deterministic processes related to different pillars of the ecological niche theory, that define the assembly of plant species at the community level (Hubbell, 2001; Maire et al., 2012; Lhotsky et al., 2016; Li et al., 2019). In this way, the assembling of the community is given by multiple factors that are summarized in abiotic conditions (e.g., availability of resources) and biotic interactions (e.g., competition for resources) that define complex habitats, determine the diversity of species and, therefore, the distribution of functions in space (Cornwell & Ackerly, 2009; Swenson & Weiser, 2010; Perry, Enright, Miller & Lamont, 2012; Arellano et al., 2017; Li et al., 2019).

Studies on the community assembly factors of plant species in tropical forests have shown contrasting positions between the dominance of biotic and abiotic selection forces at local study scales (Swenson & Enquist, 2009; Kraft et al., 2015; Chave, 2013; Zhang et al., 2018). On the one hand, it is recognized that abiotic factors, such as topography, generate variations in the spatial resources of the soil through changes in slope, roughness, and elevation, which can determine community assemblage when these conditions are significant constraints for species that are not functionally adapted to these conditions. (Cosme et al., 2017; Li et al., 2019). On the other hand, biotic interactions, such as

functional density dependence, generate competitive filters that determine the assembling of the community based on the similarity or difference in strategies between individuals and neighboring species and predominates when the environment becomes less limiting (McNickle & Dybzinski, 2013; Clark et al., 2018; Li et al., 2019). This contrast generates uncertainty about which factors and to what strength determine the assembly of plant communities at the local scale in tropical forests (McNickle & Dybzinski, 2013; Clark et al., 2018; Li et al., 2019). In particular when local climatic variability matter at local scales, it is still unclear what factors and in what proportion define the community assembly. In tropical dry forests (TDF), extreme drought periods and the water resources available to plants, conditioned by washing and the accumulation of water caused by topography at a local scale, are abiotic factors that can determine to a greater extent the coupling of plant communities based on their functional trait adaptations (Luzuriaga et al., 2012; Pizano & García, 2014; Bartlett et al., 2016; García-guzmán et al., 2016; Méndez-Toribio et al., 2020; Zuleta et al., 2018). However, at a local scale in TDF, species functional attributes that promote the coexistence of biotic interactions or trait strategy exclusion (functional density dependence, FDD) can determine the assembly of plant communities in the same proportion than environmental filters (Guzmán-M et al., 2018). Understanding the assembly mechanisms in the TDF will allow generating clear guidelines on the influence of abiotic and biotic filters on the assembly of plant species. Applying this knowledge to the capacity of the species and their functional strategies to support a specific topographic condition and design arrangements of species with functional strategies that can coexist in the same space without competing for strategy resources.

Consequently, this research aims to determine the influence of local environmental processes and the effects of functional density dependence on the functional distribution patterns of plant species in a TDF of Colombia. Specifically, we want to (1) Evaluate how changes in local topography determine the space occupied by plant species based on their functional characteristics, (2) Identify how the functional density dependence determines the space occupied by plant species based on their functional traits, and (3) Analyze to what proportion the occupation of the space for the plant species is determined by the local topography control on their functional traits and which by density dependence. Here, due to the local drought variation generated by topography changes acting on a particular suite of traits, some species can be filtered in a given area in response to changes in water availability and nutrient leaching. Thus, environmental filtering is expected to dominate community assembly, as it determines the space where species can survive, filtering species with similar functional traits locally. However, under less limiting environments, it is expected that species with the same functional strategy present a negative functional density dependence in which, at a short distance from individuals of the same species and from species with similar functional strategies, competitive exclusion is generated that will lead to a greater number of functional strategies. It will demonstrate biotic competition between individuals with the same strategy and a niche complementarity that promotes coexistence between individuals with different functional strategies.

Methods

Study site

In 2019 we established a 10-ha permanent plot at the Cerro La Potrosa, La Guajira (Colombia) (N 11° 05' 5.1" W 72° 33' 57.8", Figure 1), as part of the initiative for monitoring TDF in Colombia, led by the Instituto Humboldt Colombia and supported by Carbones del Cerrejon Limited at La Guajira. The plot area has 948.3 mm of total annual precipitation, 2006.2 mm year¹ total annual evapotranspiration, and 37.6°C mean annual temperature (Baez & Trujillo, 2014). This TDF is part of the Serranía del Perijá foothills in Northern South America. We recorded 17883 individuals of trees with a DBH (diameter at breast height – 1.30m) upper than 2.5 cm). For each tree, we estimated the total height (m), measured DBH with a diameter tape and located the spatial position within the plot of each individual tree species at a 1m spatial resolution.

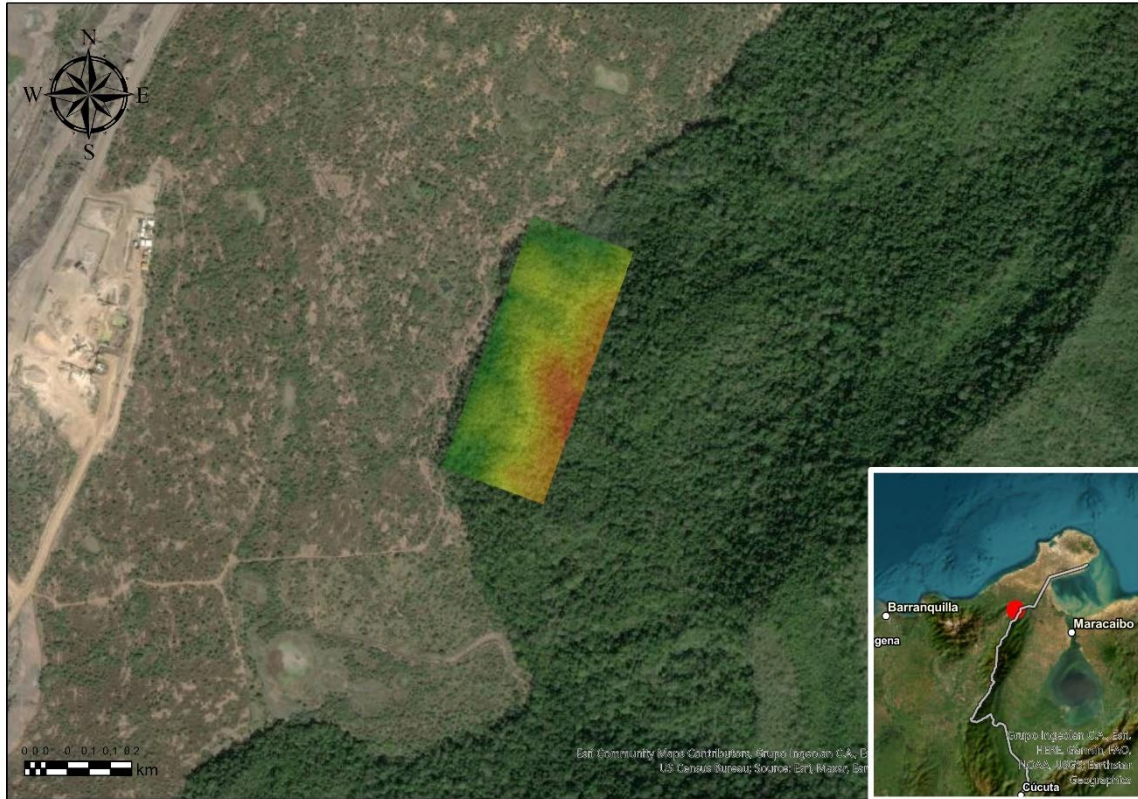


Figure 1. The 10-ha TDF permanent plot was established at Cerro La Potrosa, La Guajira, Colombia (Carbones del Cerrejón Limited).

Functional trait characterization for tree species

From the species pool in the plot, we randomly selected at least five individuals per species and collected between five and ten exposed leaves for measuring leaf traits and a 15 cm section of a branch for measuring wood traits. Following the Salgado-Negret (2015) methods, we calculated 12 leaf and wood functional traits per species, which are related to functions of water balance, light interception, tissue investment, water regulation, photosynthetic capacity, and hydraulic safety-efficiency trade-offs (Table 1; Pizano & García, 2014; Salgado-Negret, 2015; González-M. et al. 2020). For individuals without values of functional traits, we imputed the values by using “*missForest*” package in R,

which uses decision trees to perform the imputation of traits at the family and genus level. (Version 4.1.2; Stekhoven and Bühlmann, 2012).

Table 1. Selected functional traits and their association with different plant functions.

Functional traits	Trait function	Reference
Leaf thickness (Lth- μm)	Biotic defense, tissue investment, resource acquisition	Salgado-Negret (2015)
Leaf dry matter content (LDMC- mg/g)	Investment in tissue and foliar defense.	Pérez-Harguindeguy et al. (2013); Díaz et al. (2016)
Wood density (WD- g/cm^3)	Hydraulic support, hydraulic safety in the use of water	Chave et al. (2009); Pérez-Harguindeguy et al. (2013);
Moisture content at fiber saturation point (WC _{max} -%)	Efficiency and safety in the use of water	Berry y Roderick (2005)
Specific hydraulic conductivity of the xylem (Kp)	Efficiency and safety in the use of water	Chave et al. (2009); Scholz et al. (2013)
Vessel density (VD- No/mm^2) and Vessel area (VA μm^2)	Efficiency and safety in the use of water	Chave et al. (2009); Scholz et al. (2013); Jacobsen et al. (2005)
Fiber cell wall thickness. (FWT- μm)	Drought resistance, hydraulic support and tissue inversion	Madsen y Gamstedt (2013); Scholz et al. (2013); Sorieul et al. (2016)
Pit area (PA- μm^2)	Efficiency and safety in the use of water	Scholz et al. (2013)
Pit aperture diameter (DA _{pit} - μm^2)	Efficiency and safety in the use of water	Scholz et al. (2013); Helmling et al. (2018)
Ray width (RW- μm) and rays density (RD- No/mm^2)	Horizontal water conduction	Barajas – Morales (1985); Barnard et al (2013); Pfautsch et al (2015)

Local topography variation

In order to determine the local environmental variations in the permanent plot related to the topography, we sample elevation differences at each 1 m, then we performed a digital elevation model (DEM) by using the contour lines shaped by the elevation sample. To do this, we used the ANUDEM interpolation method, which determines terrain variations with a high resolution (Hutchinson, Xu, & Stein, 2011). By using the “terrain” function in R (version 4.1.2) from the package “raster”, we calculated three key topographic variables.

Altitude index (m) defined as the elevation of a point in space relative to sea level, whereas the higher the elevation tree species are located, the higher is the constraints due to a rapid runoff at the top of hills. The topographic roughness index (Ruggedness index) means how homogeneous or heterogeneous the terrain is concerning the surrounding cells (Wilson et al., 2007), where a higher index value indicates greater terrain roughness and therefore, greater runoff by sudden elevation changes. Finally, the average slope (slope index, °), where the higher the level of inclination of the land, the less water availability for the trees because greater erosion processes and soil instability are promoted due to greater runoff (Nadal-Romero et al., 2014). To define the topographic habitats inside the permanent plot, we calculated the topographic index (TI) as the sum of the normalized topographic variables with mean 0 and variance 1. Higher values of this topographic index indicate greater limiting conditions for the trees due to high elevation values, roughness and slope that favor greater leaching of nutrients from the hills to the valleys.

Setting functional density dependence

We used the individuals' X and Y spatial location within each 10 x 10 m subplot to define the effects of functional density dependence between species and individuals across the permanent plot. Performing the mapping of all the individuals of the tree species in the R software (version 4.1.2), to evaluate the minimum distance between each individual and its nearest neighbors of the plot and determine its spatial dependence (Vallejo & Galeano, 2009). For this, the "dist" function of the "stats" package in the R software version 4.1.2 was used for each individual to calculate the Euclidean average distance for the nearest neighbors at both of the same species (Intraspecific distance index) and for different species

(Interspecific distance index). This allows us to model the effective distance in which different functional strategies of individuals develop so that they can coexist without competing for resources among themselves.

Data analysis

To define the functional space of the community, we evaluated the trait probability density functions (TPD) following Carmona et al. (2016). Individuals measured the average value of each trait and the data extracted from the environmental variables and distances for each individual were used. First, an analysis of the variance inflation factor (limit equal to 3) was performed to reduce functional autocorrelation (Millas, 2014). Subsequently, the functional space of the plot was defined, through a principal component analysis, the environmental space through the classification of the topographic index, and the effects of FDD through the classification of the inter and intraspecific distance of the average nearest neighbors. The comparison of the functional space of the TPD, the topographic index and the distance indices was used to analyze the influence of the local topography and the FDD effects on the space of occupation of each plant species based on their functional strategies. This makes us possible to determine the most probable spaces where the species and individuals were concentrated in the different topographic and distance categories shaped. Where the TPD made it possible to define the probabilities of occurrence of the functional traits for the species and the functional indices with respect to the total space sampled based on the aboveground biomass calculated for each individual and summarized at the species level. This was estimated based on the allometric equations type I and type II suggested by Alvarez (2012).

In this way, the functional richness index used, indicates how much of the functional space a given community occupies and the spectrum of strategies shaped by that community (Carmona et al., 2016). Thus, we also use the functional dissimilarity index that indicates how much the functional space of one selected community is shared concerning the optimal functional space of the entire community (Carmona et al., 2016). These indices were modeled in a Generalized Additive Mixed Model ("gamm" function of the "gamm4" package in R) with the topographic index, the intra- and interspecific distance index to verify the topographic influence and the FDD. Finally, a Gamm multivariate model was carried out to define the effects of the three variables on the functional assembly of the community.

Results

The topographic index (min: -0.6, max: 11.47, mean: 0.0015) shows an increase in stress conditions at the local space for the plot (Figure 1d, red areas), given the increase in slope (min: 0.0012, max: 0.9654, mean: 0.3345; Figure 1b), elevation (min: 203.77, max: 273.55, mean: 231.42; Figure 1c) and roughness (min: 0.002, max: 0.91, mean: 0.22; Figure 1a) of the terrain. While in conditions of low elevation and low roughness that is reflected in flat terrain within the plot (Figure 1d, blue areas). The variable with the greatest representativeness for the index was the slope, given its similarity of areas with low slope and high slope with the areas with the lowest and highest topographic index, respectively. We found that the areas with less roughness, less slope and less elevation are the most predominant within the plot marked by the blue zones. Additionally, the areas with the greatest roughness, steepest slope, and highest elevation are concentrated in the middle area of the plot (150 m to 400 m on the Y axis) and in the lower left area (150 to 200 m on the X axis, with 0 to 20 on the Y axis), which represents the hilly areas.

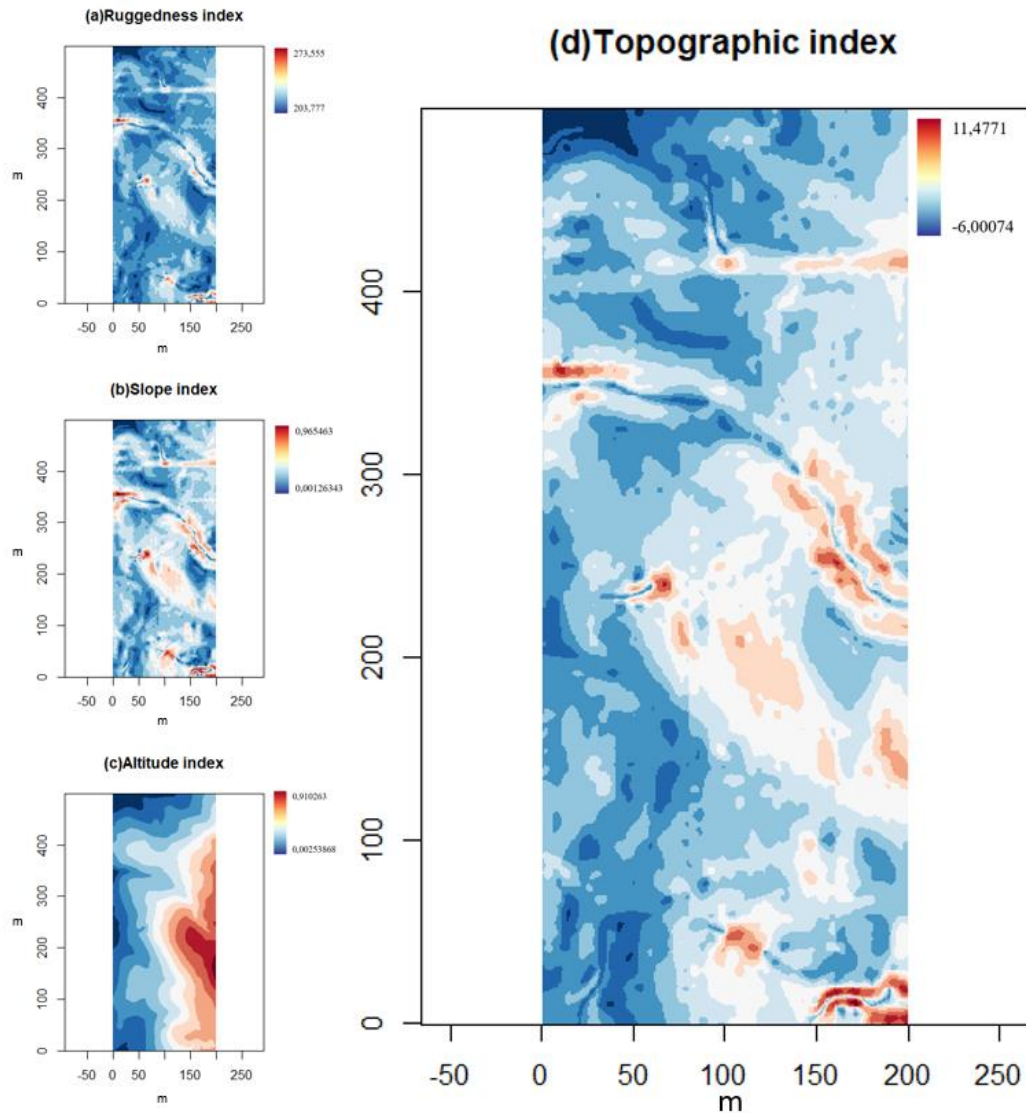


Figure 2. Topographic variables at the TDF 10-ha permanent plot. A) Ruggedness index, b) Slope index, c) Altitude index. D) Topographic index. The color gradient from blue to red indicates the increase in the indexes. Thus, dark blue areas indicate low roughness, low slope and low elevation (valleys), while dark red areas indicate high roughness, high slope and high elevation (hilly).

The generalized multiple additive models for topography (topographic index) fitted well with functional richness distribution and functional dissimilarity ($R^2 = 0.82$; $R^2 = 0.67$, respectively). Functional communities at the two extreme sides of the topographic index gradient have low functional richness (0.74 to 38.07, Figure 2a) but high functional dissimilarity (>0.55 , Figure 2b). In contrast, high functional richness and low dissimilarity

were concentrated between 38.07 to 75.41 of the topographic index (Figure 2a, <0.55 , Figure 2b).

Thus, the effect of the functional dependence of the density (FDD) on the functional assembly of the plot can also be appreciated. The generalized multiple additive models for the interspecific distance index and intraspecific distance index showed a good fit with functional richness distribution and functional dissimilarity ($R^2 = 0.54-0.90$, $p < 0.001$). Where, for the distance of the interspecific neighbors, a tendency was found toward a decrease in functional richness (81.17 to 0.74; Figure 2c) and an increase in functional dissimilarity (0.09 to 0.99; Figure 2d) as the distance increases (>2 , Figure 2c and 2d). However, at small distances, there are communities where functional richness decreases ($F_{Rich} < 81.17$; Figure 2c) and functional dissimilarity increases ($F_{Diss} > 0.09$; Figure 2d). On the other hand, this behavior is more evident when the closest mean distance of the conspecific neighbors is evaluated. Where, at smaller distances (<192.08 ; Figure 2e and 2f) richness increases (0.12 to 68.70; Figures 2c) and functional dissimilarity decreases (1 to 0.16; Figure 2f).

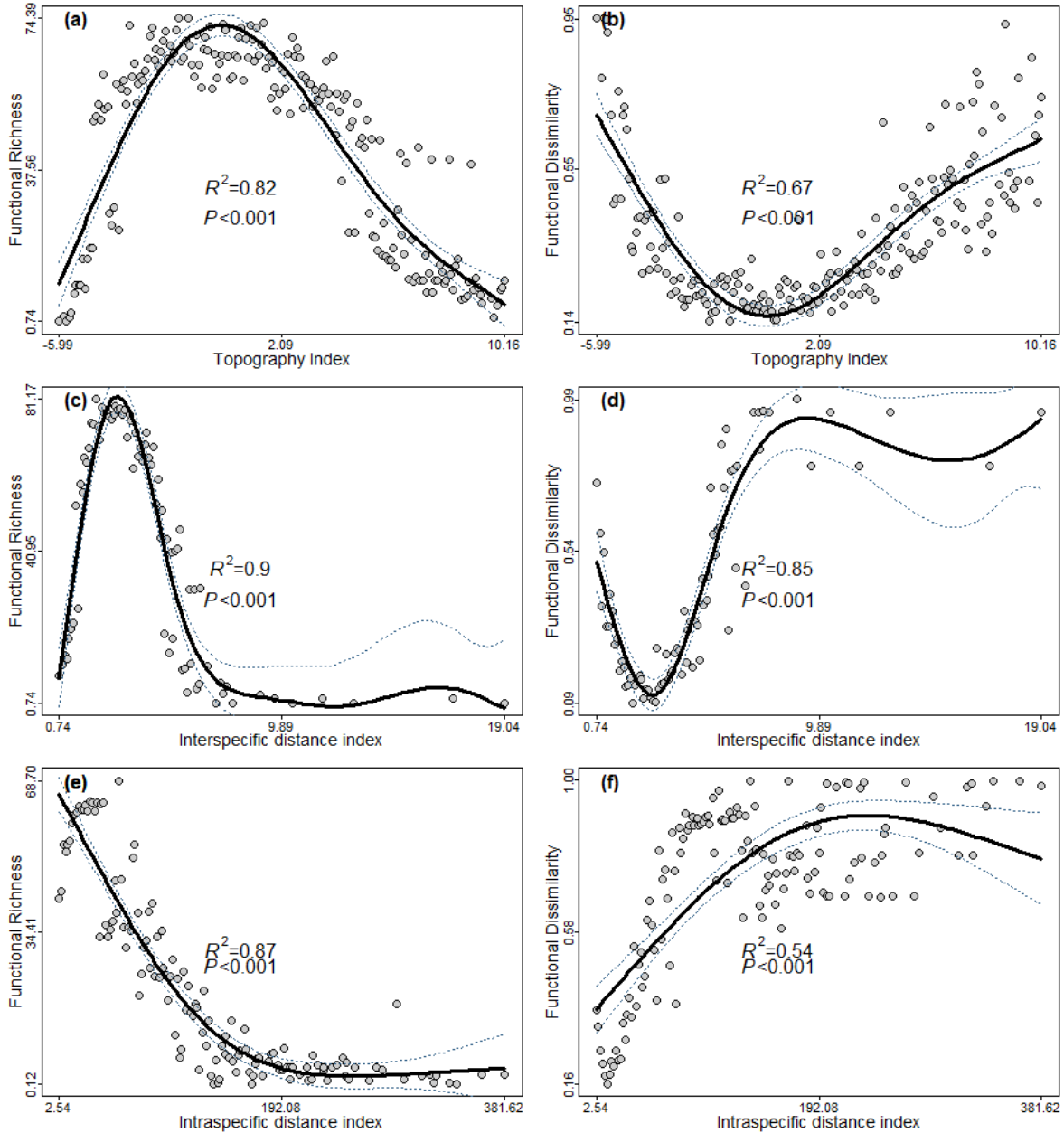


Figure 3. Gamma distribution model for functional richness and functional dissimilarity as a function of the topographic index, interspecific distance index and intraspecific distance index (a) relationship of the topographic index on functional richness, (b) relationship of the topographic index on functional dissimilarity, (c) relationship of the average minimum distance of interspecific nearest neighbors on functional richness, (d) relationship of the average minimum distance of interspecific nearest neighbors on functional dissimilarity, (e) relationship of the average minimum distance of intraspecific nearest neighbors on functional richness, (f) relationship of the average minimum distance of intraspecific nearest neighbors on functional wealth. The gray dots represent the value of the functional richness and functional dissimilarity index constructed with the trait probability density function (TPD) for each category in the topographic index and the distance indices.

Finally, to determine the proportion of the two factors on the functional assembly, we carried out a model that relates the richness and functional diversity with the variables of topography and distance (Table 1 and Table 2, respectively). We found a significant effect of the three variables on functional richness ($P < 0.001$). However, when we evaluated the non-linear effects, it was the topographic index the only variable with significant effects on functional richness ($P = 4.97\text{e-}05$ ***). On the other side, for functional dissimilarity we find a high significance ($P < 0.001$) of the topographic and density dependence variables, but when we see the non-linear effects of each variable, we only see an appreciable effect of the distance of neighboring individuals of the same species ($P = 0.099$).

Table 2. Explained proportion of topography and density dependence variables on functional richness. Generalized multiple additive models. Significance codes 0 ‘****’ 0.001 ‘***’ 0.01 ‘**’ 0.05 ‘.’ 0.1 ‘ ’ 1

	<i>Estimate</i>	<i>STD Error</i>	<i>T value</i>	<i>p-Value</i>
<i>Intercept</i>	40.8932	0.4951	82.6	<2e-16 ***
<i>Topography index</i>	1.957	1.998	11.365	4.97e-05 ***
<i>Interspecific distance index</i>	1	1	1.987	0.162
<i>Intraspecific distance index</i>	1	1	0.640	0.426
R^2			0.221	

Table 3. Explained proportion of topography and density dependence variables on functional dissimilarity. Generalized multiple additive models Significance codes 0 ‘****’ 0.001 ‘***’ 0.01 ‘**’ 0.05 ‘.’ 0.1 ‘ ’ 1

	<i>Estimate</i>	<i>STD Error</i>	<i>T value</i>	<i>p-Value</i>
<i>Intercept</i>	0.655818	0.004745	138.2	<2e-16 ***
<i>Topography index</i>	1	1	2.185	0.1426
<i>Interspecific distance index</i>	1	1	1.691	0.1966
<i>Intraspecific distance index</i>	1	1	2.762	0.0998 .
R^2			0.01164	

Discussion

Environmental filters and biotic interactions, are generally recognized as the mechanisms underlying community assembly for tree species in tropical forests (Perry, Enright, Miller, & Lamont, 2012; Arellano et al., 2017; Li et al. al., 2019). In particular, the TDF experiences environmental constraints that can determine the niche occupation of species, which respond through their functional traits to be able to adapt to these particular environmental conditions (Chaturverdi et al., 2020; González et al., 2020). However, it is still not clear at a local scale how the influence of the environment and biotic factors affect the functional assembly of plant species. In this way, our study sought to understand the influence of abiotic and biotic factors on community assembly in TDF. We evaluated that both topography and functional density dependence differentially affect the functional distribution of plant species in the TDF. Our results showed that: 1) at the local scale, both functional topography and density dependence differentially affect the functional distribution of plant species in the TDF. There is a topography gradient that affects the availability of resources in the plot, where at the extremes of the topographic gradient were found a low functional richness and a high dissimilarity, indicating an optimal strategy for the community in the intermediate areas of the gradient. 2) In terms of the effects of functional density dependence at the species and individual level, we found that as lower the density of individuals lower the functional richness and higher the functional dissimilarity. 3) The topography index showed significant importance for functional richness at a local scale but not for functional dissimilarity. Interestingly no effects were found for the functional density dependence in intraspecific and interspecific distance index.

Contrasting effects of topography as a local determinant for functional richness and dissimilarity in TDF

The topographic index at the local scale showed to be a determinant factor for the functional richness and dissimilarity in our TDF community. As we expected, we found a topographic gradient which may be associated with differences in resources available, where the hilly areas had more limiting topographic conditions, in consequence, a decrease in the functional richness and an increase in functional dissimilarity, generating a filter in the number of very different functional strategies at the functional optimum of the community. This behavior describes the filter effects of water availability on functional strategies, which can be explained by high water constraints at this side of the plot. Here, species with strategies towards hydraulic security are more common, which are mostly adapted to tolerate negative pressures caused by the low availability of resources (Chaturverdi et al., 2020; Caleño et al., 2023). Our results are consistent with the reported dominance of topography as a limiting factor in the availability of resources for plants at the local scale (Enoki & Abe, 2004; Detto, Muller-Landau, Mascaro & Asner, 2013; Severin et al., 2015; Zuleta et al., 2018), where a tendency of the species to increase the density of the wood and reduce the area of its vessels has been found as strategies oriented toward hydraulic security in response to the limiting topographic conditions found in the hills of the Amazonian forests (Cosme et al., 2017).

In contrast to our expectations, however, the topographic factor is acting on both ends of the gradient, finding the same behavior of richness and functional dissimilarity both in

areas with limitations and in the valley the availability of a great resource is associated with topographic conditions. This responds, to the differential occupation of niches in response to the availability of resources reported for the TDF (Chaturverdi et al., 2020; Caleño et al., 2023). Likewise, in Colombian TDF, Caleño et al. (2023) found that the abiotic filter given by soil nutrients restricts the functional assembly of the community, since it conditions the species with safe strategies to areas with low availability of the resources, and efficient strategies in areas with high water availability. That supports the behavior associated with our results in the topographic gradient, when these topographic conditions become more or less stressful with respect to the average, species with differential functional strategies begin to appear, in response to the colonization of these topographic spaces (valleys and hills) not occupied (Cavenders-Bares et al., 2004; Satdichanh, Millet, Heinemann, Nanthavong & Harrison, 2015; Subedi, Hogan, Ross, Sah & Baraloto, 2019; Chaturverdi et al., 2020).

These results agrees with what was found by Cosme et al. (2017), who highlight that on a local scale, the hydro-edaphic climatic conditions determine the composition of the species and their patterns through the hydraulic features of the plants; which determines a substantial similarity of the species by environmental filtering between the valleys and the hills, generated by the availability of water in the soil in tropical forests of the Amazon. In the same way, Diémé, Armas, Rusch and Pugnaire (2019) found in a greenhouse experiment with plant species in Senegal, that the functional traits of the seedlings and therefore, their distribution in space varies according to the availability of nutrients and water on the ground. This supports the influence of the environment found in this study, for

species poorly adapted to tropical dry forest, restricting their distribution to the topographic conditions found at the extremes of the gradient.

In contrast, in the middle zones of the topographic gradient, an increase in the number of strategies was found, very similar to the functional optimum of the community. Which could be influenced by the functional response of the species to the most expected conditions of the TDF in Colombia, where it has been reported that the optimal strategies of the TDF species are given by a variation of their strategies between safety and hydraulic efficiency with a high investment in tissues to resist the negative pressures generated by drought (González et al. 2020). Our results show that in the average conditions of the plot, we find this functional optimum of the TDF in response to the functional adaptation for the most expected dry conditions for this ecosystem, which restricts the suboptimal strategies of the TDF to the extreme topographic conditions found in the gradient. However, it is worth emphasizing that to have greater certainty about the variations of the available resources in the topographic gradient, it is essential to include the role of soil nutrients in future approaches.

Density dependence drives functional assembly at the local scale

As we expected, the effects of the functional density dependence influence both individuals and species community assemble. Here, as higher the individual's density (abundance) increases the functional richness is our plot, while, as the distances increase between individuals, functional richness decreases and functional dissimilarity increases. According to Paine et al. (2012), the density dependence filter factors act to a greater extent when the

functional strategies move away from the functional optimum of the community because there is a greater risk of mortality due to other biotic interactions, such as predation, by presenting singularities in their strategies and functional traits; which agrees with our results when there is an increase in distances and an increase in functional dissimilarity. Likewise, the increase in the number of strategies, very similar to the functional optimum at short distances between individuals of different species, probably occurs because the similarity of strategies between species produces a competition filter that prevents the grouping of similar strategies in different species in the same space, which generates different adaptations and functional expressions in response to this competition (Janzen, 1970; Connell, 1971; Cavenders-Bares et al., 2004; McNickle & Dybzinski, 2013). Additionally, this increase in functional expressions when we observe in distances of individuals of the same species could be due to biotic competition and functional plasticity between individuals with the same strategy around the search for resources, which produces a niche complementarity within the same species allowing coexistence between individuals with the same functional strategy but expressed differently (McNickle & Dybzinski, 2013). However, contrary to what was expected when the distances decreased between strategies of individuals of different species, we found a decrease in functional strategies very different from the optimal functional of the community. This can be explained according to Zang et al. (2021), who pointed out that this absence of the density dependent filter can be related to the grouping of individuals of species with limited dispersion, the interactions in juvenile stages of the species or a more significant effect of local variations of the environment. This response could be related to the similarity limit hypothesis, which establishes that there is a limit in which species with similar or redundant strategies or functional expressions can coexist without generating competition for the use of resources

(Yannelli et al., 2017); Therefore, a competitive exclusion is generated in which only some species with functional strategies different from the community optimum can be established.

Topography or functional density dependence, which is more critical in the TDF assembly?

As we expected for TDF, the abiotic filter evaluated from the topography has a significant effect on the functional richness of the community given the limitations in terms of drought and resource availability reported for this ecosystem (Luzuriaga et al., 2012; Pizano & García, 2014; Bartlett et al., 2016; García-Guzmán et al., 2016; Méndez-Toribio et al., 2020). Our results are consistent with the importance of the local-scale topographic filter for the assemblage of plant communities found in various Amazonian tropical and Asian subtropical forests (Zuleta et al., 2018; Li et al., 2019). The topographic filter is important of habitats with greater stress affecting the availability of light, nutrients and soil moisture (Li et al., 2019). However, although each factor evaluated in this research shows the importance in the functional assemblage, when we explore the combined effects of the topographic variables and those associated with the functional density dependency filters, they do not express a significance on the functional dissimilarity. This differs from what was found by Guzmán-M et al. (2018), who establish that the competitive filter given by biotic interactions determines the assembly of the community in the same proportion as environmental filters for dry ecosystems. However, the combined effects of topography and functional dependence on density may be offset by turnover and functional redundancy, where a group of species with similar functional strategies may respond differentially to

environmental effects and biotics interactions in search of the dynamic balance of the community (McNickle & Dybzinski, 2013; Yannelli, et al. 2017). The density dependent filter can be more important in the average conditions of the topographic gradient where there is a greater number of functional strategies very similar to the optimum of the community.

Additionally, the functional responses of the species may probably be conditioned not only by the abiotic environment and the density dependent filter but also by biotic interactions such as predation and dispersal, which may be determinants of community structure and the performance of species in the ecosystem (Hubble, 1980; Swenson & Weiser, 2010; Perry, Enright, Miller, and Lamont, 2012; McNickle & Dybzinski, 2013; Li et al., 2019; Clark et al., 2018). Generating the need to explore the influence of other biotic factors in the functional assemblage of the tropical dry forest in Colombia in future research.

Functional assembly of the TDF as a management tool

Understanding the topographic and functional density factors that interact in TDF communities is essential to comprehensively understanding the mechanisms that condition the local assemblage of plant communities in this ecosystem. This would allow an advance in the strategies for the restoration and integral management of the tropical dry forest in Colombia. It is contributing to the fulfillment of the first restoration approach defined in the National Program for the Conservation and Restoration of the TDF in Colombia (PNCBST; Minambiente, 2021), which seeks to recover and maintain the ecosystem capacity of the TDF through the recovery of the function of degraded areas. This can be achieved by

defining species arrangements with functional strategies adapted to the limiting topographic conditions of the terrain. That generates greater certainty in restoration designs in response to different local environmental conditions and reducing the competitive biotic filter with species with similar strategies or functional expressions, reducing costs, recovering ecosystem functionality, and increasing success in sustainable management of this ecosystem (Avella-Muñoz et al., 2022).

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References

- Alvarez, E., Duque, A., Saldarriaga, J., Cabrera, K., de Las Salas, G., del Valle, I., ... & Rodríguez, L. (2012). Tree above-ground biomass allometries for carbon stocks estimation in the natural forests of Colombia. *Forest Ecology and management*, 267, 297-308.
- Arellano, A., Umaña, M. N., Macia, M. J., Loza, M. I., Fuentes, A., Cala, V., Jorgensen, P. M. (2017). The role of niche overlap, environmental heterogeneity, landscape roughness and productivity in shaping species abundance distributions along the Amazon–Andes gradient. *Global Ecology and Biogeography*, 26, 191–202.
- Avella Muñoz, A., Garzón Fierro E. M., Páez Díaz, M. J., & Ordosgoitia, D. (2022). *Restauración ecológica: Principios y prácticas*. Ministerio de Ambiente y Desarrollo Sostenible de Colombia-Fundación Natura.
- Báez, L. y F. Trujillo (Eds.). 2014. *Biodiversidad en Cerrejón*. Carbones de Cerrejón, Fundación Omacha, Fondo para la Acción Ambiental y la Niñez. Bogotá, Colombia. 352 p.
- Barajas – Morales, J. (1985). Wood structural differences between trees of two tropical forests in Mexico. *IAWA Bulletin n.s.*, Vol. 6 (4). Instituto de Biología, Universidad Nacional Autónoma de México. Coyoacán, México, D. F.
- Barnard DM, Lachenbruch B, McCulloch KA, Kitin P, Meinzer FC (2013) Do ray cells provide a pathway for radial water movement in the stems of conifer trees? *Am J Bot* 100:322–331.
- Bartlett, M. K., Zhang, Y., Yang, J., Kreidler, N., Sun, S. W., Lin, L., Hu, Y. –H., Cao, K. – F., Sack, L. (2016). Drought tolerance as a driver of tropical forest assembly: resolving

- spatial signatures for multiple processes. *Ecology*. 97(2), 503-514.
- Berry, S. L., y Roderick, M. L. (2005). Plant-water relations and the fibre saturation point. *New Phytol.*, 168, 25– 37.
- Caleño-Ruiz BL, Garzón F, López-Camacho R, Pizano C, Salinas V and González-M R (2023). Soil resources and functional trait trade-offs determine species biomass stocks and productivity in a tropical dry forest. *Front. For. Glob. Change* 6:1028359. doi: 10.3389/ffgc.2023.1028359
- Carmona, C. P., De Bello, F., Mason, N. W., & Lepš, J. (2016). Traits without borders: integrating functional diversity across scales. *Trends in ecology & evolution*, 31(5), 382-394.
- Cavenders-Bares, J., Ackerly, D. D., Baum, D. A., y Bazzaz, F. A. (2004). Phylogenetic Overdispersion in Floridian Oak Communities. *The American Naturalist*, 163 (6), 823-843.
- Chaturvedi, R. K., Tripathi, A., Raghubanshi, A. S., & Singh, J. S. (2020). Functional traits indicate a continuum of tree drought strategies across a soil water availability gradient in a tropical dry forest. *Forest Ecology and Management*, 118740. doi:10.1016/j.foreco.2020.118740
- Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N. G. y Zanne, A. E. (2009). Towards a worldwide wood economics spectrum. *Ecol. Lett.*, 12, 351– 366.
- Chave, J. (2013). The problem of pattern and scale in ecology: what have we learned in 20 years?. *Ecology Letters*, 16, 4–16. doi: 10.1111/ele.12048.
- Clark, A. T., Detto, M., Muller-Landau, H., Schnitzer, S., Wright, S. J., Condit, R., Hubbell, S. P. (2018). Functional traits of tropical trees and lianas explain spatial structure across multiple scales. *Journal of ecology*, 106, 795-806. doi: 10.1111/1365-2745.12804.

- Connell, J. H. (1971). On the role of natural enemies in preventing competitive exclusion in some marine animals and rainforests. En: Den Boer P. J., Gradwell G. R., editores. Dynamics of populations: Proceedings of the advanced study institute on dynamics of numbers of populations. Wageningen. Center for Agricultural Publishing and Documentation. pp. 298-312.
- Cornwell, W. K., y Ackerly, D. D. (2009). Community assembly and shifts in the distribution of functional trait values across an environmental gradient in coastal California. *Ecological Monographs*. 79, 109–126.
- Cosme, L. H. M., Schiatti, J., Costa, F. R. C., y Oliveira, R. S. (2017). The importance of hydraulic architecture to the distribution patterns of trees in a central Amazonian forest. *New Phytologist*, 215, 113–125.
- Detto, M., Muller-Landau, H. C., Mascaró, J., y Asner, G. P. (2013). Hydrological networks and associated topographic variation as templates for the spatial organization of tropical forest vegetation. *PLoS ONE*, 8(10), e76296. doi:10.1371/journal.pone.0076296.
- Díaz, S., Kattge, J., Cornelissen, J. H. C., Wright, I. J., Lavorel, S., Dray, S. et al. (2016). The global spectrum of plant form and function. *Nature*, 529, 167– 171.
- Diémé, J. S., Armas, C., Rusch, G. M., y Pugnaire, F. I (2019). Functional responses of four Sahelian tree species to resource availability. *Flora*, 254, 181–187.
- Enoki, T., y Abe, A. (2004). Saplings distribution in relation to topography and canopy openness in an evergreen broad-leaved forest. *Plant Ecology*, 173(2), 283-291.
- García-guzmán, G., Trejo, I., & Sánchez-coronado, M. E. (2016). Forest Ecology and Management Foliar diseases in a seasonal tropical dry forest: Impacts of habitat fragmentation, 369, 126–134. <http://doi.org/10.1016/j.foreco.2016.03.043>
- González-M. R., Posada, J. M., Carmona, C. P., Garzón, F., Salinas, V., Idárraga-Piedrahita,

- Á., Pizano, C., Avella, A., López-Camacho, R., Norden, N., Nieto, J., Medina, S. P., Rodríguez-M, G. M., Franke-Ante, R., Torres, A. M., Jurado, R., Cuadros, H., Castaño-Naranjo, A., García, H., Salgado-Negret, B. (2020) Diverging functional strategies but high sensitivity to an extreme drought in tropical dry forests. *Ecol Lett.* 2021 Mar;24(3):451-463. doi: 10.1111/ele.13659. Epub 2020 Dec 14. PMID: 33316132.
- Gusmán-M, E., de la Cruz, M., Espinosa, C. I., Escudero, A. (2018). Focusing on individual species reveals the specific nature of assembly mechanisms in a tropical dry-forest. *Perspectives in Plant Ecology, Evolution and Systematics*, 34, 94-101. doi: 10.1016/j.ppees.2018.07.004.
- Helmling, S., Olbrich, A., Heinz, I. y Koch, G. (2018). Atlas of vessel elements. *IAWA J.*, 39, 250-352.
- Hubbell, S. P. (1980). Seed predation and the coexistence of tree species in tropical forest. *Oikos*, 35, 214-229.
- Hubbell, S. P. (2001). *The Unified Neutral Theory of Biodiversity and biogeography*. Princeton University Press, Princeton. NJ, USA, pp. 1–375.
- Hutchinson, M., Xu, T., & Stein, J. (2011). Recent Progress in the ANUDEM Elevation Gridding Procedure. In T. Hengel, I. Evans, J. Wilson, & M. Gould (Eds.), *Proceedings of the Geomorphometry* (pp. 19–22). Redlands, California: International Society for Geomorphometry.
- Jacobsen, A.L., Ewers, F.W., Pratt, R.B., Paddock, W.A. y Davis, S.D. (2005). Do xylem fibers affect vessel cavitation resistance? *Plant Physiol.*, 139, 546– 556.
- Janzen, D. H. (1970). Herbivores and the number of tree species in tropical forest. *The American Naturalist*, 104, 501:528.
- Kraft, N. J. B., Valencia, R., y Ackerly, D. D. (2008). Functional traits and niche-based tree

- community assembly in an Amazonian forest. *Science*. 322, 580–582.
- Kraft, N. J. B., Adler, P. B., Godoy, O., James, E. C., Fuller, S., Levine, J. M. (2015). Community assembly, coexistence and the environmental filtering metaphor. *Functional Ecology*. 29, 592–599. doi: 10.1111/1365-2435.12345.
- Lhotsky, B., Kovacs, B., Onodi, G., Csecserits, A., Redei, T., Lengyel, A., Kertesz, M., y Botta-Dukat, Z. (2016). Changes in assembly rules along a stress gradient from open dry grasslands to wetlands. *Journal of Ecology*, 104, 507–517. doi: 10.1111/1365-2745.12532.
- Li, Y., Bin, Y., Xu, H., Ni, Y., Zhang, R., Ye, W., Lian, J. (2019). Understanding Community Assembly Based on Functional Traits, Ontogenetic Stages, Habitat Types and Spatial Scales in a Subtropical Forest. *Forests*, 10, 1055. doi: 10.3390/f10121055.
- Luzuriaga, A. L., Sánchez, A. M., Maestre, F. T., Escudero, A. (2012). Assemblage of a semi-arid annual plant community: abiotic and biotic filters act hierarchically. *PloS one*. 7(7), e41270.
- Madsen, B. y Gamstedt, E.K. (2013). Wood versus plant fibers: Similarities and differences in composite applications. *Advances in Materials Science and Engineering*, 2013, 1–14.
- Maire, V., Gross, N., Börger, L., Proulx, R., Wirth, C., Pontes, L. S., Soussana, J. F., Louault, F. (2012). Habitat filtering and niche differentiation jointly explain species relative abundance within grassland communities along fertility and disturbance gradients. *New Phytol*. 196, 497–509.
- McNickle, G. G. y Dybzinski, R. (2013). Game theory and plant ecology. *Ecology Letters*, 16: 545–555. doi: 10.1111/ele.12071.
- Méndez-Toribio, M., Ibarra-Manríquez, G., Paz, H., y Lebrija-Trejos, E. (2020).

Atmospheric and soil drought risks combined shape community assembly of trees in a tropical dry forest. *Journal of Ecology*, 108, 1347–1357. doi: 10.1111/1365-2745.13355.

Ministerio de Ambiente y Desarrollo Sostenible, (2021). Programa nacional para la conservación y restauración del bosque seco tropical en Colombia. Plan de Acción 2020-2030 / Ministerio de Ambiente y Desarrollo Sostenible. Dirección de Bosques, Biodiversidad y Servicios Ecosistémicos: Ospina Arango, Olga Lucía (Ed.); Instituto de Investigación Recursos Biológicos Alexander von Humboldt: Alcázar Caicedo, Carolina; Avella Muñoz, Edgar Andrés; Norden Medina, Natalia; García Villalobos, Daniel Hernán; García Martínez, Hernando; Castellanos Castro, Carolina; González-M, Roy. ---- Bogotá D.C.: Colombia. 78 p.: il. ISBN: 978-958-5551-56-5

Millas, J. (2014). Tolerance and Variance Inflation Factor. Wiley StatsRef: Statistics Reference Online. <https://doi.org/10.1002/9781118445112.stat06593>.

Nadal-Romero, E., Petric, K., Verachtert, E., Bochet, E., & Poesen, J. (2014). Effects of slope angle and aspect on plant cover and species richness in a humid Mediterranean badland. *Earth Surface Processes and Landforms*, 39(13), 1705–1716. doi:10.1002/esp.3549

Paine, C. E. T., Norden, N., Chave, J., Forget, P.-M., Fortunel, C., Dexter, K. G., & Baraloto, C. (2011). Phylogenetic density dependence and environmental filtering predict seedling mortality in a tropical forest. *Ecology Letters*, 15(1), 34–41. doi:10.1111/j.1461-0248.2011.01705.x

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P. et al. (2013). New handbook for standardised measurement of plant functional traits worldwide. *Aust. J. Bot.*, 61, 167– 234.

- Perry, G. L. W., Enright, N. J., Miller, B. P., Lamont, B. B. (2012). Do plant functional traits determine spatial pattern? A test on species-rich shrublands. Western Australia. *Journal of Vegetation Science*. Doi: 10.1111/j.1654-1103.2012.01476.x.
- Pfautsch S, Hölttä T & Mencuccini M (2015). Hydraulic functioning of tree stems—fusing ray anatomy, radial transfer and capacitance. *Tree Physiology Advance Access published July 9*.
- Pizano, C., y García, H. (2014). *El Bosque Seco Tropical en Colombia*. Instituto Alexander von Humboldt. Bogotá. D.C., Colombia. 349 pp.
- R Core Team (2017) R: A language and environment for statistical computing; version 4.1.2. Available: <http://www.R-project.org/>
- Salgado-Negret, B. (ed.) (2015). *La ecología funcional como aproximación al estudio, manejo y conservación de la biodiversidad: protocolos y aplicaciones*. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt. Bogotá, D. C. Colombia. 236 pp.
- Satdichanh, M., Millet, J., Heinemann, A., Nanthavong, K., y Harrison, R. (2015). Using Plant Functional Traits and Phylogenies to Understand Patterns of Plant Community Assembly in a Seasonal Tropical Forest in Lao PDR. *PLoS ONE*, 10 (6): e0130151. doi:10.1371/journal.pone.0130151.
- Scholz, A., Klepsch, M., Karimi, Z. y Jansen, S. (2013). How to quantify conduits in wood? *Front. Plant Sci.*, 4, 1– 11.
- Severin D. H., Harter, D., Steinbauer, M. J., Gallego-Puyol, D., Fernández-Palacios, J., Anke Jentsch, A., y Beierkuhnlein, C. (2015). Climate vs. topography – spatial patterns of plantspecies diversity and endemism on a high-elevationisland. Division of Biology, Kansas State University. Manhattan, Kansas, USA. *Journal of Ecology*, 103, 1621–

1633. doi: 10.1111/1365-2745.12463.

- Sorieul, M., Dickson, A., Hill, S.J. & Pearson, H. (2016). Plant fibre: Molecular structure and biomechanical properties, of a complex living material, influencing its deconstruction towards a biobased composite. *Materials (Basel)*, 9, 1– 36.
- Stekhoven, D.J. & Bühlmann, P. (2012). MissForest–Non-parametric missing value imputation for mixed-type data. *Bioinformatics*, 28, 112–118.
- Subedi, S., Hogan, J. A., Ross, M. S., Sah, J. P., y Baraloto, C. (2019). Evidence for trait-based community assembly patterns in hardwood hammock forests. *Ecosphere*, 10(12), e02956. 10.1002/ecs2.2956.
- Swenson, N. G., y Enquist, B. J. (2009). Opposing assembly mechanisms in a Neotropical dry forest: Implications for phylogenetic and functional community ecology. *Ecology*, 90 (8), 2161- 2170.
- Swenson, N. G., y Weiser, M. D. (2010). Plant geography upon the basis of functional traits: an example from eastern North American trees. *Ecology*. 91(8), 2234-2241.
- Vallejo, M. I. y Galeano, G. (2009). Cambios a corto plazo en los patrones de distribución espacial de nueve especies de plantas comunes en un bosque nublado al sur-occidente de Colombia. *Caldasia*, 31(1), 77-98.
- Wilson, MFJ, O'Connell, B., Brown, C., Guinan, JC, Grehan, AJ, (2007). Análisis de terreno multiescala de datos de batimetría multihaz para el mapeo de hábitats en el talud continental. *Geodesia Marina* 30: 3-35.
- Yannelli, F. A., Koch, C., Jeschke, J. M., & Kollmann, J. (2017). Limiting similarity and Darwin's naturalization hypothesis: understanding the drivers of biotic resistance against invasive plant species. *Oecologia*, 183(3), 775–784. doi:10.1007/s00442-016-3798-8

- Zhang H., Chen, H. Y. Y., Lian. J., John, R., Ronghua, L., Liu, H., Ye, W., Berninger. F., Ye, Q. (2018). Using functional trait diversity patterns to disentangle the scale-dependent ecological processes in a subtropical forest. *Functional Ecology*, 32, 1379–1389. doi. 10.1111/1365-2435.13079.
- Zang, L., Xu, H., Li, Y., & Zang, R. (2021). Conspecific negative density dependence of trees varies with plant functional traits and environmental conditions across scales in a 60-ha tropical rainforest dynamics plot. *Biotropica*, 53(2), 693-702.
- Zuleta, D., Russo, S. E., Barona, A., Barreto-Silva, J. S., Cardenas, D., Castaño, N., ... & Duque, A. (2018). Importance of topography for tree species habitat distributions in a terra firme forest in the Colombian Amazon. *Plant and Soil*, 450(1), 133-149.