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Plant trait assembly in species-rich forests along elevation in the northwest Andes of Colombia

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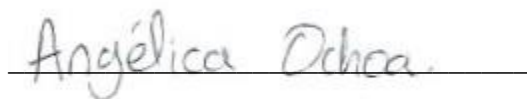
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Angélica Liliana Ochoa Beltrán

02 de Junio 2021

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Abstract

Plant trait assembly in species-rich forests along elevation in the northwest Andes of Colombia

The Andean forests harbor an astonishing plant diversity, which hampers the understanding of the main drivers of species assemblage along the elevational gradient. In this study, we used the multivariate methods RLQ and Fourth corner to identify the main determinants of plant trait assembly in the northwestern Andean forests of Colombia. We evaluated the relationship between six functional traits and three groups of environmental drivers: climate, soil fertility, and symbiotic root associations (mycorrhizae and nitrifying bacteria). Our findings showed that five functional groups represented the communities in the Andes, where two main axes explain 95.75% of the variability. The first is associated with the leaf economic spectrum and the second with the trade-off between survival/growth. Furthermore, we found that the interaction of regional (climatic variables) and local factors (soil fertility, symbiotic root associations), played a key role in determining the assembly of plant communities in our study area.

Keywords: Community assemble, functional traits, environmental drivers, Andean Mountains

Resumen

Ensamblaje de los rasgos funcionales en bosques ricos en especies a lo largo del gradiente altitudinal en el noroeste de los Andes de Colombia

Los bosques andinos albergan una amplia diversidad, lo que vuelve complejo el entendimiento del ensamblaje de las comunidades a lo largo de su gradiente altitudinal. En este estudio, usamos los métodos multivariados *RLQ* y *Fourth corner* para comprender el ensamblaje de los bosques andinos del noroeste de Colombia. Estos métodos evaluaron la relación entre seis rasgos funcionales y tres grupos de impulsores: ambientales (clima y fertilidad del suelo), asociaciones de raíces simbióticas (micorrizas y bacterias nitrificantes) y tamaño del árbol (grandes y pequeños). Nuestros resultados mostraron que las comunidades de los Andes están representado por cinco grupos funcionales, donde el 95,75% de la variabilidad es explicada por dos ejes principales. El primero está asociado con el espectro económico de la hoja y el segundo con el equilibrio entre supervivencia / crecimiento. Además, encontramos que la interacción de factores regionales (variables climáticas) y factores locales (fertilidad del suelo, asociaciones de raíces y tamaño de los árboles) determinaron el ensamblaje de las comunidades en nuestra área de estudio.

Palabras claves: Ensamblaje comunitario, rasgos funcionales, impulsores ambientales, Andes.

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Introduction

Andean forests represent the hottest hotspot of diversity on Earth (Myers et al., 2000; Orme et al., 2005) as well as one of the most threatened regions by deforestation and climate change (Aide et al., 2013; Duque et al., 2021; Rodríguez et al., 2006; Sánchez-Cuervo & Aide, 2013). To assure an effective forest conservation in this endangered ecosystem, an improved understanding of the mechanisms determining species assembly along tropical elevational gradients is needed. One meaningful approach that has been shown to help identifying the underlying mechanisms shaping forest structure and function along environmental gradients is the use of functional traits (Booth & Swanton, 2002; Keddy, 1992; McGill et al., 2006). Functional traits can inform us about the probability of plant success along with changes in the environmental conditions (Götzenberger et al., 2012; Körner et al., 1989; I. Wright et al., 2004, 2005). A trait-based approach can also help overcome some of the challenges associated with high taxonomic complexity, providing new insights into the main drivers of species coexistence, and thus, on the maintenance of such an astonishing level of species diversity (Malizia et al., 2020; Myers et al., 2000).

Leaf traits have been previously used to identify plant adaptation across the functional economic spectrum along elevational gradients (Agudelo et al., 2019; Blonder et al., 2017; Ding et al., 2019; Homeier et al., 2021; van de Weg et al., 2009). One advantage of morphological leaf traits is that they are relatively low labor-intensive measurements and a good proxy to assess the trade-off between acquisition and resource allocation (Asner et al., 2016; Homeier et al. 2021, Muscarella et al., 2016; Reich, 2014; Shipley et al., 2006; Wright et al., 2004). Along elevational gradients, a handful of studies have found that species at lower elevations tend to have acquisitive characteristics mainly due to greater availability of light and nutrients (Agudelo et al., 2019; Ding et al., 2019; Finegan et al., 2015; Read et al., 2014). On the contrary, species at high elevation tend to have conservative characteristics due to constraints in resources availability, such as light and nutrients (Agudelo et al., 2019; Ding et al., 2019; Finegan et al., 2015; Read et al., 2014). In addition to light availability and nutrients, other studies have shown other factors such as vapor pressure deficit and solar radiation, also as important drivers of leaf trait variation

among plant communities (Grossiord et al., 2020; Wieczynski et al., 2019). Thus, plant strategies represented by trait assembly may be the result of a product of several factors that covariate together rather than the answer to an individual factor or process.

Likewise, the wood-specific gravity (g cm^{-3}), hereafter called wood density, has shown to be a very efficient trait to characterize the trade-off between hydraulic conductivity and nutrients, which determines plant resistance to embolism (Chave et al., 2009; Reich et al., 2003; Worthy & Swenson, 2019). This trait has also shown to be a good proxy for life history of tropical tree species (Wright et al., 2010). Overall, acquisitive species have low wood density due to low investment in tissue construction to ensure rapid growth, while conservative species are associated with high wood density and greater survival to hydraulic or biomechanical damage (Baraloto et al., 2010; Chave et al., 2009; Muscarella et al., 2016; Pinho et al., 2019; Poorter et al., 2010; Reich, 2014; Shen et al., 2016). Hence, the use of both leaf and woody traits to identify the main determinants of plant assembly, could help to disentangle the extent to which climate and soil properties determine forest function and species turnover along steep climatic gradients in tropical forests.

Tropical forest structure can also change across strata due to a systematic reduction of light availability from canopy to understory (Capers & Chazdon, 2004; Montgomery & Chazdon, 2001). Across forest strata, to co-exist, plants have developed divergent strategies of trait adaptation to compete for light and other resources (Agudelo et al., 2019; Liu et al., 2012; Niinemets, 2010, 2016; Santiago & Wright, 2007). For example, in the presence of low availability of light, such as at the ground level in closed-canopy forests, plant species favor conservative water and nutrients use and high light capture (Poorter, 2009; Salgado-Luarte & Gianoli, 2012). In contrast, in the light-exposed canopy, plant species have a positive correlation with photosynthetic rate and resource allocation (Liu et al., 2012; Salgado-Luarte & Gianoli, 2012). Understanding the influence of changes in light availability on trait adaptation at a local scale along with regional changes in climate and edaphic properties will shed new insights on the mechanisms that promote species coexistence in tropical mountain ecosystems.

Local variation in soil fertility is also a key determinant of species fitness and tree community assembly (Jager et al., 2015; Ordoñez et al., 2009). However, the concomitant variability of climate and soils (Körner, 2007) has questioned the acquisitive-conservative plant response spectrum as a universal rule along elevational gradients. Likely important modifiers of both climatic and edaphic controls, symbiotic root associations (e.g.,

mycorrhizae and nitrogen-fixing bacteria), have been largely overlooked in studies about plant trait assembly. Symbiotic root associations can enhance plant nutrient availability as well as modify plant responses to environmental constraints such as water or light limitation (Dixon et al., 1994; Hernández-Vargas et al., 2019; Maherali, 2020; L. Shi et al., 2017; Valladares et al., 2007). Assessing the role of soil fertility and root symbiotic associations as determinants of the functional assembly of plant species along elevational gradients could inform us about prominent strategies to lessen the ongoing impact of global change on the functioning of Andean forest ecosystems.

The goal of this study is to assess the main drivers of plant trait assembly along elevational gradients in the northwestern Andean forests of Colombia. We evaluated the role played by climate, soil fertility, and symbiotic root associations on shaping the assembly of six functional traits (leaf area, specific leaf area, dry leaf matter content, leaf thickness, leaf toughness, and wood density) along an elevational gradient spanning 2850 m. Traits were measured *in situ* to 1086 morpho-species in nine 1-ha plots. The main research questions are: i) Can we differentiate changes in tree functional assembly along the elevational gradient in the northwestern Andean forests of Colombia? We expect a gradual change from acquisitive to conservative strategies along the elevational gradient. ii) What are the main environmental drivers of plant trait assembly along the elevational gradient? We expect climate variability to override soil fertility and symbiotic root associations as a determinant of plant trait assembly. iii) Can local differences in resource availability (e.g. light) between large trees ($DAP \geq 10\text{cm}$) and small trees ($1 \leq DAP < 10\text{cm}$) determine differences in trait assembly? We expect a differential response in as well as in the drivers of trait composition due to changes in light availability between canopy and understory.

1.Methods

1.1 Study Area

The study area is located in the northwest region of Colombia between 5°50' and 7°78' North and 74°61' and 77°67' West. This region encompasses an elevational gradient highly variable in terms of climate, and soils. We established nine (9) permanent monitoring 1-ha (100 m × 100 m) plots between 50 and 2900 m asl (Figure 1-1). The distance between plots ranged from 22.1 to 271.7 km. In Colombia, the Andean region contains only approximately 20% of its original natural cover, primarily due to historical deforestation (Etter et al., 2008).

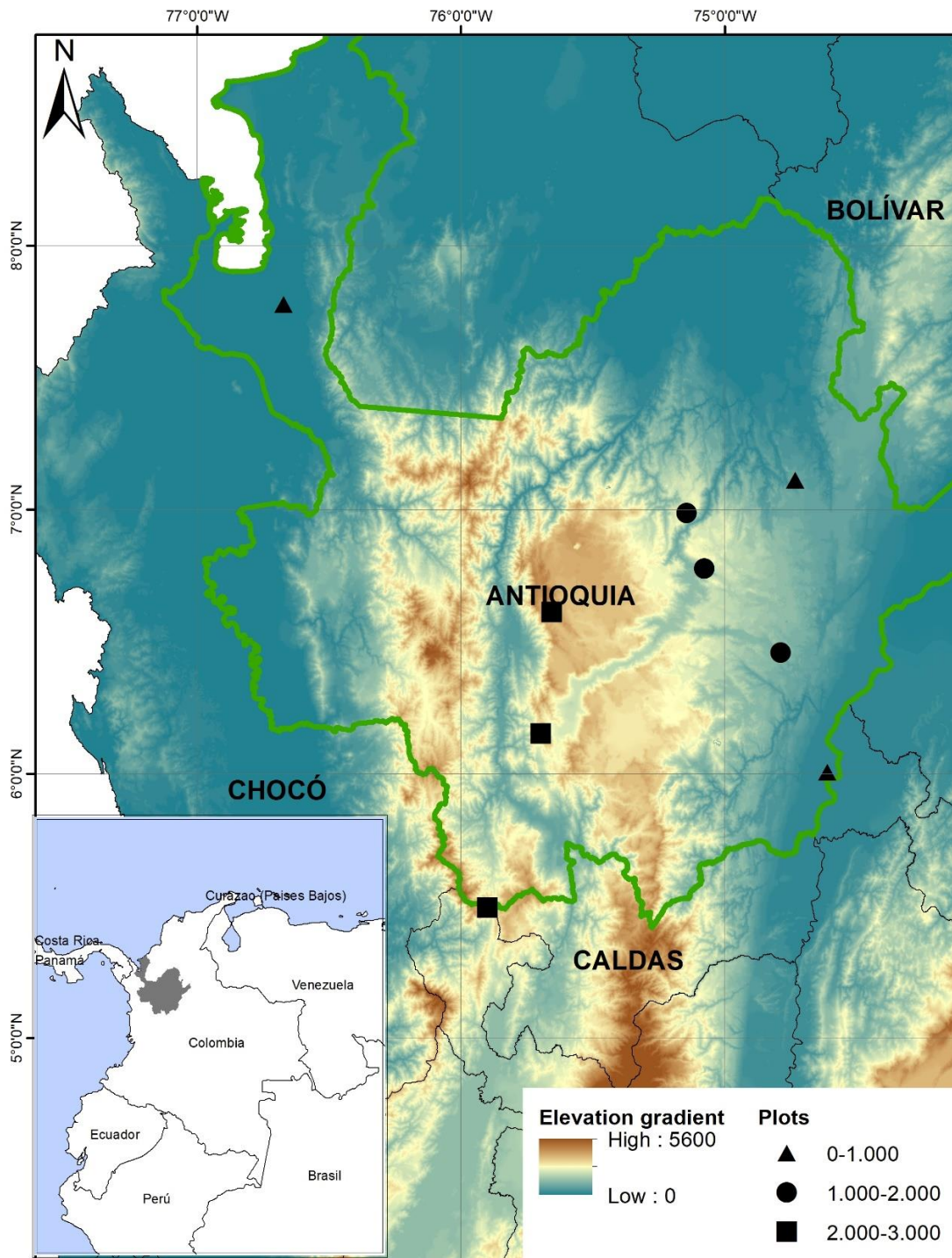


Figure 1-1. Plots localization in the northwest of the Andes in Colombia. Squares indicate the precise localization of each plot and the colors of the squares represent the change in the elevational gradient.

1.2 Tree species abundance (L matrix)

In each 1 ha plot (100 m × 100 m), all trees with a diameter at breast height (DBH) ≥ 10 cm (hereafter referred to as large trees) were mapped, tagged, and measured. Likewise, shrubs and small trees with 1 cm ≤ DBH < 10 cm (hereafter referred to as small trees) were tallied in a 0.16 ha subplot (40 m × 40 m) located near the center of each plot (Figure 1-2). Voucher specimens were collected for each potentially unique species in each plot. We collected vouchers in all cases in which there was any doubt as to whether an individual plant was the same species as another individual that was already collected within the same plot. Taxonomic identifications were made by comparing the specimens with herbarium material and with the help of specialists in particular plant groups. All of the vouchers are kept at the University of Antioquia's Herbarium (HUA). The plants that were identified at the level of genus and family were classified as morphospecies based on differences in vegetative character morphology. We built a community matrix ($n \times p$) with species abundance information, where sites are in rows and species in columns (hereafter referred to as L matrix).

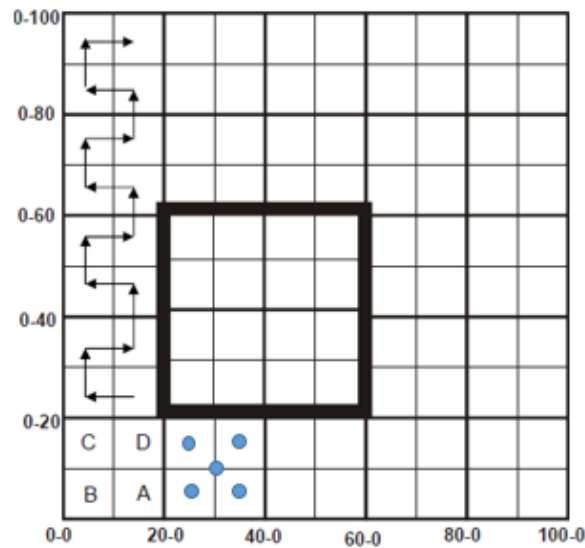


Figure 1-2. Plot design and georeferentiation. The arrows indicate the sequence followed for the individual numbering within the 20x20 quadrants and through each 20x100 strip. The box with the thickest line corresponds to the subplot of 40x40 m (0.16 ha), where the 1 cm individuals were included. Blue points show taking soil samples inside a 20m x 20m quadrant.

1.3 Environmental variables (R matrix)

We used climatic and edaphic information to characterize each plot. Each environmental variable was included in a $n \times m$ matrix, where sites are in rows and environmental values in columns (hereafter R matrix). Climatic data were downloaded from Worldclim version 2.1. (1970-2000) with a resolution of 30 arcsec \sim 1 km (Annex A) (Fick et al., 2017). The climatic variables are mean annual temperature (MAT °C), temperature seasonality (T.s), mean annual precipitation (PP mm), precipitation seasonality (P.s), solar radiation (Srad in $\text{kJ m}^{-2} \text{day}^{-1}$), wind speed (Wind in m s^{-1}), vapor air pressure (VAP in Kpa), vapor pressure deficit (VPD in Kpa). VPD was calculated as the difference between saturated vapor pressure and VAP. The soil variables assessed were pH, calcium (Ca in meq pre 100g soil), magnesium (Mg in meq pre 100g soil), potassium (K in meq pre 100g soil), phosphorus (P in ppm), and organic matter (OM in %) (Annex B). We used the mean concentration per plot calculated from 25 composite soil samples taken in each 20 x 20 m quadrant in the 1-ha plot (Figure 1-2). Soil samples were analyzed in the Biogeochemical Analysis laboratory of the Department of Forest Sciences at the Universidad Nacional de Colombia-Medellin.

To incorporate the potential contributions of symbiotic root association (SRA) in explaining plant trait assembly along the elevational gradient, individuals were assigned an SRA status either as arbuscular mycorrhizal (AM), ectomycorrhizal fungi (EcM), or nitrogen-fixing bacteria (Nfix) based on the genus- or family-level designations provided in Steidinger et al. (2019). We chose these two taxonomic levels to increase the ability to provide SRA assignments to the dataset; this choice is supported by the fact that SRA is largely conserved at the genus and family level (Maherali et al., 2016; Tedersoo et al., 2018). Here, we restricted matches for our genera and families to only those present in North and South America in the compiled list of Steidinger et al. (2019). Any genus or family lacking symbiotic root assignment was manually checked and, when possible, assigned SRA based on primary literature searches. We used the above information and L matrix (tree species abundance matrix) to calculate each SRA proportion as the ratio between the abundance of individuals with EcM, AM, or Nfix association and the total number of individuals in each plot.

1.4 Trait sampling (Q matrix)

In the nine plots, we assessed six morphological traits: leaf area (LA), specific leaf area (SLA), leaf dry matter content (LDMC), leaf thickness (LT), leaf toughness (Lth), and small branches' wood density (WD). LA is associated with plant fitness to compete for light and to regulate water balance. SLA and LDMC represent the trade-off between resource acquisition, plant productivity, and carbon storage (Albert et al., 2010; Cornelissen et al., 2003). LT and Lth are related to adaptations to harsh climatic conditions and herbivory defenses (Cornelissen et al., 2003; Perez-Harguindeguy et al., 2016). Finally, WD primarily represents the trade-off between survival and growth (Wright et al., 2010) and hydraulic safety (Cornelissen et al., 2003; Perez-Harguindeguy et al., 2016).

We took samples of five mature leaves from five different individuals belonging to the 80% most abundant species per plot. In the remaining 20% individuals, the samples were taken in as many individuals as possible, ensuring at least one individual for the very rare species. To assess WD, we took one sample from a mature branch per individual. The size of the samples was around 2-3 cm in diameter and 10 cm long. Since for some species within the plot was not possible to measure directly the WD due to the small size of the individuals and the lack of mature branches, the missing values were filled hierarchically. First, the missing WD values per individual were assigned based on the average value of the same species in other plot. If the value were not available at the species level, the value by genus was used and finally by family.

We selected light-exposed leaves when possible. However, we excluded those species that had either small individuals with few leaves/branches or were out of reach due to height. Fresh weight, leaf thickness (LT), and leaf toughness (LTh) were measure *in situ*, while the other traits were measured in the lab. The data was organized in a $p \times s$ trait matrix, where the rows have the s trait's mean value per species and the columns the p species (hereafter referred as to Q matrix). To build this matrix, we used the species with information on all six traits, which correspond to 75% of the morphospecies registered in the nine plots. LA, SLA, LT, and Lth were log-transformed to reduce the bias on trait distributions (Kerkhoff & Enquist, 2009).

We used the Pearson correlation coefficient to assess the correlation between the community weighted mean (CWM) of each trait as well as the environmental variables and elevation. Elevation is used here as a valid surrogate of temperature ($r = -0.99$).

1.5 Data analysis

To assess plant trait assembly in the northwestern Andean forests of Colombia, we used Correspondence analysis RLQ and Fourth Corner Analysis (Dolédec et al., 1996; Legendre et al., 1997; Ter Braak et al., 2012). The Correspondence analysis RLQ and Fourth Corner Analysis are two alternative methods that integrate information stored in the R matrix (sites x environmental characteristics), L matrix (sites x species abundance), and Q matrix (functional traits x species). The RLQ is a multivariate method that reduces the variability of the three matrices (RLQ) by applying ordination procedures (Dolédec et al., 1996). The RLQ assigns scores to each species, samples, traits, and environmental variable along orthogonal axes, to visualize the structure of the data. The RLQ analysis was performed using the *RLQ* function. The Fourth Corner Analysis is a multivariate permutation test that relates the R, L, and Q matrices to generate a matrix with association scores (Legendre et al., 1997). This analysis was run employing the *fourthcorner* function. Both analyses were performed using the *ade4* R package (Dray et al., 2007). The significance of the associations obtained from both methods, RLQ and Fourth Corner Analysis, was tested by applying a permutation procedure that randomizes 49,999 times the samples and species abundance data (L) separately and then combines those outputs (model 6: combination of the outputs of models 2 and 4) (Dray & Legendre, 2008). The large number of environmental variables can generate a multi-testing issue and report a false correlation. To minimize that possibility, we performed a high number of permutations in the randomization test for the fourth corner and RLQ analysis as proposed by Dray et al. (2014). See Annex C for further information on the methods of randomization.

To assess our first research question, which aimed to differentiate and identify functional groups along the elevational gradient, we applied the k-means method using the *kmeans* function available in the *stats* R package (Hartigan & Wong, 1979) to the two first trait orthogonal axes derived from the RLQ analysis. The optimal number of clusters was estimated with the elbow method, which minimizes the within-cluster sums of squares using the *fviz_nbclust* function available in *factoextra* R package (Alboukadel & Mundt, 2020). We compared the distribution of each functional group per trait with the RLQ structure to determine the position of each functional group along the conservative - acquisitive leaf/wood-density economic spectrum. Significant differences between functional groups (FG) were calculated using the Tukey Honestly Significant (*Tukey HSD*) test.

To answer the second question, we used the Fourth Corner Analysis to test for the correlation between each trait and climatic ($n = 11$) and edaphic variables ($n = 11$). Individual correlation between each trait and each environmental variable was tested following the permutation procedure describe above. And finally, to answer the third question, we repeated the same analysis (Fourth Corner) using the two tree cut-off sizes: only large trees ($DBH \geq 10$ cm) and only small trees ($1 \text{ cm} \leq DBH < 10$ cm). Thus, the Fourth Corner Analysis was employed to analyze the influence of the climatic and edaphic variables on determining trait functional assembly according to tree size cut-off (large and small trees).

2. Results

2.1 Patterns of change with elevation

Eight out of the 17 variables evaluated showed a significant correlation with elevation. OM and AM were positively associated, while MAT, VAP, VPD, Srad, Mg, and Nfix were negatively associated (Annex D). Regarding functional traits, when we included all individuals ($DBH \geq 1$ cm), we found a negative relationship between LA/SLA with elevation, but a positive one with LT (Figure 2-1 and Annex E). The significant trait-elevation relationship differed when the analysis was carried out separately by tree cut-off size categories. Overall, LTh remained significant only for large trees, while LA for small trees. The LT was statistically significant, in both large and small trees (Figure 2-1).

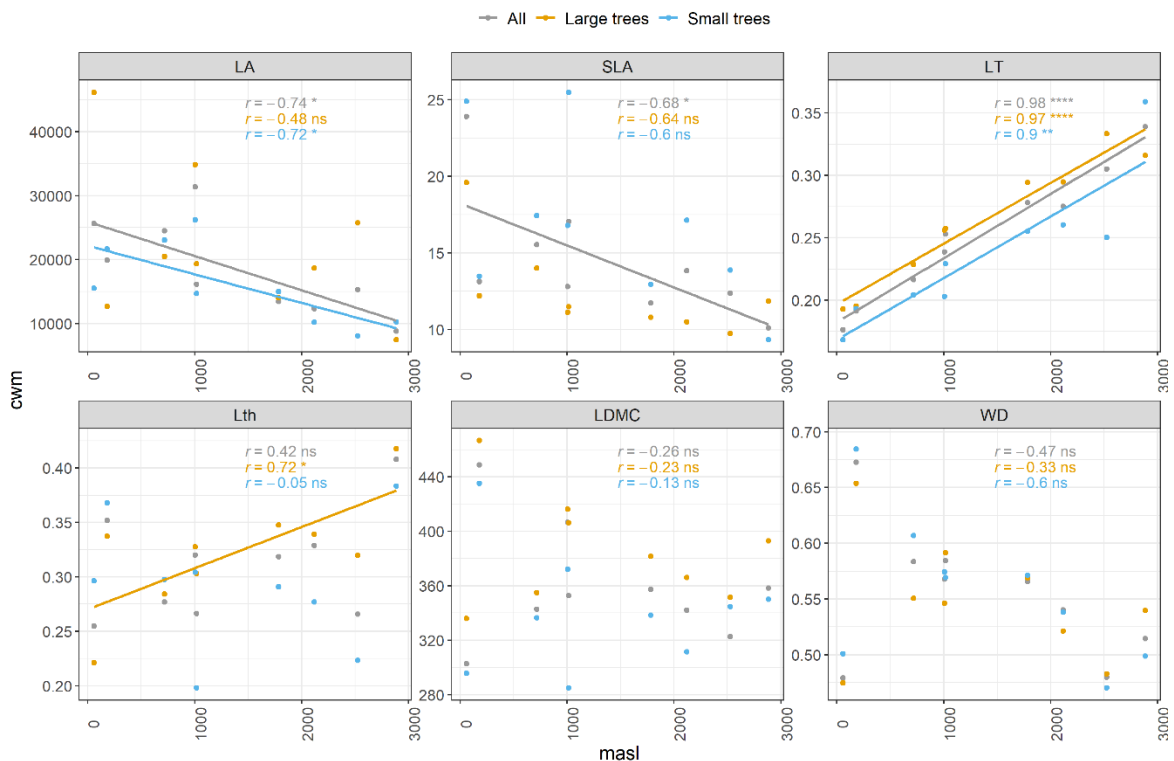


Figure 2-1. Relationship between traits and elevation in the northwest Andes of Colombia. LA: leaf area (mm²), SLA: specific leaf area (mm² mg⁻¹), LDMC: leaf dry matter content (mg), LT: thickness (mm), Lth: toughness (N mm), WD: wood density (g cm⁻¹). Gray: all individuals (DBH ≥ 1 cm), orange: large individuals (DBH ≥ 10 cm), blue: small individuals (1 cm ≤ DBH < 10 cm). Not significant (ns), 0.05 (*), 0.01 (**), 0.001 (***).

2.2 Definition of functional groups

According to the RLQ analysis, we found five main functional groups (FG) along the elevational gradient in Northwestern Andean forest (RLQ permutation test: model 2, p-value: 0.00106 and model 4, p-value: 0.00002) (**¡Error! No se encuentra el origen de la referencia.**). The first two RLQ orthogonal axes explained most of the trait-environment relationships (Total explained inertia 95.76%; see Table 2-1). The first functional group (FG1; red) was characterized by low WD and intermediate SLA. Some representative species were *Miconia acanthocoryne*, *Ladenbergia macrocarpa*, and *Miconia micropetala*. The second functional group (FG2; orange) was characterized by high SLA, but thin-soft leaves with low dry matter content in their leaf and woody tissues. Some representative species were *Allomaieta pancurana*, *Allomaieta hirsuta*, and *Piper urabaensis*. The species of this group were primarily located in low elevations with warm weather and relatively fertile soils. The third functional group (FG3; yellow) was characterized by high WD and LDMC, and was located along the entire elevation gradient, being more representative of areas with high VPD, low soils fertility, but high presence of N-fixing root associations. Some representative species were *Palicourea angustifolia*, *Matayba arborescens*, and *Tapirira guianensis*. FG3 falls within the acquisitive second half of the leaf/wood-density economic spectrum. The fourth functional group (FG4; purple) was characterized by low SLA, but high LT and Lth, and was primarily located between middle and high elevations. FG4 belongs to the conservative extreme of the leaf/wood-density economic spectrum. Some representative species were *Matudaea colombiana*, *Billia rosea*, and *Eschweilera antioquiensis*. Finally, the fifth functional group (FG5; blue) was characterized by high LDMC, LT, and Lth. FG5 was located at high elevations and at the conservative extreme of the leaf economic spectrum, but low WD (**¡Error! No se encuentra el origen de la**

referencia.). Some representative species were *Miconia multiplinervia*, *Schefflera trianae*, and *Tibouchina lepidota*.

Table 2-1. RLQ Statistics. Each Ax represents the first five orthogonal axes with their respective Eigenvalues (Eig), Projected inertia (Eig %), and Cumulative projected inertia (%) (Accumulative). The two first orthogonal axes decomposition with their covariance (covar), R matrix variance (sdR), Q matrix variance (sdQ) and Q-R correlation (corr).

Outputs of permutation test which alternative hypothesis is "greater" and p-value is estimated as: (number of random values equal to or greater than the observed one + 1) / (number of permutations + 1).

Total inertia: 4,16					
	Ax1	Ax2	Ax3	Ax4	Ax5
Eig	3,23	0,75	0,13	0,03	0,01
Eig %	77,66	18,10	3,04	0,84	0,27
Acumulative	77,66	95,76	98,81	99,65	99,92

Eigenvalues decomposition:					
	Eig	covar	sdR	sdQ	corr
1	3,23	1,80	2,48	1,22	0,59
2	0,75	0,87	1,44	1,39	0,43

Permutation test (randtest)					
	Test	Obs	Std.Obs	Alter	Pvalue
1	Model 2	4,16	3,98	greater	0,00006
2	Model 4	4,16	15,26	greater	0,00002

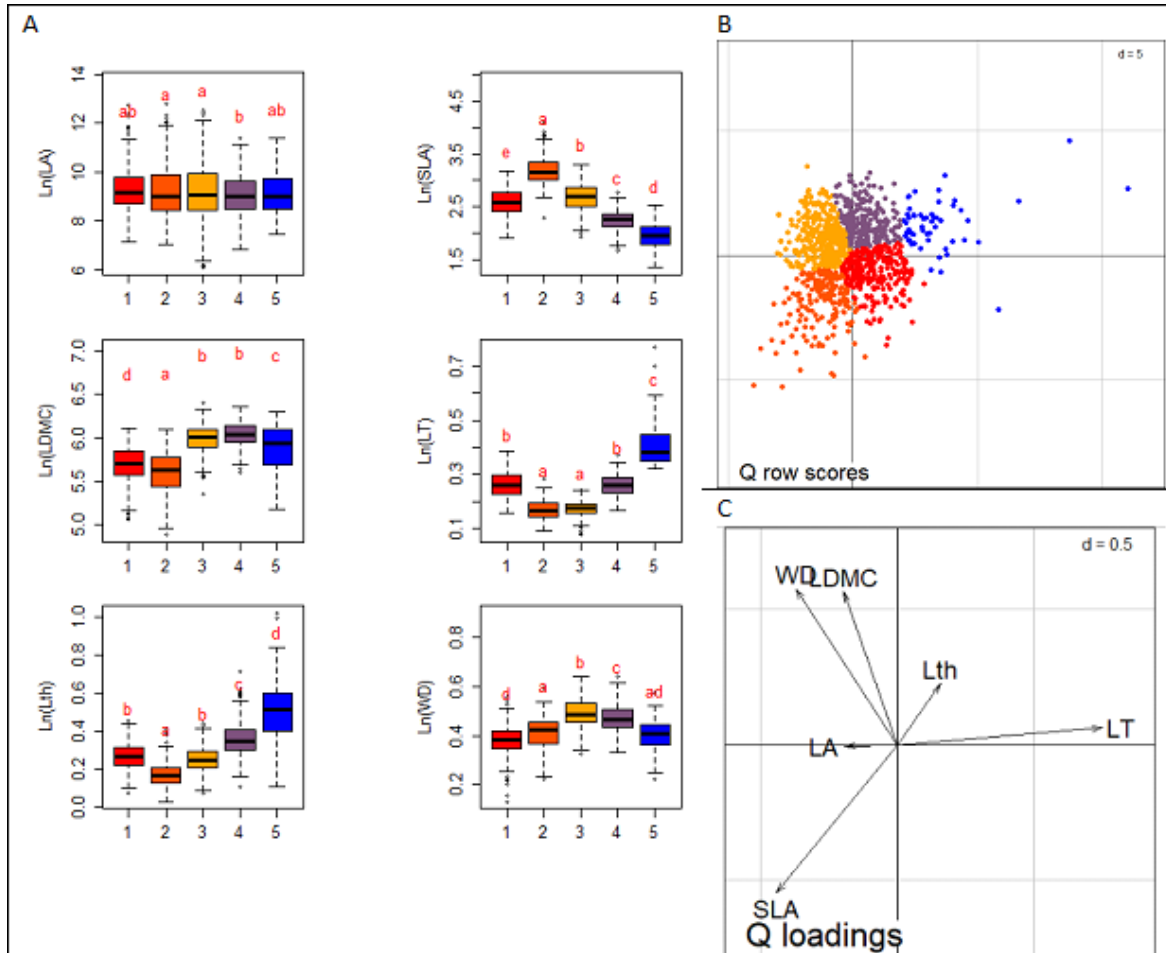


Figure 2-2. A: Boxplot of trait per functional group resulting from the k-mean analysis. Tukey's test estimated the significant mean differences with a 95% confidence level. B: Species clustering according to K-mean results (Q row scores) and eigenvalues. C: traits lineal combination (Q loadings). LA (Leaf area), SLA (Leas specific area), LDMC (leave dry matter content), LT (Leaf thickness), and Lth (leaf toughness).

2.3 Traits-environment relationship for different cut-off tree sizes

When all individuals ($DBH \geq 1$ cm) were included, the fourth corner analysis revealed that temperature and some related climatic variables, such as atmospheric water vapor (VAP)

and vapor pressure deficit (VPD), positively influenced traits associated with photosynthetic rates (SLA and LA) and resistance to embolism (WD). However, VAP and VPD were negatively associated with leaf thickness (LT). Other relevant variables were symbiotic root associations with both mycorrhizal types as well as nitrogen-fixing bacteria. The results showed that increased EcM association enhanced leaf toughness (Lth), while increased AM association decreased EcM. An increase in N-fixing association was also positively associated with WD. Finally, there was a negative correlation between soil Mg concentration and LT (Figure 2-3).

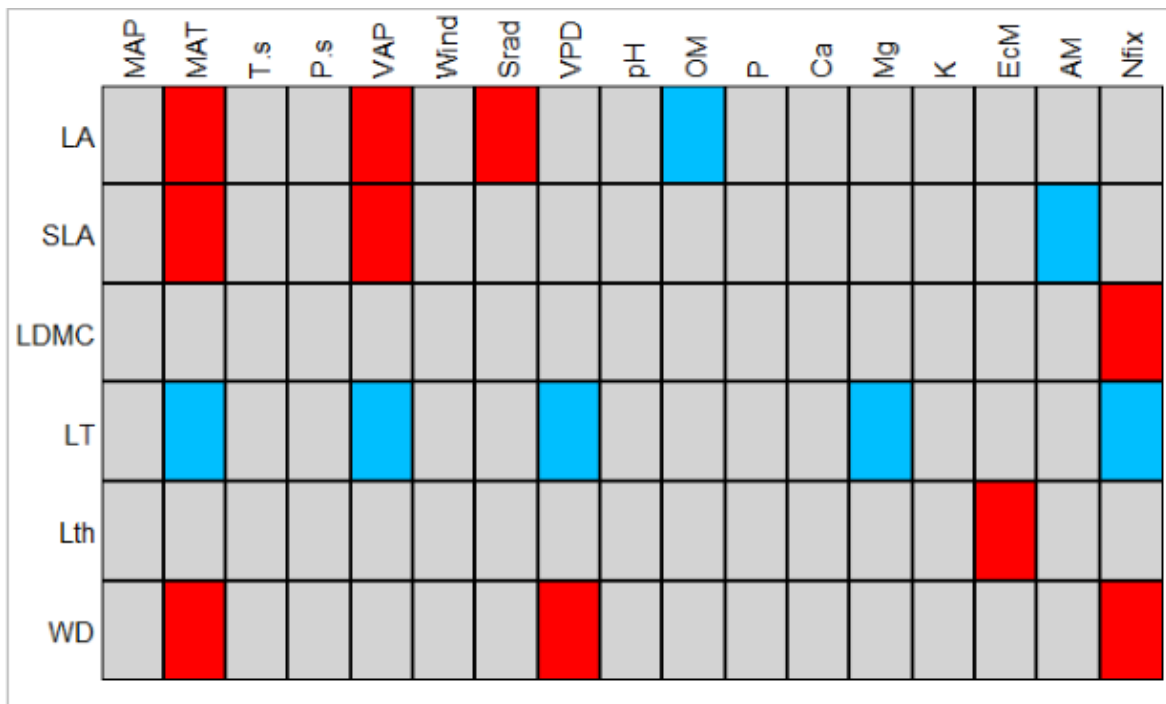


Figure 2-3. Fourth-corner analysis for all individuals (DBH \geq 1 cm). Red cells represent positive correlation and blue ones a negative correlation ($\alpha \leq 0.05$). Traits: LA (Leaf area), SLA (Leaf specific area), LDMC (leave dry matter content), LT (Leaf thickness) and Lth (leaf toughness). Environmental factors: MAT (mean annual temperature), MAP (mean annual precipitation), VAP (Water vapor pressure), Wind (Wind speed), SRad (Solar radiation), VPD (Vapor pressure deficit). Edaphic variables: soil nutrients (Ca, K, Mg, P), OM (organic matter content), EcM (ectomycorrhizal fungi), AM (arbuscular mycorrhizal fungi) and Nfix (Nitrogen fixing bacteria).

The fourth corner analysis on large (DBH \geq 10 cm) and small trees (1 cm \leq DBH < 10 cm) categories produced partially differentiated environment-trait correlations. The increase of

Figure 2-4. Outputs of the fourth-corner analysis for large trees (A) and small trees (B), Cell in red represents a positive correlation and blue a negative one ($\alpha \leq 0.05$). Traits: LA (Leaf area), SLA (Leaf specific area), LDMC (leaf dry matter content), LT (Leaf thickness), and Lth (leaf toughness). Environmental factors: MAT (mean annual temperature), MAP (mean annual precipitation), VAP (Water vapor pressure), Wind (Wind speed), SRad (Solar radiation), VPD (Vapor pressure deficit). Edaphic variables: soil nutrients (Ca, K, Mg, P), OM (organic matter content), EcM (ectomycorrhizal fungi), AM (arbuscular mycorrhizal fungi) and Nfix (Nitrogen fixing bacteria).

3. Discussion

In this study, we found environmental heterogeneity as a key driver of plant fitness and trait assembly in wet tropical forests of the Northwest Andes. The climatic variation, together with soil fertility and symbiotic root associations, shaped plant trait assembly along the elevational gradient (Annex D). There were five main functional groups that could be distinguished along the conservative/acquisitive spectrum (van de Weg et al., 2009). Furthermore, the environment-trait relationships partially differed according with plant size (small vs. large trees) and position across forest strata (understory vs. canopy, respectively). Taken together, our study shows that a combination of local-scale factors, such as microclimatic variation, soil fertility and symbiotic root associations within forests, along with regional climatic heterogeneity, largely drives plant adaptation and species coexistence along tropical elevational gradients.

3.1 Functional groups

The distribution of functional groups shifted from an acquisitive strategy in lowlands, characterized by thin leaves with low dry matter content per area (FG2), to a conservative one in highlands, which was characterized by thick and resistant leaves with high dry matter content per area (FG4 and FG5) (Agudelo et al. 2017, Ding et al., 2019; van de Weg et al., 2009). Plant adaptation to environmental heterogeneity along the elevational gradient was mainly associated with two functionally independent axes. On one hand, the first RLQ axis represented the aforementioned leaf economic spectrum, in which plants have developed mechanisms of protection against physical/biological hazards by increasing LT and Lth at lower temperatures, but increasing SLA and LA to improve their photosynthetic efficiency in warmer lowlands (Agudelo et al., 2017; Körner et al., 1989; Reich, 2014; Wright et al., 2005). On the other hand, the second RLQ axis represented a growth trade-off, which was positively correlated with LDMC and WD. The growth trade-off highlights the capability of plants to acquire and store resources, and thus, to accumulate carbon (Hodgson et al.,

2011; Wilson et al., 1999; Jager et al., 2015). Although the wood density did not show a clear pattern along elevation, our results agree with other studies in lowlands that have demonstrated a positive correlation with low fertility (Ter Steege et al. 2006). However, our findings suggest a still unexplored relationship between WD and the association with nitrogen-fixing bacteria, which could support the positive correlation observed between WD and nitrogen accumulation in species with low growth rates (Martin et al., 2014) in the understory.

The first functional group (red) is composed of 273 species, which are characterized by the low cost to build tissue and leaf located in the middle leaf economic spectrum. These species are widely distributed along the elevation gradient, being more representative in middle-high elevations (2000 -2500 m asl). These species, according to the economic spectrum raised by (I. Wright et al., 2004), have an equilibrium between photosynthetic rate (SLA and LA) and leaf life span (LT and Lth) but low tissue construction (LDCM and WD). Therefore, this species can adapt to varied environments, which means they could tolerate climatic variations and interventions.

187 species are in the second functional group (orange), have acquisitive leaf traits, and low cost to build tissue. Thus, those species have fast growth to increase their efficiency in light and nutrients capture, as well as hydraulic conductance (I. Wright et al., 2004; Zhao et al., 2017). This FG is limited to low elevations and environments with favorable conditions. Furthermore, this species could be successful in open forests or early successional states of forests since those have more light availability.

The third functional group (yellow), with 338 species, is located in the middle leaf economic spectrum and has a high cost to build tissue. The species of this FG are distributed throughout the elevational gradient. It leads us to believe that these species could have higher adaptability to climatic variations, which may be due to the relationship between photosynthetic efficiency and low growth rates (Blundo et al., 2015; S. J. Wright et al., 2010). Thus, these species prioritize the accumulation of dry matter and more resistant stems (high WD), giving them greater resistance and durability. These species also have the commercial importance of their high wood densities.

The fourth functional group is represented by species with conservative leaf traits and high costs to build tissue. This FG has 234 species located in all elevations, mainly in high and middle elevations. The characteristics of those species make them tolerant to low light

availability environments and with harsh conditions. For this reason, they are considered as understory species (Blundo et al., 2015; S. J. Wright et al., 2010) and more advanced stages of succession (Blundo et al., 2015).

Finally, the fifth group (blue) is the group with fewer species, only 54. Furthermore, this group is limited to the high altitudes, developing conservative strategies in their leaf and low accumulation of matter in their tissues. Given its narrow distribution and its conservative characteristics and not very hardwoods, it is considered that this group may be the most sensitive before to climatic variations (Hernández-Vargas et al., 2019), so greater attention should be paid to conservation strategies.

3.2 Drivers of plant trait assembly

In contradiction to our second hypothesis, we found that environmental heterogeneity and symbiotic root associations were all significant drivers of plant trait plasticity and adaptation along elevation in the wet tropical Andean forests. The relevant climatic variables in our study area were MAT, VAP, VPD, and Srad, which favored SLA but reduced LT. A decrease of SLA but an increase of LT with the decline in temperature has also been reported in similar studies on tropical elevational gradients (Asner et al. 2018; Ding et al. 2018). In this study, we hypothesize that these functional changes may be primarily due to lower cell growth but higher development of cell walls and mesophyll tissue to improve the distribution and density of stomata at low temperatures (Körner et al., 1989; Wright et al., 2005). A decrease in the evaporative demand at higher elevations may also regulate the foliar accumulation of mobile nutrients (Homeier et al. 2021), as was revealed in our study for N (here understood as an increase of organic matter) and Mg. Although our study area did not present limitations due to water since they are humid forests, our analysis highlighted that in an environments with a high vapor pressure deficit (low altitudes), plants increased their WD, likely as a strategy to avoid cavitation (Swenson & Enquist, 2007). It has also been shown that WD is related to reducing the conduction spaces and the thickness of the fiber walls to allow a more efficient hydraulic conductivity (Chave et al., 2009; Poorter et al., 2010).

However, we did not find a trend between WD and elevation, as it was observed with DVP, VAP, and Nfix. It may be because WD does not necessarily reflect the plants' strategy developed to maintain equilibrium among water stress, generate resistance, and support

(Chave et al., 2009). For example, López Camacho et al., (2020) showed the conductivity increases in plants with low pore density, but high pits diameter. On the other hand, the tracheates and fibers length is related to both plants' conduction and support.

Soil fertility also played a major role in shaping trait assembly along elevational gradients (Cárate-Tandalla et al. 2018). Both Mg and OM were negatively and positively correlated with elevation, respectively. The negative correlation between magnesium in soils and leaf thickness emphasizes on the importance of Mg concentration in leaves to enhance photosynthesis (Tränkner et al., 2018; Wang et al., 2018). Alternatively, the negative correlation between leaf area and organic matter points to N limitation in high/cold elevations due to low decomposition and mineralization rates (Tanner et al., 1998; Liu et al., 2012; Homeier et al. 2021). Nitrogen is an essential nutrient involved in photosynthetic capacity in plants with an acquisitive strategy (Wright et al., 2004) that positively contributes to light-harvesting and electron transportation (Niinemets, 2010). The influence of OM and Mg on the functional traits of the leaves pinpoints to physiological limitations for plants in tropical montane forests that reduces photosynthetic efficiency and the use of N (Camenzind et al., 2017; Fisher et al., 2013; Tanner et al., 1998). Conversely, in our study area, phosphorus did not correlate significantly with any functional trait, which indicates that, in this region, P was not a limiting for trait development (van de Weg et al., 2009). This lack of correlation may be due to either the high variability in P concentration along the elevation gradient (Annex B and Annex D) (Asner et al., 2016) or the relative young age of the Andean soils that supposes a low limitation of Phosphorus (Asner et al., 2016; Fisher et al., 2013).

In the whole plant community (DBH \geq 1cm), our findings suggest contrasting roles among symbiotic root associations in promoting plant growth. It is likely that the higher concentration of organic matter in highland soils is at least partially driven by lower decomposition and mineralization rates due to colder temperatures (Tanner et al., 1998). The higher abundance of AM associations in sites with lower temperatures (Annex D) may reflect greater plant reliance on symbiotic acquisition of N and P in those constrained environments (Shi et al., 2020). There is some evidence that AM fungi can access nutrients from organic matter, particularly through associations with hyphosphere-associated bacteria (Bunn et al., 2019; Nuccio et al., 2013), although studies in other geographic regions have found the abundance of AM associations is negatively correlated with

elevation (Koele et al., 2012; Steidinger et al., 2019). In contrast, we found that the abundance of N-fixing associations were more associated with areas containing higher availability of nutrients, such as lowlands. This distribution may possibly reflect the availability of key co-factors such as iron or molybdenum in sustaining the functioning of this symbiosis. Since N-fixing association was positively associated with WD and LDMC, our results also suggest a primary role of this symbiosis enhancing plant carbon assimilation. However, as shown below, this trend was consistent only for small trees (Figure 2-4B), suggesting that N-fixing associations may enhance carbon accumulation mainly in earlier stages of development of shade-tolerant species. Regarding EcM associations, our findings revealed a positive association with leaf toughness (Lth). This may reflect greater allocation to plant defenses, given the slower rate of nutrient cycling in EcM dominated forests compared to AM dominated forests (Phillips et al., 2013). Alternatively, it could be related with the greater acquisition of micronutrients, which are essential in lignin synthesis and may favor greater resistance of plant tissues.

3.3 Traits-environment relationship for different tree size cut-off.

When we split the whole dataset into large ($DBH \geq 10$ cm) and small trees ($1 \text{ cm} \leq DBH < 10$ cm), our results showed only partial differences in the extent to which the explanatory variables differentially determined plant trait assembly. Only in the large trees, wind speed and solar radiation, which are promoters of boundary layer conductance (Tränkner et al., 2018), were positively correlated with the SLA. That means species have more exposed area per mass unit, and thus, higher photosynthetic and growth rates (Niinemets, 2010). For climatic variables, however, the main difference was the influence of temperature seasonality on determining WD for large trees but mean annual temperature for small trees. In large trees, a greater WD has been shown to be a good strategy to resist droughts and water shortage mainly due to the ongoing increase of temperature (Esquivel-Muelbert et al., 2017; Zuleta et al., 2017). However, for small trees, the increase of WD appears to respond to slow-growing shade-tolerant species that tend to accumulate carbon due to their positive association with nitrogen-fixing bacteria that enhance the metabolic performance under reduced availability of light but higher MAT. In this case, a greater WD in small trees at higher MAT should help to reduce the conduction spaces and the thickness of the fiber

walls, which allow for a more efficient hydraulic conductivity (Chave et al., 2009; Poorter et al., 2010).

Regarding soil fertility, Mg had a more significant influence on large trees (high SLA y low LT) due to this nutrient is highly associated with the harvest of light and the photosynthetic efficiency of plants (Tränkner et al., 2018; Wang et al., 2018). Conversely, K influenced small-trees, highlighting the prevalence of carbon assimilation (high LDCM) in harsh environments with low concentration of K. The importance of K lies on its control of plant enzymatic activities as well as the diffusion and translocation of photoassimilates for photosynthetic control (Tränkner et al., 2018; Wright et al., 2005). The importance of carbon assimilation in small species was also shown in the positive correlation between OM and LT. To our knowledge, no studies have yet evaluated the influence of tree size on mycorrhizal association-functional trait relationships. While our study suggests these relationships, such as between SLA and mycorrhizal type, are tree size-dependent, more research is needed among symbiotic root associations and different sizes or stages of plant development to improve our mechanistic understanding of their effects on trait assembly.

4. Conclusion

In conclusion, our study demonstrates that multiple factors (climate, soil fertility, and symbiotic root association) play key roles in shaping plant trait assembly in the northwest Andes of Colombia. The five functional groups represent the high plant diversity (> 1000 species) found in our study area can be summarized along two functional axes primarily associated with the leaf economic spectrum and the survival/growth trade-off. Likewise, our study emphasize on the importance of considering small individuals as well as local factors, such as soil fertility and symbiotic root associations to better understand the drivers of plant trait assembly along complex environmental gradients, and thus, the likely response of these forests to the ongoing climate change. Finally, we find the necessity to study deeply the unexplored relationship found between symbiotic root associations and functional traits. Furthermore, future studies should evaluate other wood traits such as pore diameters, pore density, hole diameter, fiber length to understand the WD role in the plant life strategy.

A. Annex: Climatic variables

Climatic values per plot in northwestern Andean mountains, Colombia. Mean annual temperature-MAT (°C), Mean annual precipitation-MAP (mm), Temperature seasonality-T.s (°C), Precipitation seasonality-Ps (mm), Wind speed-Wind (m/s) and Solar rad- S.rad (KJ m⁻¹ day⁻¹) were downloaded from the free climate data set Woldclim version 2.1. (1970-2000) with a resolution of 30 arcsec ~ 1 km. Vapor pressure deficit-DVP (KPa) was calculated with the difference between the moisture in the air and the moisture that the air can hold when it is saturated (DVP=SVP-VAP), with $SVP = \frac{610.7 \times 10^{7.5T}}{237.3+T}$.

Site	Elev	MAP	MAT	T.s	P.s	VAP	Wind	SRad	VPD
Carepa	58	2518	26	25,79	47,16	2,93	1,71	18320,58	0,71
Puerto Triunfo	180	2788	27	35,05	41,00	2,87	0,89	17640,42	0,86
Segovia	717	3803	23,2	33,13	41,44	2,52	1,08	17852,58	0,55
Porce	1006	2108	21,9	41,97	42,04	2,28	0,97	17722,67	0,56
Maceo	1016	3014	22,6	40,64	33,46	2,35	0,92	17739,00	0,61
Anorí	1784	4354	17,5	46,73	43,04	1,81	1,07	17830,42	0,52
Angelópolis	2118	2197	16,2	33,95	38,27	1,58	0,98	17488,33	0,41
Jardín	2525	2617	14,6	20,49	35,89	1,45	0,96	17354,17	0,21
Belmira	2885	2203	11,9	32,97	48,35	1,20	1,17	17624,08	0,26

B. Annex: Soil variables

pH: measured potentiometric method in a ratio of 1 to 2, MO: organic matter measured combustion method (%), Ca (calcium) Mg (magnesium) y K (potassium) cations were determined by atomic absorption spectrophotometry using neutral and 1N ammonium acetate (meq pre 100g soil), P: phosphorus determined by ultraviolet-visible spectrophotometry (ppm), probability of association per place with EM (ectomycorrhizas) AM (arbuscular mycorrhizas) Nfix (nitrogen-fixed bacteria).

Site	Elev	pH	MO	P	Ca	Mg	K	EM	AM	Nfix
Carepa	58	5,78	7,70	0,87	11,28	7,39	0,22	0,02	0,49	0,04
Puerto Triunfo	180	6,06	8,47	35,32	5,18	6,08	0,13	0,06	0,58	0,13
Segovia	717	3,94	6,65	1,08	0,32	0,12	0,08	0,00	0,73	0,06
Porce	1006	4,18	4,52	4,28	0,12	0,13	0,08	0,00	0,78	0,04
Maceo	1016	3,56	5,42	1,67	0,42	0,17	0,24	0,01	0,66	0,02
Anorí	1784	3,87	4,33	5,52	0,29	0,10	0,17	0,04	0,81	0,04
Angelópolis	2118	4,74	23,3	14,1	9,29	1,52	0,26	0,02	0,72	0,00
Jardín	2525	4,78	12,19	4,8	0,31	0,13	0,18	0,00	0,78	0,00
Belmira	2885	3,57	28,50	4,38	0,14	0,11	0,14	0,25	0,72	0,02

C. Annex: R Documentation: RLQ and Fourth corner

The inputs of this analysis are:

Matrix L: the abundances of p species at n sites ($n \times p$)

Matrix R: the measurements of m environmental variables for the n sites ($n \times m$)

Matrix Q describing s species traits for the p species ($p \times s$)

Fourth corner analysis

The fourth-corner measures the link between three tables described above by a Pearson correlation coefficient when the trait and environmental variables are quantitative, or by a Pearson Chi2 and G statistic when the two variables are qualitative, or by Pseudo-F and Person r when one variables is quantitative and other qualitative (this was the one we used in this paper). This method has been developed by Legendre et al (1997) and extended in Dray and Legendre (2008).

RLQ analysis

RLQ analysis performs a double inertia analysis of the R and Q table with a link expressed by a contingency table (L). The rows of L correspond to the rows of R and the columns of L correspond to the rows of Q. Previously to RLQ test, we perform a separate analyses of each matrix: Correspondence analysis (`dudi.coa`) is applied to L matrix and a multivariate analysis with mixed quantitative variables and factors (`dudi.hillsmith`) is applied to Q and R matrices.

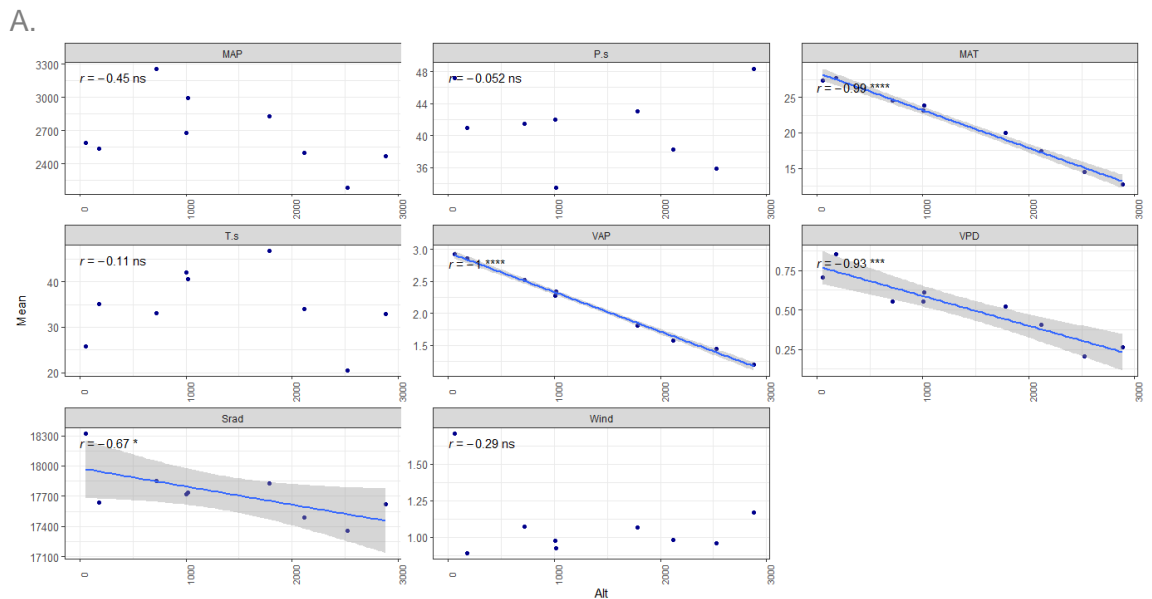
Permutation test

This test is built into the `fourthcorner` function, however for RLQ is available by the function `randtest.rlq`. The different models available are:

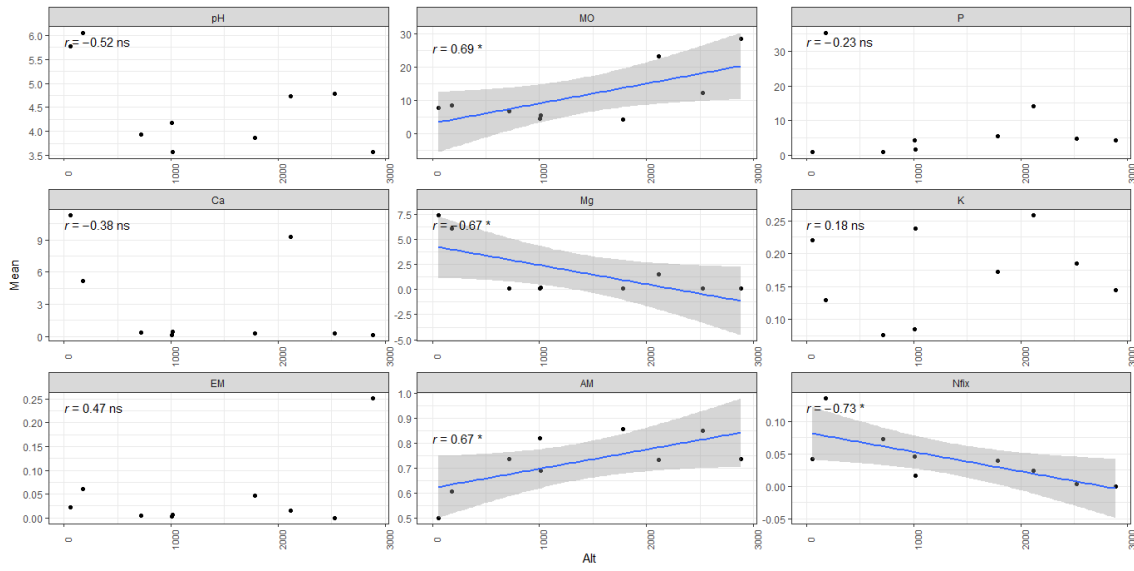
- Model 1: Permute values for each species independently (i.e., permute within each column of matrix L).
- Model 2: Permute values of sites (i.e., permute entire rows of table L).
- Model 3: Permute values for each site independently (i.e., permute within each row of table L).
- Model 4: Permute values of species (i.e., permute entire columns of table L). The model 1-4 were developed by Legendre et al. (1997).
- Model 5: Permute values of species and after (or before) permute values of sites (i.e., permute entire columns and after (or before) entire rows of table L). This model is strictly equivalent to permuting simultaneously the rows of tables R and Q, as proposed by Doledec et al. (1996).
- Model 6: combination of the outputs of models 2 and 4. Dray and Legendre (2008) and ter Braak et al. (2012) showed that all models (except model 6) have inflated type I error (This is the model used in this paper)

D. Annex: Environmental gradients in Northern Andean Mountain

A. Climate: MAT: Mean annual temperature (°C), MAP: Mean annual precipitation (mm), T.s: Temperature seasonality (°C), P.s: Precipitation seasonality (mm), VAP: Water vapor pressure (KPa), Wind: Wind speed (m/s), SRad: Solar rad (KJ m⁻¹ day⁻¹), DVP: Vapour pressure deficit (KPa). B. Soil and symbiotic association: MO: organic matter (%), Ca (calcium) Mg (magnesium) y K (potassium) cations (meq pre 100g soil), P: phosphorus (ppm), probability of association per place with EM (ectomycorrhizas) AM (arbuscular mycorrhizas) Nfix (nitrogen fixed bacteria).



B.



E. Annex: Trait information per sampled site

LA: leaf area (mm²), SLA: specific leaf area (mm² mg⁻¹), LDMC: leaf dry matter content (mg), LT: thickness (mm), Lth: toughness (N mm), WD: wood density (g cm⁻¹)

Site	LA	SLA	LDMC	LT	Lth	WD
Carepa (58 masl)	30008,55	19,87	339,48	0,19	0,24	0,50
Puerto Triunfo (180 masl)	19362,02	12,83	447,25	0,20	0,35	0,68
Segovia (717 masl)	24318,90	15,06	344,39	0,22	0,28	0,59
Porce (1006 masl)	32310,38	12,38	409,48	0,24	0,32	0,57
Maceo (1016 masl)	16608,01	16,94	352,91	0,25	0,27	0,59
Anorí (1784 masl)	14764,42	11,52	365,61	0,28	0,33	0,57
Angelópolis (2188 masl)	12786,70	13,61	344,09	0,28	0,33	0,54
Jardín (2525 masl)	16292,80	12,16	329,63	0,31	0,28	0,49
Belmira (2855 masl)	9292,93	10,10	359,29	0,34	0,41	0,52

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