Functional Differences between Andean Oak (*Quercus humboldtii* Bonpl.) Populations: The Importance of Intraspecific Variation

Valentina Castañeda, Andriana Corrales and Adriana Sánchez

Universidad del Rosario
Facultad de Ciencias Naturales
Bogotá, Colombia
2022

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Valentina Castañeda, Andriana Corrales and Adriana Sánchez

Tesis presentada como requisito para obtener el título de:

Biólogo

Director

Adriana Sánchez, PhD

Co-director

Adriana Corrales, PhD

Facultad de Ciencias Naturales
Programa de Bilogía
Universidad del Rosario
Bogotá, Colombia
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Valentina Castañeda-León

Abstract

Monodominant tree communities can have phenotypic trait variation (intraspecific variation) as extreme as the trait variation across a forest with higher species diversity. An example of such forests are those composed of *Quercus*, an important genus of woody angiosperms in the montane neotropical forest. The Andean oak, or *Quercus humboldtii* Bonpl., is the sole member of this genus in South America and a characteristic component of montane ecosystems. Although there are several studies on the ecology and genetic structure of this species, there are few studies on the functional trait diversity among populations. Understanding functional traits can improve our comprehension of how organisms respond to various environmental conditions. In this study, we aimed to evaluate differences in six functional traits in individuals of the Andean oak, in two ontogenetic stages (juveniles and adults) from three sampling sites with contrasting environmental conditions. Additionally, using T-statistics to compare variance at different organizational levels, we assessed the impact of external and internal filters. We found significant differences in all functional traits between adults and juveniles, and among sampling sites. Internal filters (e.g., factors such as competition, facilitation, and microhabitat heterogeneity) also had a stronger influence, compared to external filters. Habitat heterogeneity or facilitation between individuals at different life stages could be influential factors in the functional differences between sites. Given that the functional diversity of Andean oak populations has been poorly explored, we need of more studies to inform conservation efforts.

Keywords*:* internal and external filters; intraspecific variation; leaf dry matter content; wood density; specific leaf area.

Introduction

The first thing that usually comes to mind when thinking about tropical ecosystems are rainforests with highly diverse plant communities and low relative abundance. Nonetheless, exceptions to the general pattern where a single tree species accounts for > 60% of the abundance [2], exist throughout the tropics [1]. These monodominant forests are rare, although community level phenotypic variation, can be as extreme as the variation observed in forests with higher species diversity [3]. As a result, in these forests community structure and ecosystem function is influenced by intraspecific variation as much as the variation among species [4,5].

An example of such monodominant forests are those composed by *Quercus* L. *Quercus* is an important genera of woody angiosperms in the Neotropics and is distributed from central Mexico to the northern part of the Andean Mountain range [6]. In Colombia, *Q. humboldtii* Bonpl. (1805) is the only representative of this genus in South America and a characteristic element of montane ecosystems [7]. This species forms monodominant forests [8] distributed in the three branches (Eastern, Central and Western Cordillera) of the Colombian Andes mountain range between the altitudes of 750 and 3450 m [9,10]. Despite their monodominance, Andean oak forests contain high levels of biodiversity and serve as refuge and critical habitat for several species of plants, animals and fungi [11]. These forests (also known in Spanish as *robledales*) are part of the biodiversity hotspot [12] of the Andes and provide important ecological services such as habitat protection, water and climate regulation [13]. Despite the many benefits they offer, Andean oak forests are one of the least known and have been historically subjected to high rates of deforestation due to the expansion of agricultural activities and wood extraction [14].

What makes *Q. humboldtii* an interesting object of study is its wide climatic adaptation. The altitudinal gradient it inhabits represents a mean temperature span of almost 20 °C (9.3 to 27.9 °C), as well as a precipitation range of ca. 2000 mm/year (dry environments with 788 mm/year to very humid with 2681 mm/year). According to Gonzalez et al. [15], the species could be divided into two climatic groupings, which differ in their adaptations to average temperature, and to low or high elevations. Also, a recent study made by Zorrilla-Azcué et al. [7], showed that the climatic fluctuations since the last glacial maximum (LGM) had effects on the population history of *Q. humboldtii*. They found that the lack of genetic structure and high genetic diversity in these populations can be attributed to historical increases in connectivity from the LGM to the present [7]. Additionally, this species has the capacity to tolerate fire disturbance. Salazar et al. [12] showed that *Q. humboldtii* has the ability to regrow after this disturbance.

Despite the number of investigations on this species, there are few studies (e.g., 16,17) on its functional traits. This could be key to understanding its broad climatic adaptation. Functional traits are heritable and well-defined characteristics that influence fitness [18], and can be morphological, physiological, or phenological. The variation in functional traits represents, to an extent, the species adaptation to the existing environmental conditions [18,19], and they have been used to study the distribution of plant species and vegetation types, and the underlying responses of functional traits to factors like temperature and precipitation [20]. Given that *Q. humboldtii* is present in a wide temperature and precipitation gradient, we would expect to find considerable functional trait variability among different populations.

Along resource availability gradients for instance, populations growing in resource-rich environments are expected to have higher growth rates, which are reflected in higher specific leaf area (SLA) and lower leaf dry matter content (LDMC), leaf thickness (LT) and/or wood density (WD). In more stressful conditions [18,21], strategies for nutrient conservation and high water use efficiency are expected. Therefore, populations of *Q humboldtii* growing in dry and nutrient poor ecosystems would be expected to have lower SLA and higher WD, LDMC and/or LT. In addition, higher specific root length (SRL) can facilitate faster growth by rapidly acquiring soil resources. This trait has been described as an analogue to SLA [22], which would imply that SRL should be highest in fertile soils. Nonetheless, Kramet-Walter et al. [23] observed the opposite and high SRL dominated in low fertility soils, especially in communities that had associations with ectomycorrhizal fungi (which is also the case of *Q. humboldtii*) [24]. High SRL can therefore facilitate the exploration of larger soil volume and enhance nutrient acquisition. Another important factor in functional traits is how these change during the ontogeny. Although little is known about trait changes [25], differences may reflect the changes plants suffer as they grow in height, as well as the changes in microenvironmental systems. For instance, there is higher soil-habitat specialization in adults [26]. However, it is poorly understood if environmental filters act on the adult and/or juvenile functional traits, to create the observed patterns of trait-environmental associations [25].

An additional fundamental point is to understand how trait values are distributed in a population and which filters (internal or external) control this process. According to Violle et al. [27], trait intraspecific variation is key to many evolutionary and ecological processes. However, traditional ecology has mostly focused on interspecific variation and, according to the community assembly theory, filters would work on the mean trait values of species. Violle et al. [27] proposed a new framework that considers the trait distribution of individuals (instead of species) at different hierarchical levels. In monodominant forests, intraspecific variation is the key driver to understand ecosystem level processes [5] and therefore, it must be considered. Additionally, by comparing functional traits against a regional pool of the Andean oak, we would be able to infer how external filters (e.g., dispersal factors, climate, environmental filtering,) can potentially affect the assembly process. Internal filters occur within a community/population and are related to factors such as microhabitat heterogeneity, facilitation and competition [27]. Under this framework, we expect external filters to be more influential in sites with more extreme conditions (e.g., low nutrient soil content and precipitation) and lead to convergent trait value distributions. Internal filters would be more predominant in environments with less abiotic restrictions and, therefore, there would be more competition or facilitation.

This study aims to understand how functional traits of the Andean oak, *Quercus humboldtii* change among populations and two ontogenetic stages (juveniles and adults). Given that these species form monodominant forests, we expect intraspecific trait variability to be important in the species' functional responses to the environment. Therefore, we also seek to understand which filters, internal or external, are more important for the coexistence of individuals within a population. We hypothesize that external filters would be more important than internal filters because they can act at both, species and individual levels.

Materials and Methods

Study Area

This study was conducted in three sites along the Eastern Andean Cordillera of Colombia. The first site was Parque Natural Chicaque (4°37´3” N, 74°18´49” W) located in the municipality of San Antonio del Tequendama, Department of Cundinamarca. This reserve has an altitude gradient from 2,000 to 2,720 m, with an average temperature of 14.5 °C, and annual rainfall of 2,500 mm [28]. The second site was in the municipality of Arcabuco located within the Department of Boyacá, in the Madre Monte natural reserve (5°46´9” N, 73°25´28” W). Madre Monte has an average temperature of 14 °C, annual precipitation between 1,000 and 1,900 mm [29] and an altitudinal gradient from 2,200 to 3,100 m [30]. The third site was in the Department of Santander, in the Santuario de Fauna y Flora Guanentá Alto Río Fonce (SFF GARF) which is a National Park located close to the municipality of Encino (6°01´09” N, 73°07´08” W). This third site has an average annual temperature of 18 °C and annual rainfall between 2,500 to 3,000 mm. All sampled Andean oak forests were in altitudes between 2,250 and 2,700 m (Fig 1).

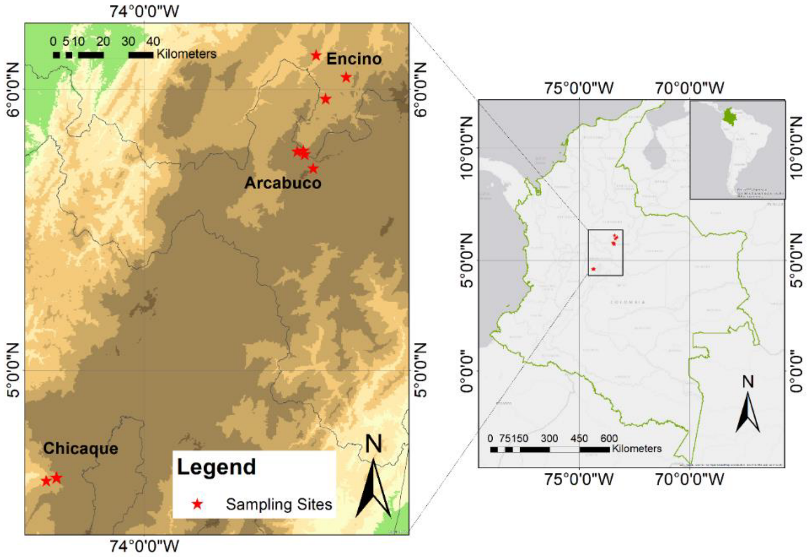

Fig 1. Location of the sampled Andean oak forests. The red stars represent the locations that were included in the analyses.

Functional Trait Sampling and Measurement

Six functional traits associated with plant growth and survival were recorded during the wet season, in November 2021 and March 2022, following standardized trait protocols [31]. In each site we sampled 20 adult and 20 juvenile individuals. These six traits are leaf area (LA (cm^2)), specific leaf area (SLA (mm^2 mg^{-1})), leaf thickness (LT (mm)), leaf dry matter content (LDMC (g g^{-1})), wood density (WD (g cm^3)), and specific root length (SRL (cm/g)). All leaf traits were measured on three healthy leaves per individual excluding the petiole. To calculate LA, fresh leaves were scanned using ImageJ [32]. To obtain leaf dry weight, leaves were dried in an oven at 70 °C for 72 h. Specific leaf area (SLA) was then calculated based on LA and leaf dry weight. For LDMC we used leaf dry weight and the leaf wet weight (measured in the field) and LT was measured at the sampling site using a digital Vernier caliper. Three measurements per leaf were averaged for LT, always consistent in the different individuals. All the leaves were collected in the same light environment (shade) in order to maintain similar conditions for juveniles and adults. To determine WD we used wood fresh volume and dry weight, wood was sampled from three branches per individual and stored in silica gel. To estimate the fresh volume of the wood, each sample was immersed in water and rehydrated for 24 h. The volume was estimated using the water displacement method [33]. Subsequently, the wood samples were dried in an oven at 70 °C for 72 h and immediately weighed after being removed from the oven [33]. Finally, for SLR, fine roots of the same individuals were sampled, stored in plastic bags, and refrigerated after collection. The roots were cleaned with tap water and scanned in an Epson Perfection V19 scanner to estimate the specific length of each root with the help of the RhizoVision Explorer software [34]. Afterwards, the root samples were dried at 70 °C for 48 h and weighed immediately after being removed from the oven.

Statistical Analysis

Data analysis was carried out in R v.4.1.0 [35]. First, using the *factoextra* package [36], we performed a principal component analysis (PCA) to visualize the values of the six traits sampled. Given that the traits were not normally distributed (tested with Shapiro-Wilk's method [35]**;** the six traits had a $p < 0.001$), we used the non-parametric U-test or Mann–Whitney to compare the average values of each functional trait between adults and juveniles in each sample site. To explore if there were differences between trait values in adults among sites, as well as juveniles, we ran a Kruskal–Wallis test using the *dplyr* package [37]. To conduct a multiple pairwise comparisons of each site, a posthoc Dunn Test using the Bonferroni method (this method is an adjustment to prevent data from incorrectly appearing to be statistically significant), was used for both adults and juveniles, using the FSA package [38].

We used "Trait statistics" (T-statistics) to understand the influence of the internal and external filters on the community assembly of *Q. humboldtii* forests [27]. We calculated the three T-statistics for all the populations together (all sampling sites) and for each site separately. In all the analyses, we treated adults and juveniles separately. The three statistics are (i) T_IP.IC, which corresponds to the ratio between the population variance and the total community variance at the individual level (individuals-populations/communities). This statistic reflects the strength of internal filters; (ii) T_IC.IR is the ratio between the community's variance and the total regional pool variance at the individual level (individuals-communities/regional pool); (iii) T_PC.PR is calculated as the ratio between the communities' variance and the total regional pool variance at the population level (populations-communities/regional pool). The last two statistics, when the regional pool is taken into account, reflect the strength of the external filters. In our sampling sites, the Andean oak is a monodominant species (especially at the canopy level), so it is important to highlight that in this case the community is the same as the population and the population/community was compared between study sites. The standardized effect size (SES) was used to compare the observed values of the three T-statistics with simulated communities ($n = 1000$ randomizations), Equation (1):

$$\mathrm{SES} = \frac{\mathrm{I_{obs}} - \mathrm{I_{sim}}}{\sigma_{\mathrm{sim}}}$$

where $\mathrm{I_{sim}}$ the average value and σ_{sim} the standard deviation of the randomized values. SES calculates the deviation between the observed and the simulated communities. When compared to random expectations, negative or positive SES values show lower or greater T-statistic values, respectively. The randomizations (null models) were adjusted to each T-statistic using the R program *cati* [39]. Using the two unilateral tests and a significance level of 5%, the importance of SES was assessed for each T-statistic and the six functional traits.

Results

Variation of Functional Traits among Populations

When considering all functional traits in the PCA analyses, the populations of adults and juveniles between sites show large overlaps. In adults, LDMC and LT contribute to the first dimension (Dim 1), whereas SRL and LA to the second (Dim 2). These two components explain 55% of the variation in the trait values (Fig 2). For the juveniles, LDMC, SLA and LT contribute to the Dim 1, while WD, LA and SRL to the Dim 2. These components explain ca. 55%.

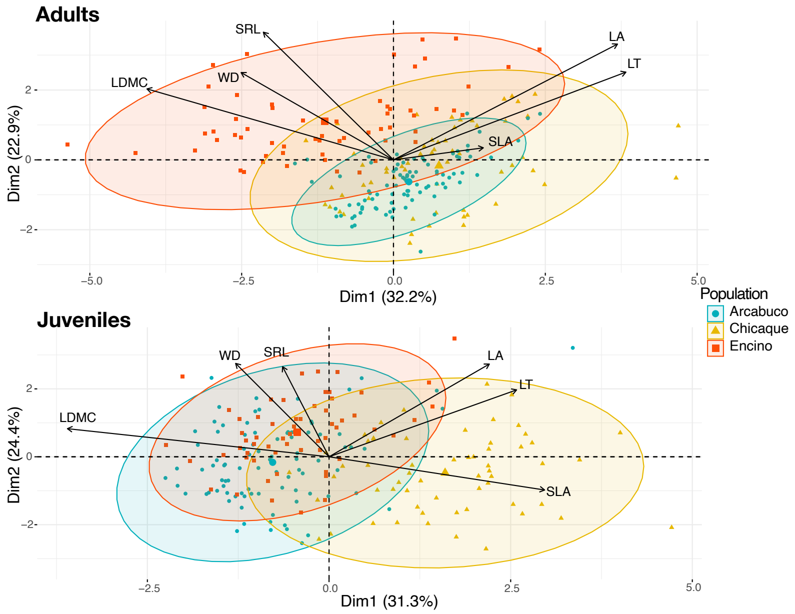

Fig 2. Principal component analysis (PCA) showing the relationship between the population of adults (first panel) and juveniles (lower panel) and the six functional traits evaluated. Each point represents an individual sampled and the sampling sites (populations) are represented in distinct colors and shapes. LA = leaf area; SLA = specific leaf area; LDMC = leaf dry matter content; LT= leaf thickness; WD = wood density; SRL = specific root length.

PCA analysis also shows that the adult individuals of Encino have higher values of LDMC, WD, and SRL; while Chicaque has higher LA, LT, and SLA values. Additionally, the population in Arcabuco has a more restricted trait distribution compared to the trait distribution of Encino and Chicaque. For the juveniles, Chicaque has the highest values for SLA, LT, and LA; Arcabuco has highest LDMC values and Encino highest WD and SRL.

Table 1. Kruskal Wallis results for adult and juvenile traits among study sites.

Trait	X^2	p value

Adults	SLA	23.580	<0.001***
	LDMC	130.210	<0.001***
	LT	1.575	**0.455**
	LA	18.183	<0.001***
	WD	69.863	<0.001***
	SRL	91.197	<0.001***
Juveniles	SLA	64.267	<0.001***
	LDMC	122.500	<0.001***
	LT	36.596	<0.001***
	LA	18.374	<0.001***
	WD	25.404	<0.001***
	SRL	54.707	<0.001***

When analyzing each trait separately, there are significant differences in all functional traits between adults and juveniles in the three populations studied ($p<0.001$; S1 Table). In addition, there are significant differences in functional traits (except for LT, $p>0.05$) among the populations of adults (Arcabuco-Chicaque, Arcabuco-Encino, Chicaque-Encino) ($p<0.001$; Table 1; Fig 3; S2 Table; S1 Fig). With respect to juveniles, all traits are significantly different between populations (Table 1; Fig 3; S2 Table; S1 Fig).

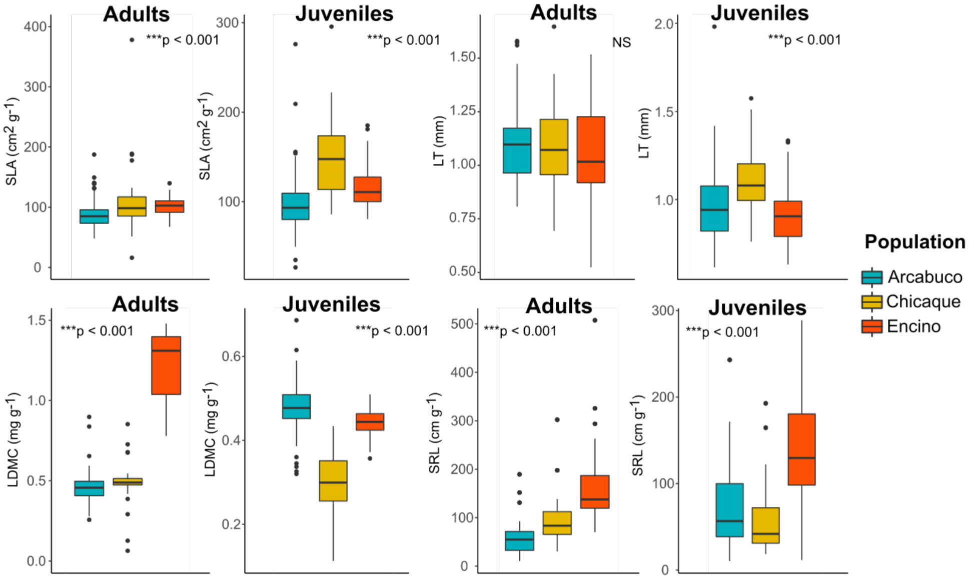

Fig 3. Functional trait variation within and between adults and juveniles in each population. Significant differences are considered when $p<0.05$. ***denotes $p<0.001$, NS = not significant. SLA = specific leaf area; LDMC = leaf dry matter content; LT= leaf thickness; SRL = specific root length. LA (leaf area) and WD (wood density) are shown in S1 Fig.

Internal and External Filters Influence *Quercus humboldtii* forests

The relation between SES of functional traits and the simulated null expectation, are shown in Fig 4 and all p-values are found in the S3 Table. For adults in the T_IP.IC (individuals-populations/communities; internal filters), SRL, SLA, and LA show significantly different and negative SES mean values. For juveniles, SRL, LDMC, SLA, LA, and LT show significantly different and negative SES mean values in the T_IP.IC. For T_IC.IR (individuals-communities/regional pool; external filters) and T_PC.PR (populations-communities/regional pool; external filters), only LDMC presents significant differences in adults and juveniles (negative SES).

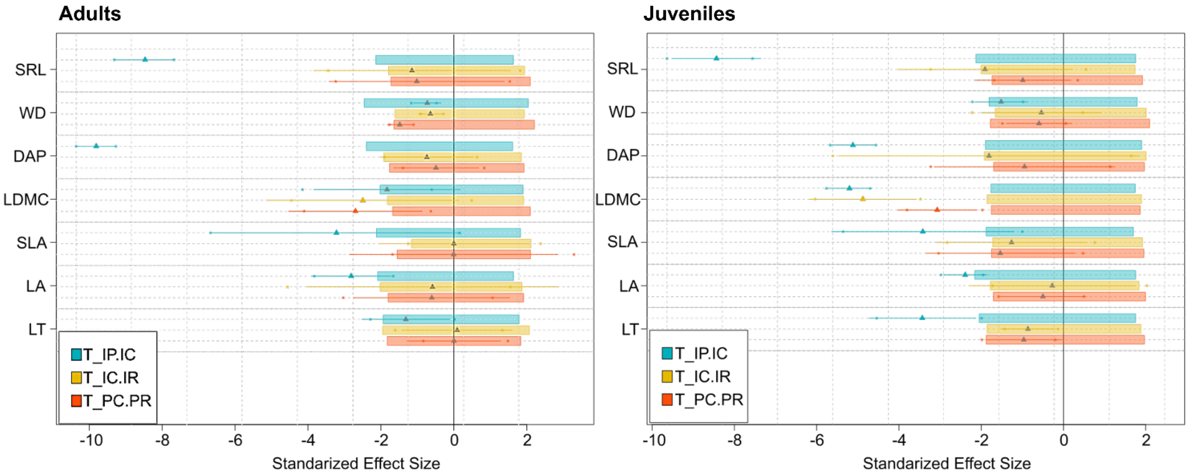

Fig 4. Standardized effect size (SES) of T-statistics of LA = leaf area; SLA = specific leaf area; LDMC = leaf dry matter content; LT= leaf thickness; WD = wood density; SRL = specific root length. The triangles represent the mean, and the segments the standard deviation of the SES values, for a given T-statistic. The boxes delimit the confidence interval. If the mean of the SES (triangle) is significantly different from the random distribution, it is found outside the box. (i) T_IP.IC (in blue): the observed ratio between the populations' variance and the total community variance at the individual level (individuals-populations/communities); (ii) T_IC.IR (in yellow): the observed ratio between the community's variance and the total regional pool variance at the individual level (individuals-communities/regional pool; (iii) T_PC.PR (in red): the observed ratio between the community's variance and the total regional pool variance at the population level (populations-communities/regional pool).

At the site level (S2 Fig) in the adults of Arcabuco we observe that for T_IC.IR, LDMC, SRL and LA have significantly lower and negative SES values than the null models. For T_IP.IC, the significantly lower and negative SES values are found in SRL, SLA and LA. For T_PC.PR. LA, SRL and LDMC present significantly lower negative SES values. For adults individuals in Chicaque we observe that only SRL show significantly lower negative SES values in T_IP.IC. Whereas T_IC.IR shows significant differences (negative SES) in LDMC and SRL. Also, we observe significantly higher differences (positive SES) in SLA for T_IC.IR. For T_PC.PR, LDMC was the only trait that presents significantly lower negative SES values. Finally, for adults in Encino, all traits except for WD, are negative and significantly different for T_IP.IC. For T_IC.IR and for T_PC.PR, only SLA has significantly lower and negative SES values compared to the null models.

On the other hand, for juveniles (S3 Fig) in Arcabuco, we observed that all six traits in T_IP.IC, except for WD and SLA, have significantly lower and negative SES compared to the null models. For T_IC.IR, LDMC, SRL and SLA shows significant differences (negative SES), while for T_PC.PR, LDMC, SLA and LA also have significantly lower and negative SES values compared to the null models. In Chicaque, for T_IP.IC, the six traits have significantly lower and negative SES values. LDMC, SRL and WD where the traits that have significant differences for T_IC.IR. For T_PC.PR, LDMC and SRL where the only traits that have significantly lower negative SES values. Lastly, for Encino, SRL, SLA and LDMC traits have significantly lower negative SES values for T_IP.IC. For T_IC.IR, SLA and LDMC present significantly lower negative SES values and for T_PC.PR, LDMC and SLA show significant differences (negative SES).

Discussion

Andean oak populations differ in most of the functional traits between juveniles and adults, as well as between sites (populations). Regarding the influence of internal and external filters our results show that, contrary to what was expected, internal filters (such as competition, facilitation, and microhabitat heterogeneity) are more influential than external filters (such as climate, environmental filtering, dispersal factors) in the three populations, in both, adults, and juveniles. The ability to colonize a wide diversity of environments and ecosystems, as well as their evolutionary history may be explained by the broad intraspecific trait variation of *Q. humboldtii*.

Functional Traits of Andean Oak Forests

According to our findings, Andean oak populations in the Colombian Andes differ in several plant functional traits (Table 1; Fig 3). These traits may provide information to understand the broad climatic adaptation of these species. Previous studies on functional traits of *Quercus humboldtii* have also shown that traits, such as SLA and WD, separate between sites as well, especially in an elevational gradient [17]. Climate is one of the main factors influencing the evolution of populations [40]. Some long-term studies indicate that variation in climatic conditions such as rainfall, can affect the direction or magnitude of trait selection [41,42]. Our results are consistent with the findings of Ramírez-Valiente et al. [40] where a reduced SLA in *Quercus suber* can be advantageous when there is low water availability. In our study, Arcabuco presents the lowest SLA and annual rainfall values (100-1900 mm) [30], compared to Chicaque and Encino which present similar precipitation values (2500-3000 mm) [43], and these results are consistent for both, adults and juveniles. The variation of SLA may be important for adjusting to different air temperatures and precipitation regimes [44], since it reflects the trade-off between water conservation and resource capture [45].

Plants have different physiological mechanisms that are reflected in leaf traits and influenced by the life stage the plant is at [46]. In this study, SLA was higher in juveniles and these results are in line with the study by Williams-Linera et al. [47], where they found that SLA differed across plant development stages. SLA and LDMC are traits that change with ontogeny [48]. Low SLA and high LDMC values (typical of adult trees), are associated with conservative growth, increased leaf longevity and more investment in leaf protection [49]. Also, Andean oak adults have higher LDMC and thicker leaves (LT) than juveniles (Table S1). High LDMC values often indicate the adaptation to resource-limited environments [50]. Higher LDMC and thicker leaves enhances the plant's ability to resist strong light while also increasing leaf biomass and keeping water in the leaves [51]. Juveniles devote more nutrients to growth which could explain the lower LDMC and LT compared to adults [50].

Wood density (WD) correlates with resistance to damage and embolism, resource allocation, as well as with growth potential [52]. Our results show that Encino adults have the highest WD and LDMC values of all populations, indicating a high investment in long-lasting and strong foliar and wood tissues. This is also related to survival and more nutrient accumulation under stressful conditions [18]. Finally, for SRL, we found the highest values for Encino. This root trait can represent the economic aspects and the environmental changes experimented by roots [53]. A study by Ostonen et al. [54] showed that depleted soils tend to have higher SRL values. Soils with higher nutrient availability would have lower SRL, because there is less need for fine root length growth. Higher SRL reflects more soil exploration by fine roots, although it can lower root longevity [55]. Additionally, higher SRL can also imply a lower dependance on mycorrhizal associations [53]. Arcabuco, on the other hand, presents the lowest SRL values, which may be indicative of fertile soils or more reliance on ectomycorrhizal symbiosis [56].

Internal and External Filters Influence *Quercus humboldtii* forests

The significant intraspecific variation between the three populations of Andean oak is especially influenced by internal filters. Although in a species with a broad climatic adaptation like *Q. humboldtii* external filters may play an important role in the assembly, based on our results, internal filters are more important (Fig 4). *Quercus humboldtii* populations have been threatened because of the high rates of deforestation (for agriculture and cattle ranching), as well as wood extraction. These could have caused structural simplifications in many oak populations [57]. However, Andean oak forests may inhabit areas with high microhabitat heterogeneity (due to, for example, changes in microclimate and soils) and soil properties may vary and influence the expression of functional traits [58]. Therefore, internal filters could create niche differentiation.

To date, the role of facilitation is unknown for this species. However, it can be an important internal filter that may be affecting the community assembly of Andean oaks. Facilitation has been assumed to occur when niche overlap is low or non-existent. Otherwise, there would competition for common resources [59]. Although, intraspecific facilitation may happen when different life stages are co-existing, adult trees can have nursing effects on recruitment [60]. If adult trees, being taller, allow the retention of low levels of moisture on the soil surface, these could facilitate the growth of seedlings that do not yet have deep roots (and affect traits like SRL or SLA) [61]. Additionally, Andean oak forms symbiotic associations with ectomycorrhizal fungi [62]. Mycorrhizal networks serve as a vital pathway for the exchange of resources between mycorrhizal fungi and plants, dividing up nutrients and water away from competing soil microorganisms and plant roots in the soil matrix. It is possible that this could provide certain network participants a competitive advantage (or disadvantage). Ectomycorrhizal networks, for example, might influence traits related to water availability by facilitating the hydraulic redistribution of soil or plant water along water potential gradients [63]. In this study, we also found that LDMC is the only trait affected by external filters in both, adults, and juveniles (Fig 4). In this particular case, external filters such as climate (temperature and precipitation) may be more definite in the distribution of LDMC values [64].

Evolutionary History Can Explain Intraspecific Variation

When talking about the ecology of a species, we cannot ignore its evolutionary history. Hooghiemstra and Flantua [65] reported that the upper limit of the forest reached an altitude of 2,000 m during the LGM (21 ka BP to ca. 14 ka BP). The upper mountain forest was compressed by about 400 m and displaced to lower elevations compared to the current altitudes. The lower mountain forest was also displaced altitudinally to lower altitudes. The demography and genetics of *Q. humboldtii* in the Andean montane forests were affected in various ways by these variations. In particular, palynological and floristic investigations have suggested migration routes that allowed the colonization of different mountain ranges [66]. This would imply, that the Andean oak forests may have remained connected over time and that populations of *Q. humboldtii* would have maintained gene flow [7].

A recent study by Zorrilla-Azcué et al. [7], demonstrates that this species has a lack of genetic structure and considerable genetic diversity. They found eight genetic clusters distributed along the three cordilleras (Western, Central, and Eastern). Two of their study sites correspond to sampled sites in this study (Encino and Arcabuco) and both are in two different genetic clusters (Figs 1, 3; S2). These findings show that although the Andean oak may be acclimating to their environment, there could also be differences responding to their genetic diversity and evolutionary history (and thus, adaptation). Evolutionary history, in addition to the internal filters and environmental factors, can be affecting trait values and could explain the functional trait differences between the three populations studied. The question remains as to how the functional traits of these populations will change in the future, as fragmentation increases and there are more restrictions to gene flow.

Conclusions

Functional traits in populations of *Quercus humboldtii* vary widely between populations of the Eastern cordillera of the Colombian Andes. These differences are mostly explained by internal filters (e.g., habitat heterogeneity, disturbance and/or intraspecific facilitation), while external factors seem to play a secondary role. There were significant differences in all functional traits between both ontogenetic stages (S1 Table), indicating ontogenetic shifts as juveniles grow. There were also differences between oak populations (except for LT in adult populations; Fig 3; S2 Table; S1 Fig). The functional differences could also be explained by the evolutionary history of this species. Genetic differentiation between populations could have led to intraspecific functional variation. Therefore, the ability to colonize a wide diversity of environments and ecosystems, as well as their evolutionary history may be explained by the broad intraspecific trait variation of *Q. humboldtii*.

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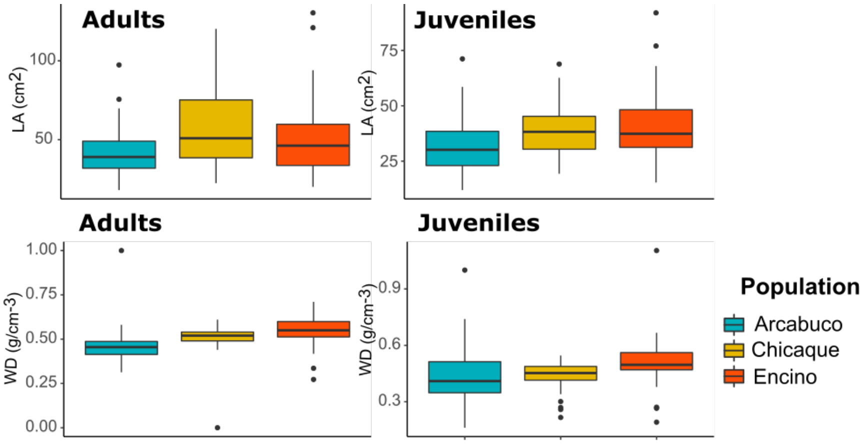
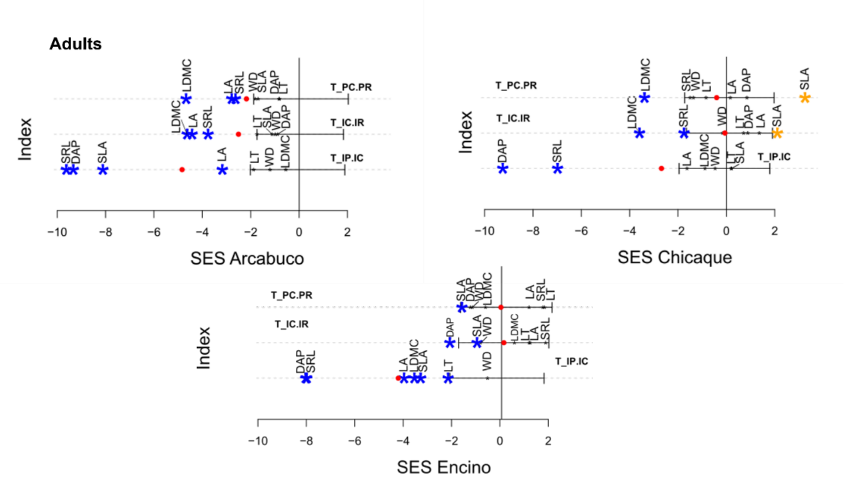
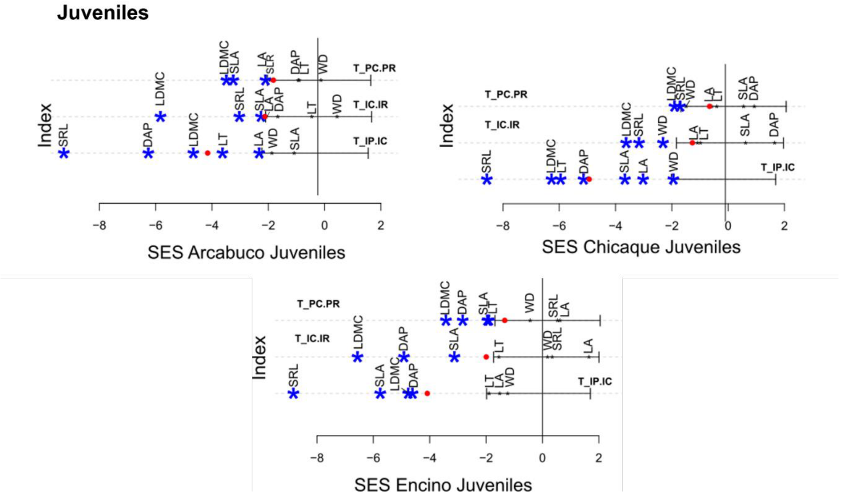
Supporting information



S1 Fig. Functional trait variation between adults and juveniles in each population. Significant differences are considered to exist when p<0.05. ***represents p<0.001. LA = leaf area; WD = wood density.



S2 Fig. Standardized effect size (SES) of the six functional traits evaluated for three T statistics according to adults of each population. The T statistics evaluated are (1) T_IP.IC: observed ratio between the variance of the populations and the total variance of the communities at the individual level; (2) T_IC.IR: observed ratio between the variance of each community and the total variance of the regional pool at the individual level; (3) T_PC.PR: the observed ratio between the communities' variance and the total variance of the regional pool at the population level (populations-communities/regional pool). The segments observed in each figure represent the expected random ranges corresponding to each T-statistic. Blue asterisks indicate significantly lower differences compared to the null models (p<0.05). Yellow asterisks indicate significantly higher differences compared to the null models (p<0.05). Red dots show the average SES of all traits for each T-statistic.



S3 Fig. Standardized effect size (SES) of the six functional traits evaluated for three T statistics according to juveniles of each population. The T statistics evaluated are (1) T_IP.IC: observed ratio between the variance of the populations and the total variance of the communities at the individual level; (2) T_IC.IR: observed ratio between the variance of each community and the total variance of the regional pool at the individual level. The segments observed in each figure represent the expected random ranges corresponding to each T-statistic; (3) T_PC.PR: the observed ratio between the communities' variance and the total variance of the regional pool at the population level (populations-communities/regional pool). Blue asterisks indicate significantly lower differences compared to the null models ($p<0.05$). Red dots show the average SES of all traits for each T-statistic.

S1 Table. Mann-Whitney Test for each population comparing adults and juveniles for each trait.

	Trait	Group	SD	Mean	p value
Chicaque	SLA	Adult	102.284	116.980	< 0.001***
		Juvenile	45.046	144.815	
	LDMC	Adult	0.105	0.490	< 0.001***
		Juvenile	0.078	0.300	
	LT	Adult	0.195	1.081	0.6938
		Juvenile	0.175	1.098	
	LA	Adult	23.639	57.541	< 0.001***
		Juvenile	11.368	38.810	
	WD	Adult	0.243	0.352	0.006
		Juvenile	0.197	0.335	
	SLR	Adult	59.923	99.889	< 0.001***
		Juvenile	47.073	60.498	
Arcabuco	SLA	Adult	24.585	89.001	< 0.010**
		Juvenile	32.437	98.653	
	LDMC	Adult	0.373	0.495	0.021
		Juvenile	0.061	0.478	
	LT	Adult	0.171	1.098	< 0.001***
		Juvenile	0.196	0.950	
	LA	Adult	13.344	40.990	< 0.001***
		Juvenile	11.015	31.900	
	WD	Adult	0.092	0.453	0.010**
		Juvenile	0.132	0.424	
	SLR	Adult	42.218	56.758	0.102
		Juvenile	53.248	70.974	
Encino	SLA	Adult	14.446	101.601	0.001***
		Juvenile	22.429	115.299	
	LDMC	Adult	1.177	2.438	< 0.001***
		Juvenile	0.032	0.441	
	LT	Adult	0.206	1.057	< 0.001***
		Juvenile	0.165	0.903	
	LA	Adult	22.870	49.993	0.011
		Juvenile	14.443	39.421	
	WD	Adult	0.080	0.552	< 0.001***
		Juvenile	0.117	0.506	

SLR	Adult	102.203	174.193	0.108
	Juvenile	67.009	140.098	

S2 Table. Dunn posthoc test results for adults and juveniles, comparing traits values in each population (sampling site).

	Trait	Comparison	Z	p value
Adults	SLA	Arcabuco-Chicaque	-3.647	< 0.001***
		Arcabuco-Encino	-4.396	< 0.001***
		Chicaque-Encino	-0.683	< 0.001***
	LDMC	Arcabuco-Chicaque	-2.350	< 0.001***
		Arcabuco-Encino	-11.174	< 0.001***
		Chicaque-Encino	-8.055	< 0.001***
	LT	Arcabuco-Chicaque	0.371	**1.000**
		Arcabuco-Encino	1.247	**0.636**
		Chicaque-Encino	0.799	**1.000**
	LA	Arcabuco-Chicaque	-4.223	< 0.001***
		Arcabuco-Encino	-2.225	< 0.001***
		Chicaque-Encino	1.824	< 0.001***
	WD	Arcabuco-Chicaque	-4.833	< 0.001***
		Arcabuco-Encino	-8.100	< 0.001***
		Chicaque-Encino	-2.227	< 0.001***
	SLR	Arcabuco-Chicaque	-4.538	< 0.001***
		Arcabuco-Encino	-9.522	< 0.001***
		Chicaque-Encino	-4.581	< 0.001***
Juveniles	SLA	Arcabuco-Chicaque	-7.961	< 0.001***
		Arcabuco-Encino	-4.031	< 0.001***
		Chicaque-Encino	3.609	< 0.001***
	LDMC	Arcabuco-Chicaque	11.023	< 0.001***
		Arcabuco-Encino	3.477	< 0.001***
		Chicaque-Encino	-6.909	< 0.001***
	LT	Arcabuco-Chicaque	-4.791	< 0.001***
		Arcabuco-Encino	1.467	< 0.001***
		Chicaque-Encino	5.714	< 0.001***
	LA	Arcabuco-Chicaque	-3.676	< 0.001***
		Arcabuco-Encino	-3.490	0.001***
		Chicaque-Encino	0.169	1.000
	WD	Arcabuco-Chicaque	-0.763	< 0.001***

	Arcabuco-Encino	-4.910	< 0.001***
	Chicaque-Encino	-3.477	< 0.001***
SLR	Arcabuco-Chicaque	1.670	< 0.001***
	Arcabuco-Encino	-5.895	< 0.001***
	Chicaque-Encino	-6.954	< 0.001***

S3 Table. p-values of the two unilateral statistical tests performed (lower and upper limit) to compare the T statistics with the random expectations, according to each functional trait and forest type.

		p-value LT	p-value LA	p-value SLA	p-value LDMC	p-value WD	p-value SRL
Adults	T_IP.IC low Arcabuco	0.05	0.01	0.01	0.16	0.09	0.01
	T_IP.IC low Chicaque	0.55	0.08	0.54	0.21	0.20	0.01
	T_IP.IC low Encino	0.03	0.01	0.01	0.01	0.17	0.01
	T_IP.IC upp Arcabuco	0.96	1	1	0.85	0.92	1
	T_IP.IC upp Chicaque	0.46	0.93	0.47	0.80	0.81	1
	T_IP.IC upp Encino	0.98	1	1	1	0.84	1
	T_IC.IR low Arcabuco	0.05	0.01	0.11	0.01	0.20	0.01
	T_IC.IR low Chicaque	0.70	0.92	0.97	0.01	0.43	0.01
	T_IC.IR low Encino	0.89	0.92	0.01	0.70	0.30	0.96
	T_IC.IR upp Arcabuco	0.96	1	0.90	1	0.81	1
	T_IC.IR upp Chicaque	0.31	0.09	0.04	1	0.58	1
	T_IC.IR upp Encino	0.12	0.09	1	0.31	0.71	0.05
	T_PC.PR low Arcabuco	0.29	0.01	0.04	0.01	0.04	0.01
	T_PC.PR low Chicaque	0.22	0.56	1	0.01	0.03	0.08
	T_PC.PR low Encino	0.93	0.85	0.01	0.29	0.14	0.94
	T_PC.PR upp Arcabuco	0.72	1	0.97	1	0.97	1
	T_PC.PR upp Chicaque	0.79	0.45	0.01	1	0.98	0.93
	T_PC.PR upp Encino	0.08	0.16	1	0.72	0.87	0.07
Juveniles	T_IP.IC low Arcabuco	0.01	0.04	0.16	0.01	0.07	0.01
	T_IP.IC low Chicaque	0.01	0.01	0.01	0.01	0.04	0.01
	T_IP.IC low Encino	0.02	0.03	0.01	0.01	0.10	0.01
	T_IP.IC upp Arcabuco	1	0.97	0.85	1	0.94	1

T_IP.IC upp Chicaque	1	1	1	1	0.97	1
T_IP.IC upp Encino	0.99	0.98	1	1	0.91	1
T_IC.IR low Arcabuco	0.42	0.04	0.02	0.01	0.73	0.01
T_IC.IR low Chicaque	0.16	0.13	0.80	0.01	0.01	0.01
T_IC.IR low Encino	0.07	0.96	0.01	0.01	0.49	0.74
T_IC.IR upp Arcabuco	0.59	0.97	0.99	1	0.28	1
T_IC.IR upp Chicaque	0.85	0.88	0.21	1	1	1
T_IC.IR upp Encino	0.94	0.05	1	1	0.52	0.27
T_PC.PR low Arcabuco	0.32	0.03	0.01	0.01	0.59	0.05
T_PC.PR low Chicaque	0.37	0.35	0.80	0.05	0.04	0.04
T_PC.PR low Encino	0.04	0.75	0.02	0.01	0.33	0.70
T_PC.PR upp Arcabuco	0.69	0.98	1	1	0.42	0.96
T_PC.PR upp Chicaque	0.64	0.66	0.21	0.96	0.97	0.97
T_PC.PR upp Encino	0.97	0.26	0.99	1	0.68	0.31