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# LACK OF VERTICAL AND HORIZONTAL FLORISTIC CONGRUENCE IN *QUERCUS INSIGNIS*-DOMINATED CLOUD FOREST STANDS IN THE MEXICAN NEOTROPICS

MIGUEL OLVERA-VARGAS*, BLANCA L. FIGUEROA-RANGEL, AND JOSÉ GUADALUPE MORALES ARIAS

Departamento de Ecología y Recursos Naturales, Centro Universitario de la Costa Sur, Universidad de Guadalajara, Jalisco, Mexico.
*Corresponding author: miguel.olvera@academicos.udg.mx

**Abstract**

**Background:** In diverse forests, it remains uncertain whether species composition of seedlings and saplings aligns with that of adult-trees, and whether similarity in composition decreases with greater geographic distance.

**Questions:** i) How do species composition, diversity, and abundance vary across three ontogenetic stages: seedlings, saplings, and adult-trees in *Quercus insignis*-dominated forests? ii) Is there vertical congruence in floristic composition among seedlings, saplings, and adult-trees? iii) How do environmental and geographic distances influence horizontal floristic patterns? Which environmental variables are the primary drivers of species composition in these forests?

**Studied species:** *Quercus insignis* and its forty-nine associated tree species.

**Study site:** Sierra de Cacoma Jalisco, west-central México.

Methods: Twenty-four 500 m² plots were sampled along a 3.5 km transect, covering a 500 m elevational gradient. In each plot, all adult-trees (DN ≥ 5 cm) were recorded by species, diameter, and height. Saplings (DN < 5 cm) were recorded in 50 m² subplots, and seedlings in eight 1 m² units within each plot. Physiographical and environmental variables were recorded to assess habitat heterogeneity.

**Results:** Floristic composition, diversity, and abundance varied significantly across the three ontogenetic stages according to NMDS and PERMANOVA analyses. Five environmental variables significantly explained species composition patterns. Mantel tests indicated no significant correlation between horizontal composition similarity and environmental distance.

**Conclusions:** The study reveals complex interactions among ontogenetic stages, species distribution and environmental heterogeneity, highlighting the role of environmental variables as critical habitat filters in shaping forest community structure.

**Keywords:** Environmental variables, floristic composition, micro-habitat filters, neotropical cloud forest, ontogenetic stages.

**Resumen**

**Antecedentes:** En bosques diversos se discute si la composición florística de plántulas y juveniles se asemeja a la de árboles adultos y si esta similitud disminuye con la distancia geográfica.

**Preguntas:** i) ¿Cómo varían composición, diversidad y abundancia de especies entre plántulas, juveniles y árboles adultos en bosques dominados por *Quercus insignis*? ii) ¿Existe congruencia vertical en la composición florística entre etapas ontogenéticas? iii) ¿Cómo influyen la distancia geográfica y ambiental en los patrones florísticos horizontales? ¿Qué variables ambientales impulsan la composición de especies?

**Especie estudiada:** *Quercus insignis* y 49 especies arbóreas asociadas.

**Sitio de estudio:** Sierra de Cacoma, Jalisco, centro-oeste de México.

**Métodos:** Se muestrearon 24 parcelas de 500 m² sobre un transecto de 3.5 km en un gradiente de 500 m. En cada parcela se registró la especie, diámetro y altura de árboles adultos (DN ≥ 5 cm), juveniles (DN < 5 cm) en subparcelas de 50 m² y plántulas en ocho unidades de 1 m². Se midieron variables fisiográficas y ambientales para evaluar la heterogeneidad del hábitat.

**Resultados:** La composición florística, diversidad y abundancia variaron significativamente entre las etapas ontogenéticas según NMDS y PERMANOVA. Cinco variables ambientales explican los patrones de composición de especies. Pruebas de Mantel revelaron correlaciones no significativas entre composición horizontal y distancia ambiental.

**Conclusiones:** El estudio revela interacciones complejas entre las etapas ontogenéticas, la distribución de especies y la heterogeneidad ambiental, destacando el papel de las variables ambientales como filtros críticos en la estructura de la comunidad forestal.

**Palabras clave:** Bosque nublado neotropical, composición florística, estadios ontogenéticos, filtros de micro-hábitat, variables ambientales.

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Seedlings and saplings are the most important ontogenetic stages in the development of forest stands, and their species composition is likely driven by the spatial distribution of reproductive adult-trees (Wang *et al.* 2017), combined with local seed dispersal, seed spreading strategies and the maximal distance of their distribution. In general, early stages of tree's life cycle (*e.g.,* seedlings and saplings) are considered more sensitive to environmental factors than adult-trees of the same species (Caron *et al.* 2021). However, there is insufficient information in scientific literature to assert whether seedlings and saplings species composition will resemble adult-tree species composition. Traditional gradient studies on changes in tree species abundance typically focus on adult-tree individuals (Collins & Carson 2004) and many studies assume that all life stages are responding similarly; they also assume that adult-trees response to gradients is stronger than seedlings and saplings response. This focus ignores that community assembly mechanisms may strongly differ between life-stages and reject the role of ontogenetic dependency: the mechanisms by which one life stage directly affects the composition of another life stage (Ramachandran *et al.* 2023). Vertical floristic congruence focuses on the similarity of species composition from the upper canopy to the forest floor. It is assessed by comparing species composition across vertical strata to determine significant floristic similarity. For instance, if the same species dominate the overstory, understory, and the forest floor, it indicates high vertical floristic congruence. Similarly, horizontal floristic congruence looks at similarity in species composition between different sites distributed in a geographical area or along an altitudinal gradient.

Different studies have also examined the effects of habitat heterogeneity either on adult-trees, saplings or seedlings, while only few studies (*e.g.,* Collins & Carson 2004, Henry & Walterss 2023, Ramachandran *et al.* 2023) have assessed the importance of habitat heterogeneity at different ontogenetic stages. Contemporary research has also shown that the need of essential resources undergoes a transition from seedlings to adults, a phenomenon referred to as ontogenetic shift (Caron *et al.* 2021). Identifying the most responsive life stage to environmental gradients will likely ascertain the life stage that regulate future species abundances. Research also suggests (Wang *et al.* 2017) that abiotic and biotic essential resources are spatially structured and control species distribution and abundance through habitat-species specific associations. Therefore, habitat filtering is an important process which shapes forest communities, and arises from species-habitat niches, or from the inability of a species to persist in all environments (Baldeck *et al.* 2013).

The decrease (or decay) in species composition similarity between two samples (species turnover), associated with the geographical distance between them is a characteristic pattern commonly described in several ecological and geographical studies (Kobayashi & Sota 2016, Basham *et al.* 2019). Distance decay of similarity in forest communities is a typical spatial pattern in biodiversity and refers to cases where the similarity in species composition between communities decreases as the geographic distance between them increases (Nekola & White 1999). The causes of distance decay can be categorized into two general types: niche-based processes and dispersal-based processes (Basham *et al.* 2019). In niche-based processes species composition is driven by environmental constraints, and in dispersal-based processes, influenced by species' movement and aggregation patterns. Both can generate spatial structures in communities (Kobayashi & Sota 2016).

Furthermore, species distribution and abundance are determined by local scale environmental variability, such as topography, micro-climate, and soil nutrient variables (Rodrigues *et al.* 2021). As a result, non-random species distribution with respect to soil nutrients and environmental gradients has been documented at various temporal and spatial scales in numerous forest communities worldwide (Comita *et al.* 2007). Temperature is one of the most critical micro-climate variables for the development and growth of juvenile tree species. It can strongly affect all phases of plant species' regeneration, from dormancy break until seedling establishment and survival (Caron *et al.* 2021). Thus, temperature variability plays a crucial role in regulating most ecological processes that affect tree growth and development. These processes include photosynthesis, respiration, bud opening, shoot growth, seed germination, and seedling mortality (Xu *et al.* 1997). At forest stand level, the distribution of thermal energy is primarily affected by topography-associated thermal gradients (He *et al*. 2017), soil nutrients availability, soil humidity, temperature, and light requirements (Werner & Homeier 2015, Jucker *et al.* 2018).

*Quercus insignis* is an Endangered species with a limited range of 472 km² according to the IUCN Red List (Jerome 2018, IUCN 2024), classified as Near Threatened on the Red List of Oaks (Oldfield & Eastwood 2007) and Critically Endangered on the Red List of Mexican Cloud Forest Trees (González-Espinosa *et al*. 2011). Despite its broad geographic distribution from Mexico to Panama, it is restricted to cloud forests and humid oak forests, with isolated populations in Mexico's Oaxaca, Veracruz, Jalisco, and Chiapas states. In Jalisco, it is found in humid ravines at 900-1400 m asl, commonly within cloud mountain forest communities, and typically with a disjunct distribution in this forest communities (Gonzalez-Villareal 1986).

Therefore, our aims in this research were: *i*.- to identify patterns of seedlings, saplings, and adult-trees in terms of species composition, diversity and abundance in *Quercus insignis*-dominated forest stands along an altitudinal gradient. We predict variations in species composition and abundance among ontogenetic stages. *ii*.- to identify whether there is vertical congruence in species composition across the three ontogenetic stages (seedlings, saplings, and adult-trees). We predict a lack of vertical floristic congruence among the three ontogenetic stages because of the complex interactions between species characteristics and environmental variables (*e.g.,* soil nutrients, environmental and physiographical characteristics, etc.), therefore, each ontogenetic stage should exhibit a distinct association with environmental conditions. *iii*.- to assess the relative importance of environmental and geographical distance on patterns of horizontal species composition across the three ontogenetic stages. We predict that horizontal species composition across ontogenetic stages is more strongly influenced by environmental gradients than by geographical distance, highlighting ontogenetic stage-specific ecological filters in community assembly; *iv*.- to reveal the best-fit environmental variables explaining variation in patterns of species composition. We expect that each ontogenetic stage will be associated to a particular set of environmental variables due to their needs for essential resource use.

## Materials and methods

*Study area.* The study area is in Sierra de Cacoma (SC) Jalisco, in west-central México (Figure 1). The SC is a forested area located in the Trans-Mexican Volcanic Belt (Morrone 2019); this is an interesting biogeographic area almost floristically unexplored. Its elevation ranges from 800 to 2,400 m asl. Climate is a sub-humid with temperatures between 18 and 28 ºC and precipitation range from 1,500 to 2,000 mm/yr (Morales-Arias *et al.* 2018). A conspicuous physiographic heterogeneity characterizes SC, allowing the interplay of different vegetation types: cloud forest, pine forest, oak forest, pine-oak forest, tropical deciduous forest, and riparian forest over low elevations (Morales-Arias *et al*. 2016). This research was undertaken in a thriving well-preserved cloud forest, located over an altitudinal range from 1,000 to 2,100 m asl., with canopy dominant trees stretching from 25 to 30 m in height and up to 1.50 m in diameter. This forest ecosystem has been free of catastrophic forest fires and logging operation, at least over the past 35 years (Personal observations).

*Sampling method.* We established 24 circular sampling plots, 500 m² each, placed approximately 100 m apart from one another along an elevational gradient of 500 m asl. and covering 3.5 kilometers (Figure 1). In each plot, we recorded all adult-trees considered as those individuals with a diameter at breast height (dbh) ≥ 5 cm and a trunk height ≥ 1.30 m, which were individually enumerated, identified to species level, and recorded. Measurements of adult-trees included species, dbh and tree height measured using a Haga clinometer.

We also established a circular 50 m$^2$ sub-plot (*radius* = 4.0 m) (*n* = 24) nested at the center of each 500 m² plot. Within these sub-plots, we recorded all saplings, defined as individuals with a trunk height ≥ 1.30 m and < 5 cm dbh. Seedlings, defined as those small individuals < 1.30 m height, were recorded in eight nested sampling units of 1 × 1 m² (*n* = 192) each, four of these sampling units were situated along the slope-terrain and four perpendicular to the slope-terrain. Species sample collections were undertaken to identify unknown tree species. Nomenclature for vascular plants followed Tropicos.org (Tropicos 2024). All plots were geo-referenced with a hand-held Global Positioning System receiver (GPS 12XL, Garmin International, Inc., Olathe, Kansas, USA).

Within each 500 m² sampling plot, we collected soil samples (approx. 10 - 15 cm below the organic material layer) from three points equally spaced, one at upper the slope, one at middle slope and one at the bottom of the slope; soil samples were mixed-up in a plastic bag to obtain a single composite soil sample. Chemical soil analyses were determined in a specialized laboratory for: organic matter (Om), pH, Cation-exchangeable capacity (CIC), total nitrogen

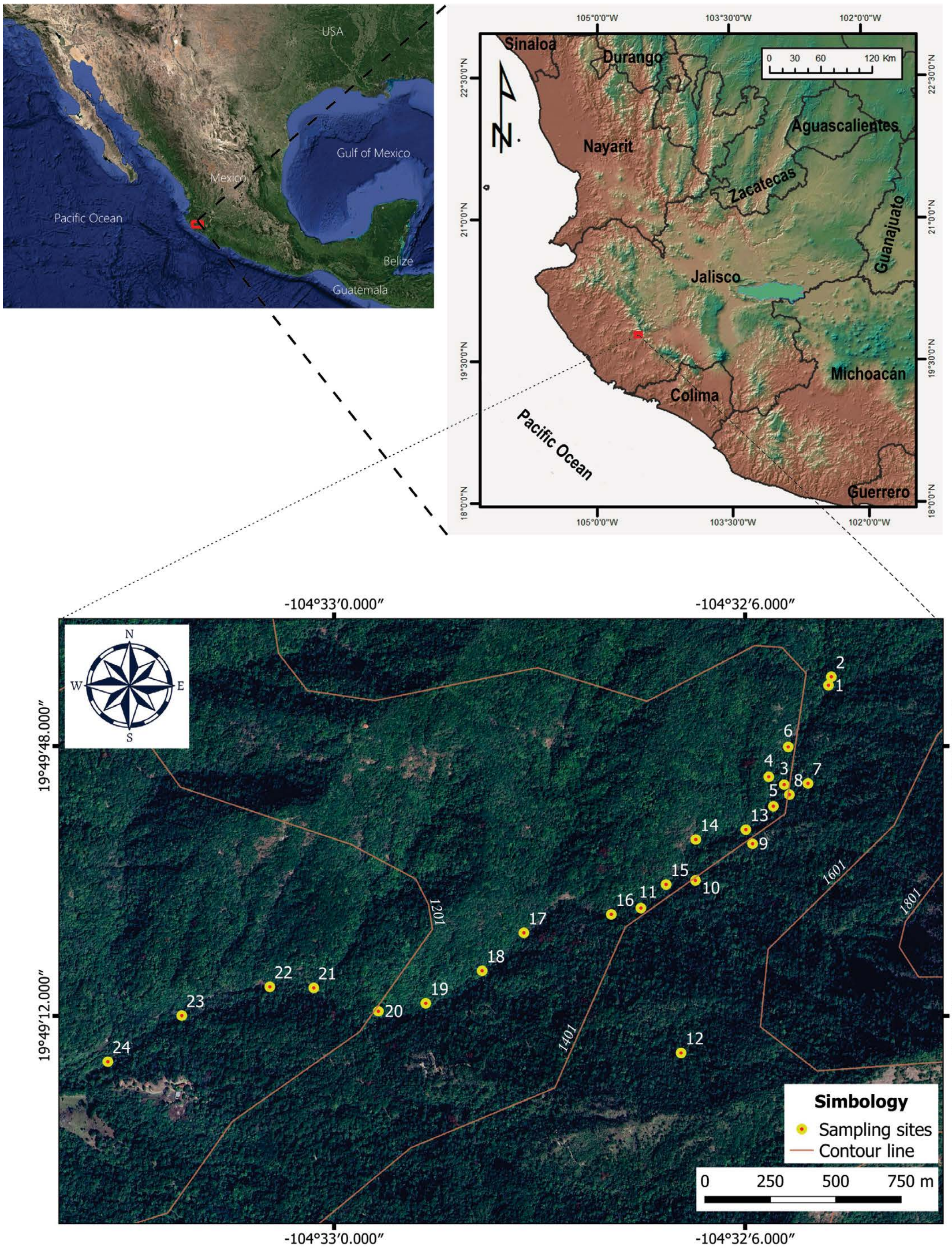

**Figure 1.** Map of the study area of the *Quercus insignis*-dominated cloud forest in the Mexican Neotropics. The figure highlights the locations of the sampled plots across the altitudinal range sampled.

(N), calcium (Ca), potassium (K), copper (Cu), iron (Fe), manganese (Mn), zinc (Zn) and sodium (Na) (Table 1). All chemical analyses were appraised by the Kjeldahl method.

*Environmental heterogeneity.* To assess the environmental heterogeneity at plot level in our study area, we recorded environmental variables, according to Olvera-Vargas & Figueroa-Rangel (2023) as in Table 1.

We computed a topographically derived thermal gradient using the heat load index (HLI) which combines slope, aspect and latitude values to estimate terrain-driven differences in solar heating (McCune & Keon 2002). To compute HLI, we first constructed a data matrix with three predictor variables for each plot (latitude, slope-inclination, and aspect). For this purpose, we implemented the non-parametric multiplicative regression method developed by McCune & Keon (2002) (equation 1). This index provides an estimate of the potential annual direct incident radiation at a specific location, offering insights into microclimatic diversity (Carroll *et al.* 2017).

$$HLI = \frac{1 - \cos\emptyset}{2} \tag{1}$$

Where θ represents the angle of incidence between the slope's normal vector and the direction of solar radiation, therefore data on latitude, slope-inclination, and aspect are crucial for HLI determination.

*Statistical analyses.* All variables were checked for normality assumptions; when necessary, we transformed variables by applying a logarithmic transformation (*e.g.,* heat load index; slope-terrain), square root transformation (*e.g.,* elevation), and Beers´ transformation (*e.g.,* azimuth) (Beers *et al.* 1966) for aspect. To avoid multicollinearity, we eliminated redundant variables by Principal Component Analysis (PCA) based on a correlation matrix with the complete set of 19 environmental variables (Table 1). PCA is a popular ordination method in community ecology employed for several purposes such as data reduction (Jolliffe 1972). We determined the meaningful principal components by the broken stick method (Jackson 1993). The broken stick method is a heuristic approach for identifying the number of significant principal components to retain in an analysis. It offers a statistical criterion to evaluate whether the variance explained by each component is meaningful or merely a result of random variation (Legendre & Legendre 2012). After performing PCA, we retained the following 16 variables: elevation, aspect, slope-terrain, catena, litter, crown competition, heat load index, pH, organic matter content, K, Ca, Cu, Fe, Mn, Zn, and Na.

We estimated diversity across the three ontogenetic stages by plot based on Hill´s numbers. Hill´s numbers are three metrics ($^{0}$D, $^{1}$D and $^{2}$D) that integrate species richness and relative abundances; the most relevant attribute of Hill´s numbers is that they do not consider sampling effort and are expressed in units of effective numbers of species; the exponent controls the sensitivity of the measure to species relative abundances as follows: species richness is represented by $^{0}$D, common species by $^{1}$D, and dominant species by $^{2}$D (Chao *et al.* 2014). To standardize sampling efforts across ontogenetic stages, we computed rarefaction and extrapolation curves. For this purpose, we examined abundance data, representing the total number of individuals sampled per species at 95 % confidence intervals using the bootstrapped method (Hsieh *et al.* 2016). We extended extrapolation up to a maximum sample size of 1,500 for the three ontogenetic stage to discover whether rarefaction-extrapolation overlapped. These analyses were performed in the *iNEXT* library. To test for differences in diversity among ontogenetic stages, we computed Kruskal-Wallis tests for every Hill´s number among the three stages, as our data did not meet assumptions of normality and homogeneity of variance (Vargha & Delaney 1998).

We used unconstrained non-metric multidimensional scaling (NMDS) (Kruskal 1964) to evaluate the vertical congruence of species composition among the three ontogenetic stages; NMDS display the position of sample units in a point cloud where distance between any two samples indicates their compositional dissimilarity. We used presence-absence data matrices of adult-trees, saplings, and seedlings and the Bray-Curtis dissimilarity index as a distance metric. This is a semi-metric measure of dissimilarity commonly used in continuous numerical or presence-absence data (Legendre & Legendre 2012). We used 200 random starting configurations and a maximum of 500 iterations with the *metaMDS* procedure. Then, we draw contour lines to demarcate the position of each ontogenetic stage spe-

**Table 1.** Environmental variables recorded in each 500 m$^2$ sample plot. Asterisk denote variables chosen through the PCA-*broken stick* method for use in Nonmetric Multidimensional Scaling analyses.

| Variable name | Acronym | Variable categories | Measured units and/or categories description | Description | Confidence interval (95%) for continuous data/ Absolute frequency for categorical data | CV (%) |
|---|---|---|---|---|---|---|
| 1. Elevation* | Elevation | | Meters above sea level | Measured at each plot with a Suunto altimeter. | 1275 ± 52 | 9.8 |
| 2. Slope-terrain* | Slope | | Percentage | Percentage of slope terrain inclination measured looking downslope. Log-transformed to make the data more symmetrical. This can help in reducing the influence of extreme slope values. | 24.6 ± 7.8 | 75.5 |
| 3. Azimuth* | Aspect | | Degrees (0 – 360°) | Azimuth of dominant direction of downward-facing slope-inclination. Log-transformed into a continuous variable (Beers *et al.* 1966). | 0.36 ± 0.19 | 122 |
| 4. Catena* | Cat | | | | | |
| | | Cat0 | Flat terrain | Slope position, ranked on a seven-point scale. | 0 | |
| | | Cat1 | Ridge slope | | 0 | |
| | | Cat2 | Upper slope | | 21 | |
| | | Cat3 | Middle slope | | 1 | |
| | | Cat4 | Lower slope | | 1 | |
| | | Cat5 | Base slope | | 1 | |
| | | Cat6 | Gully/ ditch | | 0 | |
| 5. Hear load index* | HLI | | Unitless | Heat load index from 0 (coolest) to 1 (warmest) (McCune and Keon, 2002). | 1.09 ± 0.06 | 12.6 |
| 6. Crown competition* | Crcp | | | | | |
| | | Crcp0 | No crown overlaps | Percentage of crown overlapping between neighboring trees within a plot, visually estimated. | 2 | |
| | | Crcp1 | Up to 15% crown overlap | | 15 | |
| | | Crcp2 | 15-30% crown overlap | | 5 | |
| | | Crcp3 | More than 30% crown overlap | | 2 | |
| 7. Humus | Hum | | Centimeter | Thickness of the decomposed plant material. | 3 ± 0. 8 | 19 |

| Variable name | Acronym | Variable categories | Measured units and/or categories description | Description | Confidence interval (95%) for continuous data/ Absolute frequency for categorical data | CV (%) |
|---|---|---|---|---|---|---|
| 8. Litter* | Ltr | | Centimeter | Litter thickness on the forest floor, generally composed of small twigs, acorns, leaves, flowers, fruits seeds and fine debris. | 5 ± 0.8 | 37 |
| 9. Organic matter content* | Omc | | Percentage | Determined in laboratory as percentage of loss ignition. | 2.7 ± 0.3 | 33.2 |
| 10. pH* | pH | | Logarithmic units (0 – 14) | Determined in laboratory. | 5.9 ± 0.3 | 10 |
| 11. Cation-Exchangeable Capacity | CEC | | Mmol $g^{-1}$ | Determined in laboratory. | 11.7± 0.6 | 7 |
| 12. Nitrogen | N | | mg/100g dry weight | Determined in laboratory. | 1270 ± 255 | 32 |
| 13. Calcium* | Ca | | mg/100g dry weight | Determined in laboratory. | 1680 ± 477 | 67 |
| 14. Potassium* | K | | mg/100g dry weight | Determined in laboratory. | 116 ± 45 | 92 |
| 15. Copper* | Cu | | mg/100g dry weight | Determined in laboratory. | 1.6 ± 02 | 33 |
| 16. Iron* | Fe | | mg/100g dry weight | Determined in laboratory. | 95 ± 21 | 53 |
| 17. Manganese* | Mn | | mg/100g dry weight | Determined in laboratory. | 36. 6 ± 8.3 | 54 |
| 18. Zinc* | Zn | | mg/100g dry weight | Determined in laboratory. | 1.6 ± 0.6 | 91 |
| 19. Sodium* | Na | | mg/100g dry weight | Determined in laboratory. | 20.3 ± 1.2 | 14 |

cies onto the NMDS ordination diagram. We applied permutational multivariate analysis of variance, via the *adonis* function (PERMANOVA) (Anderson & Walsh 2013), on the Bray-Curtis dissimilarity matrix to test for significant differences among ontogenetic stages on the basis of 999 permutations. PERMANOVA was used to test for differences in centroids among the groups, that is, shifts in the location of data within the multivariate space (Moreno *et al.* 2018). For these analyses, we used *vegan* (Oksanen *et al.* 2013) and *ggplot2* libraries.

To identify the most influential environmental variables that best correlate with patterns of floristic composition at each ontogenetic stage, we fitted significant environmental vectors to the NMDS with 999 permutations using the *envfit* function. Then, we used the *ordisurf* function to visualize the relationships of species composition of each stage in relation to changes in the most significant environmental gradients. *Ordisurf* uses generalized additive models (GAM) to fit surfaces of environmental variables in two dimensional ordinations using thin-plate splines as a smooth response across the NMDS ordination; for all these multivariate analyses, we used *vegan* library (Oksanen *et al.* 2013).

We also assessed the relative importance of environmental and geographical distance on compositional dissimilarity in the three ontogenetic stages, for this purpose we used the partial Mantel test based on Pearson´s product-moment correlation, using the *Euclidean* dissimilarity index, together with spatially constrained permutation procedure by means of Moran Spectral Randomization (MSR) (Crabot *et al.* 2019). The Mantel test is a statistical technique concerning distance-decay associations; it evaluates the correlation between two distance matrices calculated between pairs of samples, together with its significance through random permutations (Mantel 1967). Although the partial Mantel test can control spatial structures, it is unable to correct the spatial autocorrelation drawback presenting inflated type I error rates (Guillot & Rousset 2013). To deal with this drawback Wagner & Dray (2015) proposed an approach using MSR creating random replicates to maintain the original data´s spatial structures but disrupting their correlations.

To run the Mantel test, for each ontogenetic stage, we built three matrices: *i*.- a floristic matrix based on species abundances of all species recorded in the 24 sample plots; we used the *Sørensen* index as a measure of similarity (equation 2).

$$SS = \frac{2a}{(2a + b + c} \qquad (2)$$

where: *a* is a shared number of species or interactions between two sites, and *b* and c are number of species or interactions only occurring at one of the plots (Koleff *et al.* 2003); *ii.*- an environmental matrix with the 16 environmental variables previously mentioned. Subsequently, a Euclidean distance matrix was calculated between each pair of plots after all environmental variables were standardized (mean = 0, variance = 1) and *iii.*- a geographical matrix with the geographical linear separation between all pairs of plots using GPS location coordinates, for this aim we used the GPS plot location coordinates. The linear distance between every pair of plots ranged from 500 m to 3 km. While computing the partial Mantel test, all correlations were statistically tested at $P < 0.0001$ using a Monte Carlo permutation with 10,000 randomizations. We performed the partial Mantel test and the Moran's Spectral Randomization (MSR) Mantel test, which controls for spatial autocorrelation by randomizing residuals in a way that preserves spatial structure. Both tests were applied using principal coordinates with the *adespatial* and *vegan* libraries in R (R Core Team 2023).

## Results

*The environmental surroundings.* The study plots were characterized by a set of heterogeneous environmental variables; some examples follow: elevation presented a coefficient of variation (CV) of 9.8 % ranging from 1,030 to 1,460 m asl. and confidence intervals (CI) of 1,275 ± 52. Slope-terrain CV was 75.5 % ranging from 6 to 80% with CI of 24.6 ± 7.8. The CV for the heat load index (HLI) was 12.6 % ranging from 0.99 to 2.12 with CI of 1.09 ± 0.06. The highest coefficient of variation of all soil chemical elements corresponded to K (116 ± 45) and Zn (1.6 ± 0.6). The upper slope was the dominant catena (class = 2) and the most recurrent class for crown competition was class = 1, referred to crown overlapping up to 15 % (Table 1). Concerning the geographic spatial distribution of the plots, the farthest distance among plots was 3 km, and the closest was 100 m (Figure 1).

*Species composition, diversity, and abundance.* We recorded 1,832 individuals distributed in 784 adults (45 genera and 50 species), 275 saplings (19 genera and 21 species) and 773 seedlings (29 genera and 31 species). When examining species composition, species diversity and abundance across the three ontogenetic stages, notable differences emerged (*see* Figure S1 and Table S1for the complete species list). The most abundant species in terms of adult-trees density were: *Ardisia compressa* Kunth (260 individuals), *Quercus insignis* M. Martens & Galeotti (99), *Matudaea trinervia* Lundell (54), *Styrax radians* P.W.Fritsch (45) and *Inga vera* Willd. (36); they collectively accounted for 63.01 % of the total adult-tree density. For saplings, *Ardisia compressa* (174 individuals) was the most abundant species, followed by *Piper rosei* C.DC. (19), *Piper villiramulum* C. DC. (17), *Urera caracasana* (Jacq.) Gaudich.

ex Griseb. (13), and *Inga vera* (12); these species accounted for 85.45 % of the total saplings density. In the case of seedlings, *Ardisia compressa* (404 individuals) was also the prevailing species, followed by *Inga vera* (86), *Prunus cortapico* Kerber ex Koehne (79), *Cordia prunifolia* I.M.Johnst. (35), and *Styrax radians* (29) all together represented 81.88 % of the total seedlings' density.

Examining the most diverse ontogenetic stage (adult-trees), only 15 (constituting 30 % of the total) out of the 50 species documented in this stage, were present across the three ontogenetic stages, albeit with varying levels of abundance (Table S1). Adult-trees and seedlings exhibited the highest levels of diversity in terms of species richness, common species, and dominant species, as assessed by the three Hill's numbers ($^0$D, $^1$D and $^2$D). In contrast, saplings displayed the lowest diversity metrics among the three ontogenetic stages, characterized by the lowest number of individuals; the rarefaction curves showed asymptotes for $^1$D, $^2$D, and incompleteness for $^0$D (Table 2 and Fig S1). According to the Kruskal-Wallis test, there were significant differences among ontogenetic stages for $^0$D (H = 47.65, $P < 0.0001$), $^1$D (H = 43.44, $P < 0.0001$) and $^2$D (H = 38.34, $P < 0.0001$).

*Vertical congruence.* Results from NMDS (*Stress* = 0.195), using presence-absence data, clearly showed distinct separation of adult-trees, saplings, and seedlings along the first two axes of the ordination diagram (Figure 2). This implies significant vertical variations in species composition among the three ontogenetic stages. PERMANOVA confirmed statistically significant differences in species composition among the three ontogenetic stages ($F = 7.51$, $R^2 = 0.178$, $P = 0.001$).

*Environmental and geographical distance revealing patterns of floristic composition.* Mantel tests revealed that floristic compositional similarity between pair of plots was not significantly correlated with environmental distance for adult-trees (*rM (MSR-Mantel)* = 0.025, $P = 0.385$); saplings (*rM (MSR-Mantel)* = 0.031, $P = 0.36$) and seedlings (*rM (MSR-Mantel)* = - 0.068, $P = 0.686$); this arose even when the effect of the geographical distance was partialled out (for adult-trees *rM (MSR-Mantel)* = 0.034, $P = 0.348$; for saplings *rM (MSR-Mantel)* = 0.074, $P = 0.236$ and for seedlings *rM (MSR-Mantel)* = - 0.059, $P = 0.629$).

*Best environmental predictors.* Results of fitting linear vectors onto NMDS ordination revealed that only five out of 16 variables, were statistically significant. Elevation was statistically significant ($P < 0.0001$) for the three ontogenetic stages; litter was only significant for adult-trees ($P < 0.05$) and seedlings ($P < 0.01$). pH ($P < 0.05$) and Ca ($P < 0.05$) were statistically significant only for saplings; slope-terrain ($P < 0.05$) only for adult-trees (Table 3).

The fitted values derived from *Ordisurf* overlaying the three ontogenetic stages onto the elevation gradient revealed outstanding patterns. Adult-trees and seedlings species exhibited sparse distribution from 1,050 to 1,400 m asl. whereas saplings showed species between 1,100 to 1,350 m asl. Only three species: *Eugenia capuli* (Ecap), *Juglans major* (Jmaj) and *Zanthoxylum mollissimum* (Zmol) were present beyond this range (Figure 3A-C).

Our findings suggest that *Q. insignis* (Qins) thrive between 1,150 and 1,350 meters above sea level, exhibiting a statistically significant correlation with elevation across all ontogenetic stages. Seedlings and adult trees of this species coexist within the range of 1,300 to 1,350 m asl, while *Q. insignis* saplings are predominantly found below 1,150 m asl. (Figure 3A, C). A relatively similar elevation co-occurrence pattern between 1,300 - 1,350 m asl was observed for *S. hintonii* (Shin), *P. villiramulum* (Pvil), *O. virginiana* (Ovir), *A. compressa* (Acom), *M. trinervia* (Mtri), and *I. vera* (Iver). For saplings, only *A. compressa* (Acom) and *S. hintonii* (Shin) were recorded at this elevation (Figure 3B).

Sapling species demonstrated an association with pH values ranging from 5.2 to 6.6. Specifically, at lower pH levels, only *I. vera* (Iver) exhibited a relationship with values around 5.2, while at higher pH levels, *Q. insignis* (Qins), *A. revoluta* (Arev), *Crotalaria micans* (Cmic), and *Vernonia* (Ver) were linked to pH values surpassing 6.6 (Figure 4A). A similar pattern was observed with Ca (calcium) levels, where most saplings species were distributed in plots with Ca values ranging from 1,300 to 1,600 (mg kg-1) (Figure 4B).

**Table 2.** Confidence intervals (95%) for Hill numbers; species richness (0D), common species (1D), and dominant species (2D) for the three ontogenetic stages in *Quercus insignis*-dominated stands.

| | **Hill numbers** | | |
|---|---|---|---|
| **Ontogenetic stage** | **$^0$D** | **$^1$D** | **$^2$D** |
| Adult-trees (n = 784) | 8.87 ± 1.03 | 5.84 ± 0.76 | 4.41 ± 0.68 |
| Saplings (n = 275) | 2.16 ± 0.51 | 1.73 ± 0.36 | 1.55 ± 0.35 |
| Seedlings (n = 773) | 4.58 ± 0.83 | 2.90 ± 0.62 | 2.39 ± 056 |

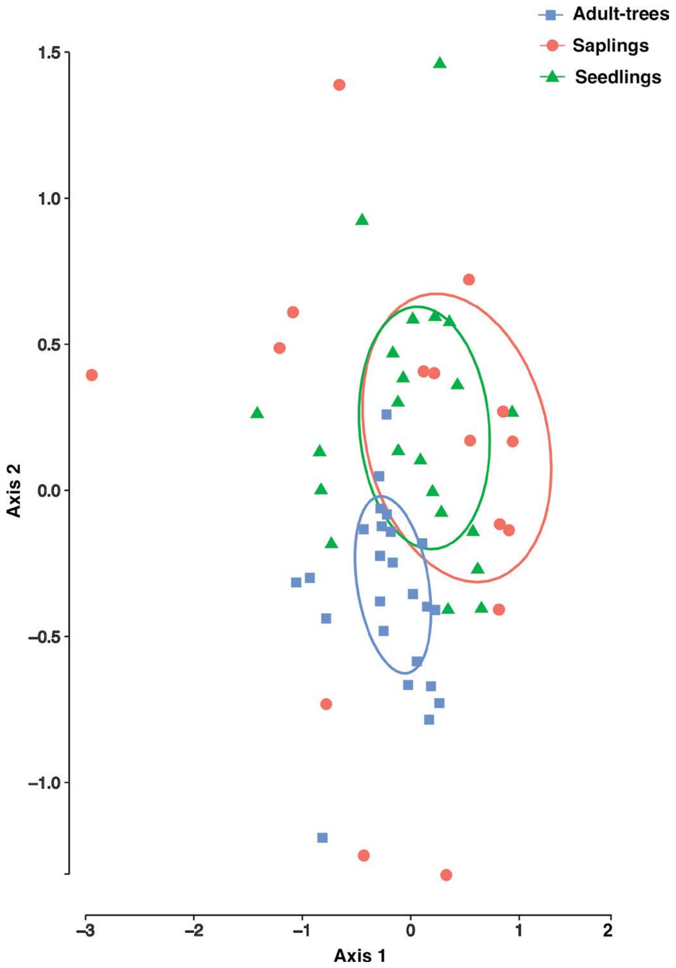

**Figure 2.** Two-dimensional nonmetric multidimensional scaling (NMDS) ordination (*Stress* = 0.195) showing the three ontogenetic stages based on presence-absence data. Adult-trees are denoted by blue squares, saplings by pink circles, and seedlings by green triangles. The different ellipses are 95 % confidence intervals around the centroids of each ontogenetic stage based in species composition. PERMANOVA was used to test for differences in centroids among groups.

An interesting finding emerged regarding the association between adult trees and litter, as well as between seedlings and litter (Figure 5A, B). In both instances, species were distributed across the entire range of litter depth values (from 2.5 to 6.5 cm).

The spatial distribution of adult-trees is notably influenced by slope terrain, with a significant contribution observed. Despite this, the distribution of adult-tree species appears relatively homogeneous across the entire sampled range of slope terrain. In the case of *Q. insignis*, its positioning was notable, occurring within the range of 20 - 25 degrees of slope inclination. However, for most species, a concentration was observed within the range of 15 - 35 degrees (Figure 6).

**Table 3.** Results of *Envfit* fitting linear vectors onto NMDS ordination. Crcp. = crown competition, HLI = heat load index, OMC = organic matter content, K = Potassium, Ca = Calcium, Cu = Copper, Fe = Iron, Mn = Manganese, Zn = zinc, Na = Sodium. Signif. codes: '***' 0.001 '**' 0.01 '*' 0.05 '. Number of permutations: 999.

| **Variable** | **Adult-trees** | | **Saplings** | | **Seedlings** | |
|---|---|---|---|---|---|---|
| | $r^2$ | **Pr(>r)** | $r^2$ | **Pr(>r)** | $r^2$ | **Pr(>r)** |
| Elevation | 0.4752 | 0.001*** | 0.4040 | 0.001*** | 0.4777 | 0.001*** |
| Aspect | 0.0021 | 0.973 | 0.2227 | 0.052 | 0.0188 | 0.824 |
| Slope-terrain | 0.2860 | 0.032* | 0.2669 | 0.059 | 0.0489 | 0.583 |
| Catena | 0.0888 | 0.351 | 0.0798 | 0.272 | 0.0460 | 0.637 |
| Litter | 0.2699 | 0.036* | 0.2420 | 0.055 | 0.4313 | 0.002** |
| Crcp | 0.0990 | 0.312 | 0.0941 | 0.310 | 0.0480 | 0.613 |
| HLI | 0.0677 | 0.456 | 0.1792 | 0.157 | 0.0072 | 0.939 |
| pH | 0.0156 | 0.851 | 0.2835 | 0.040* | 0.0412 | 0.655 |
| Omc | 0.0102 | 0.911 | 0.0520 | 0.572 | 0.0179 | 0.826 |
| K | 0.2446 | 0.051 | 0.0424 | 0.472 | 0.1541 | 0.175 |
| Ca | 0.0754 | 0.440 | 0.3272 | 0.015* | 0.0373 | 0.691 |
| Cu | 0.2497 | 0.2497 | 0.1949 | 0.105 | 0.0167 | 0.850 |
| Fe | 0.1352 | 0.238 | 0.0429 | 0.608 | 0.1113 | 0.323 |
| Mn | 0.0387 | 0.651 | 0.0094 | 0.916 | 0.1128 | 0.289 |
| Zn | 0.0002 | 0.998 | 0.2563 | 0.077 | 0.0095 | 0.909 |
| Na | 0.0815 | 0.379 | 0.3330 | 0.051 | 0.0327 | 0.714 |

## Discussion

*Patterns of species composition, species diversity and abundance.* Our results revealed that species composition, species diversity and absolute abundance differed among the three ontogenetic stages, with the highest values, in all cases, for adult-trees, followed by seedlings and finally saplings. The pattern of decreasing abundance from adult-trees to saplings is consistent with previous studies. This overarching pattern has been linked to several factors, such as variations in resource allocation, both intra- and interspecific competition, and environmental heterogeneity (Jevon *et al.* 2020, Jiang *et al.* 2022). However, our findings partially differ from other studies. For instance, Martínez *et al.* (2013) showed that seedling densities in a temperate forest have complex spatial associations with conspecific and heterospecific adults, with no clear patterns between adult trees and their conspecific seedlings densities. These authors indicate that *Ilex aquifolium* and *Crataegus monogyna* seedlings are positively associated with conspecific adults at small scales, suggesting favorable microenvironments, but *C. monogyna* shows negative associations at larger scales, reflecting competition. Patterns of seedling abundance are driven by adult tree distribution, seed production, climate, competition, and mast seeding events, underscoring the interplay of factors shaping recruitment dynamics. Differences between ontogenetic stages indicate that sites favorable for establishment and survival during early stages may become unsuitable for survival in later stages (Havrilla *et al.* 2021). Understanding how seedlings and saplings respond to microhabitat variations is crucial for determining microhabitat suitability for their establishment and its subsequent impact on canopy structure and species composition. Previous research suggests that species composition, species diversity and relative abundances can vary significantly based on factors like soil properties, topography, microclimate, and disturbance history. Our findings, which indicated that various environmental factors were statistically associated with each ontogenetic stage, are in accordance with the results of Seiwa (2007) who found that resource partitioning and species coexistence shape seedling and sapling dynamics by driving variations in growth rates and survival strategies based on resource availability. For example, *Betula platyphylla* var. *japonica*

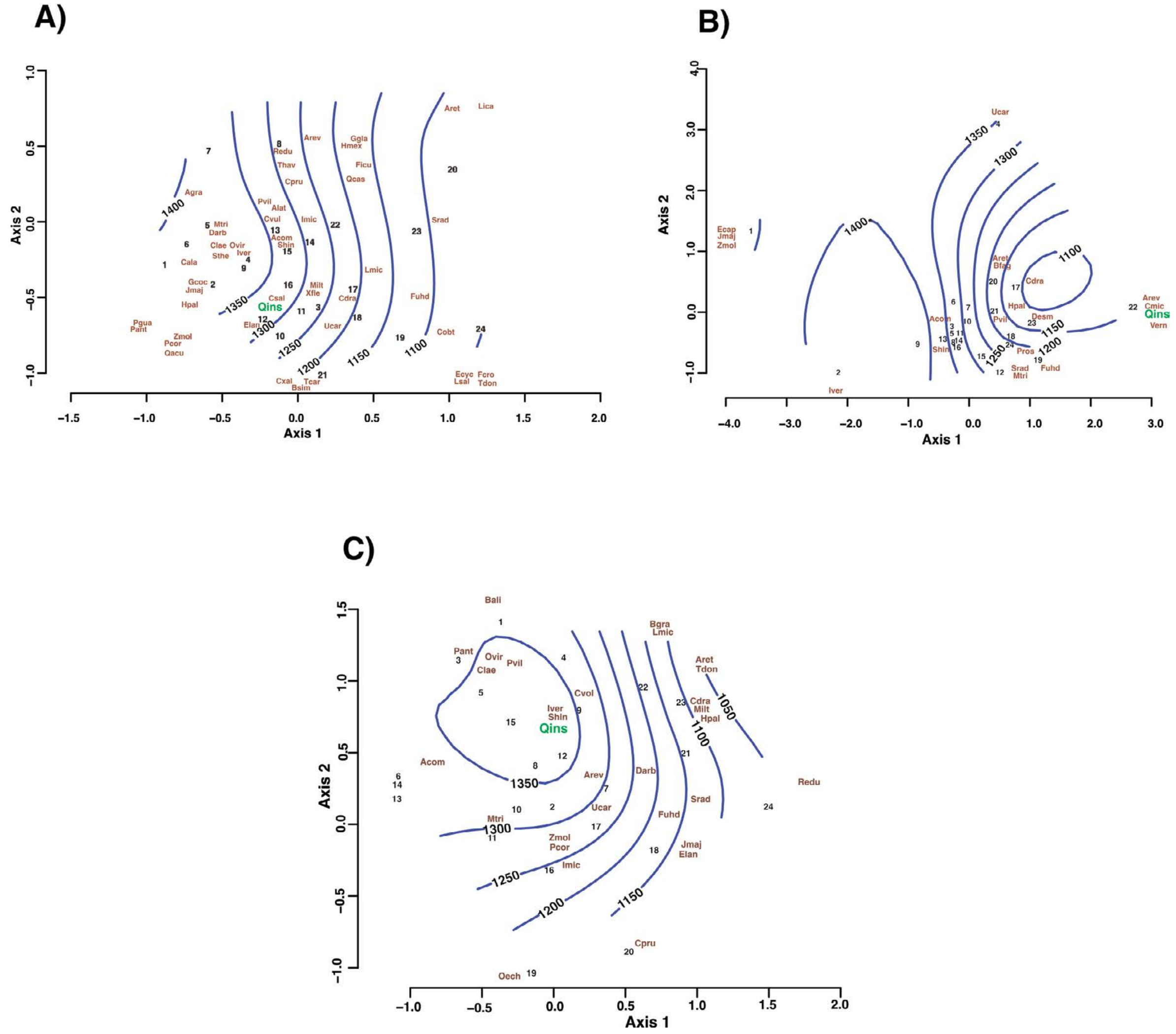

**Figure 3.** Two-dimensional nonmetric multidimensional scaling (NMDS) ordination showing the three ontogenetic stages with elevation. Contour isolines in the figure represent the relationship between species distribution and the elevation gradient; A) represent seedlings, B) saplings and C) adult-trees. Acronyms as in Table S1.

thrives in high-light environments, adapting to succeed in canopy gaps, while *Quercus mongolica* balances higher growth in light-rich areas with reduced survival, further impacting the canopy species composition. This underscores the importance of understanding how seedlings and saplings respond to microhabitat variations, as this is crucial for determining microhabitat suitability for their establishment and its subsequent impact on canopy structure and species composition.

In terms of species abundance, we found a nearly twofold difference between the absolute number of adult-trees and seedlings compared to saplings. This suggest that seed germination and subsequent seedling establishment may not be a limiting obstacle for forest regeneration in our study area, given the absolute number of seedlings recorded in our study plots. However, the transition from seedlings to saplings and likely from saplings to adult-trees may be more challenging due to various ecological and environmental factors, two primary challenges affect seedling survival are: (i) competition for resources, as seedlings struggle to obtain sufficient light, water, and nutrients in densely vegetated areas, with limited sunlight significantly hindering their growth (Chang-Yang *et al*. 2021); and (ii) biotic stressors, such as herbivory, and abiotic stressors, including moisture variability, temperature fluctuations, and physical disturbances, which further threaten their survival and render them more vulnerable than mature trees (Jing *et al*. 2024). While our data does not offer strong evidence to determine the reasons behind recording more seedlings than saplings and the associated disparity in absolute numbers, it is generally assumed that the seedling stage represents a critical bottleneck in the life cycle of trees (Chang-Yang *et al.* 2021, Yao *et al.* 2020). A lack of recruitment can hinder the development of forest stand structure by impeding the replacement of canopy species (Quinteros-Gómez *et al.* 2021). All else being equal, species undergoing more pronounced self-thinning among juvenile trees are likely to achieve lower adult-tree densities (Perea *et al.* 2021).

Although seedlings represent only a fraction of a tree species' full life span, those that survive this bottleneck can reveal essential characteristics of the juvenile and adult-trees populations (Chang-Yang *et al.* 2021). In our case, species abundances data suggest that such "bottleneck" from seedling to sapling stage was nearly 35 % (absolute number of seedlings and saplings was 773 and 275, respectively).

Thus, our results suggest such differences could be the result of a strong signal of habitat filtering, either biotic or abiotic or both, or even interspecific competition. Habitat filtering refers to the process through which species are selectively favored or excluded from a community based on their ability to adapt to specific abiotic (*e.g.,* soil properties, light availability, moisture levels, etc.) and biotic (*e.g.,* inter- or intraspecific competition, herbivory, pathogens, etc.) environmental conditions to the prevailing conditions (Li *et al.* 2018).

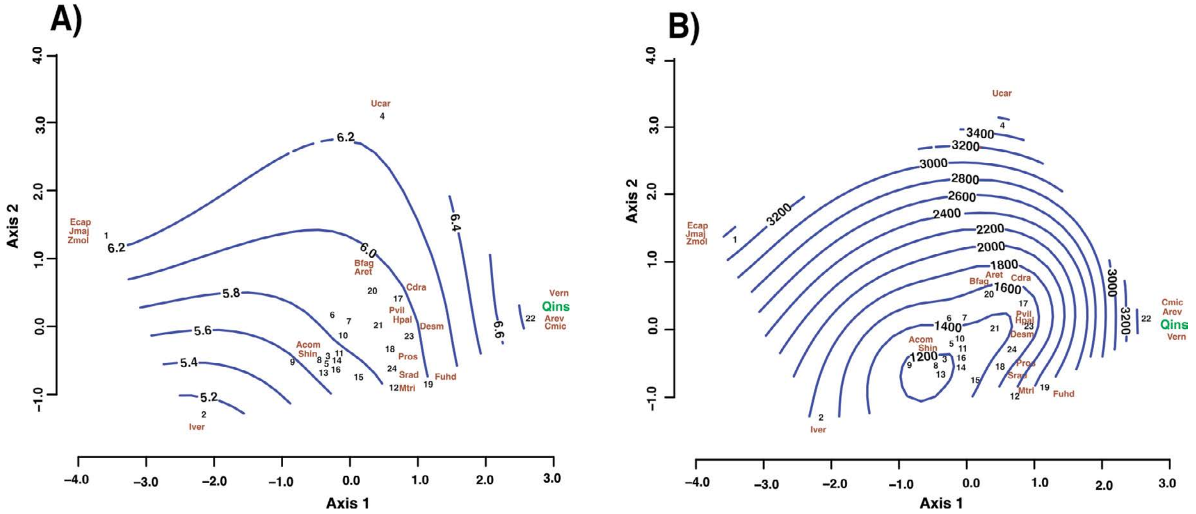

**Figure 4.** Two-dimensional nonmetric multidimensional scaling (NMDS) ordination showing saplings with A) pH and B) Ca. Contour isolines within the figure represent the relationship between species distribution and the pH and Ca gradient.

According to our results, we documented 275 saplings compared to 784 adult-trees. This discovery raises an intriguing question: what could account for the presence of a greater number of adult-trees than saplings in our study area? An alternative explanation may lie in a legacy effect (*sensu* Perea *et al*. 2021) that has left its mark on the current abundance and species composition of adult-trees. Consequently, a reduced number of saplings might persist over time, eventually integrating into the adult-trees stage as part of the successional processes. The legacy effect, according to Perea *at al.* (2021), highlights the lasting impact of seed dispersal, species interactions, and environmental conditions in shaping plant community structure and influencing species assembly across ontogenetic stages. Nevertheless, to enhance the persuasiveness of our inferences and extend them to our study area, it may be necessary to assess the importance of the legacy of seed dispersal concerning both intraspecific and interspecific spatial patterns across ontogenetic stages, as suggested by Perea *et al* (2021).

In a similar sequence of ideas, Kanagaraj *et al.* (2011) observed strong habitat structuring for juvenile trees while reproductive-sized trees showed weak habitat structuring. This was interpreted as a result of strong habitat filtering, acting upon trees at the transition from recruits to juveniles.

Furthermore, the sapling layer indeed represents a transitional stage in the life cycle of trees, characterized by relatively rapid growth and development. Unlike the adult tree layer, where individuals have already passed through this stage and exhibit a wide range of ages, saplings may progress through this phase more quickly as they grow into mature trees (Zhu *et al.* 2015). Therefore, the relatively shorter duration of individuals in the sapling layer may indeed influence density requirements.

It is plausible that lower densities of saplings may still be adequate for ensuring the replenishment of the canopy layer over time, given the faster turnover rate in the sapling stage (Kobe 1999). This suggests that the observed lower density of saplings may be a natural outcome of the dynamic processes occurring within this forest ecosystem.

*Is there a lack of floristic vertical congruence?* Results from NMDS and PERMANOVA confirmed our prediction concerning the lack of vertical species congruence among the three ontogenetic stages. However, besides the spatial environmental heterogeneity in our study area, it might be rather expected to find lack of floristic vertical congruence in the three ontogenetic stages, given the fact that we found the contrasting differences in species absolute abundance among the three ontogenetic stages. Thus, the fact that we found clear differences in abundance and species composition, between adult-trees and saplings and between seedlings and saplings, could be explained by one of two likely alternatives: one, in terms of failure of species recruitment processes, mainly at sapling stage, as we previously discussed in this paper and two, in terms of either niche differentiation or neutral processes among species with similar resource use (Li *et al*. 2017).

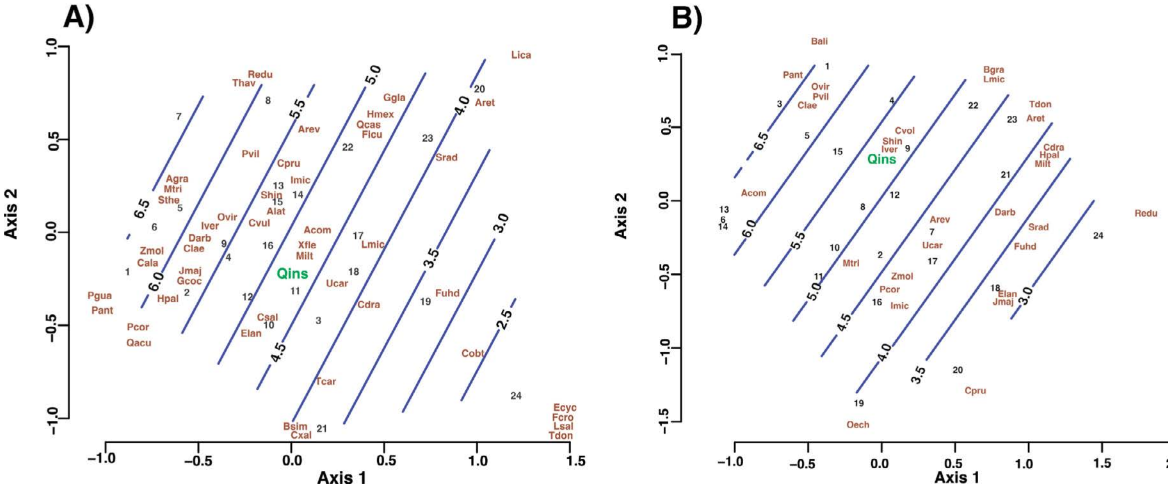

**Figure 5.** Two-dimensional nonmetric multidimensional scaling (NMDS) ordination showing the distribution of adult-trees A) and seedlings B) with litter. Isolines within the figure depict the relationship between species distribution and the litter gradient.

Smith *et al.* (2021) reports a lack of congruence between ground-layer versus epiphyte-layer lichen strata in boreal forests. Such lack of congruence was primarily attributed to the utilization of distinct field-sampling methods for each stratum. In our study, we used sampling plots, nested within each other, for both adult-trees and saplings, and we tested differences among ontogenetic stages with rarefaction-extrapolation curve estimations. For seedlings, samplings units were placed at the center of the overall plot, ensuring consistency and minimizing any incongruences associated with varying sampling methods.

The lack of significant correlations between geographic distance and environmental distance in Mantel tests across all three ontogenetic stages suggests that the plots do not exhibit environmental similarities, particularly those in close proximity. Thus, the absence of an association between species composition and geographic separation of the plots may not be attributed to the effect of environmental heterogeneity in our study area. Instead, other factors such as seed dispersal or neutral processes are likely influencing the observed floristic patterns. The pure spatial component, this is the portion of variation in species composition that cannot be explained by environmental factors and attributed solely to spatial processes, could be interpreted as evidence of neutral processes such as dispersal limitation (Kasel *et al.* 2017) which is commonly described as the restriction of species movement between sites. This can lead to differences in species composition between sites. These findings suggest that neither the environmental nor the geographical distance, accounted for the patterns in species composition between pair of plots. Results indicate that the species composition of the three ontogenetic stages was not spatially structured.

*Environmental fit.* The environmental predictors that most effectively accounted for the variation in species composition varied across each of the three ontogenetic stages, except elevation which consistently emerged as a significant factor across all three stages, indicating a shared response to elevation among the different ontogenetic stages.

Elevational gradients play a crucial role in influencing the distribution of species during the seedling-sapling stages by reshaping environmental variables, leading to gradients in climate and resource availability (Wang *et al.* 2017). Despite elevation being identified as a statistically significant environmental variable across all three ontogenetic stages, we posit that it could potentially encompass finer-scale variables measured in this study, such as HLI, slope terrain,

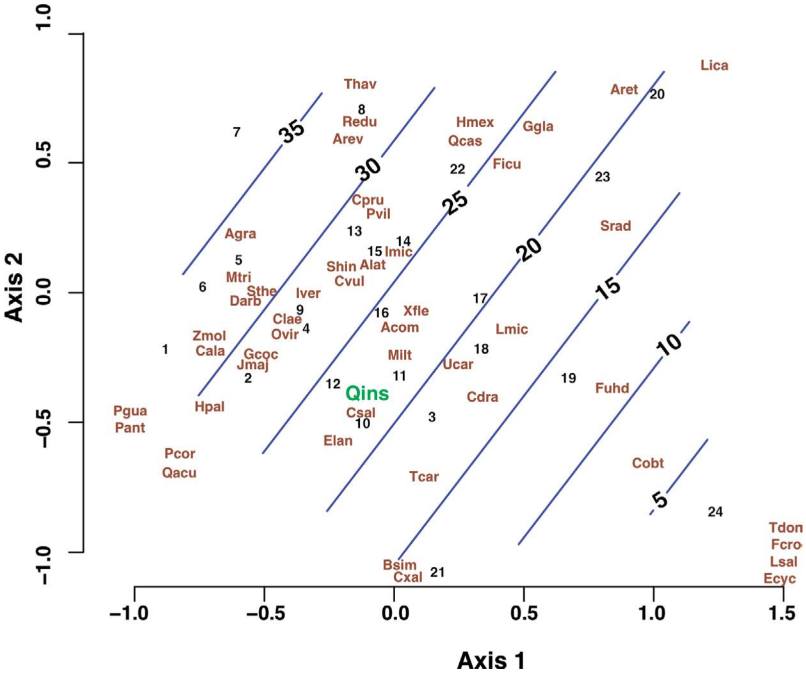

**Figure 6.** Two-dimensional nonmetric multidimensional scaling (NMDS) ordination, showing the distribution of the adult-trees with respect to Slope-terrain. Contour isolines within the figure depict the relationship between species distribution and the Slope-terrain gradient.

catena, etc. These last environmental variables may be obscured by the elevation gradient in our study area. Recent research has emphasized the association between spatial changes in species richness and thermal energy, as well as environmental heterogeneity. However, the specific roles of these factors in cross-taxon congruence remain relatively unexplored (Ramos *et al.* 2021).

The significance of slope terrain exclusively for adult-trees may elucidate this fine-scale effect. The interplay of moisture and optimal temperature facilitates continuous leaf litter decomposition, leading to enriched soil nutrients. Research indicates that warm and moist conditions stimulate decomposer activity, thereby enhancing decomposition rates (Canessa *et al*. 2021). Previous studies have documented correlations between soil nutrients and terrain slope, highlighting the connection between elevation and local environmental conditions (Costa *et al.* 2005).

Our findings revealed that, among the various soil parameters, only pH and calcium (Ca) content were statistically significant for saplings. In species-rich mixed forests situated on nutrient-poor parent material, litter, pH, and Ca assume crucial roles. Calcium is frequently identified as one of the most influential exchangeable cations. However, excessive calcium may outcompete other soil nutrients, such as magnesium, potassium, and phosphorus, thereby reducing their availability and accessibility to plants. (Tilk *et al.* 2017). Our results suggest that pH and Ca collectively constitute the edaphic-niche for seedlings and saplings, exerting a robust structuring effect on the distribution of tree species in tropical forests. Conversely, lower pH values lead to diminished availability of Ca (John *et al.* 2007).

We identified statistically significant differences between adult-trees and litter, as well as between seedlings and litter. The well-established understanding that litter accumulation can influence the growth and survival of seedlings supports these results. Recent studies highlight the crucial role of canopy trees in regulating the type and quantity of litter on the forest floor (Jean *et al.* 2020). Moreover, a strong correlation has been observed between soil moisture, canopy composition, and litter accumulation, which directly affects the seedbank and further influences the success of forest regeneration (Daněk *et al.* 2022). Consequently, the impact of litter on seedling establishment and survival is likely to vary, contingent on canopy species composition, with broadleaf litter potentially hindering seedling establishment more than needle litter cover (Wang *et al.* 2022). Moreover, these effects may be influenced by micro-physiographic conditions.

Forest managers must evaluate the association between litter type and accumulation concerning seedling establishment. It is crucial to recognize that litter cover, while capable of fostering positive impacts on seedling establishment and growth, can also exert adverse effects such as physical barrier to seedling emergence, this is particularly problematic for small-seeded species or allelopathic effects, substances may inhibit seed germination and seedling growth (Loydi *et al.* 2013). The intricate interplay between these factors may consequently influence the composition and structure of forest ecosystems. Recent investigations suggest that litter can limit the transition from seed to seedling but may facilitate plant development after seedling establishment. Additionally, litter has a minimal impact on the vegetation community, with the exception of its influence on species richness (Zhang *et al.* 2022).

We distinguished significant variation in composition, diversity and absolute abundance across the three ontogenetic stages, with adult-trees exhibiting the highest values, followed by seedlings and saplings. The lack of vertical species congruence among these stages suggests a potential influence of habitat filtering. Our data indicates that these patterns may be attributed to distinct responses to fine-scale environmental factors, such as litter, soil pH, and Ca, with saplings being the least abundant ontogenetic stage and particularly sensitive to these variables. We found a twofold difference in the number of adult trees and seedlings compared to saplings, suggesting challenges in transitioning from seedlings to saplings. The lack of floristic vertical congruence among stages, confirmed by NMDS and PERMANOVA, indicates potential recruitment failures or niche differentiation.

A comprehensive understanding of the dynamics governing species composition and abundance across ontogenetic stages is essential, not only aid in recognizing vulnerable life stages but also guides the formulation of strategies to enhance resilience and promote regeneration within forest ecosystems.

## Supplementary material

Supplemental data for this article can be accessed here: https://doi.org/10.17129/botsci.3634

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