

Original Articles

Environmental factors shaping structure and their limited influence on floristic composition in tropical montane forests of southern Ecuador

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Abstract

Tropical montane forests harbor high biodiversity and develop under heterogeneous topographic, climatic, and soil conditions. However, the influence of these environmental factors on their ecological dynamics remains poorly understood. This study was conducted to provide baseline information on the mechanisms underlying biodiversity in this complex mountain landscape. Specifically, we aimed to: (i) determine the floristic composition and forest structure of these ecosystems, and (ii) evaluate the effect of environmental gradients on species floristic composition and structural attributes in southern Ecuador. Across six localities, the tree community was sampled (composition, basal area, density, diameter, and maximum height) and edaphic, climatic, and topographic properties were characterized at the subplot level. Four discrete floristic groups and marked structural differences were identified among the evaluated forests. Environmental factors (mainly elevation and pH) explained a minor fraction of the floristic variation. In contrast, slope, elevation (associated with precipitation, temperature, and evapotranspiration gradients), and soil properties (depth, CEC, texture, and acidity) significantly modulated forest structure. We conclude that environmental factors determine density, biomass, and canopy height in these ecosystems. However, their weak influence on floristic composition suggests that community assembly is primarily mediated by biotic interactions or stochastic processes.

Keywords: Andes, ecological theory, conditioning factors, community assembly, conservation.

Introduction

Tropical montane forests are among the most diverse ecosystems on Earth, characterized by high levels of endemism and covering approximately 305 million hectares globally (FAO & UNEP, 2020; Salinas et al., 2021). Currently, these ecosystems are severely threatened by anthropogenic deforestation and fragmentation, which are occurring at a faster rate than in tropical lowlands (Cuesta et al., 2009; Hamilton, 1995). Despite this, the Ecuadorian Andes still harbor extraordinary species richness, positioning them as global biodiversity hotspots (Myers et al., 2000; Richter, 2008).

Beyond their biogeographical value, these ecosystems serve as crucial settings for testing community assembly theories, which debate the relative importance of deterministic and stochastic processes (Chase & Myers, 2011). On the one hand, ecological niche theory and environmental variables maintain that abiotic gradients select for specific functional traits, thus restricting species presence based on local climatic and edaphic limitations (Keddy, 1992; Kraft et al., 2015). On the other hand, the unified neutral theory of biodiversity postulates that floristic composition in hyperdiverse systems is largely determined by ecological drift, demographic stochasticity, and dispersal limitation (Chave, 2004; Rosindell et al., 2011). Understanding how environmental filters interact with stochastic dynamics remains a fundamental challenge in Andean ecosystems, where rugged topography amplifies both spatial isolation and niche differentiation.

Despite the vast biodiversity of the Andean flank, comprehensive ecological assessments in Ecuadorian montane forests have historically remained fragmented (Grubb & Whitmore, 1966; Armenteras et al., 2017). At a regional scale, classical and contemporary literature has predominantly focused on macroecological elevational gradients, consistently documenting a monotonic decline in species richness, canopy height, and primary productivity with increasing elevation (Gentry, 1988; Homeier et al., 2010; Jørgensen et al., 2011). This overarching trend, widely reported across both the Andes and other global tropical montane ecosystems (Kappelle & Brown, 2001; Culmsee et al., 2011), establishes altitude as a primary proxy for floristic turnover due to its direct control over temperature and moisture regimes (Aiba & Kitayama, 1992; Báez et al., 2015).

Nevertheless, this macroclimatic focus often oversimplifies community assembly mechanisms at a local scale. Comparable studies throughout Neotropics demonstrate that micro-scale variations in topography and edaphic properties operate as environmental mosaics that frequently mask or distort the linear effects of altitude (Duivenvoorden, 1995; Culmsee & Leuschner, 2013). In geologically complex environments, such as karst and sandstone formations

between 1,400 and 2,700 m a.s.l. (Becking, 2004), factors such as slope dynamics, soil depth, and nutrient availability impose rigorous mechanical and chemical constraints on plant establishment (Beck et al., 2008; Merckx et al., 2015). Consequently, the extraordinary tree species wealth in Andean montane forests cannot be attributed solely to thermal lapse rates; rather, it is heavily driven by small-scale edaphic-topographic heterogeneity that multiplies available ecological niches (Homeier et al., 2010). This multifactorial interaction underscores the critical need to decouple climate from local soil constraints to effectively identify the true drivers of forest structure and floristic composition.

To contribute to the understanding of ecological patterns in the Andean-Amazonian region, this research analyzes the environmental determinants of forest structure and floristic composition in six distinct areas of southern Ecuador. The study was conducted to generate baseline information on the mechanisms that support biodiversity in this complex mountainous landscape. To this end, the specific objectives were: (i) to determine the floristic composition and forest structure of these ecosystems, and (ii) to evaluate the effect of environmental gradients on species composition and forest structure.

Material and methods

Study Area and Sampling Design. The study was conducted across six 1-ha permanent plots distributed around latitude 04 °S within the Zamora Chinchipe province in southern Ecuador, with four plots established on the eastern flank of the Cordillera Real de los Andes and two in the upper valley of the Nangaritza River within the Cordillera del Cóndor (Figure 1). To ensure landscape scale representativeness and capture the complex environmental heterogeneity of the northern Andean flank, the sampling design explicitly encompassed a wide elevational gradient (900 to 2,400 m a.s.l.) and four contrasting geological substrates that typify the region's primary soil lineages; these included forest communities on Andean Tepuis (Nangaritza Tepui at 1,120 m and Nangaritza Río at 900 m a.s.l.) situated over hyper acidic, oligotrophic quartzitic sandstones of the Hollín Formation (Cretaceous), metamorphic formations (San Francisco at 2,100 m a.s.l.) over weathered micaceous schists, Tertiary volcanic substrates (Tapichalaca at 2,400 m and Numbala at 1,200 m a.s.l.), and recent alluvial or colluvial sediments (Padmi at 900 m a.s.l.) in the Zamora River valley. In each of these study areas, a square 100 m x 100 m plot was delimited and further subdivided into a regular grid of 25 subplots 20 m x 20 m (400 m²) following standardized protocols for tropical forest dynamics (Condit, 1998), which effectively captured local-scale topographic and edaphic

variations within each macro-site. Within this census design, all woody individuals with a diameter at breast height (DBH ≥ 10 cm) were systematically tagged, mapped, measured, and identified in their entirety, corroborating the taxonomy of critical specimens through comparison at the LOJA herbarium of the Universidad Nacional de Loja, in accordance with the Angiosperm Phylogeny Group classification system (APG IV, 2016) and the MOBOT TROPICOS nomenclatural database.

Environmental Characterization and Explicit Predictor Selection. For each of the 150 subplots (25 subplots 6 plots), a comprehensive set of climatic, edaphic, and topographic variables was compiled, with edaphic characterization performed via the systematic collection of topsoil composite samples (0-20 cm depth) across five strategic core points (the four vertices and the center) within each 1-ha plot. The resulting chemical and textural analyses were executed

in the laboratories of the Universidad Nacional de Loja following standardized INIAP protocols, quantifying organic matter via the Walkley-Black volumetric method, pH via potentiometry in a 1:2.5 soil-to-water ratio, Cation Exchange Capacity (CEC) via the formaldehyde method, total nitrogen through the high-pH indophenol blue reaction, and macro and micronutrient concentrations (K^+ , Mg^{2+} , Ca^{2+} , Fe^{3+} , Al^{3+}) via Olsen solution extraction followed by atomic absorption spectrometry. Concurrently, local topography was captured by measuring slope (%) along the subplot face parallel to the incline using a clinometer, while altitude (m a.s.l.) was recorded with an altimeter at its four vertices to generate a true subplot level average value; simultaneously, 19 macroclimatic bioclimatic variables were extracted from the WorldClim global database at a spatial resolution of 30 arc seconds (≈ 1 km²) using the central geographic coordinates of each macro site. To identify and eliminate multicollinearity, thereby preventing over parameterization in downstream multivariate

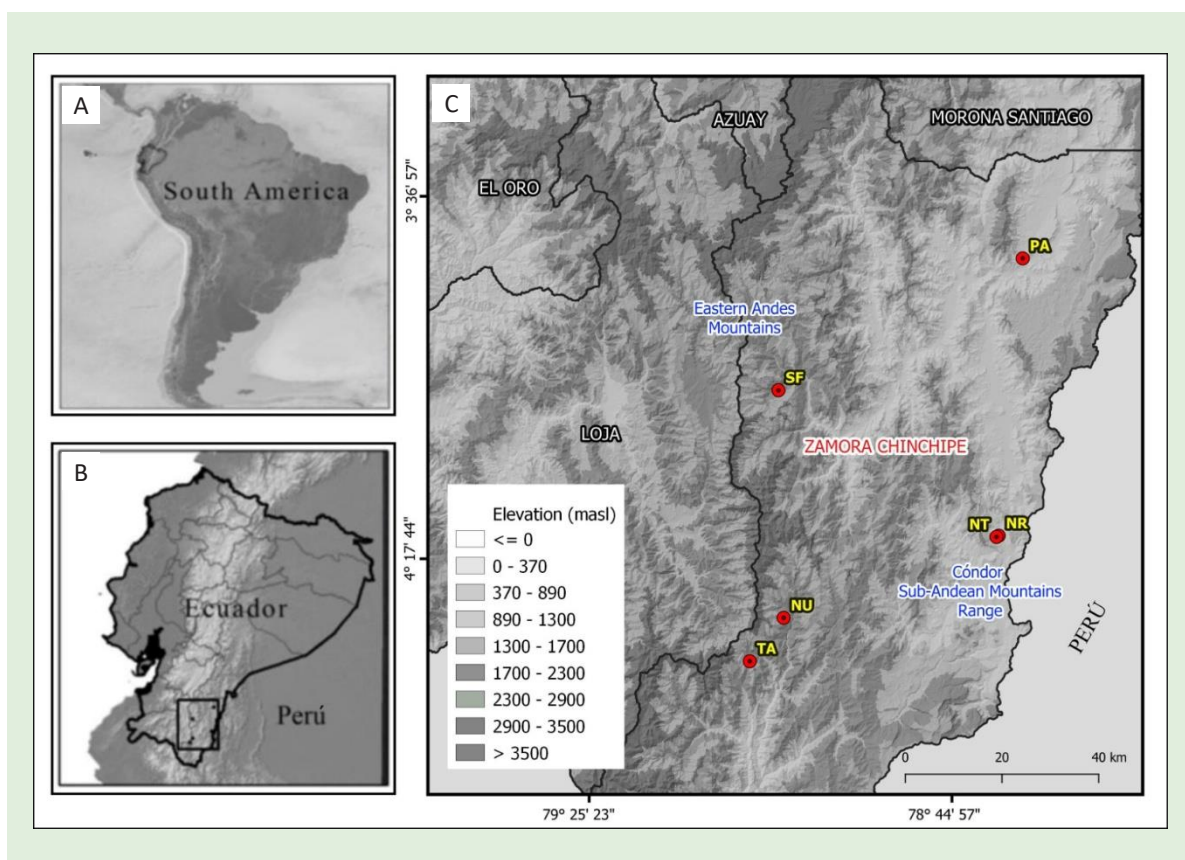


Figure 1. Geographic positioning of the six study areas, distributed in the tropical montane forests, province of Zamora Chinchipe, southern Ecuador: A) Location of Ecuador in South America; B) Location of study sites in the southern region of Ecuador; C) Location of each study site. SF: San Francisco (Reserva Biologica Estación San Francisco); TA: Tapichalaca (Tapichalaca Nature Reserve); NU: Numbala (Reserva Ecologica Numbala); PA: Padmi (Estación Experimental El Padmi); NR: Nangaritza Rio and NT: Nangaritza Tepuy (both in the Area de Conservación de la Asociación de Trabajadores Autónomos San Miguel de las Orquídeas).

models, a rigorous predictor selection protocol was applied based on a Spearman correlation matrix ($r > 0.7$ $P < 0.05$), under which a climatic topographic decoupling was executed because WorldClim variables exhibited extreme collinearity with altitude ($r > 0.85$). Given that the 1 km² resolution of this global database is insufficient to resolve the steep microclimatic variations typical of rugged Andean terrain, these macroclimatic variables were excluded, retaining altitude as a robust, integrative proxy for temperature lapse rates and atmospheric moisture regimes (Körner, 2007). Likewise, edaphic redundancy filtering was applied due to a strong absolute inverse correlation detected between the clay and sand textural fractions ($r = -0.94$), leading to the exclusion of sand content and the retention of clay as a surrogate indicator for soil water holding capacity (Schawe et al., 2010); consequently, only seven non-collinear and ecologically relevant environmental predictors were retained for all subsequent statistical modeling analyses: soil depth (cm), pH, clay content (%), cation exchange capacity (CEC, cmol_c kg⁻¹), altitude (m a.s.l.), slope (%), and organic matter content (%).

Floristic Composition and Deterministic Assembly. Taxonomic composition and the delimitation of discrete forest types under deterministic processes were evaluated using an Indicator Species Analysis (ISA; Dufrêne & Legendre, 1997) via the *indicspecies* package. Forest types were categorized into Floristic Groups (FG) comprising species with a high Indicator Value (IndVal > 0.70 ; $P < 0.05$). To determine environmental effects on species composition, a Canonical Correspondence Analysis (CCA) was applied to the abundance matrix of 150 subplots. Soil data (1-ha scale) were uniformly assigned to their corresponding subplots under the assumption of geological homogeneity at that scale. The multivariate inferential framework was validated using non-parametric permutation tests (999 permutations) for constrained ordinations, testing the global significance of the CCA, its individual axes, and the marginal effect of each predictor. Significance testing strictly followed this biostatistical framework (Oksanen et al., 2019) using the *vegan* package in R.

Community Structure and Environmental Drivers. To evaluate forest structure in relation to environmental factors, four response variables were calculated per subplot: basal area, stem density, maximum DBH, and maximum height. Relationships with the seven environmental predictors were modeled using Ordinary Least Squares (OLS) Multiple Linear Regressions. Models were optimized via stepwise backward elimination based on the Akaike Information Criterion (AIC). Model assumptions (homoscedasticity, normality of residuals, and the absence of influential outliers) were rigorously verified using residual diagnostic plots (Quinn & Keough, 2002). To address shared variance

among predictors and quantify the independent contribution of each explanatory variable, a Hierarchical Variance Partitioning Analysis was performed using the *hier.part* package. All statistical analyses were conducted in R software v4.3.2.

To represent forest structure and species composition across the study sites, profile diagrams were adapted from the vegetation profiles of Yaguana (2020). These diagrams utilized a representative 100 X 10 m belt centered within each plot, integrating field data, topographic slopes, and empirical observations to elucidate temporal dynamics in the montane forests of southern Ecuador. Visual refinements were subsequently performed using Gemini (Google) to depict specific environmental gradients such as soil depth, moisture, altitude, and canopy cover while strictly preserving the integrity of the collected structural data.

Results

Floristic composition and indicator species. Floristic composition analysis revealed marked heterogeneity and high species turnover (β -diversity) among the evaluated sites. Each of the six plots exhibits a highly distinct taxonomic identity with minimal species overlap. Conversely, a notable homogeneity was observed at the generic level, suggesting a shared evolutionary history coupled with intensive local speciation or selective processes. As a prominent result of this structural configuration, key taxa were identified as significant indicator species of specific ecological and edaphic conditions. In the Numbala plot, for instance, the unusual abundance of the gymnosperms *Retrophyllum rospigliosii* and *Pectinopitys harmsiana* (Podocarpaceae) stands out as an atypical phenomenon for Andean forests, where this group generally exhibits significantly low densities. Furthermore, ecological connectivity and floristic flow between specific ecosystems are evidenced by the shared presence of *Chrysophyllum sanguinolentum* (between Nangaritza Tepuy and Nangaritza Río) and *Graffenrieda emarginata* (between Nangaritza Tepuy and San Francisco). Likewise, this study highlights the indicator value of several taxa with highly restricted or endemic geographical and ecological distributions. Species such as *Dacryodes uruts-kunchae* and *Pagamea dudleyi* act as strict indicators of sandstone formations in the Cordillera del Cóndor and other Andean tepuis of southeastern Ecuador and eastern Peru. An exceptional case of ecological disjunction is represented by *Jacaranda densicoma* in the Nangaritza Tepuy plot, a sandstone-plateau indicator taxon that floristically links this region to the Guiana Shield across a geographical gap of over 2,000 km. Additionally, *Humiria balsamifera* stands out as a critical indicator of white-sand habitats, representing the only record of this species within Ecuadorian territory. Finally,

local endemism as a trait of habitat specificity is confirmed by *Sciodaphyllum ferrugineum*, a diagnostic and common element of the montane forest in the San Francisco Reserve, and by the stilt root palm *Iriartea deltoidea* in the Padmi plot, which functions as an indicator species of the upper altitudinal limit for tree populations of the western lowland Amazon.

Influence of environmental factors on floristic composition. The Canonical Correspondence Analysis (CCA) demonstrated that floristic composition in the studied tropical montane forests is strongly modulated by a complex environmental gradient, wherein altitude acts as the primary macro-explanatory driver, co-assisted by local edaphic properties. The model accounted for 16% of the total cumulative variance across the first five axes ($F = 3.80$; $P = 0.001$; Figure 2), revealing a significant floristic segregation that clearly delineates four environmentally and spatially distinct floristic

groups (FG1–FG4). These groups are further nested into two major vegetational typologies: Sub-Andean Forests (FG1 and FG2) and Andean Forests (FG3 and FG4).

Species turnover (β -diversity) and structural shifts among these groups responded distinctly to edaphic and topographic gradients segregated by axes:

- CCA Axis 1 was structured by an edaphic gradient of fertility and texture ($P = 0.001$). Toward the positive end, Sub-Andean Forests (sites PA, NR, and NT) exhibited a robust affinity for higher soil pH, clay content, and cation exchange capacity (CEC). However, the nature of the geological substrate induced a sharp internal bifurcation: FG1 (sites NR and NT; 900–1,100 m a.s.l.) consolidated as a community strictly adapted to the oligotrophic conditions

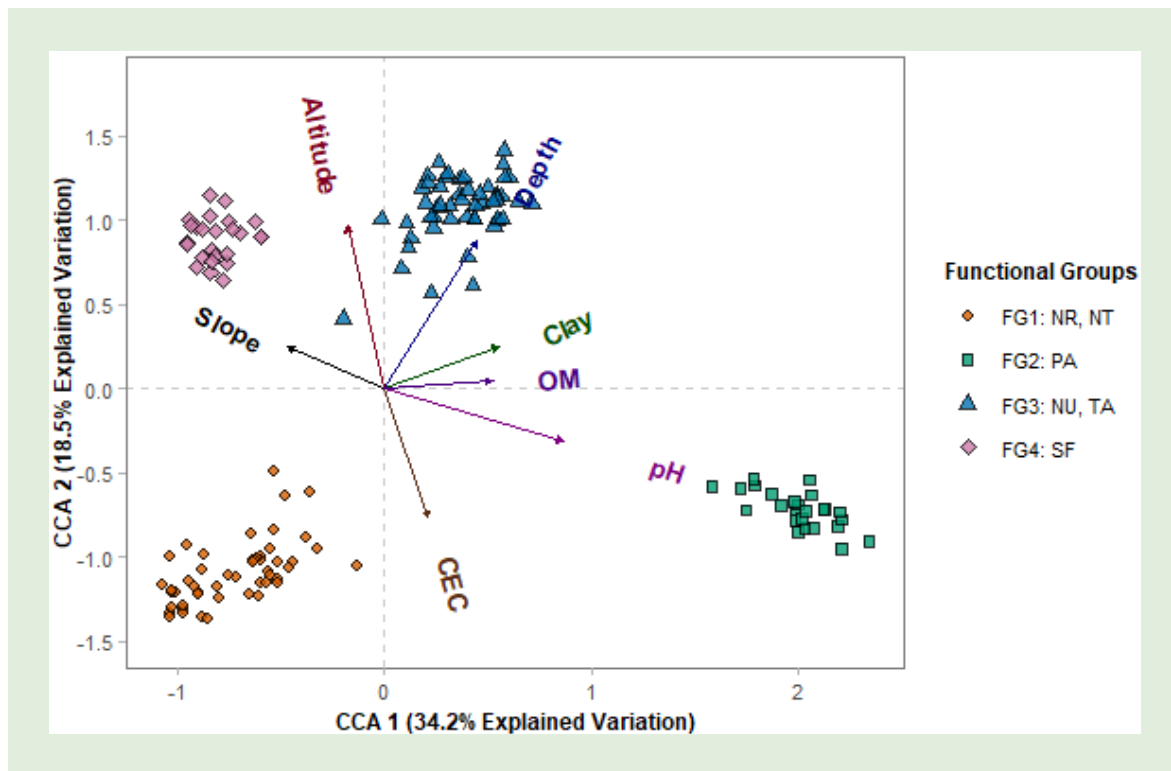


Figure 2. Canonical Correspondence Analysis (ACC) of factors influencing species distribution (all species included in the analysis) among montane tropical forests of southern Ecuador. The group of Sub-Andean Rainforest comprises FG1 formed by Nangaritza Rio and Nangaritza Tepuy (NR-NT orange diamond), FG2 formed by Padmi forest (PA, green square). The Andean Rainforest, include FG3 formed by Numbala and Tapichalaca (NU-TA blue triangle) and FG4 formed by San Francisco Forest (SF pink diamond). The factors indicated with black arrows showed a significant correlation ($P < 0.05$) with the floristic composition of the sampling units. The gray colored arrow represents a non-significant influence of the factor on the community composition. Abbreviations for the factors studied: clayey soil texture (Clay); elevation (Altitude); soil depth (Depth); organic matter (OM); soil acidity (pH); cation exchange capacity (CEC); and slope (Slope).

of highly acidic, sandy soils, whereas FG2 (site PA; lower altitude) differentiated by colonizing less acidic, clay-dominated substrates.

- CCA Axis 2 reflected a trade off between the altitudinal gradient and physical substrate constraints ($P = 0.001$). This axis governed the distribution of Andean Forests (FG3 and FG4; sites NU, TA, and SF), which displayed an inverse relationship with soil depth and fertility, but a positive correlation with steep slopes and high elevations (2,100–2,400 m a.s.l.). Floristic divergence within this altitudinal belt was driven by local geology: FG3 (sites NU and TA) is restricted to tertiary volcanic substrates, whereas FG4 (site SF; ~2,100 m a.s.l.) responds exclusively to metamorphic mica-schist substrates.

The diagnostic value of this environmental segregation was validated by the indicator species analysis, which identified 24 key taxa with high niche specificity for the discrimination of the four groups (Table 1). The asymmetrical distribution of these species reflects distinct structural responses of the vegetation to their respective ecological niches: FG4 exhibited the highest floristic specialization with 11 indicator species, followed by FG1 (7 species) and FG2 (4 species), whereas the rigorous conditions of the volcanic substrate in FG3 supported only 2 indicator species.

Influence of environmental factors on community structure. Multiple regression analysis (Table 2) indicated that between 29% and 81% of the variation in the structure of tropical montane forests in southern Ecuador can be explained by combinations of environmental variables. The clay content, the CEC and the slope have a negative correlation with basal area. The pH and altitude positively influenced this variable. The variable with the greatest independent effect on the basal area was CEC (38%). Density was influenced by the combination of clay content in the soil (positive effect), pH (negative), organic matter (positive effect), altitude (negative) and slope (negative). Of this variation, 53% were associated with the organic matter content. The height of the tallest trees was negatively associated with the clay content, the cation exchange capacity and the organic matter content in the soil. Additionally, in plots with higher pH and at higher altitudes, trees tend to be tall. Of the variation in the maximum height of the trees, 28% was explained by organic matter, 22% by pH and 20% by CEC. The DBH of the largest individuals in the forests was negatively influenced by the combination of clay content, cation exchange capacity and slope, being positively influenced by pH and soil depth. The soil depth explained 46% of the variation in the maximum DBH.

Profile-diagrams. The vertical structure and dominant floristic composition of the montane forests of southern Ecuador are represented in the profile-diagrams (Figure 3). The six forests exhibited marked differences in their structure and floristic composition, driven primarily by an altitudinal gradient and, at a local scale, by edaphic filters. Within the upper altitudinal belt (2,100 – 2,400 m a.s.l.), characterized by low temperatures and high precipitation, the vegetation featured coriaceous leaves and a high density of epiphytes, segmenting into three distinct structural profiles according to topography. The Tapichalaca forest, located at the highest elevation and on steep slopes, was notable for harboring regional endemic taxa such as *Magnolia palanana* and *Vasconcellea palandensis*. The Numbala forest exhibited a monumental structural profile, concentrating mature individuals that exceeded 80 cm in diameter at breast height (DBH) and reached total heights of up to 45 m, heavily dominated by the last remnants of native regional conifers: *Retrophyllum rospigliosii* and *Pectinopitys harmsiana*. Conversely, the San Francisco forest recorded the highest stem density, with a pronounced dominance of *Graffenrieda emarginata*. Furthermore, both the San Francisco and Tapichalaca communities develop on unstable substrates prone to frequent landslides.

In contrast, the forests located within the lower altitudinal belt (< 1,200 m a.s.l.) bifurcated into two dissimilar structural and floristic units strictly regulated by local physicochemical soil properties. The Nangaritza profile (Río and Tepuy) was established on shallow, acidic, sandy soils covered by a dense, mattress-like organic layer (“*bamba*”), where specialized species such as *Dacryodes uruts-kunchae*, *Pagamea dudleyi*, *Humiria balsamifera*, and *Jacaranda densicoma* developed longitudinal root systems adapted for anchoring onto rocky outcrops. In contrast, the Padmi forest profile, situated on deeper clayish soils with relatively higher pH values, displayed a markedly differentiated architecture and composition, characterized by the absolute dominance of the stilt palm *Iriarteia deltoidea* (Figure 3).

Discussion

In this study, we characterized six forest communities located in hilly areas in southern Ecuador to verify whether there is a regional pattern of floristic composition and structure for these forests or whether climatic, edaphic and topographic factors cause significant differences between them. Communities are expected to change along environmental gradients, with the replacement of species from one habitat to another (Whittaker, 1960; MacArthur, 1965). In fact, we found floristically distinct groups and wide structural variation, which can be explained, although only partially, by the environmental

Table 1. Indicator value (IV) tree species of the four floristic groups discriminated in montane tropical forests of southern Ecuador. FG1: formed by Nangaritza Rio and Nangaritza Tepuy; FG2: formed by Padmi forest; FG3: formed by Numbala and Tapichalaca; FG4: formed by San Francisco forest.

Species	Floristic Group	IV > 0.7	P-value
<i>Chrysophyllum sanguinolentum</i> (Pierre) Baehni	FG1	0.81	<0.001
<i>Miconia</i> spp.		0.81	
<i>Pagamea dudleyi</i> Steyerem.		0.72	
<i>Jacaranda densicoma</i> Mart. ex DC.		0.70	
<i>Humiria balsamifera</i> Aubl.		0.70	
<i>Ocotea</i> spp.		0.70	
<i>Graffenrieda harlingii</i> Wurdack		0.70	
<i>Iriartea deltoidea</i> Ruiz & Pav.	FG2	0.96	<0.001
<i>Grias peruviana</i> Miers		0.96	
<i>Sorocea trophoides</i> W.C. Burger		0.95	
<i>Sapium marmieri</i> Huber		0.84	
<i>Retrophyllum rospigliosii</i> (Pilg.) C.N. Page	FG3	0.70	<0.001
<i>Nectandra laurel</i> Klotzsch. ex Ness		0.70	
<i>Clusia</i> spp.	FG4	0.92	<0.001
<i>Alchornea grandiflora</i> Müll. Arg.		0.87	
<i>Clethra revoluta</i> (Ruiz & Pav.) Spreng.		0.76	
<i>Graffenrieda emarginata</i> (Ruiz & Pav.) Triana		0.75	
<i>Vismia tomentosa</i> Ruiz & Pav.		0.72	
<i>Naucleopsis francisci</i> C.C. Berg		0.71	
<i>Sciodaphyllum ferrugineum</i> (Willd. ex Schult.) Decne. & Planch		0.70	
<i>Elaeagia karstenii</i> Standl.		0.70	
<i>Matayba inelegans</i> Radlk.		0.70	
<i>Prunus opaca</i> Benth.Walp		0.70	

Table 2. Environmental factors (predictor variables) that explain the differences in structural variables (response variables) in tropical montane forests in southern Ecuador. Percentages represent the hierarchical partition of variances of the predictor variables. The direction of the effect of each environmental variable was shown as positive (+) or negative (-). DBH: diameter at breast height; OM: organic matter content, CEC: cations exchange capacity.

Response variables	Predictor variables	F	P-value	R ²
Basal area (m ² ha ⁻¹)	Clay (-) (15%), pH (+) (14%), CEC (-) (38%), Altitude (+) (14%), Slope (-) (19%)	21.49	<0.0001	0.41
Density (individuals ha ⁻¹)	Clay (+) (16%), pH (-) (14%), OM (+) (53%), Altitude (-) (11%), Slope (-) (5%)	13.33	<0.0001	0.29
Height (tallest tree)	Clay (-) (16%), pH (+) (22%), CEC (-) (20%), OM (-) (28%), Altitude (+) (14%)	128.1	<0.0001	0.81
DBH (largest tree)	Clay (-) (18%), pH (+) (8%), CEC (-) (12%), Depth (+) (46%), Slope (-) (16%)	34.9	<0.0001	0.53

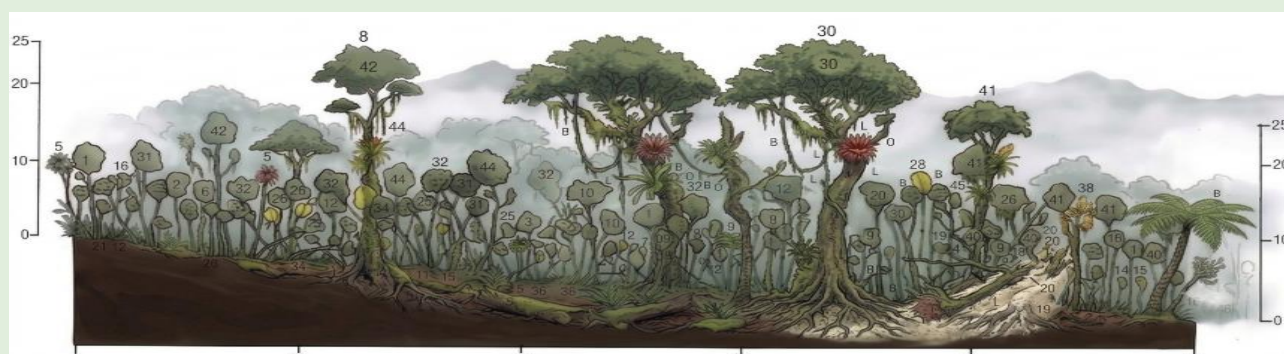
Andean Forests (2,135 – 2,153 – 2,411 m a.s.l.)

Numbala



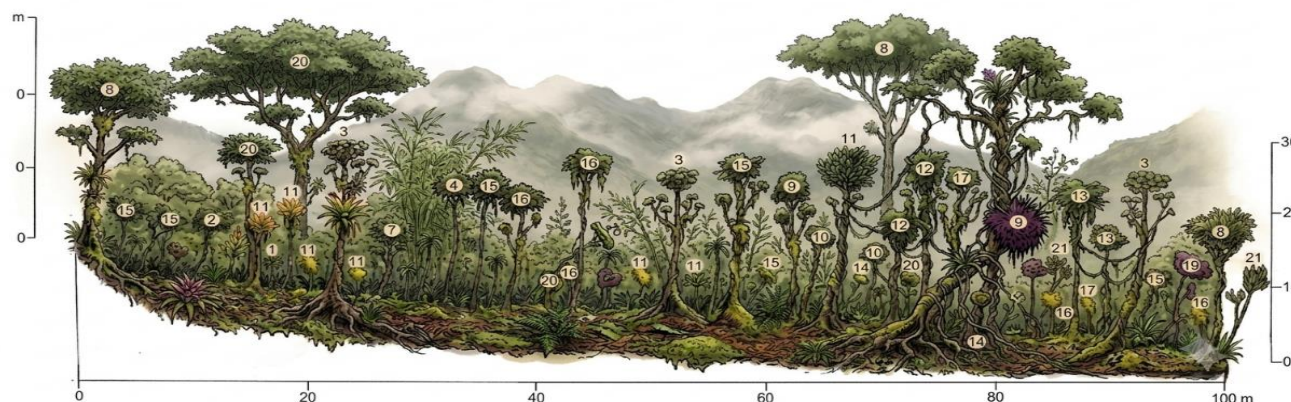
Retrophyllum rospigliosii (29), *Handroanthus chrysanthus* (14), *Nectandra laurel* (21), *Hyeronima asperifolia* (15), *Picnophytis hamsiana* (26), *Jossia aequatoria* (6), *Aegiphila cuatrecassasi* (1), *Psychotria brachiata* (7), *Endlicheria sericea* (8), *Guatteria decurrens* (13), *Piptocoma discolor* (23), *Casearia ovalis* (4), *Roupala montana* (30), *Cecropia montana* (5), *Myrcianthes rhopaloides* (18), *Prunus huantensis* (27), *Trichilia pallida* (32), *Weinmannia sorbifolia* (34), *Vochysia aurantiaca* (35), *Aniba* sp. (2), *Ficus insipida* (10), *Porouma cecropiifolia* (25), *Pouteria capacifolia* (1), *Calatola costaricensis* (3), *Ficus maxima* (11), *Podocarpus oleifolius* (24), *Palicourea amethystina* (22).

San Francisco



Clusia sp. (8), *Graffenrieda emarginata* (12), *Alchornea glandiflora* (1), *Elaeagia kerstenii* (9), *Vismia tomentosa* (44), *Prunus opaca* (34), *Clethra revoluta* (6), *Iseria krausei* (18), *Sciadophyllum ferruginum* (38), *Matayba ineleqans* (19), *Hedyosmum goudotianum* (14), *Miconia* sp. (6), *Andesanthus lepidotus* (43), *Podocarpus sprucei* (32), *Purdiaea nutans* (37), *Hyeronima alchornoides* (16), *Inga striata* (17), *Naucleopsis francisci* (28), *Nectandra subbullata* (30), *Ocotea* sp. (31), *Meliosmas* sp. (20), *Alzatea verticillata* (2), *Miconia jahnii* (21), *Symplocos peruviana* (40), *Calyptanthus pulchella* (4), *Pourouma minor* (33), *Weinmannia fagaroides* (44), *Cecropia montana* (5), *Magnolia zamorana* (41), *Endlicheria oreocola* (10), *Hyeronima oblonga* (16), *Guarea subandina* (13), *Miconia punctata* (23), *Myrsine coriacea* (26), *Hyeronima asperifolia* (15), *Clusia elliptica* (7).

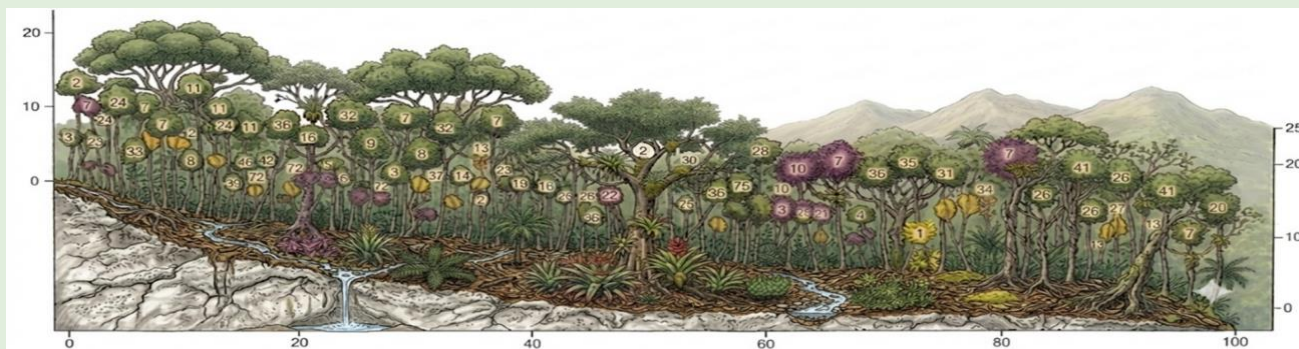
Tapichalaca



Nectandra laurel (20), *Hyeronima asperifolia* (15), *Miconia punctata* (16), *Cecropia montana* (3), *Guarea kunthiana* (11), *Palicourea amethystina* (17), *Ficus insipida* (8), *Sciadophyllum ferruginium* (21), *Croton lechleri* (5), *Elaeagia kerstenii* (6), *Hedyosmum goudotianum* (14), *Ruagea pubescens* (18), *Guarea pterorhachis* (12), *Guettarda speciosa* (13), *Miconia* sp. (10), *Mycianthes rhopaloides* (4), *Abatia parviflora* (1), *Aparisthmium cordatum* (7), *Palicourea ovalis* (17).

Sub-Andean Forests (953 – 956 – 1,135 m a.s.l.)

Nangaritza Rio



Chrysophyllum sanguinolentum (7), *Aspidosperma megalocarpon* (3), *Nectandra* sp. (28), *Pagamea dudleyi* (33), *Dacryodes uruts-kunchae* (10), *Miconia* sp. (26), *Dystovomita paniculata* (12), *Ocotea* sp. (30), *Pseudolmedia laevigata* (36), *Helicostylis tomentosa* (19), *Aniba* sp. (2), *Macrolobium gracile* (24), *Ladenbergia* sp. (22), *Inga* sp. (21), *Meliosma* sp. (25), *Centronia laurifolia* (5), *Roucheria laxiflora* (38), *Stilpnophyllum grandifolium* (40), *Otoba parvifolia* (32), *Protium subseratum* (35), *Guatteria* sp. (18), *Tapirira guianensis* (41), *Euterpe precatoria* (13), *Micropholis guyanensis* (27), *Osteophloeum platyspermum* (31), *Ladenbergia oblongifolia* (22), *Chrysochlamys bracteolata* (21), *Inga acreana* (6).

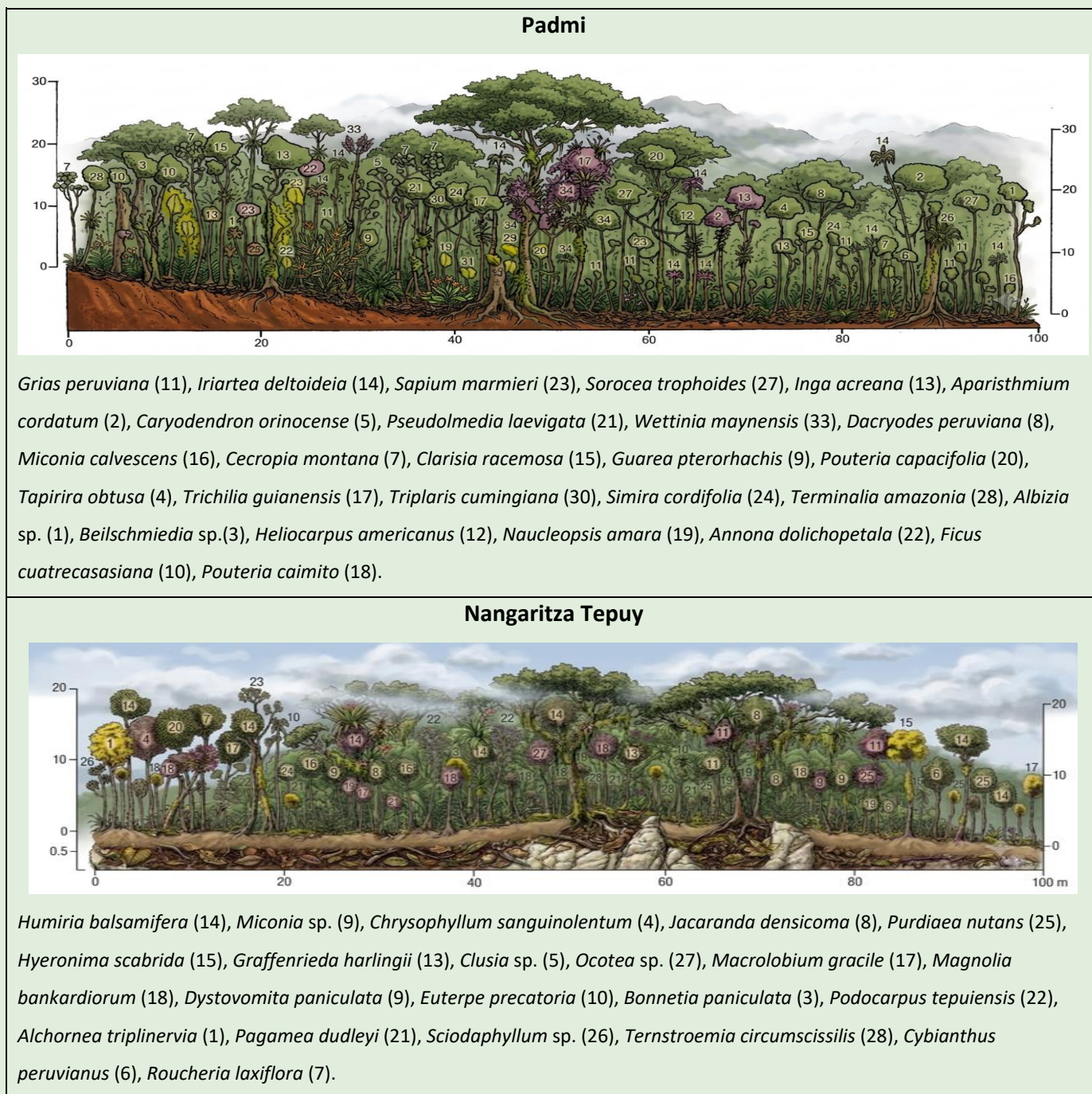


Figure 3. Profiles of tree vegetation in the six study areas in the montane forests of southern Ecuador.

factors analyzed, especially by the altitude and associated climatic factors, but also by some soil properties. However, most of the differences between the six forests studied remain unexplained.

Do environmental factors explain the floristic composition between the montane forests of southern Ecuador? The absence of a clear linear pattern between species richness and altitude, coupled with the high proportion of floristic and structural variance left unexplained by our environmental variables, challenges traditional paradigms of ecological determinism along Andean gradients (Gentry, 1988; Tuomisto et al., 2003). Although we identified macro environmental climate drivers and secondary edaphic filters that segregate Sub-Andean Pluvial Forests (SPF) from Andean Pluvial Forests (APF), differences at the local scale (intra gradient) suggest that niche-based mechanisms lose predictive capacity within these high diversity ecosystems. Consequently, our findings support the tenets of the Unified Neutral Theory of Biodiversity and Biogeography (Chave, 2004), suggesting that community assembly in these forests is predominantly governed by stochastic processes and dispersal limitation.

The high residual or unexplained variance in our multivariate models (e.g., the CCA) is conventionally interpreted in classical literature as mathematical noise or a reflection of unmeasured environmental variables. However, from the perspective of contemporary community ecology (Chave, 2004; Rosindell et al., 2011), this phenomenon constitutes indirect yet robust evidence of ecological drift. In hyperdiverse systems featuring a high representation of rare or low-density species such as those documented in the sub-Andean plots of Nangaritza and Padmi the probability of an individual being replaced following a disturbance or gap dynamic depends more on the stochastic proximity of available propagules than on an adaptive competitive advantage tied to the microhabitat. The *per capita* functional equivalence postulated by Chave (2004) becomes highly relevant here: at the one-hectare scale, colonization success within canopy gaps appears to operate as a stochastic “recruitment lottery” (Sale, 1977), wherein local abundance is a historical reflection of demographic chance rather than strict niche specialization.

Furthermore, the floristic similarity or divergence among plots sharing the same altitudinal range and analogous climatic conditions highlights the role of dispersal limitation as a key neutral force. The biogeographical separation of communities across ecologically equivalent substrates or distances indicates that species do not occupy all sites where their physiological niche is viable, simply because they have failed to reach them (Chave, 2004). This dynamic mitigates the strict environmental determinism found by Tuomisto

et al. (2003) in the western Amazon, suggesting that the rugged topography of southern Ecuador does not solely generate ecological gradients; rather, it primarily functions as a physical barrier that fragments metapopulations, thereby exacerbating the effects of geographical isolation and demographic drift.

Finally, it is crucial to recognize that stochasticity interacts with local biotic factors that warrant future exploration. The massive ecological dominance of certain woody taxa in specific plots (e.g., *Retrophyllum rospiglosii* in Numbala) could initially be interpreted as a superior adaptation to the local niche. Nonetheless, under the neutral framework, this pattern can also emerge from a historical “priority effect” a stochastic mass dispersal event or a large scale past disturbance that allowed this species to monopolize physical space. Once the canopy is established by these large-statured trees, the forest architecture is altered, modifying light and water dynamics for subsequent generations in a deterministic manner, even though its origin was strictly altered. Thus, our data suggest that the montane forest structure in southern Ecuador behaves as a complex system, wherein environmental rigor acts as a macro evolutionary framework, while demographic chance and stochastic assembly dictate the fine-scale composition of the community.

In this context, the floristic segregation among sites observed at a local scale could be partially linked to dispersal limitation and stochastic processes associated with ecological drift. Although the present study does not employ direct analytical methods (such as community null models or explicit spatial analyses) to quantify the exact contribution of stochasticity, the local scale of our analysis allows us to propose these mechanisms as plausible explanations that complement the effect of environmental filters.

Is the community structure driven by environmental factors? Unlike floristic composition, the structure of tree communities in the montane forests of southern Ecuador does not appear to be driven by successional processes or gap dynamics, but primarily by the physical and chemical properties of the soil. Our results indicate that forest exuberance represented by biomass, basal area, and tree sizes are greater at higher altitudes where soils are deeper, more acidic, and sandier. Contrary to expectations, climatic variables associated with the altitudinal gradient did not reach stress thresholds limiting tree growth or longevity. Instead, edaphic factors explained up to 81% of the variation in canopy height, with texture, pH, and organic matter content emerging as the primary determinants of forest architecture, consistent with patterns observed in other Neotropical regions (Quesada et al., 2012).

Soil depth and topography emerge as critical filters for biomass development. On steep terrain, despite high light incidence, runoff

and landslide processes (Ließ et al., 2011) limit establishment and growth, resulting in smaller, less dense forests. Furthermore, our data reveals an unexpected negative correlation between Cation Exchange Capacity (CEC) and forest exuberance. This phenomenon is explained by the shallow depth of soils with high CEC (e.g., Nangaritza Tepuy), where the volume of soil explorable by roots is insufficient to compensate for high surface fertility. In these contexts, water stress during periods of high evapotranspiration and mechanical instability during heavy rainfall act as physical constraints that restrict the development of large woody structures.

The structural contrast observed between Numbala and Tapichalaca, despite their geographical proximity, illustrates how chemical edaphic filters and stochastic processes can decouple the relationship between spatial closeness and physiognomic similarity (Gentry, 1988). Our results suggest that the driving factor behind the suppression of tree growth and the lower biomass in Tapichalaca is severe metal toxicity, specifically driven by critical concentrations of exchangeable aluminum (Al^{3+}), which are 22 times higher than those recorded in Numbala.

In tropical montane ecosystems, high leaching caused by intense precipitation acidifies the soil, triggering the solubilization of aluminum into its most active phytotoxic form, Al^{3+} (Brunner & Sperisen, 2013). At the physiological level, elevated concentrations of this ion rapidly inhibit cell division and elongation at the root apex, inducing a stunted, rigid, and poorly branched root system (Kochian et al., 2005). In mountain forests, this structural damage severely restricts the tree's capacity to absorb water and critical nutrients such as phosphorus and calcium while also compromising mechanical anchorage on steep slopes (Graefe et al., 2008). As a direct consequence, aluminum stress acts as an adverse environmental filter that limits net primary productivity. This translates into a significant reduction in canopy height, stem diameter, and overall basal area, a pattern widely documented across highly weathered and acidic soils in the Neotropics (Quesada et al., 2012).

Conversely, the structural exuberance and exceptional biomass accumulation in Numbala reflect not only an environment free from the selective pressure of Al^{3+} but also the influence of biotic stochasticity and community assembly processes. The massive local dominance of large-statured gymnosperms, such as *Retrophyllum rospigliosii*, exerts a "phylogenetic priority" or niche selection effect (Chave, 2004). If the initial establishment of this species was mediated by stochastic successful dispersal events or random historical disturbances that favored its past regeneration, its current massive architecture microclimatically alters the site, monopolizing resources and increasing the plot's biomass values. Thus, the divergence between both forests demonstrates that montane forest

architecture is not governed by a single linear gradient, but rather by a complex interaction wherein edaphic rigor constrains the structural potential of the forest (as in Tapichalaca), while biotic chance and ecological dominance maximize this potential (as in Numbala).

Structural and floristic differentiation of the tree communities. The pronounced structural and floristic segregation observed along the altitudinal gradient in southern Ecuador reinforces the paradigm of niche based environmental filtering as a primary mechanism structuring tropical montane forest communities (Gentry, 1988; Homeier et al., 2010). Our results demonstrate a clear decoupling between macroclimatic factors which operate as a first-order regional filter and localized edaphic properties that modulate community assembly at finer spatial scales. In the upper altitudinal belt (2,100–2,400 m a.s.l.), macroclimatic rigor characterized by persistent cloud cover, low temperatures, and continuous water saturation restricts nutrient mineralization and limits soil development (Körner, 2007). Nevertheless, the structural heterogeneity recorded among Numbala, San Francisco, and Tapichalaca demonstrates that these high altitude forests are not physiognomically uniform. For instance, the Podocarpaceae family eludes the metabolic constraints through resource-conservative strategies and high wood mechanical density, allowing them to accumulate significant biomass and successfully compete against angiosperms in specific topographic positions (Aiba et al., 2005). Likewise, the high stem density (*stem packing*) in San Francisco functions as an ecomorphological response of opportunistic and stress-tolerant species to maximize light interception under chronically overcast sky, a pattern widely documented in the shallow, nutrient-poor soils of the northern Andes (Graefe et al., 2008). Conversely, below 1,200 m a.s.l., the attenuation of regional thermal constraints allows edaphic filters to emerge as the dominant force driving beta diversity, providing robust empirical validation for the "edaphic specialization hypothesis" in the Neotropics (Tuomisto et al., 2003; Fine et al., 2005). This floristic divergence is particularly evident when contrasting the Nangaritza and Padmi forests under analogous macroclimatic regimes. In Nangaritza, severe phosphorus deficiency and low cation exchange capacity (CEC) induce the development of specialized, shallow root architectures beneath a thick organic litter layer; this operates not merely as an anchoring mechanism, but as a critical functional trait to mitigate nutrient leaching and optimize mycorrhizal symbiosis (Tanner et al., 1998). In contrast, the Padmi forest highlights the structural advantages of deep, highly fertile clayish soils, where the overwhelming quantitative dominance of the palm *Iriartea deltoidea* serves as a biological indicator of higher soil pH, base saturation, and water retention

capacity (Pitman et al., 2001; Quesada et al., 2012). By relying on stilt roots that facilitate rapid vertical growth without the costly metabolic investment required by dense woody xylem, *I. deltoidea* successfully monopolizes space in nutrient-rich, deep soils, shifting community structure toward high-biomass stands dominated by palms. In synthesis, while regional lapse rates delineate the macroevolutionary boundaries of species distribution, local-scale soil physicochemical properties dictate the fine architecture and biomass allocation of these montane ecosystems.

Conclusions

Structural and floristic assembly of tropical montane forests in southern Ecuador incorporate a relevant stochastic component, besides the predictable effects of environmental factors. The considerable unexplained variation found in our models can be interpreted as a plausible indication that the species composition of these forests, even more than their structure, are influenced by processes aligned with neutral theory, rather than responding exclusively to niche-based determinism. While abiotic factors provide a baseline for environmental filtering, the high species richness and prevalence of rare species highlight ecological drift as a highly potential mechanism shaping these ecosystems. Framed as a tentative hypothesis at a local scale, these findings contribute to a broader ecological debate on community assembly. Future research should integrate biotic interactions and explicit spatial analyses to further clarify the mechanisms governing species distribution in these complex mountain landscapes.

Authors contributions

CYP problem conception, research design, data collection and paper writing. DLS and NPL data collection, data analysis and paper writing. GD paper writing.

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AI use declaration

During the preparation of this work, the authors used Gemini (version Gemini 1.5 Pro, Google) to assist in generating the descriptive profiles of the six study plots. Specifically, the tool was utilized to synthesize and structure textual descriptions of each plot's floristic composition, structural characteristics, soil properties (edaphic conditions), and climate, as well as to suggest modifications and layout improvements for the corresponding schematic diagrams of the study areas. Following this generation, the authors thoroughly reviewed, verified, and edited all outputs to ensure scientific accuracy, ecological consistency with the raw field data, and alignment with academic standards. The authors take full responsibility for the final content of this manuscript.

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