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Biodiversity and structural analysis of forests at the altitudinal boundary between dry and montane forests: response of tree diversity to altitudinal variation in the northeastern Peruvian Andes

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Forests at the altitudinal limits between seasonally dry tropical forests (SDTF) and montane forests in northeastern Peru are key for biodiversity and ecological connectivity. Sixteen 0.1-ha plots were surveyed along a 1900–2700 m a.s.l. gradient, recording 133 species, 76 genera, and 47 families, reflecting high floristic heterogeneity. Diversity indices showed a unimodal pattern, peaking in the transition zone between 2300 and 2500 m (Hill_{q1} = 22.36; Hill_{q2} = 15.92; estimated richness = 49 species). Diversity decreased at lower SDTF elevations (1900–2100 m) and higher montane sites (>2500 m), likely due to thermal and water limitations. Species dominance shifted along the gradient: *Vachellia aroma* and *Inga adenophylla* dominated SDTF, whereas *Aiouea montana*, *Clethra revoluta*, and *Ilex scopulorum* characterized montane forests. Beta diversity revealed pronounced species replacement and highlighted plot S08 as an ecotone with species from both ecosystems. Diameter-class distributions followed an inverted “J” pattern, indicating active regeneration in both ecosystems, with higher recruitment in SDTF. Altitude drives species replacement and shapes a unimodal diversity pattern. We recommend restoring dominant SDTF species, such as *Vachellia aroma* and *Inga adenophylla*, in degraded lower-elevation areas, and conserving ecotonal belts as altitudinal corridors to enhance biodiversity and climate resilience areas, and conserving ecotonal belts as 32 altitudinal corridors to enhance biodiversity and climate resilience.

KEYWORDS

altitudinal gradient, Chachapoyas, diversity indices, floristic diversity, montane forests, seasonally dry tropical forest

1 Introduction

Tropical forests play a central role in global climate regulation, carbon cycling, and the maintenance of terrestrial biodiversity, while exhibiting high structural and functional complexity across broad environmental gradients (Pan et al., 2011; Malhi et al., 2010; Malhi et al., 2014). Their distribution and functioning are shaped by the interaction between climate, topography, and edaphic conditions, resulting in pronounced spatial heterogeneity in floristic composition, productivity, and ecological processes (Girardin et al., 2014). In this context, climatic and altitudinal gradients within the tropics provide an ideal framework for evaluating forest ecosystem responses to variations in temperature and water availability, factors of particular relevance under scenarios of global climate change (Malhi et al., 2010).

Within this broad array of ecosystems, tropical seasonally dry forests (TSDF) represent one of the most distinctive, vulnerable, and yet least studied forest biomes in the Neotropics (Pennington et al., 2009; Dirzo et al., 2011; Dryflor et al., 2016). These forests are characterized by pronounced climatic seasonality, with extended dry periods that impose strong physiological constraints and favor the dominance of species and functional strategies adapted to water stress, such as deciduousness, high wood density, and high water-use efficiency (Sánchez-Azofeifa et al., 2014; Poorter et al., 2016). Despite these limiting environmental conditions, TSDF harbor high levels of floristic diversity, endemism, and ecological uniqueness, often concentrated within relatively small geographic areas, which has led to their recognition as global priorities for conservation and scientific research (Pennington et al., 2009; Dryflor et al., 2016).

From a structural and functional perspective, TSDF are commonly dominated by families such as Fabaceae (Leguminosae) and Bignoniaceae, whose species exhibit key adaptations related to biological nitrogen fixation, drought tolerance, and the efficient exploitation of soils with high nutrient variability (Guzman et al., 2021). However, despite their ecological importance, these forests have been identified as among the most threatened tropical ecosystems worldwide, with less than 10% of their original extent remaining in many countries. This dramatic reduction is primarily driven by conversion to agricultural and livestock activities, habitat fragmentation, and their limited representation within formal protected area networks (Miles et al., 2006; Hoekstra et al., 2005; Dryflor et al., 2016).

In Peru, inter-Andean tropical seasonally dry forests comprise three major floristic groups—coastal, inter-Andean, and eastern forests, reflecting pronounced environmental and biogeographic heterogeneity (Linares-Palomino et al., 2011; Linares-Palomino et al., 2022). These ecosystems span a wide altitudinal range that, in some regions of northern Peru, exceeds 2,000 m a.s.l., particularly in inter-Andean valleys associated with the Marañón River basin (Linares-Palomino et al., 2011; Marrufo Huamán, 2023). In this region, TSDF exhibit exceptionally high levels of endemism, estimated at approximately 33% of woody plant species, along with pronounced floristic turnover (Marcelo-Peña et al., 2016; Marcelo-Peña et al., 2025). These patterns have been attributed to the complex Andean topography and historical processes of climatic isolation that have promoted the evolutionary differentiation of plant communities (Särkinen et al., 2012; Marcelo-Peña et al., 2025).

Nevertheless, despite their well-recognized biological importance, scientific research on TSDF in Peru remains limited, particularly with regard to systematic ecological studies and analyses across altitudinal gradients. This constraint hampers a comprehensive understanding of

their dynamics and limits the development of effective conservation strategies (Delgado-Paredes et al., 2020; Marcelo-Peña et al., 2025). This knowledge gap is reflected in the scarcity of long-term monitoring plots in dry forests, in contrast to the relatively large number of studies and permanent plots established in montane forests. In the department of Amazonas, for example, several floristic assessments based on monitoring plots have been conducted in montane forests (Añazco Urbina et al., 2021; Culqui et al., 2024; Sánchez Zamora et al., 2024), whereas only a single study has specifically focused on the establishment of vegetation monitoring plots in dry forests (Tarrillo Cieza, 2024).

In this context, the establishment of evaluation plots in TSDF of northern Peru represents a strategically important initiative to improve ecological knowledge of these highly vulnerable ecosystems. Given the high biodiversity of the Amazonas department and the urgent need to generate baseline information to support conservation efforts, the installation of 16 study plots was undertaken at the altitudinal boundaries between TSDF and montane forest ecosystems in the district of Sonche, Chachapoyas Province. This effort aims to contribute to the characterization of vegetation structure and composition in the dry forests of northeastern Peru.

2 Materials and methods

2.1 Study area

This study was conducted along the altitudinal boundaries between tropical seasonally dry forest (TSDF) and montane forest ecosystems in the district of Sonche, Chachapoyas Province, northeastern Peru. At the provincial scale, montane forests cover approximately 66.76% of the territory (1,852.78 km²), whereas dry forest ecosystems account for 33.11% (918.96 km²). According to the Peruvian life zone map, these dry forests are classified as tropical premontane dry forest, tropical lower montane dry forest, and tropical premontane desert shrubland [Instituto Nacional de Recursos Naturales (INRENA), 1995]. In addition, they correspond to the inter-Andean seasonally dry forests of the Marañón Valley as defined in the national ecosystem map [Ministerio del Ambiente (MINAM), 2019].

Both seasonally dry tropical forests (SDTF) and montane forests in the Amazonas Department provide essential ecosystem services. In particular, SDTF serve as refuges for a high diversity of fauna (Guzman et al., 2021; Coronel-Castro et al., 2024), contribute to soil stability by reducing erosion and landslide risk, and supply important forest resources such as timber, fuelwood, fruits, and medicinal plants. Moreover, these ecosystems play a key role in hydrological regulation by storing and gradually releasing water into streams and rivers. Nevertheless, these ecosystems face increasing anthropogenic pressures associated with agricultural expansion, illegal logging, forest fires, climate variability, and institutional limitations for sustainable management. These pressures have driven ongoing processes of degradation and fragmentation (Figuerola et al., 2016; Coronel-Castro et al., 2024), such that currently slightly more than 10% of the area over which this ecosystem is distributed in the province (108.7 km²) is degraded [Ministerio del Ambiente (MINAM), 2021].

At the local scale, the district of Sonche covers an area of approximately 120 km² and spans an altitudinal range from 1,554 to 2,845 m a.s.l. [Ministerio del Ambiente (MINAM), 2019]. Two main ecosystem types

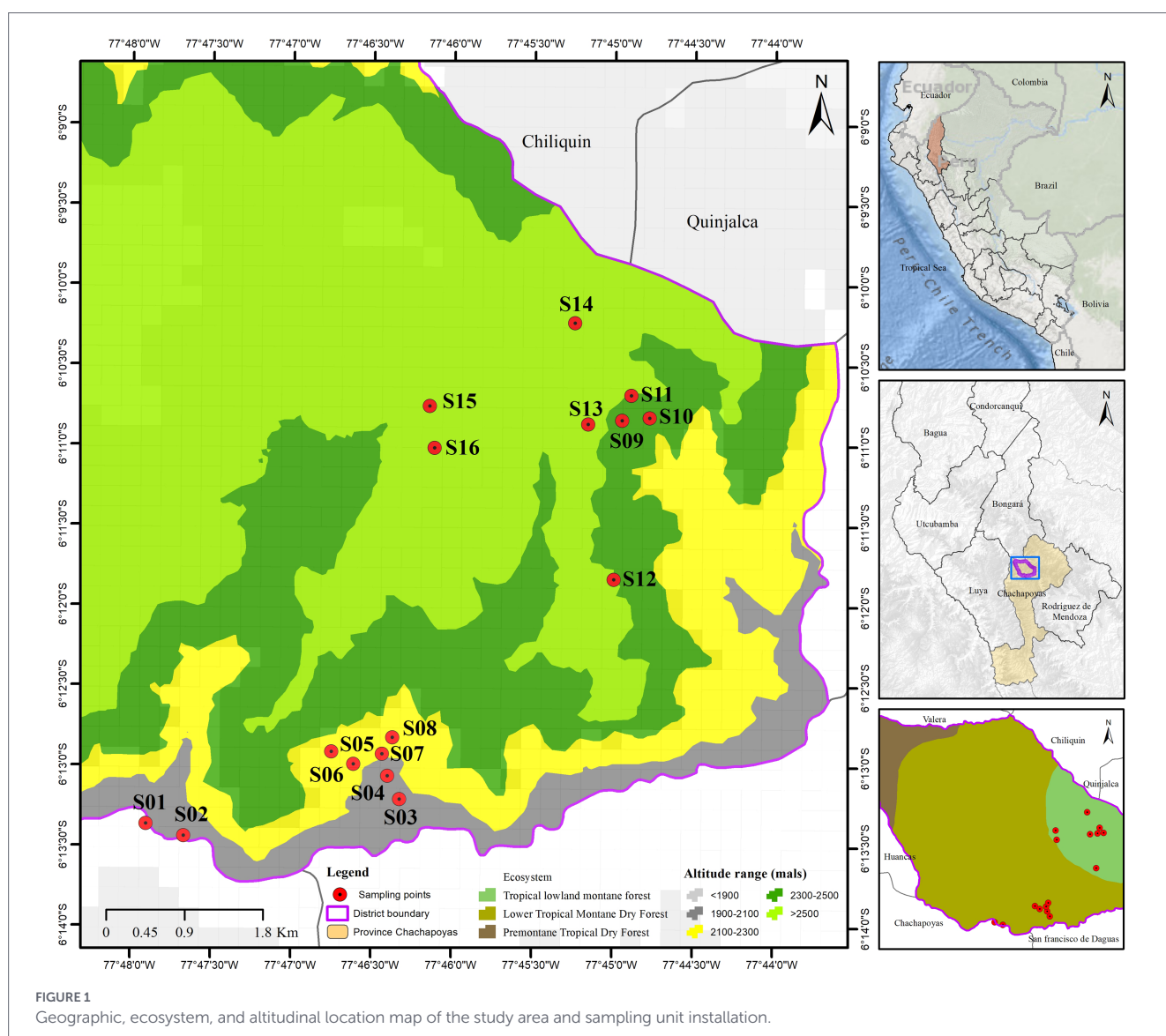
are recognized within the study area. Tropical seasonally dry forests dominate the landscape, covering nearly 89% of the territory, primarily as tropical premontane dry forest (bs-PT) and tropical lower montane dry forest (bs-MBT). In contrast, montane forests account for the remaining 11% and correspond to tropical lower montane humid forest (bh-MBT) [Instituto Nacional de Recursos Naturales (INRENA), 1995].

Climatic and topographic conditions vary markedly along the altitudinal gradient and strongly influence vegetation structure and composition. In lower and mid-elevation areas, where TSDF predominate, conditions are warmer and drier, and the terrain is rugged, characterized by steep slopes, deep valleys, and well-defined ravines (Rodríguez Achung et al., 2010; Mapcarta, 2025). Vegetation in these areas is mainly composed of deciduous, spiny, and open-canopy tree species adapted to environmentally restrictive conditions (Tarrillo Cieza, 2024). In contrast, higher elevations corresponding to humid montane forests experience lower temperatures and greater moisture availability [Instituto Nacional de Recursos Naturales (INRENA), 1995], which favor denser and more structurally complex vegetation with closed canopies and a high abundance of epiphytes, mosses, and ferns (Sánchez Zamora et al., 2024).

2.2 Establishment of sampling units and tree species inventory

For the establishment of the sampling units, a digital elevation model (DEM) with a spatial resolution of 30 m was used (Farr et al., 2007). The study area was stratified into four altitudinal classes at 200 m intervals (1900–2,100, 2,100–2,300, 2,300–2,500, and 2,500–2,700 m a.s.l.) (Figure 1) within a Geographic Information Systems (GIS) environment using ArcGIS software version 10.8 (Bricca et al., 2025). The first two strata corresponded to seasonally dry tropical forests, whereas the two upper strata were associated with montane forests. This stratification allowed the sampling design to be structured along the altitudinal gradient and ensured adequate representation of the environmental and ecological conditions of the study area (Khadanga et al., 2023).

Within each altitudinal stratum, potential plot locations were identified through a spatial selection process in GIS and subsequently refined in the field using a targeted sampling approach. This refinement considered criteria of accessibility, safety, and the presence of continuous and representative forest cover, allowing the exclusion of disturbed or



fragmented areas and ensuring comparable environmental conditions within each altitudinal class (Queinnec et al., 2022; Khadanga et al., 2023).

Based on this procedure, four sampling plots were established per stratum (50 × 20 m; 0.1 ha each), following designs widely used in studies of tropical and montane forests (Fujiki et al., 2016; Aguirre Mendoza et al., 2021a; García-Cox et al., 2023). A minimum distance of 100 m was maintained between plots in order to reduce spatial autocorrelation and avoid pseudoreplication (Rodrigues Silva et al., 2019; Aguirre Mendoza et al., 2021b).

Additionally, to evaluate the representativeness and adequacy of the sampling effort, species accumulation curves were analyzed based on the cumulative increase in species richness as a function of the number of sampled plots per ecosystem (seasonally dry tropical forest and montane forest). This analysis was conducted using randomization procedures in the R statistical environment, employing the vegan and iNEXT packages (Callaghan et al., 2022; Sánchez Zamora et al., 2024; Repetto et al., 2024). The tendency of the curves to approach an asymptote was used as an indicator of sampling completeness, whereas the lack of stabilization was interpreted as a limitation of the applied effort (Castro-Souza et al., 2024). Within each plot, all tree with a diameter at breast height (DBH) ≥ 10 cm, measured at 1.30 meters above the base of the trunk, were assessed. For each individual, an identification code, total height, and bole height were recorded, following standardized protocols (Rodrigues Silva et al., 2019; Toasa et al., 2020). Tree species were identified directly in the field by botanists experienced in the local flora, based on the recognition of vegetative and reproductive morphological characters. When necessary, identifications were verified using specialized taxonomic literature and reference collections, following standard procedures commonly applied in tropical and montane forest inventories (Gaem et al., 2022; García-Cox et al., 2023).

2.3 Data processing and analysis

The tree composition of the montane forests was analyzed by estimating species richness (S) through the direct count of the total number of recorded families, genera, and species, which constitutes a basic yet fundamental measure for characterizing local floristic diversity (Carvajal-Hernández et al., 2014; Ramírez Huila and Ayoví Garces, 2022). Additionally, the Importance Value Index (IVI) was estimated for each species by combining three structural components: relative abundance (RA), relative frequency (RF), and relative dominance (RD), the latter based on the total basal area of each species. The IVI was then used to compare the most representative species along the altitudinal gradient, allowing the identification of those with the highest ecological relevance, following the approach proposed by Yeboah et al. (2022). To calculate the IVI, the following formula was used:

$$IVI_i = RA_i + RF_i + RD_i$$

Where:

$$RA_i = \frac{\text{Number of individuals of species } i}{\text{Total number of all individuals}} \times 100$$

$$RF_i = \frac{\text{Number of plots in which a species is found}}{\text{Total number of plots}} \times 100$$

$$RD_i = \frac{\text{Total basal area of species } i}{\text{Total basal area of all species}} \times 100$$

Alpha diversity was assessed using the Hill numbers framework, which parsimoniously integrates traditional diversity metrics (Shannon and Simpson) within a unified framework of effective diversity. This approach allows comparisons of species richness ($q = 0$), abundance-weighted diversity ($q = 1$), and the dominance of common species ($q = 2$), thereby reducing redundancy among indices and facilitating consistent ecological interpretations across ecosystems and altitudinal strata (Hsieh et al., 2016; Penny et al., 2025). The equation applied was as follows:

$$D = \left(\sum_{i=1}^S p_i (ri)^\ell \right)^{1/\ell}$$

Where D is diversity, S is the number of species, p_i is the proportion of all individuals belonging to species i , ri is the rarity of species i , defined as $1/p_i$, and ℓ is the exponent that determines the scale of rarity over which the mean is taken (Roswell et al., 2021).

In addition, beta diversity was assessed using the Sørensen similarity index (S), based on presence-absence matrices of tree species among plots and across altitudinal strata. This index allowed the quantification of floristic turnover along the altitudinal gradient and represents a synthetic, robust, and widely used metric in studies comparing plant communities (Carvajal-Hernández et al., 2014; Karami et al., 2021):

$$S = \frac{2a}{2a + b + c}$$

Where a represents the number of shared species between two sites, and b and c correspond to the species exclusive to each site (Karami et al., 2021).

Forest structure was characterized through the distribution of individuals into diameter classes (5-cm intervals) (De Cáceres et al., 2019; Abreu Neto et al., 2021) and height classes (5-m intervals) (Junyan et al., 2014), which allowed identifying structural trends, regeneration patterns, and successional stages of the forest.

Finally, a Multiple Correspondence Analysis (MCA) was performed using the FactoMineR package in RStudio v4.4.1 (Lê et al., 2008) to explore the associations among the abundance of taxonomic families, DBH classes, height classes, and altitudinal ranges. This analysis focused on the most dominant taxonomic families, enabling the identification of key structural and ecological patterns in relation to the environmental gradient.

3 Results

3.1 Effort and representativeness of floristic sampling

The species accumulation curve estimated for the SDTF of the Sonche district, fitted using the Clench model, showed a progressive

increase in species richness as the sampled area increased. The shape of the curve exhibited a clear tendency toward saturation, although it did not fully reach the asymptote. The estimated total richness ($S^* = 79.51$ species) exceeded the observed number of species, suggesting the presence of additional species that were not recorded during sampling. Similarly, in montane forests, the species accumulation curve displayed a progressive trend toward stabilization as the sampled area increased. The initial increase in richness was rapid, followed by a gradual decrease in slope, indicating a reduction in the rate of incorporation of new species. The approach of the curve to the estimated asymptote ($S^* = 126.78$) suggests that the applied sampling effort was adequate to capture a representative proportion of the floristic diversity of this ecosystem. Overall, although complete stabilization was not achieved in either case, the results indicate that the sampling effort was sufficient to describe general diversity patterns, while acknowledging that increased sampling could allow the detection of additional species (Figure 2).

3.2 Tree composition

In the forests of the Sonche district, 133 tree species were recorded, belonging to 47 families and 76 genera (Supplementary Table 1). Species, genus, and family richness exhibited a pattern clearly structured by elevation and ecosystem type (Figures 3a–c), reflecting a pronounced floristic differentiation along the gradient. In seasonally dry tropical forests, occurring between 1,900 and 2,300 m a.s.l., the lowest levels of tree diversity were observed, consistent with the more restrictive climatic conditions of this altitudinal belt. In contrast, the 2,300–2,500 m a.s.l. interval, corresponding to montane forests, concentrated the highest floristic richness, indicating more favorable environmental conditions for the establishment and coexistence of a greater number of taxa. Above 2,500 m a.s.l., a slight decline in tree richness was recorded, suggesting a possible combined effect of lower temperatures and edaphic limitations. Overall, these results reveal a unimodal richness pattern along the altitudinal gradient, with a peak in the mid-montane zone and a

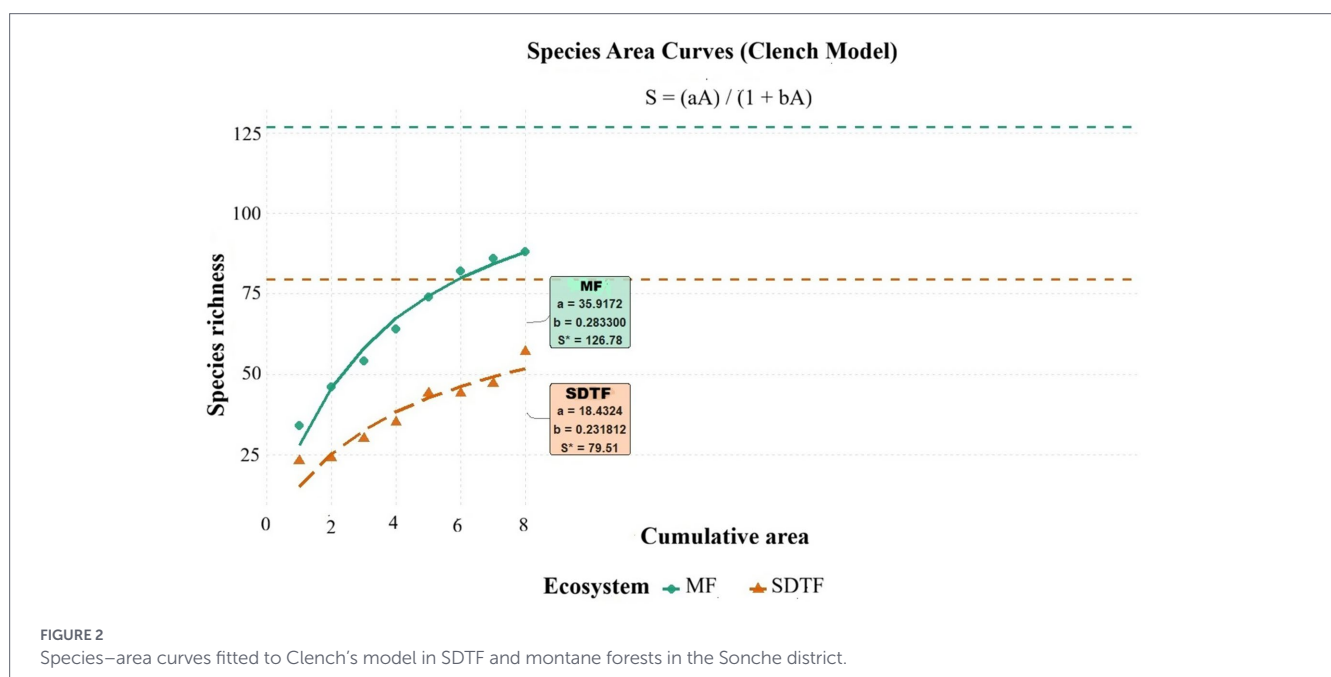
decline at both the lower dry forest elevations and the uppermost altitudes.

3.2.1 Importance value index

Table 1 presents the Importance Value Index (IVI) of tree species along the altitudinal gradient from 1900 to 2,700 m a.s.l. in the forests of the Sonche district. In the lower altitude range (1900–2,100 m), *Vachellia aroma* exhibited the highest IVI (12.97), associated with its high abundance and relative dominance, followed by *Inga adenophylla* and *Clusia rigida*, which consistently contributed to the characteristic forest structure of SDTF. Between 2,100 and 2,300 m, *Escallonia paniculata* and *Myrsine oligophylla* reached the highest IVI values (>10), reflecting a floristic transition with a progressively more uniform distribution of dominance among various taxa. In the 2,300–2,500 m range, *Aiouea montana* stood out for its high structural dominance, while *Ilex scopulorum* and *Hieronyma oblonga* maintained intermediate values. Finally, at 2500–2700 m, *Clethra revoluta* and *Clusia hylaeae* were the most important tree species. These patterns confirm a well-defined altitudinal floristic succession and high structural complexity within the ecosystem.

3.2.2 Predominance of tree flora by altitude gradient

The predominance of tree species in the forests of Sonche is influenced by elevation and the ecological characteristics of the ecosystem (Supplementary Table 1; Table 1). In the altitudinal range of 1900–2,100 m a.s.l., there is a high dominance of species adapted to dry and warm conditions, including *Vachellia aroma*, *Clusia rigida*, *Inga adenophylla*, *Vernonanthura patens*, and *Buddleja longifolia* (Figure 4a). In the 2,100–2,300 m range, the floristic composition reflects a transition zone toward humid montane forest. Although important records of species typical of dry environments were still found, such as *Vachellia aroma*, *Clusia rigida*, and *Vernonanthura patens*, the most abundant species were *Myrsine oligophylla* and *Escallonia paniculata*, which indicate the



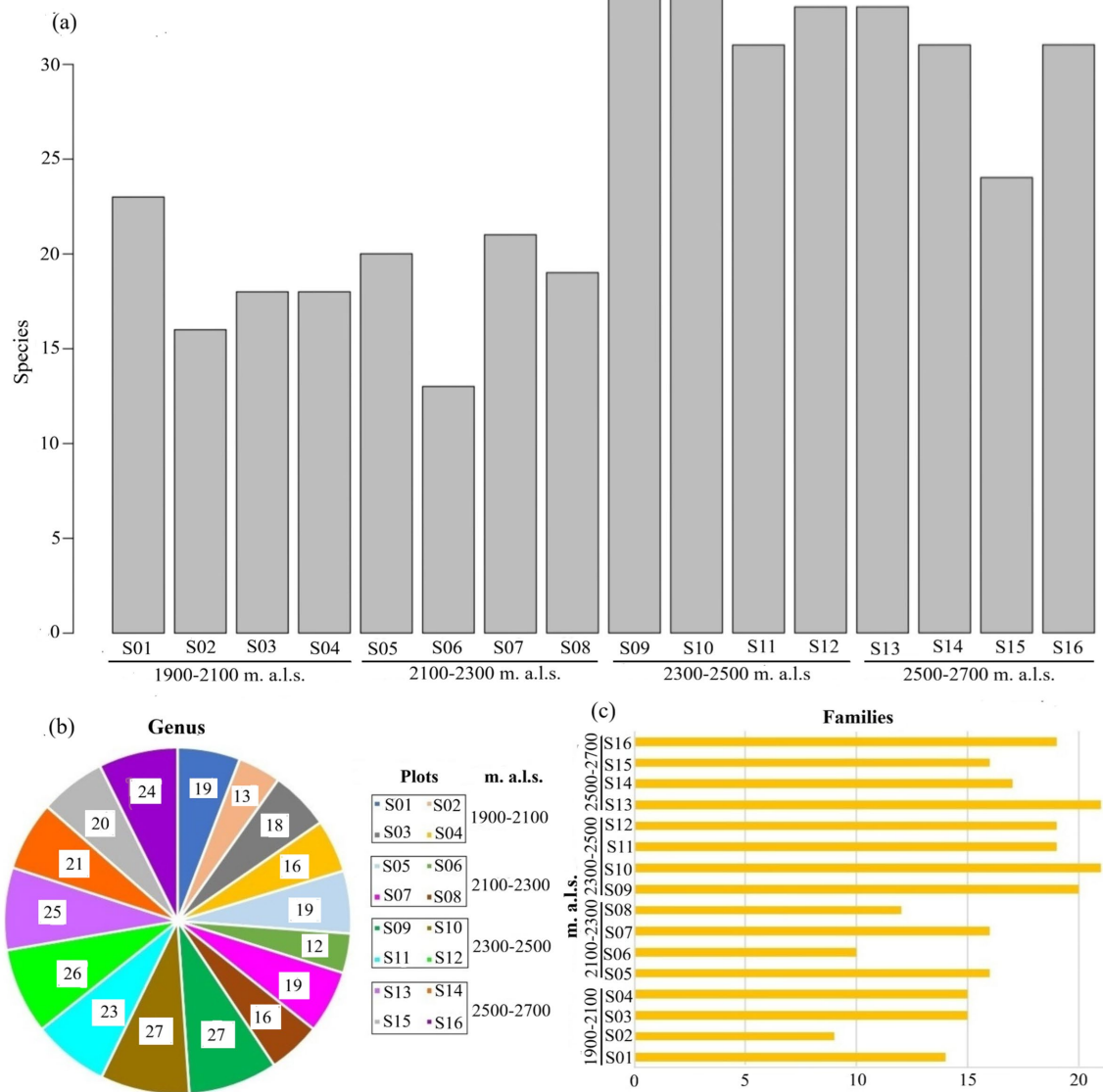


FIGURE 3
Richness of tree flora in the forests of the Sonche district along different altitudinal gradients: (a) species richness, (b) genus richness, and (c) family richness.

presence of more temperate and humid conditions (Figure 4b). Between 2,300 and 2,500 m a.s.l., the presence of species characteristic of humid montane forests increases, including *Aiouea montana*, *Ilex scopulorum*, *Critoniopsis pycnantha*, *Cyathea austropallescens*, *Hieronima oblonga*, and *Clusia multiflora* (Figure 4c). Finally, in the 2,500–2,700 m altitudinal range, species typical of high and cold environments prevail, such as *Clethra revoluta*, *Ilex quitensis*, *Hesperomeles ferruginea*, *Cyathea delgadii*, and *Clusia hylaeae* (Figure 4c). This pattern demonstrates floristic turnover along the altitudinal gradient, primarily driven by variations in temperature, humidity, and forest structure, factors that directly influence the composition and distribution of tree communities.

Distribution of tree flora by ecosystem of the 15 most important tree species recorded in the forests of the Sonche district, 11 were found exclusively in a single ecosystem, indicating a marked ecological segregation. Six species were restricted to dry forests, while *Escallonia paniculata*, although present in montane forests, showed a strong preference for dry forests, reflecting the dominance of certain species in this ecosystem. Standardizing the data as percentages allows for

comparison of the relative contribution of each ecosystem, highlighting species' ecological specialization and emphasizing the complementary importance of dry and montane forests for the conservation of local tree diversity (Figure 5).

3.3 Diversity indices

3.3.1 Alpha diversity

The results of the alpha diversity analysis based on Hill numbers, presented in Table 2, reveal contrasting patterns between SDTF and montane forests. In the SDTF (1900–2,300 m a.s.l.), alpha diversity was moderate, although clear variations were observed between the two altitudinal ranges evaluated. In plots located between 1900 and 2,100 m a.s.l. (S01–S04), species richness (Hill q0) was relatively high and homogeneous (17–23 species), accompanied by moderate values of Hill q1 and q2, suggesting communities with intermediate evenness and moderate dominance.

TABLE 1 Tree species with the highest Importance Value Index (IVI) by altitudinal range in the forests of the Sonche district, northeastern Peru.

Altitude range (m.a.l.s)	Species	AA	RA (%)	AF	RF (%)	AD	RD (%)	IVI
1900–2,100	<i>Vachellia aroma</i>	54.00	18.00	4.00	5.33	9.83	15.58	12.97
	<i>Inga adenophylla</i>	22.00	7.33	4.00	5.33	6.12	9.70	7.46
	<i>Clusia rigida</i>	29.00	9.67	4.00	5.33	4.00	6.34	7.11
	<i>Ficus maroma</i>	12.00	4.00	2.00	2.67	5.57	8.83	5.16
	<i>Vernonanthura patens</i>	20.00	6.67	3.00	4.00	2.98	4.72	5.13
	<i>Buddleja longifolia</i>	17.00	5.67	3.00	4.00	2.99	4.74	4.80
	<i>Escallonia pendula</i>	10.00	3.33	3.00	4.00	4.13	6.55	4.63
	<i>Allophylus densiflorus</i>	15.00	5.00	3.00	4.00	2.72	4.31	4.44
	<i>Ficus maxima</i>	11.00	3.67	2.00	2.67	4.26	6.75	4.36
	<i>Solanum asperolanatum</i>	12.00	4.00	4.00	5.33	1.30	2.06	3.80
2,100–2,300	<i>Escallonia paniculata</i>	45.00	14.24	3.00	4.17	6.51	13.65	10.68
	<i>Myrsine oligophylla</i>	46.00	14.56	4.00	5.56	4.82	10.10	10.07
	<i>Vachellia aroma</i>	26.00	8.23	3.00	4.17	5.91	12.39	8.26
	<i>Vernonanthura patens</i>	27.00	8.54	4.00	5.56	3.06	6.42	6.84
	<i>Allophylus densiflorus</i>	20.00	6.33	2.00	2.78	4.25	8.91	6.01
	<i>Clusia rigida</i>	24.00	7.59	3.00	4.17	2.40	5.03	5.60
	<i>Alnus acuminata</i>	11.00	3.48	3.00	4.17	3.68	7.71	5.12
	<i>Roupala monosperma</i>	18.00	5.70	2.00	2.78	2.60	5.45	4.64
	<i>Mauria peruviana</i>	13.00	4.11	4.00	5.56	1.30	2.73	4.13
	<i>Ferreyranthus excelsus</i>	6.00	1.90	3.00	4.17	0.80	1.68	2.58
2,300–2,500	<i>Aiouea montana</i>	50.00	10.48	4.00	3.01	18.55	15.30	9.60
	<i>Ilex scopulorum</i>	30.00	6.29	4.00	3.01	10.22	8.43	5.91
	<i>Hieronyma oblonga</i>	24.00	5.03	4.00	3.01	7.64	6.30	4.78
	<i>Critiopsis pycnantha</i>	25.00	5.24	3.00	2.26	7.12	5.87	4.46
	<i>Myrcianthes rhopaloides</i>	21.00	4.40	4.00	3.01	4.96	4.09	3.83
	<i>Cyathea austropallescens</i>	25.00	5.24	4.00	3.01	3.53	2.91	3.72
	<i>Clusia multiflora</i>	23.00	4.82	3.00	2.26	4.58	3.78	3.62
	<i>Clethra revoluta</i>	15.00	3.14	4.00	3.01	4.70	3.88	3.34
	<i>Mollinedia lanceolata</i>	19.00	3.98	3.00	2.26	3.02	2.49	2.91
	<i>Cyathea caracasana</i>	16.00	3.35	4.00	3.01	2.40	1.98	2.78
2,500–2,700	<i>Clethra revoluta</i>	34.00	7.85	4.00	3.45	7.13	8.17	6.49
	<i>Clusia hylaeae</i>	21.00	4.85	3.00	2.59	6.70	7.68	5.04
	<i>Hieronyma oblonga</i>	18.00	4.16	4.00	3.45	5.37	6.16	4.59
	<i>Ilex quitensis</i>	29.00	6.70	3.00	2.59	3.70	4.24	4.51
	<i>Hesperomeles ferruginea</i>	28.00	6.47	2.00	1.72	4.07	4.67	4.29
	<i>Alchornea triplinervia</i>	13.00	3.00	2.00	1.72	6.21	7.12	3.95
	<i>Cyathea delgadii</i>	22.00	5.08	3.00	2.59	3.27	3.75	3.81
	<i>Miconia neriifolia</i>	19.00	4.39	3.00	2.59	2.78	3.19	3.39
	<i>Nectandra laurel</i>	15.00	3.46	4.00	3.45	2.83	3.24	3.39
	<i>Myrcianthes myrsinoides</i>	18.00	4.16	2.00	1.72	2.85	3.27	3.05

In contrast, in the 2,100–2,300 m a.s.l. range (S05–S08), greater variability in richness (13–21 species) and a more pronounced reduction in q1 and q2 relative to q0 were observed, particularly in plots S06 and S08. This pattern indicates lower evenness and a

stronger influence of dominant species in SDTF plots at higher elevations. Conversely, montane forests (2300–2,700 m a.s.l.; S09–S16) exhibited the highest alpha diversity values. In plots located between 2,300–2,500 m a.s.l. (S09–S12), species richness (Hill q0)

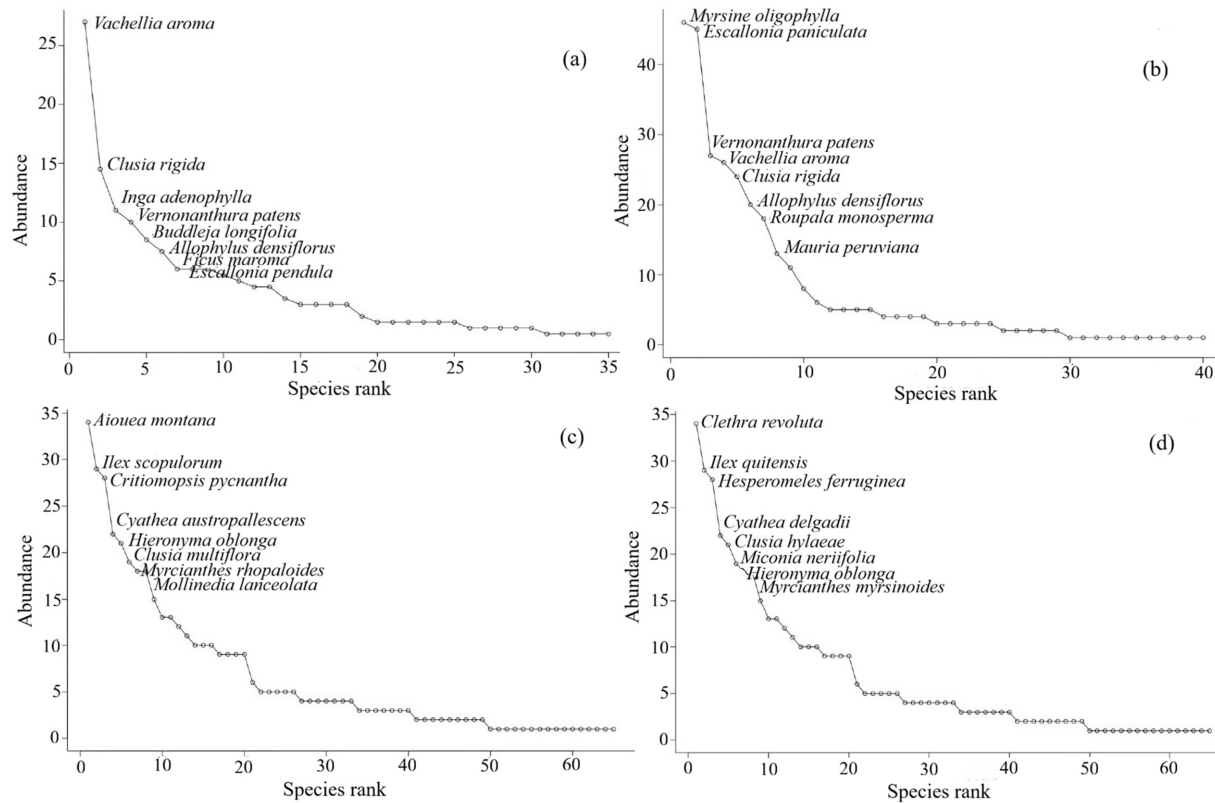


FIGURE 4

Rank-abundance curves of tree species across different altitudinal gradients in the forests of the Sonche district: (a) 1900–2100 m a.s.l., (b) 2100–2300 m a.s.l., (c) 2300–2500 m a.s.l., and (d) 2500–2700 m a.s.l.

TABLE 2 Alpha diversity of tree communities in seasonally dry tropical forests (SDTF) and montane forests in the district of Sonche, Chachapoyas Province, estimated using Hill numbers (q0: species richness; q1: Shannon effective diversity; q2: Simpson effective diversity).

Sampling plots	Hill_q0	Hill_q1	Hill_q2
S01	23	15.8770	10.9523
S02	17	11.3627	7.8671
S03	18	11.1956	7.3359
S04	19	13.7764	10.7761
S05	21	12.9405	8.5765
S06	13	9.3431	7.4377
S07	21	13.1343	9.1721
S08	19	9.3933	5.1941
S09	34	22.5930	15.1595
S10	34	22.3271	13.7778
S11	30	24.1812	20.3636
S12	33	20.9420	14.3949
S13	31	20.3419	14.9695
S14	31	23.5398	18.5274
S15	24	13.1279	8.8259
S16	31	22.7642	18.0505

was high (30–34 species), together with elevated Hill q1 and q2 values, indicating diverse and relatively even communities with moderate dominance. In the upper range, between

2,500–2,700 m a.s.l. (S13–S16), species richness remained comparable (24–31 species), although greater variability in q1 and q2 was observed. Plots such as S14 and S16 showed high evenness, whereas S15 exhibited higher dominance.

Overall, these results indicate a decrease in tree community evenness with increasing elevation in both ecosystems, as well as clear structural differences between SDTF and montane forests.

3.3.2 Beta diversity (similarity)

The analysis of floristic similarity among tree species in the evaluated plots of the forests of the Sonche district, based on the Sørensen index, reveals three well-defined groups (Figure 6). The first group (S01–S07) is associated with lower elevations and SDTF, with a mean similarity of 44% (range: 22–77%). These plots are characterized by lower plant diversity and a higher dominance of a few species, reflecting more homogeneous environmental conditions. The second group (S09–S16) comprises higher-elevation areas and plots located in montane forests, with an average similarity of 43.7% (range: 28–68%). This group is dominated by communities adapted to cold and humid environments, exhibiting high diversity and a relatively even distribution of species. Finally, plot S08 forms an independent group because it is located in a transitional zone, with a mixed floristic composition that combines elements from both groups, representing an intermediate ecosystem with distinct characteristics. Overall, these results demonstrate a clear floristic differentiation associated with altitudinal gradients and local ecological conditions in the forests of Sonche.

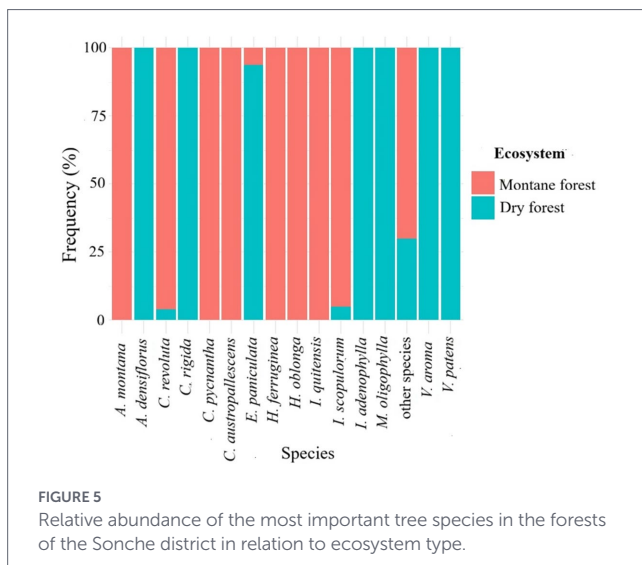


FIGURE 5
Relative abundance of the most important tree species in the forests of the Sonche district in relation to ecosystem type.

3.4 Diametric and altimetric structure of trees

The graphs in Figure 7 show the frequency distribution of trees in the SDTF and montane forests of the Sonche district according to diameter classes. In the SDTF (Figure 7a), the diameter structure exhibits a typical inverted “J” pattern, with a marked dominance of small-diameter individuals. The highest frequency occurs in the 10–15 cm DBH class (409 individuals), followed by the 15–20 cm class (151 individuals). Beyond 20 cm in diameter, abundance decreases sharply, with fewer than 40 individuals in the 20–25 cm class and very low values in diameter classes above 30 cm, indicating a limited representation of large trees and a relatively homogeneous structure.

In montane forests (Figure 7b), a similar structural pattern is observed, although with a wider range of diameter classes. The 10–15 cm class shows the highest frequency (502 individuals), followed by the 15–20 cm (244 individuals) and 20–25 cm (82 individuals) classes. Unlike SDTF, montane forests include individuals in larger diameter classes, reaching up to 45–50 cm, although at low frequencies (<10 individuals). Overall, the results indicate forests structurally dominated by young trees, with differences associated with the ecological conditions of each ecosystem.

Figure 8 presents the histograms of tree height classes for the two ecosystems evaluated in the Sonche district. In the SDTF, a marked dominance of low- to medium-height individuals is observed. The 0–5 m (128 individuals) and 5–10 m (429 individuals) classes account for the highest frequencies, together representing more than 90% of the recorded individuals. In contrast, height classes above 10 m show very low frequencies (<10%), indicating a limited presence of tall trees and reflecting a simple vertical structure dominated primarily by young and developing individuals.

In turn, montane forests exhibit a more complex vertical structure compared to SDTF. The greatest abundance is concentrated in intermediate height classes, particularly 5–10 m (639 individuals) and 10–15 m (141 individuals), which together comprise more than 85% of the recorded individuals. Lower classes (≤ 5 m) also maintain a substantial representation (130 individuals), suggesting continuous recruitment. In addition, the presence of individuals in height classes

above 15 m, although at low frequencies (<10%), indicates greater vertical stratification and a relatively better-developed forest structure.

Floristic-structural variation as a function of the altitudinal gradient Multiple correspondence analysis (MCA) enabled an integrated visualization of the distribution and associations of the ten most dominant tree families in the forests of the Sonche district along the altitudinal gradient and between ecosystem types, simultaneously incorporating individual abundance and structural attributes (diameter and height classes) (Figure 9). The main MCA axes effectively captured the floristic and structural differentiation associated with environmental variation. At lower elevations (1900–2,100 m a.s.l.), Fabaceae and Clusiaceae clustered closely, whereas between 2,100 and 2,300 m a.s.l. a marked association between Asteraceae and Primulaceae was observed, reflecting tree communities dominated by shorter individuals with intermediate diameters. From a structural perspective, this pattern confirms that the water stress characteristic of dry forests constrains vertical tree growth. In contrast, at higher elevations (2300–2,700 m a.s.l.), Lauraceae, Melastomataceae, Clethraceae, and Aquifoliaceae predominated, being associated with trees of larger diameters and greater heights adapted to colder and more humid conditions. Overall, the analysis reveals a gradual segregation of families between ecosystems and along the altitudinal gradient, highlighting elevation and environmental conditions as key determinants of forest composition and structure in the Sonche district.

4 Discussion

The results of this study provide relevant empirical evidence on the ecological role of seasonally dry tropical forests (SDTFs) at altitudinal limits and their transition toward montane forests, a component that has historically been underrepresented in Andean ecological research (Cueva et al., 2019). Although tropical dry forests have been widely recognized for their high functional specialization, pronounced climatic seasonality, and high proportion of endemic species, most studies have focused on latitudinal gradients or lowland environments (Siyum, 2020). In contrast, altitudinal gradients linking these ecosystems with montane forest formations have received limited attention, constraining our understanding of the ecological processes that structure such transitions (Murga-Orrillo et al., 2021).

In the Sonche district, SDTFs exhibited a relatively homogeneous floristic structure, characterized by low tree species richness and strong dominance by a few species, notably *Vachellia aroma*, *Inga adenophylla*, *Clusia rigida*, and *Myrsine oligophylla* (Aguirre Mendoza et al., 2021a, 2021b). This pattern reflects communities dominated by species highly tolerant to water stress (Dirzo et al., 2011; Galván-Cisneros et al., 2023; Rodríguez and Oyuela-Andino, 2023), with high relative density, small to intermediate diameters, and a predominance of young individuals (Montenegro-Hoyos et al., 2022; Ramírez et al., 2022). Consequently, the observed structural dominance suggests a simplified forest organization typical of Andean and Neotropical SDTFs, where a small number of species control most of the space and resources, limiting vertical stratification and promoting rapid regeneration dynamics (Pennington et al., 2000).

The vertical structure of SDTFs further supports this interpretation, as individuals between 0 and 10 m in height predominate. In dry

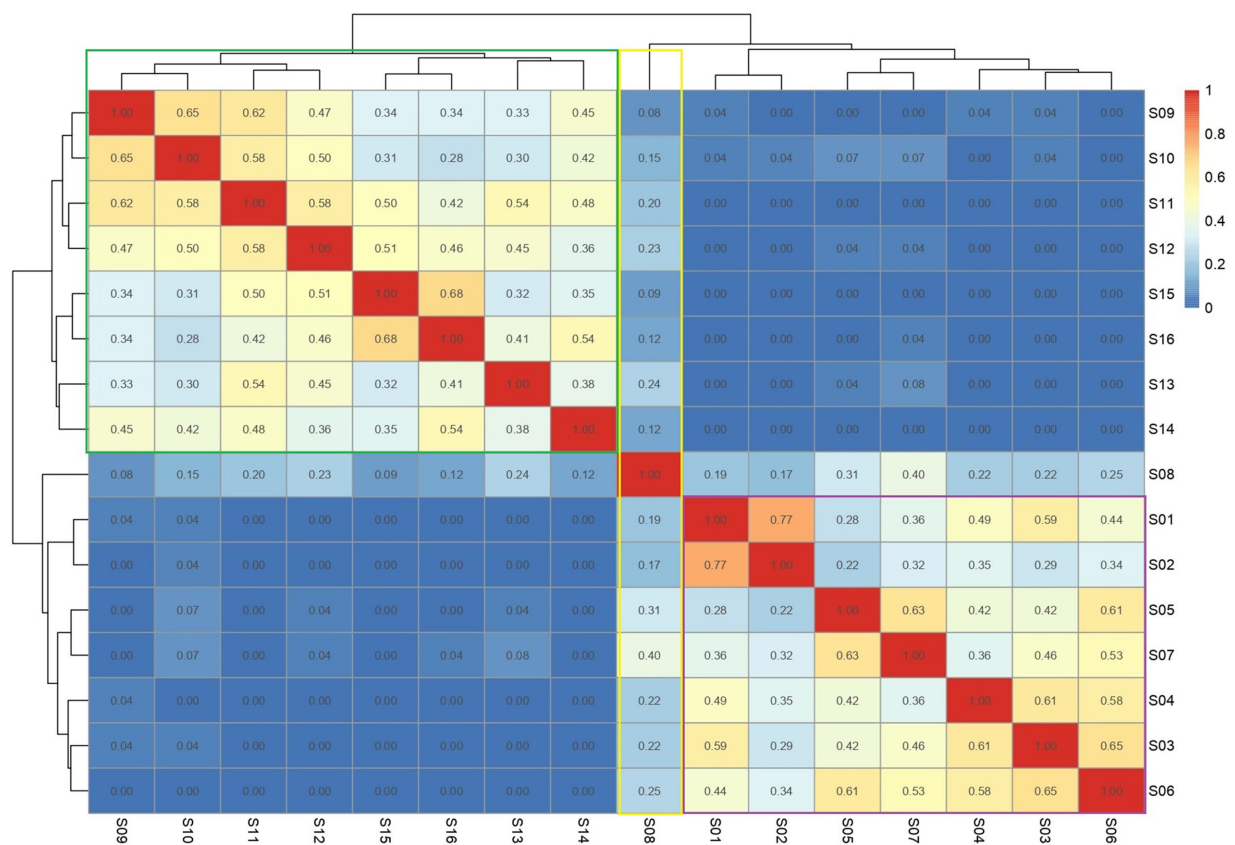


FIGURE 6 Analysis of floristic similarity between plots in the forests of the Sonche district, based on the Sorensen index.

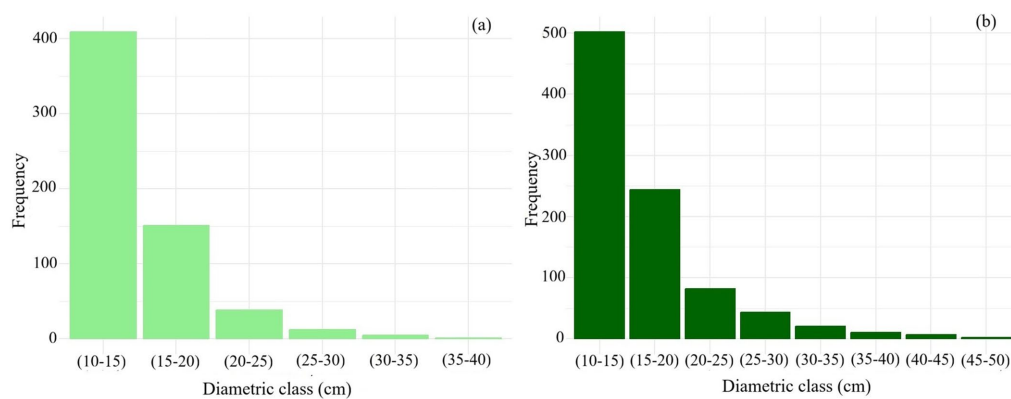


FIGURE 7 Distribution of tree frequency according to diameter in the forests of the Sonche district: (a) diameter class of dry forests, and (b) diameter class of montane forests.

environments, limited water availability constrains vertical stem growth and favors species adapted to seasonal stress conditions (Pennington et al., 2000). These adaptations include functional strategies such as deciduous phenology, small or semi-persistent leaves, and deep root systems that optimize water use but do not necessarily promote the development of tall, complex canopies (Miles et al., 2006). However, this pattern may also reflect continuous recruitment coupled with lower survival of mature trees under prolonged drought conditions. Consistently, the inverted “J-shaped” diameter distribution recorded in SDTFs is characteristic of forests with high

regeneration rates and elevated mortality of large individuals, a pattern widely documented in dry forests across Latin America (Reis et al., 2017).

In contrast, montane forests exhibited greater floristic heterogeneity and more evenly distributed Importance Value Index (IVI) values among multiple species, including *Aiouea montana*, *Clethra revoluta*, *Ilex quitensis*, *Ilex scopulorum*, *Hieronyma oblonga*, and *Clusia multiflora*. This pattern reflects less restrictive environmental conditions, associated with higher precipitation and moderate temperatures (Cueva et al., 2019). Tree species richness peaked

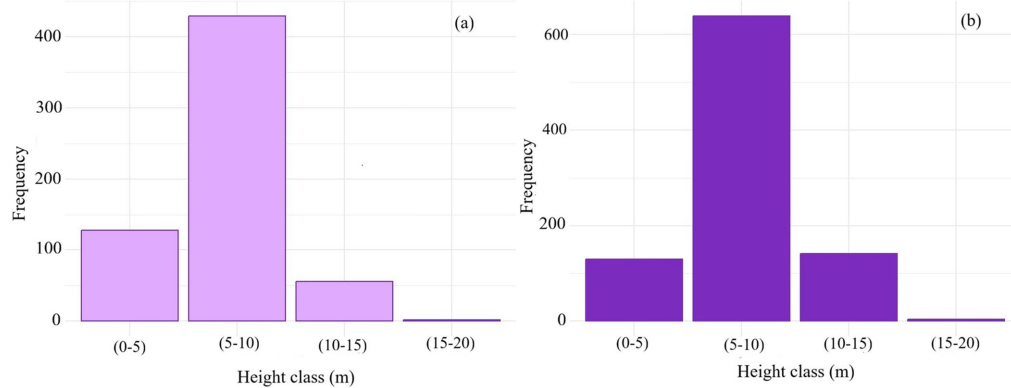


FIGURE 8
Distribution of tree height classes in the forests of the Sonche district: **(a)** height class in dry forests, and **(b)** height class in montane forests.



FIGURE 9
Multiple correspondence analysis (MCA) showing the floristic-structural differentiation of the dominant families according to the altitudinal gradient.

between 2,300 and 2,500 m a.s.l., following a unimodal pattern characteristic of montane ecosystems, where diversity reaches its maximum at mid-elevations (Li et al., 2023). This pattern has been attributed to a combination of favorable climatic conditions, increased moisture availability, and high structural heterogeneity, which facilitate the coexistence of species with both tropical and montane affinities (Sánchez Zamora et al., 2024). Conversely, at elevations above 2,500 m a.s.l., diversity declines progressively due to thermal constraints and more severe environmental filters that limit the establishment of less-adapted species (Bañares-de-Dios et al., 2024).

The transition between SDTFs and montane forests along the altitudinal gradient highlights the central role of water availability and elevation-modulated climatic conditions in shaping forest composition and architecture, in agreement with patterns observed in other Andean gradients (Blundo et al., 2012). Beta diversity analysis using the Sørensen index confirmed a clear floristic differentiation between both ecosystems; however, this transition is not abrupt. Instead, an ecological continuum is evident, where typical dry forest species coexist with montane forest elements, particularly in ecotonal plots such as S08. This pattern of floristic overlap has been widely documented in tropical altitudinal gradients and reflects the interaction of climatic,

edaphic, and topographic factors rather than the presence of rigid environmental thresholds (Veintimilla et al., 2019; Guzmán et al., 2025). In this context, altitude modulates the hydric filters characteristic of dry forests through its interaction with thermal gradients and changes in soil structure, allowing the persistence of mixed communities (Krömer et al., 2013).

From a biogeographic perspective, the tree species composition recorded at altitudinal limits supports the hypothesis that montane dry forests function as contact zones and potential ecological corridors between contrasting bioclimatic regions (Blundo et al., 2012). Nevertheless, most available studies lack spatial designs capable of capturing this complexity, as they are based on isolated plots or inventories without altitudinal continuity (Malizia et al., 2020). In this regard, the scarcity of permanent plots in dry forests of northern Peru limits the assessment of temporal dynamics, species turnover rates, and responses to climatic variability—processes that require continuous sampling along environmental gradients (Baez et al., 2015; Malizia et al., 2020).

Multiple correspondence analysis (MCA) reinforced these patterns by revealing clear associations between dominant plant families and specific environmental conditions. In lower SDTF zones, Fabaceae and Clusiaceae were associated with warm and dry environments, characterized by fast-growing species with efficient water use (Aguirre Mendoza et al., 2021a, 2021b; Galván-Cisneros et al., 2023). At intermediate elevations, Asteraceae and Primulaceae were linked to smaller-stature trees, suggesting nutrient limitations that constrain structural development (Montenegro-Hoyos et al., 2022). In montane forests, Lauraceae, Melastomataceae, Clethraceae, and Aquifoliaceae dominated the floristic composition, reflecting adaptations to cold and humid environments and to organic matter-rich soils (Tejedor Garavito et al., 2014; Guzmán et al., 2022).

From a conservation perspective, our results support a shift toward strategies that recognize the altitudinal gradient as an integrated ecological unit, in which the conservation of SDTFs and montane forests is complementary for maintaining connectivity, ecosystem resilience, and the provision of ecosystem services under climate change (Killeen and Solorzano, 2008). The conservation of ecological corridors between 1900 and 2,700 m a.s.l. is a priority to facilitate species movements and altitudinal range shifts associated with global warming (Meza Mori et al., 2020; Meza-Mori et al., 2025). SDTFs are not merely the lower end of the altitudinal gradient, but rather a distinct and vulnerable component of the Andean ecological system, structured by restrictive environmental conditions that favor communities dominated by a few drought-adapted species (Pennington et al., 2009). Their degradation would have disproportionate effects on landscape connectivity, hydrological regulation, and the ecological stability of the entire system (Miles et al., 2006; Malhi et al., 2014; Dryflor et al., 2016).

Likewise, the values of the Importance Value Index (IVI) provide a robust empirical basis for linking observed structural patterns with concrete actions in ecological restoration and climate change adaptation. In the 1900–2,100 m a.s.l. range (seasonally dry tropical forest), low diversity and high dominance of *Vachellia aroma* and *Inga adenophylla* reflect functionally simplified communities that are nonetheless critical for system stability. Their high abundance, drought tolerance, wide distribution, and capacity for biological nitrogen fixation (Bax et al., 2021) make them priority candidates for the revegetation of degraded soils and for facilitating the establishment of less stress-tolerant species (Fremout et al., 2021; de Araújo et al., 2024). However, these species are highly vulnerable to the projected increase in the

duration and intensity of dry periods, which may increase mortality and reduce natural regeneration (Campo et al., 2023). In the transitional zone between 2,100 and 2,300 m a.s.l., the pronounced ecotonal character is expressed in a relatively balanced community structure, indicating high sensitivity to relatively small changes in temperature and precipitation at the climatic boundary between dry and montane forests (Elsen et al., 2018). In the mid-montane forest (2300–2,500 m a.s.l.), where the unimodal peak of diversity is concentrated, climate vulnerability increases due to the dominance of species adapted to environmentally stable conditions, with low thermal variability and predictable hydrological regimes (Gillani et al., 2025). Furthermore, in the high montane forest (2500–2,700 m above sea level), species adapted to cold and humid climates face a high risk of local extinction due to the lack of available altitudinal space to migrate in the face of the upward shift of climatic niches (Mata-Guel et al., 2023).

Finally, this study presents limitations that should be considered when interpreting the results. Increased sampling effort would improve the representativeness of tree diversity, particularly in transition zones between SDTFs and montane forests (Chao et al., 2014). Moreover, the absence of soil analyses and biomass estimates constrains our understanding of the functional processes regulating forest structure and productivity (Pan et al., 2011; Poorter et al., 2015). Future research should integrate edaphic variables, carbon stocks, and population dynamics to more accurately assess the ecological resilience of these ecosystems under climate change.

5 Conclusion

This study demonstrates that tree diversity along the altitudinal gradient in the district Sonche does not follow a non-linear pattern, but rather a unimodal one, with a maximum between 2,300 and 2,500 m a.s.l., near the transition zone between SDTF and montane forest. In this context, this diversity peak, together with the systematic shifts in species dominance, confirms the existence of a well-defined altitudinal floristic succession and a high level of structural complexity within the ecosystem. Furthermore, our results allow a precise identification of both the most sensitive segments of the gradient and the structurally most important species, which are simultaneously the most vulnerable to climate change. At lower elevations (1900–2,100 m), communities dominant by *Vachellia aroma* and *Inga adenophylla* which are key to the stability of the SDTF, are highly sensitive to the projected increase in the duration and intensity of dry periods, potentially increasing mortality and limiting regeneration. Similarly, in the mid-montane forest (2300–2,500 m), where the diversity maximum is concentrated, dominant species adapted to historically stable environmental conditions show high vulnerability to rising temperatures and changes in precipitation seasonality. Finally, in the upper montane forest (2500–2,700 m), strictly montane species that sustain canopy structure under cold and humid climates face a high risk of local extinction due to the lack of available altitudinal space for upward migration. Taken together, we propose that conservation should focus on the entire altitudinal gradient as an integrated functional unit, as the loss of dry forest at lower elevations or montane forest at higher elevations would compromise ecological integrity, landscape connectivity, and the provision of ecosystem services throughout the system.

Data availability statement

The original contributions presented in the study are included in the article/[Supplementary material](#), further inquiries can be directed to the corresponding authors.

Author contributions

EC-C: Methodology, Writing – review & editing, Writing – original draft, Investigation, Conceptualization. EP-M: Formal analysis, Methodology, Data curation, Writing – review & editing. RR: Conceptualization, Writing – review & editing, Methodology, Formal analysis, Investigation, Data curation, Validation. JC: Software, Methodology, Writing – review & editing. AD: Methodology, Writing – review & editing, Software. MO-C: Supervision, Writing – review & editing, Resources, Funding acquisition. AH-P: Project administration, Writing – review & editing, Methodology, Writing – original draft.

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/ffgc.2026.1765957/full#supplementary-material>

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