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RESEARCH

Exploring plant α- and β-diversity patterns along tropical altitudinal gradients in the Southern Andes of Ecuador: a potential pathway to biodiversity conservation

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Abstract
The Tropical Andes provide ideal opportunities to study diversity patterns along altitudinal gradients. However, they remain poorly characterized, particularly in terms of detailed, ground-level data. The α- and β-diversity trends of vascular plants were studied along an altitudinal gradient from 1000 to 4200 m in the Jubones and the Cajas National Park areas, located in southern Ecuador, using stratified sampling transects to generate floristic inventories with 146 sampling points surveyed in total. This gradient included dry tropical forests restricted to inter-Andean valleys, montane forests, páramo, and *Polylepis* Ruiz & Pav. forests. A total of 891 species belonging to 391 genera and 118 families were recorded. Our findings for all plant species revealed a clear hump-shaped richness pattern, with peaks between 2800 and 3500 m with high endemism (13.6%). β-diversity was highest at lower elevations, then decreased with altitude. Marked variations in the diversity patterns were found with in-depth observations of the different growth forms of trees, shrubs, and herbs. Climatic factors such as temperature and precipitation were key determinants of species composition among the studied regions. Understanding diversity distribution in these regions is critical for predicting future plant refugia and developing effective conservation strategies in the face of climate change.

Keywords Andes · Biodiversity refugia · The Cajas National Park · The Jubones Valley

Introduction

Across mountain regions, the interactions among climatic factors (temperature, precipitation, atmospheric pressure, etc.) strongly influence the distribution and abundance of plant species and therefore determine the overall productivity of an altitudinal gradient and its

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biodiversity levels (Gentry 1988; Rahbek et al. 2019). Particularly, biodiversity data collected along altitudinal gradients will also reflect the combined effects of regional peculiarities (meso- and microclimate, geology, geomorphology, etc.) with the general altitudinal phenomena (Gentry 1988; Körner 2007; Gentili et al. 2013). Consequently, the pattern in which plant species richness changes with altitude can exhibit various shapes. Specifically, a hump-shaped curve with maximum richness at mid-altitudes was observed on a mountain in Norway (Grytnes et al. 2006), in the grassland pastures of the European Alps (Fontana et al. 2020), in dryland ecosystems in China (He et al. 2023), or in the tropical and subtropical forests in northwest South America (Malizia et al. 2020). Other patterns include a linear decline, as seen in high-altitude alpine regions (Sekar et al. 2023), the high tropical Andes (Cuesta et al. 2017), or in temperate and tropical montane forests (Gentry 1988; Homeier et al. 2010); and even a U-shaped pattern as identified for herbs in some temperate mountain regions (Zhang et al. 2016). Overall, it has been demonstrated that understanding the distribution of species diversity along altitudinal gradients is crucial for conservation, as patterns are often driven by environmental constraints and/or anthropogenic pressures. In addition, the possible presence of endemic species in such systems can highlight their evolutionary importance and conservation value (Di Musciano et al. 2024).

The Tropical Andes are among the regions with the highest plant diversity in the world (Pérez-Escobar et al. 2022), with approximately 45,000 plant species (Myers et al. 2000), ~ 15% of the global total, accounting for only 1% of the world's surface area (Pennington et al. 2010). This hyper-diversity and the unusual presence of endemic species are related to these mountain systems' complex topography and biogeographic history (Richter et al. 2009; Pennington et al. 2010). The timing and rate of Andean uplift have been highly uneven across its range, influencing regional climate, hydrological conditions, nutrient cycling, landscape development, and thus potential plant evolution mechanisms at a continental scale (Pérez-Escobar et al. 2022). For these reasons, the Andes mountains of South America are considered privileged sites for understanding ecosystem and ecological function along with variations in biodiversity, particularly by investigating altitudinal gradients (Malhi et al. 2010; Rahbek et al. 2019).

It is well known that Tropical Andes are characterized by high floristic β-diversity, which is partly related to the high diversity of the ecological communities in these environments and the presence of plant species with narrow geographic ranges and high habitat specialization (Gentry 1988; Quintana et al. 2017a; Cuesta et al. 2017; Rahbek et al. 2019). To date, most studies have highlighted peaks in diversity at intermediate altitudes along the Andean mountains. For example, Kessler (2001) described a hump-shaped curve for some plant families in the Bolivian Andes, with peaks at mid-elevations or constant values from the lowlands to mid-elevations, followed by a marked decline at high elevations. Similar patterns have been observed in other studies across the Andes, although differences in the elevation of the maximum peak richness have been recorded (Kessler 2000; Krömer et al. 2005; Salazar et al. 2013). In contrast, studies of trends in specific growth forms along altitudinal gradients have revealed discordant patterns. For example, Gentry (1988) reported a linear decrease in woody plant richness with altitude in Andean forests, from the lowland tropics (1500 m) to near the tree line (3100 m). Similarly, Cuesta et al. (2017) demonstrated a clear decline in species richness with increasing elevation (from 3200 to 5500 m) in highland Andean ecosystems, including Puna and Páramo species. In contrast, Cueva et al. (2019) reported a linear increase in the number of tree species in the Andean dry forests of Ecuador with elevations from 1700 to 2500 m.

It is unclear whether a general relationship exists between species richness and elevation under tropical montane conditions, given their variability in terms of climatic, topographic,

and altitudinal gradients (Kessler 2000). Published studies have captured only a small portion of the biodiversity patterns present in the tropical Andes. Specifically, studies in southern Ecuador have been limited to a few altitudinal ranges or only woody plants, particularly trees (Gentry 1988; Cabrera et al. 2019; Cueva et al. 2019; Jadán et al. 2021), even though most vascular plants in tropical areas generally belong to non-tree growth forms (Jørgensen and León-Yánez 1999). Overall, comprehensive studies on elevational gradients based on all growth forms (herbs, shrubs, and trees) have not yet been conducted in this region. Consequently, understanding α- and β-diversity patterns in under-explored mountain areas—characterized by diverse altitudinal and environmental conditions—is crucial for predicting future shifts in plant distribution during a period of global climate change that threatens biodiversity worldwide (Parolo and Rossi 2008; Malhi et al. 2010; Cuesta et al. 2017; Tovar et al. 2022).

In the present study, the diversity patterns of vascular plants were investigated along an altitudinal gradient spanning two important regions of the southern Ecuadorian Andes, providing a baseline for future studies on biodiversity trends. According to the IUCN (2024), such areas should be of special conservation interest, as nearly 76% of the recorded endemic species are classified under some threat category. α- and β-diversity patterns of trees, shrubs, and herbaceous species were analysed across elevations from 1000 to 4200 m – from 1000 to 3000 m in the Jubones Valley and from 3300 to 4200 m in the Cajas National Park (CNP). These two areas encompass several Andean ecosystems, including dry tropical forests restricted to inter-Andean valleys, montane forests, *Polylepis* Ruiz & Pav. forest, and high-elevation grasslands-páramo. Specifically, this study attempts to answer the following questions: 1) How does vascular plant species richness (α-diversity) change along the altitudinal gradient within the target areas? 2) Are there differences in β-diversity among altitudinal levels from low to high elevations? 3) How do α- and β-diversity patterns along altitudinal gradients change by growth forms (trees, shrubs, and herbs)? 4) What are the main climatic constraints associated with these variations?

Materials and methods

Study area

The study was carried out in the Andean mountains of southern Ecuador in the province of Azuay and the northern part of Loja province (Fig. 1). Floristic data were collected in 146 sampling points distributed in the important conservation areas of Cajas National Park (CNP; 2°50' S/79°13' W, WGS84) and Jubones Valley (3°20' S/79°18' W, WGS84).

The Jubones Valley is located in a special area of the Andes within the transitional zone between the Northern Andes and the Central Andes, known as the "Amotape-Huancabamba" depression (Weigend 2002). The sampling points in the Jubones Valley were located in dry tropical forests restricted to inter-Andean valleys, one of the least studied ecosystems in Ecuador (Quintana et al. 2017a). At the lowest elevations, seasonal climate variations encourage the growth of deciduous species and cacti such as *Espostoa frutescens* Madsen and *Armatocereus godingianus* (Britton & Rose) Backeb. Here, there is a scarcity of perennial grasses while shrubs dominate, and only a few tree species grow, such as *Vachellia macracantha* (Humb. & Bonpl. ex Willd.) Seigler & Ebinger, *Tara spinosa* Britton & Rose, and *Tecoma stans* (L.) Juss. ex Kunth. From 2100 to about 2400 m, there is a transitional vegetation zone adapted to increasingly humid conditions. Above 2400 m, the

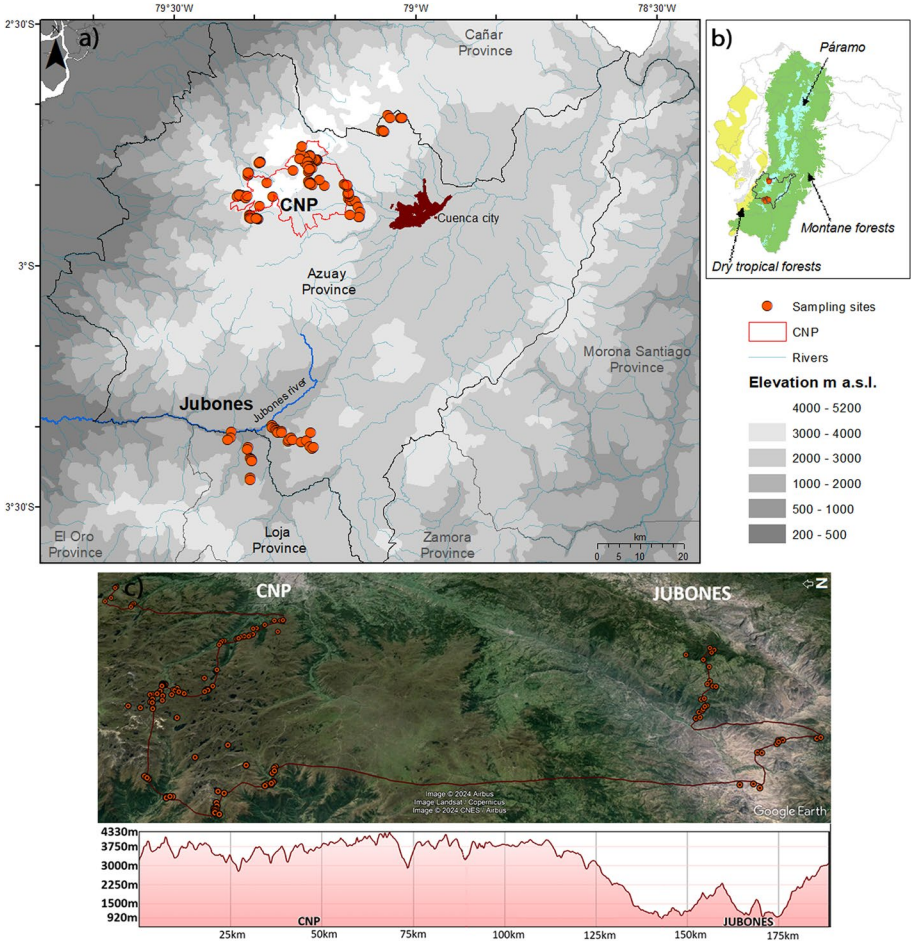


Fig. 1 Map of the study area, **a)** showing the distribution of the146 sampling points (orange dots) along the altitudinal gradient from 1000 to 4200 m, in the Jubones Valley (1000 to 3000 m) and CNP (3300 to 4200 m) in the southern Ecuadorian Andes, **b)** regional context map highlighting the vegetation zones covered within the sampling points, light blue (páramo), ligth green (montane forest), and yellow (dry tropical forest), **c)** elevation profile showing the vertical distribution of all sampling points across the gradient

montane forest appears, similar to that described in the CNP (Fig. 2a). In the CNP, sampling was conducted in montane forests dominated by trees that can reach 15 m in height, such as *Hedyosmum cumbalense* H.Karst., *Weinmannia fagaroides* Kunth, *Myrcianthes rhopaloides* (Kunth) McVaugh, and *Ocotea infrafoveolata* van der Werff. Genera such as *Miconia* Ruiz & Pav., *Viburnum* L., and *Piper* L. characterized the subcanopy (Minga et al. 2021). Páramo hosts plant species adapted to extreme climatic conditions and is dominated by tussocks such as *Calamagrostis intermedia* (J. Presl) Steud. or species such as *Plantago* L. spp. that can form rigid cushions, along with shrubs belonging to the genera *Gynoxys* Cass., *Diplostephium* Kunth, and *Baccharis* L. The genus *Polylepis*, endemic to the Andes, is the only tree that forms forested patches above 3400 m (Minga et al. 2016; Romoleroux et al. 2019; Ansaloni et al. 2022). These forest patches were also sampled in the study reported here (Fig. 2b).

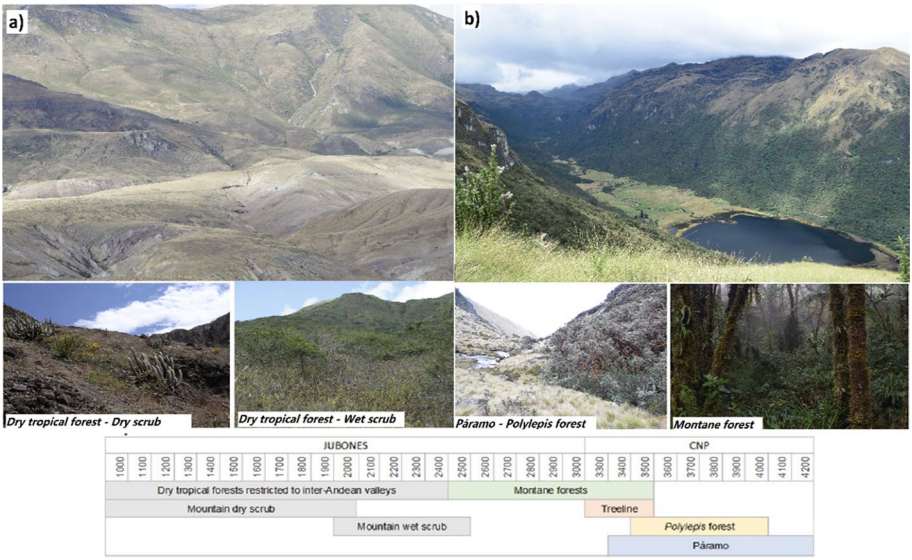


Fig. 2 Vegetation types sampled along the altitudinal gradient from 1000 to 4200 m in the southern Ecuadorian Andes, **a)** Jubones Valley (1000 to 3000 m), with dry tropical forest restricted to inter-Andean valleys, **b)** CNP (3300 to 4200 m), with páramo, *Polylepis* and montane forests. Below, a schematic diagram illustrates the vegetation types

As described, the vegetation of the Jubones region changes progressively with increasing altitude, transitioning into montane forest and converging with the vegetation of the CNP on the western side. Therefore, we consider the sampling points from both regions as part of a continuous altitudinal gradient in order to capture the greatest possible variation in vegetation types and plant species for studying altitudinal patterns in our study area.

In the Jubones Valley, the soils are formed from rhyolitic rocks, which are rich in siliceous sediments and have a pH of 6—7 (Hall and Calle 1982). The climate ranges from arid to humid. Below 2000 m, it is highly seasonal, with annual precipitation of around 1100 mm and marked dry seasons lasting between 5 and 6 months. During this dry season, the precipitation can remain below 100 mm, resulting in a desert-like climate. The annual temperature in this area varies from 15 °C to 28 °C (Hasan and Wyseure 2018). The CNP consists of volcanic-origin soils with high organic matter content (20%), acidic pH, high porosity, and high water retention capacity. The annual precipitation ranges from 800 to 1300 mm. The temperatures within this area show strong diurnal variation with average daytime temperatures between 6 °C and 18 °C around 3000 m and between 3 °C and 6 °C at about 4000 m. Temperatures below 0 °C occasionally occur above 4100 m throughout the year (Ansaloni et al. 2022).

Floristic sampling

Fieldwork was conducted in CNP from January to June 2016 and in the Jubones Valley from January to September 2017 – 2018. A total of 146 sampling points were established between 1000 and 4200 m elevation (Table 1), restricted to areas with minimal human

Table 1 Summary of the sampling units across the altitudinal gradient, including the number of transects and subplots surveyed within each altitudinal band, and quadrant data obtained from previous regional surveys

	Altitudinal bands m a.s.l																				
	Jubones Valley																				
	1000	1100	1200	1300	1400	1500	1600	1700	1800	1900	2000	2100	2200	2300	2400	2500	2600	2700	2800	2900	3000
Transects	1	4	1	2	1	2	3	2	2	3	1	1	1	1	1	1	1	1	1	1	1
Subplots	10	40	10	20	10	20	30	20	20	30	10	10	10	10	10	10	10	10	10	10	10
Quadrants	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

	Altitudinal bands m a.s.l									
	CNP									
	3300	3400	3500	3600	3700	3800	3900	4000	4100	4200
Transects	2	4	14	14	15	11	2	4	-	-
Subplots	20	40	140	140	150	110	20	40	-	-
Quadrants	-	-	-	-	7	20	10	4	5	2

disturbance. Elevations below 1000 m were excluded because the lowest part of the Jubones Valley (~ 700 m) has been highly degraded by human activities over time (e.g., logging). The elevations between 3100 and 3200 m were not sampled due to the limited accessibility of well-preserved vegetation fragments.

At each sampling point, we established 50 × 10 m stratified transects (Fig. S1). Trees (DBH ≥ 2.5 cm) were recorded within the entire transect area (500 m^2). Within this main transect, subplots were systematically placed along its length to sample other growth forms. Shrubs (perennial woody plants ≥ 50 cm in height) were recorded in ten 5 × 2 m subplots (10 m^2), totalling 100 m^2 per transect. Herbaceous species were recorded in ten 1 × 1 m subplots (1 m^2), totalling 10 m^2 per transect. Due to high stem density and clonality, shrub abundance was quantified by visually estimating the percentage cover (%) per subplot. Herb abundance was estimated using the Braun-Blanquet cover-abundance scale (Braun–Blanquet 1979). Epiphytic growth forms were not included, as the sampling design was unsuitable for capturing them.

To improve the representation of vegetation at the highest elevations (3700 – 4200 m) in CNP, we incorporated additional unpublished data from quadrants (3 × 3 to 5 × 5 m) from previous regional surveys, representing 42% of the total sampling points in the CNP (Table 1).

Species were identified and deposited in the collections of the Herbarium of the University of Azuay (HA), Cuenca, Ecuador. The classification system adopted follows the Angiosperm Phylogeny Group (APG IV 2016). The endemic status of the recorded species was determined based on the Red Book of Endemic Plants of Ecuador (León-Yánez et al. 2011) and Tropicos (2024).

Environmental data

To identify the main bioclimatic factor shaping the altitudinal trends in the study area, the following bioclimatic data was extracted: temperature (°C), precipitation (mm), and solar radiation (kj m^{-2} day^{-1}) (see Fig. S1), from the WorldClim version 2.1 dataset (Fick and Hijmans 2017) at a spatial resolution of 30 s ≈ 1 km^2). To obtain slope and aspect data, a digital elevation model (DEM) was built to generate slope and aspect maps in ArcGIS 10.6.1.

Data analysis

For the analyses, the 146 sampling points distributed along the 1000 – 4200 m altitudinal gradient, along with the additional dataset (> 3700 m), were grouped into 100—m altitudinal bands. This allowed to perform a synthesis of altitudinal biodiversity data (Gentili et al. 2013; Sekar et al. 2023). In total, 31 altitudinal bands were defined (1000 – 3000 and 3300 – 4200 m), each containing a variable number of transects and, consequently, subplots (Table 1).

Analysis of α- and β-diversity patterns by growth form: trees, shrubs, and herbs

Patterns of α- and β-diversity were analysed separately for each growth form: trees, shrubs, and herbs, using abundance matrices based on the number of individuals for trees and percent cover for shrubs and herbs.

Because different ecological processes can drive biodiversity patterns at different spatial scales, and overlooking one scale may lead to incomplete or biased interpretations (Chase and Knight 2013; Tello et al. 2015), we analysed the α- and β-diversity patterns of each growth form at two spatial scales. At a small scale, we calculated diversity among individual transects (n = 146) within each altitudinal band to capture species richness and heterogeneity within each band. At a large scale, we pooled the species composition of all transects within each altitudinal band (n = 31) to calculate diversity between bands.

Since differences in sampling effort (i.e., varying numbers of transects per altitudinal band) could influence the observed diversity patterns, we applied the individual-based rarefaction method of Gotelli and Colwell (2001) at both spatial scales. Rarefied species richness was calculated by resampling (1000 times) the abundance matrices to a fixed number of individuals (for trees) or a fixed percent cover (for shrubs and herbs). The specific values for individual or cover varied depending on the spatial scale (see Online Resource 2). As another metric of alpha diversity, we calculated the exponential Shannon index using the formula: $\exp(H\prime) = exp\left(-\sum_{i=1}^{S} p_i \ln p_i\right)$, where S is the total number of species in the community, and p_i is the proportion of individuals of the species i (Jost 2007).

Beta diversity was calculated using the Bray–Curtis dissimilarity index with the "betapart" package in R (Baselga and Orme 2012), by computing pairwise dissimilarities between individual transects (small scale) and altitudinal bands (large scale). The resulting mean dissimilarity values were then used to fit the GAMM models. We compared the observed and expected β-diversities under a null model, following Tello et al. (2015). This null model maintains the number of species and their abundance distribution while randomizing the spatial location of species occurrences among transects within each altitudinal band at the small scale, and among altitudinal bands at the large scale. We ran 999 randomizations on the rarefied matrices. The mean β-diversity values from the null distributions were compared with the observed values at each spatial scale. The difference was then divided by the standard deviation of the null distribution to calculate standardized effect sizes (SES), representing the degree to which β-diversity deviates from the null expectation.

To reveal the patterns of α- and β-diversity along the altitudinal gradient, we modelled rarefied species richness, exponential Shannon diversity, and Bray–Curtis dissimilarity as functions of elevation. We employed generalized additive mixed models (GAMMs) to account for the expected non-linear responses of diversity metrics and to accommodate the hierarchical structure of our sampling design (Wood 2006; Zuur et al. 2009). Models were fitted using the "mgcv" package in R (Wood 2011). To account for non-independence among sampling units, site (Jubones and CNP) was included as a random effect in the large-scale analyses, while altitudinal bands were treated as random effects in the small-scale models. To account for the nature of the response variables, we employed Quasi-Poisson error distributions for species richness (count data) to handle overdispersion where necessary. For continuous variables, such as the exponential Shannon index and β-diversity indices, a Gaussian distribution with a log-link function was applied after verifying the normality of residuals. In all models, we implemented regression splines as smoothers.

Models were fitted separately for each diversity metric, growth form, and spatial scale.

Analysis of α- and β-diversity patterns for total vascular plant species

To assess total vascular plant α- and β-diversity, we integrated all growth forms (trees, shrubs, and herbs) into a single dataset, due to disparities in abundance metrics (e.g.,

number of individuals for trees and percentage cover for shrubs and herbs). Specifically, we built a presence/absence matrix to standardize the data and ensure comparability. The α-diversity was estimated using area-based rarefaction; because the sampled area differed among growth forms, species richness was scaled to the minimum sampling unit (10 m^2). We then calculated β-diversity using the Sørensen dissimilarity index, which is specifically suited for binary data. These metrics were then used to fit the GAMM models to examine diversity patterns along the altitudinal gradient. Additionally, we performed the partitioning of total β-diversity into its two additive components, turnover and nestedness (Baselga et al. 2025).

Endemism of species

The number of endemic species was plotted in a heatmap to represent their richness across each altitudinal band (from 1000 to 4200 m). This was performed for all plant species, as well as independently for each growth form (trees, shrubs, and herbs).

Influence of environmental drivers on species composition

To test the influence of environmental drivers on changes in species composition across transects, we performed a canonical correspondence analysis (CCA) for total species as well as for each growth form separately. The subset of environmental variables used was selected based on a combination of Pearson's correlation coefficient to reduce the degree of multicollinearity. The least correlated environmental variables were chosen with a correlation index below 0.75, such as mean temperature (°C), annual precipitation (mm), mean solar radiation (kJ m^{-2} day^{-1}), slope (degrees), and aspect (degrees), designated as relative east aspect (sine of aspect) and relative north aspect (cosine of aspect). The Monte Carlo permutation test was performed to assess the significance of ordination axes. The CCA analysis was carried out using CANOCO version 4.5 (Lepš and Šmilauer 2003).

Results

A total of 891 vascular plant taxa—comprising 123 tree species, 239 shrub species, and 529 herb species—belonging to 391 genera and 118 families were recorded across 146 sampling points along an altitudinal gradient from 1000 to 4200 m in the Jubones Valley (1000–3000 m) and the CNP (3300–4200 m) (Fig. 3a; Table S1). The Jubones Valley accounted for a total of 380 species, belonging to 234 genera and 91 families. In terms of growth forms, herbs contributed to the highest α-diversity in terms of number of species (48%), followed by shrubs (31%) and trees (21%) (Fig. 3a-b). The families exhibiting the highest number of species were Asteraceae, Poaceae, Fabaceae, Solanaceae, and Malvaceae, which together represented around 30% of the total sampled species. The CNP encompassed a total of 569 species, belonging to 238 genera and 86 families. Herbaceous species represented 65% of the total α-diversity, followed by shrubs (24%) and trees (11%) (Fig. 3a-b). The families exhibiting the highest number of species were Asteraceae,

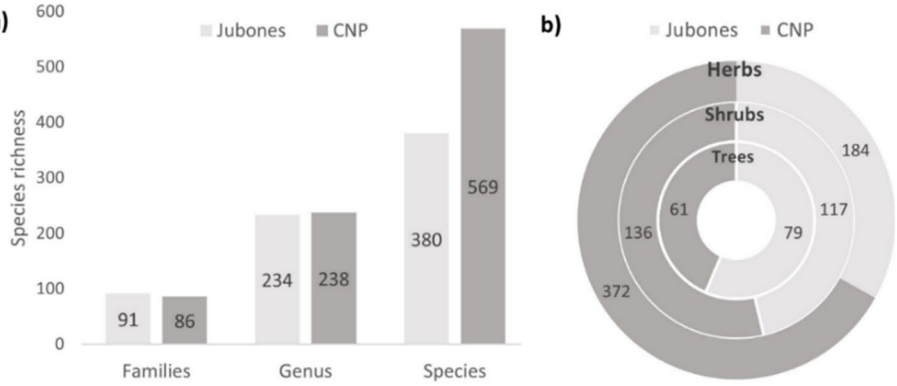


Fig. 3 Number of vascular plant species by taxonomic level and growth form, **a)** number of families, genera, and species, and **b)** total number of species by growth form (trees, shrubs and herbs) recorded in the Jubones Valley (1000 to 3000 m) and CNP (3300 to 4200 m) in the southern Ecuadorian Andes

Poaceae, Cyperaceae, Rosaceae, and Melastomataceae, comprising 41% of the total number of species.

α- and β-diversity patterns by growth form

The GAMM models calculated for the different growth forms revealed distinct patterns. For trees, a hump-shaped pattern was observed, with the highest richness occurring around 2700–3000 m. In contrast, the lowest richness was found at both ends of the altitudinal gradient, between 1000–1500 m and 3800–4200 m. At the larger scale, the overall pattern remained the same, although the peak shifted slightly, expanding to a broader range between 2700 and 3500 m. The exponential Shannon index followed the same patterns as previously described (Fig. 4; Table S2).

Shrub species exhibited a bimodal pattern along the altitudinal gradient, reflecting two peaks present in the two investigated regions. At the small scale, shrubs showed two slight diversity peaks around 1700–2000 m and 3200–3500 m. This bimodal pattern became more pronounced at the large scale, where both peaks were more clearly defined. The first peak occurred between 1600–1900 m, while the second peak at higher elevations (3400–3600 m) reached the highest overall diversity values. This pattern was consistent for both species richness and exponential Shannon diversity (Fig. 4; Table S2).

Herbaceous species richness exhibited a scale-dependent pattern along the altitudinal gradient. At the small scale, richness showed a unimodal trend with a peak between 2900 and 3400 m. In contrast, at the larger scale, a bimodal pattern emerged, with peaks around 1400–1800 m and a more pronounced peak between 3400 and 3800 m. The exponential Shannon diversity index followed a similar pattern (Fig. 4; Table S2).

The β-diversity analysis, based on the Bray–Curtis dissimilarity index, conducted between each pair of transects (small scale) and between each pair of altitudinal bands (large scale), revealed distinct patterns for trees, shrubs, and herbs. However, each growth form exhibited similar β-diversity trends across both spatial scales, with overall higher β-diversity observed at the small scale.

The β-diversity pattern for trees at both spatial scales showed an inverted hump-shaped curve, with the lowest values occurring at mid-elevations (2400–2900 m). In contrast, the

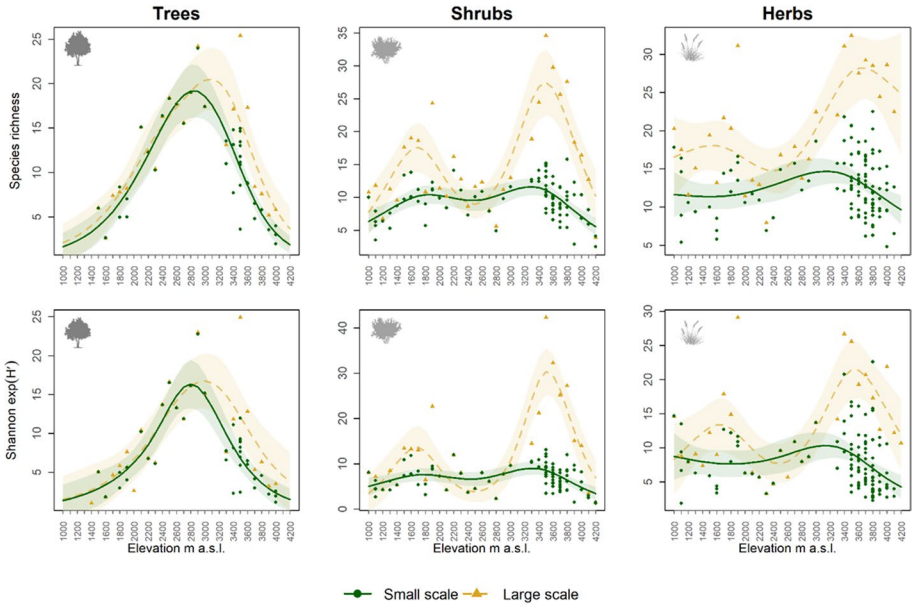


Fig. 4 Altitudinal patterns of α-diversity for trees, shrubs, and herbs at both small and large scales, along an altitudinal gradient from 1000 to 4200 m in the southern Ecuadorian Andes (Jubones Valley from 1000 to 3000 m; CNP from 3300 to 4200 m). The graphs depict the smoothed relationships between rarefied species richness and the exp-Shannon diversity index with elevation, obtained by fitting GAMMs. The shaded areas represent the 95% confidence intervals

highest β-diversity was observed at lower elevations, followed by slightly lower—but still elevated—values at higher elevations. Shrubs exhibited an unimodal β-diversity pattern along the altitudinal gradient. At the small scale, dissimilarity peaked between 2200—2800 m, whereas at the large scale, the peak shifted slightly higher, emerging around 2800 and 3200 m. At both scales, β-diversity declined around 3200 m. Herbaceous species showed a scale-dependent β-diversity pattern. At the small scale, dissimilarity reached its maximum values between 2000 and 2600 m, followed by a marked decline above 2800 m. At the large scale, this pattern was much less pronounced, showing a slight increase around 2200—2800 m (Fig. 5; Table S3).

The null model analysis revealed that observed β-diversity was consistently higher than expected under the null distribution across both spatial scales and for all growth forms (see Table S5). Standardized effect sizes (SES) were markedly higher at the large scale (SES = 46.36 for trees, SES = 52.90 for shrubs, and SES = 52.85 for herbs) than at the small scale (SES = 23.14 for trees, SES = 37.87 for shrubs, and SES = 41.62 for herbs).

α- and β-diversity patterns for total vascular plant species

Regarding α-diversity, the GAMMs calculated for all vascular plant species at the small scale revealed a hump-shaped pattern, with the highest richness peak between 2800—3500 m, whereas the lowest values were recorded at both extremes of the altitudinal gradient, particularly at 1100—1400 m (Jubones Valley) and at 3900—4200 m (CNP) (Fig. 6; Table S4). In contrast, total β-diversity followed a different trend. High dissimilarity values

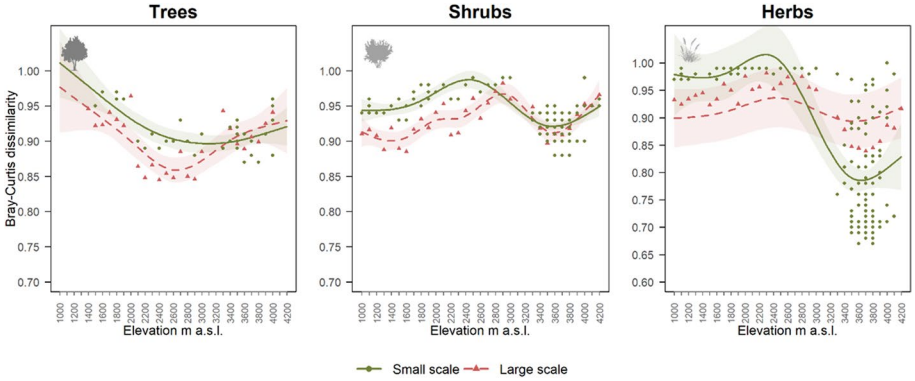


Fig. 5 Altitudinal patterns of β-diversity for trees, shrubs, and herbs at both small and large scales, along an altitudinal gradient from 1000 to 4200 m in the southern Ecuadorian Andes (Jubones Valley from 1000 to 3000 m; CNP from 3300 to 4200 m). The graphs depict the smoothed relationships between the Bray–Curtis dissimilarity index with elevation, obtained by fitting GAMMs. The shaded areas represent the 95% confidence intervals

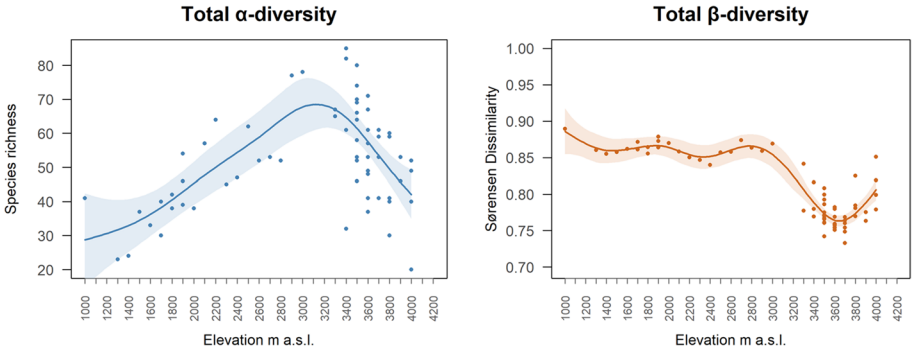


Fig. 6 Altitudinal patterns of α- and β-diversity for total vascular species at small scale, along an altitudinal gradient from 1000 to 4200 m in the southern Ecuadorian Andes (Jubones Valley from 1000 to 3000 m; CNP from 3300 to 4200 m). The graphs depict the smoothed relationships between species richness and β-Sørensen dissimilarity index with elevation, obtained by fitting GAMMs. The shaded areas represent the 95% confidence intervals

were recorded at lower elevations (1000 m) and remained relatively constant until mid-elevations. Above 3000 m, a marked decline in β-diversity was observed, followed by a slight increase at the highest elevations above 3800 m (Fig. 6; Table S4). Partitioning of total β-diversity revealed that species replacement (turnover) was the dominant process across the gradient (mean β-replacement = 0.806), while nestedness contributed minimally to the overall pattern (mean β-nestedness = 0.038).

Endemism of species by growth form and total vascular plant species

Remarkably, 13.6% (121 spp.) of the registered species are endemic to Ecuador, including 50 herb, 48 shrub, and 23 tree species; only 1% are introduced (12 spp.). The highest endemism was found in the CNP region, with a total of 87 species, while 42 endemic species

were recorded in the Jubones Valley. The distribution of these endemic species by growth form exhibited a distinct separation along the altitudinal bands. Endemic herbs were at their maximum richness above 3400 m, with little or no presence at lower elevations. On the other hand, endemic shrub species were recorded at both extremes of the altitudinal gradient, ranging from 1000—2000 m and 3300—4000 m. Tree endemism was prevalent at mid to high elevations between 2100 and 3600 m (Fig. 7).

Influence of environmental drivers on species assemblage

The first two axes of CCA ordination analysis conducted for all vascular plant species, with eigenvalues of 0.925 and 0.615, explained the largest amount of variance in the data, which is strongly associated with environmental variables, accounting for 62% of the variance (Fig. 8; Table 2). As expected, temperature and precipitation were the main environmental drivers. Particularly, in the Jubones Valley, species composition was strongly correlated with increasing values of temperature and solar radiation, especially in the transects at lower elevations. Whereas species occurrence in the CNP is associated with increasing precipitation values, noticeable at mid-elevations, with slope (°) exerting a comparatively minor influence. The Monte Carlo permutation test indicated significant statistical differences for both the ordination axes and tested variables ($p = 0.001$). Temperature, precipitation, solar radiation, and slope were significant in explaining the variable effect (i.e., gradients) on the species/samples across the study area (all with $p < 0.001$). However, temperature (LambdaA = 0.87) and precipitation (LambdaA = 0.35) exhibited the highest levels of variance, with a clear correlation with the 1 st canonical axis. Separate CCA analyses for trees, shrubs, and herbs revealed a consistent ordination pattern with those observed for total species, with temperature and precipitation remaining the most influential environmental variables (see Fig. S2; Table S6).

Discussion

Our study, performed in a scarcely studied area of the tropical Andes of southern Ecuador, revealed a noteworthy variability in α- and β-diversity patterns (i.e., trees, shrubs, and herbs) both along a remarkable altitudinal gradient ranging from 1000 to 4200 m and between the two target regions of Jubones and CNP. Overall, diversity patterns were largely driven by herbaceous species and strongly associated with climatic gradients, highlighting

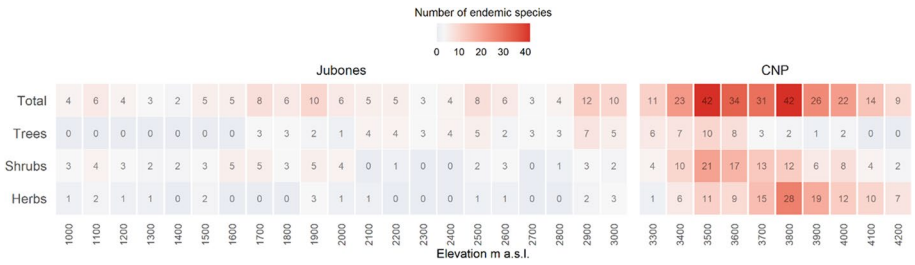


Fig. 7 Heatmap showing the richness of endemic species for total vascular plants, as well as for trees, shrubs and herbs, along an altitudinal gradient from 1000 to 4200 m in the southern Ecuadorian Andes (Jubones Valley from 1000 to 3000 m; CNP from 3300 to 4200 m)

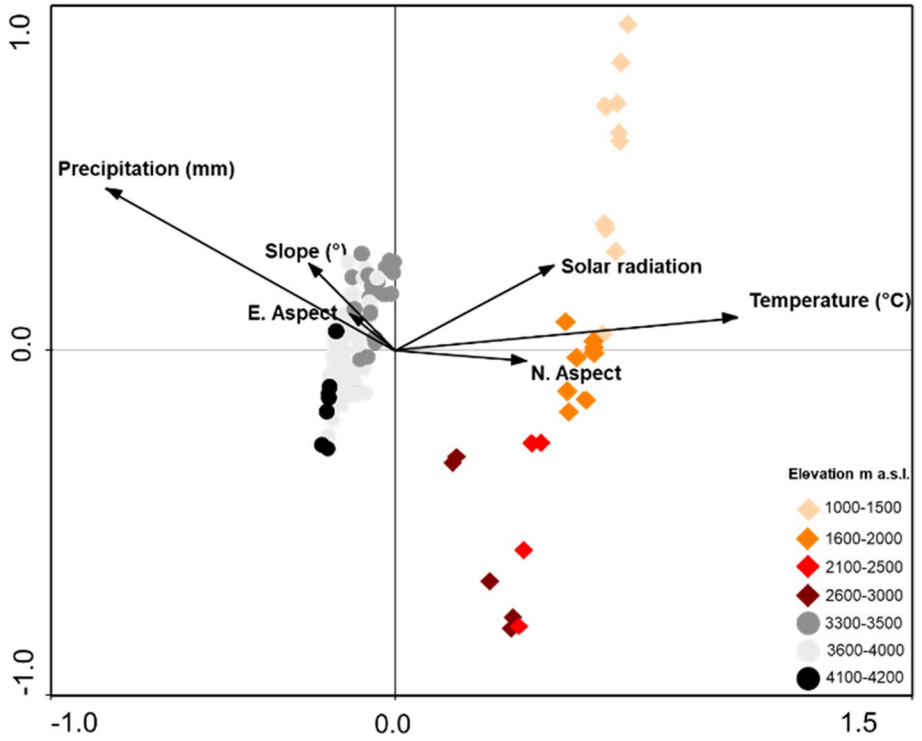


Fig. 8 Canonical Correspondence Analysis (CCA) of total vascular plants along an altitudinal gradient from 1000 to 4200 m in the southern Ecuadorian Andes. Environmental variables are represented by arrows, while sample scores are indicated by diamonds (Jubones Valley from 1000 to 3000 m) and circles (CNP from 3300 to 4200 m)

Table 2 Results of the Canonical Correspondence Analysis (CCA) carried out for total vascular plants along an altitudinal gradient from 1000 to 4200 m, in Jubones Valley (1000 to 3000 m) and CNP (3300 to 4200 m) in the southern Ecuadorian Andes, (n = 146 transects). The analysis is explained by the full set of environmental variables: temperature, precipitation, solar radiation, slope, and aspect

Axes	1	2	3	4	Total inertia
Eigenvalues	0.92	0.61	0.35	0.27	21.36
Species-environmental correlations:	0.99	0.91	0.84	0.83	
Cumulative % variance of species data	4.3	7.2	8.9	10.2	
Cumulative % variance of species-environment relation	37.3	62.2	76.7	87.6	
Sum of all eigenvalues					21.36
Sum of all canonical eigenvalues					2.47
Variable	LambdaA	P	F		
Temperature	0.87	0.000	11.83		
Precipitation	0.35	0.000	4.97		
Solar radiation	0.27	0.000	3.76		
Slope	0.22	0.000	3.21		
Eastness	0.07	0.169	1.13		
Northnes	0.07	0.650	0.94		

the key role of temperature and precipitation in structuring plant communities across contrasting Andean ecosystems and climates (Portalanza et al. 2024). Despite the novel results for the region and the interesting scenario on the biodiversity levels across growth forms, we emphasise that the current study presents some limitations linked to the lack of sampling between 3100 and 3200 m and the limited coverage above 4000 m. This partially constrained our ability to fully characterize transitional and upper-elevation diversity patterns.

α-diversity patterns

Regarding total species richness, we identified a unimodal relationship between species richness and altitude characterized by a hump-shaped pattern. This pattern is in line with other studies in the tropical Andes (e.g., Kessler 2001; Krömer et al. 2005; Salazar et al. 2013; Malizia et al. 2020), which have also documented mid-elevation peaks in species richness. However, considering both the elevation range of the diversity peak and the patterns at the growth-form level, our study differs from other ones conducted across the tropical Andes. Specifically, the richness peak for fully sampled vascular plants occurred at relatively high elevations (2800–3500 m), while the peaks for trees, shrubs, and herbs were all above 2700 m. Differences among studies (e.g., Kessler 2001; Malizia et al. 2020) likely reflect variation in elevation range, taxonomic scope, growth forms considered, and spatial extent, emphasizing the context-dependence of richness–elevation relationships in the Andes.

In addition, this great discrepancy in comparison to previous studies can be ascribed to the spatial complexity of the Andean Mountain system, where both topography and climate, in terms of temperature and precipitation regimes, play crucial roles in shaping biodiversity patterns. In this direction, also proximity to the Amazon system seems to play a crucial role in defining the regional variability of the α-diversity (Fadrique et al. 2026). Additionally, regional factors such as nutrient availability, slope variation, geological disturbances, environmental history, and other unclear factors may also influence local species abundance, as stressed by previous authors (Richter et al. 2009; Rahbek et al. 2019). It is important to emphasize that in the study reported here, various vegetation zones were observed to coexist within the same altitudinal range. Specifically, the montane forest, treeline, páramo, and *Polylepis* forest were all recorded around 3500 m. The coexistence and overlapping of different vegetation zones at the same elevation likely contribute to the observed peak in species diversity.

On the other hand, the transects at both extremes of our altitudinal gradient showed a significantly reduced number of species. This trend likely reflects the extreme climatic conditions at these elevations and the limited adaptability of species to survive in such environments. In the Jubones Valley, the long seasonal dry periods with higher temperatures contrast with the colder conditions, including occasional frost, in the Cajas National Park (CNP). Accumulation curves indicated that additional sampling effort is needed above 4000 m. However, since these altitudes represent the upper limit of vegetation distribution, extending up to 4200 m in the southern mountains of Ecuador (Minga et al. 2016; Ansaloni et al. 2022), a substantial increase in species richness is not expected. Instead, greater species rarity would most likely be expected, as shown by Sklenář et al. (2021). In the Jubones Valley, increasing the sampling effort would likely result in a higher species count. However, compared to Quintana et al. (2017a), who reported 313 species in dry tropical forests restricted to the inter-Andean valleys across Ecuador, around 65% of such diversity was collected in the current study, with 203 species that are characteristic of this vegetation type.

One of the most striking results of this study was the variation in diversity patterns observed across different growth forms. Regarding α-diversity, this reveals not only shifts in the peaks of maximum richness for trees and herbs, but also notable changes in shrub patterns. This reflects, in part, the complex interactions between species' physiological adaptations to the different environmental types across the altitudinal range. In detail, the maximum peak of tree species richness (2700—3500 m) corresponds to the high montane evergreen forest. Montane forests are well known for their high species diversity largely due to the unique microclimatic conditions of these areas, which include significant fluctuations in day/night temperatures, high relative humidity, and frequent rainfall, including drizzle and mist (Bush and Silman 2004; Körner 2007). The higher explanatory power (R^2) of large-scale models compared to small-scale ones indicates that regional climatic gradients are the primary drivers of α-diversity. Conversely, the lower explanatory power (R^2) at the small scale, particularly for herbs, suggests that local environmental heterogeneity and micro-habitat specialization play a significant role in community assembly (Körner 2007; Tello et al. 2015).

Shrub species exhibited richness peaks in transitional zones, both at mid-elevations in the Jubones Valley (1700–2000 m) and at higher elevations in the CNP (3200–3600 m). Shrubs often exhibit adaptations that allow them to thrive in these intermediate conditions between distinct ecosystems. Indeed, for certain Andean shrub genera, these transitional areas represent centres of diversity, such as *Ribes* L. or *Nasa* Weigend genera (Mutke et al. 2014). Their resilience to biotic and abiotic fluctuations, such as water, light, and nutrient availability, enables them to colonize transitional zones and, at the same time, modifies certain climatic factors (i.e., night air temperature) (D'Odorico et al. 2010). In the dry tropical forests restricted to inter-Andean valleys, shrubs may play a crucial role in maintaining biodiversity by supporting the creation and persistence of biological corridors that connect grasslands, shrublands, and forests, thereby providing a stable environment for more sensitive growth forms (Mutke et al. 2014).

β-diversity patterns

Total β-diversity exhibited consistently high Bray–Curtis dissimilarity values, indicating strong compositional differentiation along the elevational gradient. These patterns, however, were not monotonic and showed contrasting trends among growth forms, suggesting that different assembly rules (e.g., environmental filtering and dispersal limitation) act selectively on trees, shrubs, and herbs. Herbaceous species exhibited a pattern where high turnover at lower and mid-elevations gave way to a decrease in β-diversity towards the high-elevation zones (about 3000 m), likely due to "biotic homogenization" driven by the severe environmental filtering of the high-Andean climate (Kessler et al. 2011). However, contrasting trends were found among other growth forms; tree species exhibited an inverted hump-shaped pattern, whereas shrub species followed a unimodal pattern. The inverted hump-shape in trees suggests a transition between two distinct stressful environments: the dry conditions at low elevations and the cold-stress at the treeline. Both elements act as marked environmental filters that increase turnover at the extremes of the gradient.

The Andes are known for their high β-diversity indices, largely due to their highly heterogeneous habitats across slopes (Homeier et al. 2010; Quintana et al. 2017a; Cuesta et al. 2017; Rahbek et al. 2019). The high turnover we observed at low

elevations is consistent with patterns reported for dry tropical forests (including drier forest ecosystems), where dispersal limitation, climatic constraints, and historical processes promote strong compositional differentiation (Pennington et al. 2000; Dryflor 2016).

Evolutionary and historical factors, as well as dispersal barriers, may be among the main determinants of species replacement, as suggested by Nanda et al. (2021). In this direction, Null model analyses (SES > 1.96) confirmed that β-diversity patterns were largely deterministic. High SES values at the large scale indicate that environmental filtering along the altitudinal gradient seems the primary driver regionally, while at the small scale, the observed species aggregation likely results from dispersal limitation and micro-habitat specialization (see Chase and Knight 2013; Tello et al. 2015). The high SES values and the high dissimilarity recorded are further supported by our partitioning of total β-diversity, showing that species turnover (replacement) is the dominant component of the observed patterns, rather than nestedness (loss/gain).

The Jubones Valley region is located within a geological boundary formed by the transition from the Northern Andes to the Central Andes, which is geographically expressed by a depression known as "Amotape-Huancabamba" (Weigend 2002). This depression, which is considered a possible center of endemism (Weigend 2002; Richter et al. 2009; Quintana et al. 2017b), can function as a biogeographic barrier for the north–south dispersal of Andean taxa. In addition, this depression may also provide a dispersal route between the lowland plant taxa of the Pacific and the humid valleys on the eastern side of the Andes (Weigend 2002; Quintana et al. 2017a, b).

The increase of β-diversity in all growth forms, at higher elevations above 3700 m in the CNP, marks a departure from the homogenization observed at 3000 m. This late-gradient increase is likely driven by the fragmented and "island-like" nature of high-altitude habitats. Indeed, higher elevations host specific habitats and environmental conditions that support unique species. In Ecuadorian páramos, up to 12 phytosociological communities can be distinguished, many of which are composed of exclusive species (Hofstede et al. 2003; Ansaloni et al. 2022). In our sampling areas above 3500 m, four communities were identified inside the páramo: a) tussock grassland, b) carpets cushion páramo, c) scrublands, and d) super-páramo scrublands dominated by *Andicolea* Mayta & Molinari, as described by Minga et al. (2016) and Ansaloni et al. (2022). The high β-diversity here is therefore an ecological reflection of habitat specialization and the presence of high-altitude micro-refugia (e.g., *Polylepis* patches). It should be noted that the number of endemic species in these high-elevation areas was high, where not only species exclusive to the Andean region of Ecuador were recorded, but also species that are exclusively endemic to the Cajas National Park. These species included, for instance: *Carex azuayae* Steyerm., *Draba steyermarkii* Al-Shehbaz, *Gentianella hirculus* (Griseb.) Fabris, *Lysipomia vitreola* McVaugh, and *Xenophyllum roseum* (Hieron.) V.A.Funk (León-Yánez et al. 2011; Ansaloni et al. 2022).

Regarding trees, the observed decrease in β-diversity towards mid-elevations (before increasing again at the treeline) could reflect the dominance of a few widespread tree species in comparison to other growth forms (Báez et al. 2015; Quintana et al. 2017a). For instance, the lower altitudes (1000 to 1400 m) of the sampling area in this study were dominated by a single tree species, *Vachellia macracantha*. In species-poor communities, the presence or absence of a few dominant taxa, especially trees, will determine changes in the light, nutrient, and soil conditions of the ecosystem, which can, in turn, lead to shifts in the entire plant community (Kessler 2000).

Environmental drivers

Climatic factors, particularly temperature and precipitation, were the main drivers of floristic variation along the elevational gradient. The effects of these factors along an altitudinal gradient differ substantially from those observed in lowlands with higher elevations, undergoing pronounced shifts mainly in temperature, precipitation, and solar radiation (Bush and Silman 2004; Körner 2007). In the study reported here, temperature and precipitation were highlighted as the most important climatic factors influencing floristic patterns.

The two sampling areas exhibited marked differences linked to climatic factors. The higher elevation areas in the Cajas National Park (3300 to 4200 m) are predominantly influenced by humid eastern currents coming from the inter-Andean and Amazonian valleys. Here, high precipitation was an important driver favouring increased biodiversity levels. Higher productivity and species richness were recorded by previous studies performed in Andean Mountain forests (Gentry 1988; Toledo et al. 2011; Godoy-Bürki et al. 2017). In contrast, the Jubones Valley area (1000 to 3000 m) is influenced by dry western currents from the Pacific coast (Pérez-Escobar et al. 2022), resulting in higher temperatures, which can exert strong control on species richness, leading to a drop in α-diversity, especially at lower elevations. The significant role of temperature in regulating floristic variation in lowland regions, with a well-defined dry season of variable length, can shape the physiognomy of vegetation types (Toledo et al. 2011). This could explain why temperature particularly affects herb and tree species diversity, decreasing richness but conserving high levels of species turnover (β-diversity). However, it contributed more to the shrub component of the vascular flora in this study; indeed, in this area, shrubs reached their peak and dominated the landscape, along with some species adapted to survive under certain drought and temperature conditions (Quintana et al. 2017a), particularly from the Fabaceae, Asteraceae, and Malvaceae families. These families are known to contain species that are specialists in dry forest habitats (Dryflor 2016). In lowlands, species turnover remained high for shrubs.

The abrupt change in β-diversity along the altitudinal gradient from about 2900 to 3300 m, reflected the dramatic changes in the composition of Andean ecosystems. After the local substitution of species at low altitudes, there is a marked change in species composition. Therefore, above 3300 m, the lower altitudinal bands do not share any species with the altitudinal bands at higher elevations. This suggests that unique environmental conditions (e.g., precipitation, cloud cover, and temperature) could restrict the colonisation of low-altitude species. While the steepness of this transition in our data might be influenced by the sampling intervals, it likely aligns with the recognised ecological threshold of the forest-páramo ecotone (timberline), where physiological constraints sharply limit the upward distribution of montane forest species (Homeier et al. 2010). Furthermore, these climatic constraints could potentially maintain a clear separation of community assembly dynamics between the Jubones Valley and the Cajas National Park.

In mountain regions, topography also plays a critical role by modifying factors such as solar radiation, slope, and aspect that foster unique ecological niches (Kessler 2000; Körner 2007). In this study, slope and solar radiation were especially correlated with the species sampled along the altitudinal gradient. Overall, the combination of climate and topography generates important environmental drivers that can shape the biodiversity patterns of vascular plants at the micro-scale, as observed in sampling areas of this study in the Tropical Andean mountains of southern Ecuador.

Conclusions and implications for conservation and future research

This study demonstrates that plant diversity along southern Ecuadorian Andean gradients is structured by strong and non-linear patterns of both α- and β-diversity, with distinct responses among growth forms and elevation zones. Species richness peaked at mid- to high elevations (ca. 2700–3500 m), while β-diversity remained high across the gradient, indicating pronounced species turnover rather than simple richness loss.

From a conservation perspective, these results suggest that different elevational zones contribute to biodiversity in complementary ways. Low- and mid-elevation ecosystems, particularly dry inter-Andean forests in the Jubones Valley, combine relatively high species richness with strong compositional turnover, supporting unique assemblages shaped by climatic stress and dispersal limitation. These systems, therefore, represent priorities for conservation despite their comparatively lower elevation. Conversely, high-elevation ecosystems in the Cajas National Park exhibited lower α-diversity but high β-diversity driven by habitat specialization and spatial fragmentation within páramo landscapes. The strong species replacement observed above the treeline highlights the importance of conserving multiple habitat types within high-Andean mosaics, rather than focusing solely on species-rich sites.

Overall, the combined analysis of α- and β-diversity emphasizes that effective conservation planning in Andean Mountain systems must account for both species richness and compositional differentiation across elevations and growth forms.

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Author contribution N.G. wrote the main manuscript text and prepared figures.; N.G. and R.G. performed statistical analyses; R.A., M.J., D.M. e N.G. performed sampling activities; N.G. and R.G. contributed to the manuscript conceptualization; S.C and D.M provided resources; R.A. and D.M. supervised the project; all authors reviewed and edited the final draft of the manuscript.

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Data availability No datasets were generated or analysed during the current study.

Declarations

Competing interests The authors declare no competing interests.

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