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Differential Elevational Diversity Between Overstory and Understory in Tropical Forests

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ABSTRACT

Understanding how biodiversity patterns vary among forest vertical strata along elevational gradients is crucial for predicting ecosystem sensitivity to global change, yet such comparisons remain scarce in tropical forests. Here, we established 16 sites along a 1500-m elevational gradient in Yunkai Mountains to compare diversity between tree and understory layers, specifically tracking two nationally protected and rare species (*Alsophila spinulosa* and *Angiopteris fokiensis*). Tree-layer α -diversity exhibited a unimodal relationship with elevation, peaking at mid elevations, whereas understory α -diversity maintained consistently higher diversity and displayed a bimodal pattern with peaks at 400–600 m and 1000–1200 m. The β -diversity of both tree and understory layers varied across elevational zones, primarily driven by species turnover of common dominant species rather than within-zone heterogeneity or rare species. However, the two rare ferns exhibited distinct elevational distributions (unimodal and U-shaped, respectively) that were decoupled from overall α -diversity. Our study demonstrates contrasting elevational responses between tree and understory strata. Consequently, effective biodiversity conservation in tropical mountain forests must integrate complete elevational gradients with vertical stratification, explicitly prioritizing the maintenance and long-term monitoring of understory microhabitats.

1 | Introduction

Mountain forest ecosystems, characterized by complex environmental gradients, nurture exceptionally rich biodiversity [1, 2]. They represent one of the world's biodiversity hotspots and hold significant importance in biodiversity conservation [3, 4]. Species diversity across global mountain ranges exhibits diverse patterns along increasing elevational gradients, including monotonic declines, low-elevation plateaus, and mid-elevation peaks [5]. In subtropical and tropical mountains in China, species richness generally shows either monotonic declines or mid-elevation peaks with increasing elevation, shaped by mountain height

and area [6, 7]. Declines in diversity at higher elevations are commonly linked to reduced temperature, smaller habitat area, nutrient limitation, and increased isolation [8, 9]; these explanations treat the forest community as a homogeneous entity [10–12]. In reality, tropical forests are vertically stratified, with the overstory and understory experiencing contrasting microenvironments: the overstory is exposed to higher radiation and climatic variability, whereas the understory is buffered by canopy shading with higher humidity but limited light [13–15]. These differences suggest that the two layers may respond differently to the same elevational gradient [16, 17]. However, most previous

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Highlights

- Overstory and understory layers exhibit contrasting nonlinear elevational patterns in α -diversity (unimodal vs. bimodal).
- Elevational differentiation in β -diversity is primarily driven by the turnover of common dominant species rather than rare species.
- Rare fern distributions are decoupled from overall diversity, underscoring the necessity of understory microhabitat conservation.

studies have focused on the tree layer or pooled all growth forms, potentially obscuring layer-specific elevational patterns [7, 9, 18]. Therefore, a simultaneous comparison of α -diversity across vertical strata is needed to assess whether elevational patterns are consistent or divergent between forest layers.

Compared to α -diversity, β -diversity, which reflects community composition variation, has received insufficient attention in elevational gradient studies [19–21]. Previous studies indicate that β -diversity does not exhibit a consistent monotonic trend along elevational gradients, and environmental factors such as climatic heterogeneity can explain part of the variation in species replacement [21]. Overall, species composition differences between communities in mountain environments primarily stem from species turnover rather than nestedness, meaning distinct elevational zones often exhibit relatively unique species assemblages rather than higher-elevation communities being mere subsets of lower-elevation ones [21, 22]. Concurrently, the contribution of rare species to community variation remains unclear. It is uncertain whether β -diversity patterns across elevational gradients are primarily driven by the turnover of widespread dominant species or influenced by partially restricted rare species [23]. This distinction has important conservation implications, as rare and endangered species of the overstory and understory may exhibit narrow elevational ranges and disproportionately influence β -diversity. However, their elevational niches and roles in community differentiation remain poorly documented.

To investigate the elevational changes in α -diversity and β -diversity across forest vertical stratification, with a focus on rare species (e.g., the tree fern *Alsophila spinulosa* and the fern *Angiopteris fokiensis*), we established 16 sample plots along an elevational gradient of nearly 1500 m in the Yunkai Mountain National Nature Reserve, Guangdong, China. The study aimed to address the following scientific questions: (1) Does forest community α -diversity exhibit nonlinear variation along the elevational gradient, and do the patterns of change in the overstory and understory layers align? (2) Does community β -diversity undergo systematic differentiation with elevation? Is this differentiation primarily manifested as compositional turnover among elevational zones, or does it stem from differences in intragroup heterogeneity within each elevational zone? (3) Is the β -diversity pattern along the elevational gradient primarily driven by the turnover of common species or by contributions from rare species? Do the distributions of the rare

species *A. spinulosa* and *A. fokiensis* show consistent relationships with overall community diversity changes?

2 | Materials and Methods

2.1 | Study Area

The study area is the Yunkai Mountain National Nature Reserve (22°13'58"–22°21'24"N, 111°08'19"–111°23'48"E) and its surrounding areas in Guangdong Province, located at Xinyi City and Gaozhou City in the southwestern part of the province (Figure 1). Situated deep within the Yunkai Mountains, the area features complex terrain with steep peaks and deep valleys, culminating in the main peak Datian Ding at 1700 m elevation. The study area predominantly exhibits mountainous topography, forming a basin-like terrain with elevated central areas and lower peripheries. The climate is classified as a humid tropical monsoon climate, characterized by an annual average temperature of 22.3°C, with annual precipitation ranging from 1776.5 to 2600 mm. High relative humidity and the synchrony of rainfall and heat contribute to a pronounced vertical zonation of vegetation. Characterized by typical evergreen broad-leaved forest vegetation, the area exhibits a complete vertical spectrum from lowland evergreen broad-leaved forests to mixed coniferous-broad-leaved forests at mid elevations. Simultaneously, the study area serves as one of the key distribution sites in Guangdong for nationally protected plants such as *A. spinulosa* and *A. fokiensis*. Consequently, this region not only provides habitat for numerous endemic and rare plant species but also offers ideal conditions for studying community diversity along elevational gradients and the responses of rare plants.

2.2 | Site Selection and Vegetation Survey

The communities within the study area are predominantly located on steep slopes. To ensure consistency in topography, soil texture, slope gradient, and aspect (south-facing), 16 sampling sites were selected along an elevational gradient from July to August 2025. At least three 20 m × 30 m standard plots were established without overlap within each sampling site, with a minimum spacing of 1 km between sites. To ensure environmental consistency within each site, the three standard plots were established on the same slope face with similar slope gradients and aspects, and in areas with visually consistent soil texture.

Within each standard plot, species composition and abundance were surveyed and recorded separately for the tree layer and the understory layer. For the tree layer, all woody stems with a diameter at breast height (DBH) $\geq$ 5 cm were identified and counted as individual trees [18, 24]. Understory species were surveyed within five 2 m × 2 m subquadrats systematically distributed across each standard plot. For the understory vegetation layer (including shrubs, herbs, ferns, and tree seedlings with DBH < 5 cm), species were identified, and their abundances were documented. Because the understory includes clonal plants (e.g., *Selaginella doederleinii*), for which delimitation of discrete genetic individuals is inherently difficult, we counted the number of independent ramets or clumps (i.e., physically distinct aboveground shoots or tufts) rather than

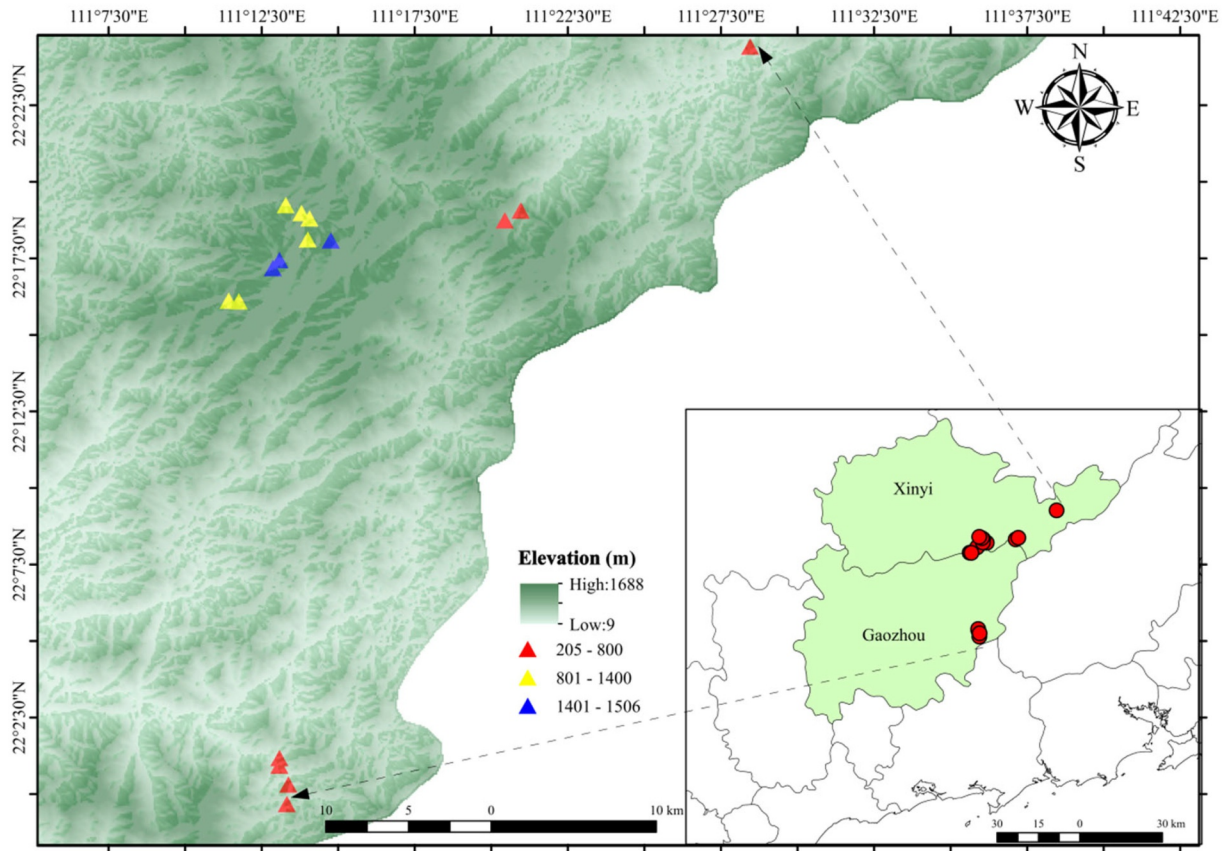


FIGURE 1 | Locations of the 16 sampling sites in a tropical montane forest in Southern China.

strict genetic individuals to reduce sampling bias [18, 24]. The distribution of sampling sites is shown in Figure 1.

For subsequent diversity analyses, the survey data from the three standard plots within each sampling site were pooled to form a single comprehensive species-abundance matrix representing that site. The elevation of each sampling site was determined by calculating the mean elevation of the centers of its three constituent standard plots. It should be noted that the sampling design was established systematically along the elevational gradient to capture overall community patterns, rather than specifically targeting the occurrences of the two nationally protected and rare ferns.

2.3 | Diversity Indicator Analysis

Based on survey data, this study selected species richness (S), Shannon–Wiener index (H'), Simpson index (D), and Pielou index (E) to calculate α -diversity indices for plots at different elevations. The formulas are as follows:

$$S = R, \quad (1)$$

$$H' = -\sum_{i=1}^S (P_i \ln P_i), \quad (2)$$

$$D = 1 - \sum_{i=1}^S P_i^2, \quad (3)$$

$$E = H'/\ln S, \quad (4)$$

where S , H' , D , and E represent species richness, Shannon–Wiener diversity index, Simpson's diversity index, and

Pielou's evenness index, respectively; P_i denotes the proportion of individuals of species i relative to the total number of individuals; R represents the number of species.

For β -diversity, the Bray–Curtis index was employed to measure and analyze dissimilarity among sampling sites along the elevational gradient [25, 26]. The Bray–Curtis index quantifies dissimilarity between different communities, with higher values indicating lower similarity—that is, fewer shared species. The formula for the Bray–Curtis index is as follows:

$$B_N = 2J_N/(N_a + N_b), \quad (5)$$

where N_a and N_b represent the number of individuals of all species in plots a and b , respectively, whereas J_N denotes the sum of the minimum number of individuals across all species.

2.4 | Data Analysis

To assess the variation patterns of community α -diversity along the elevational gradient, four commonly used diversity indices were calculated for both the tree layer and understory plants: species richness, Shannon–Wiener index, Simpson index, and Pielou's evenness index. Index calculations were based on species-abundance data within each sampling site, implemented using the *vegan* package in R 4.2.2. The relationships between diversity indices and elevation were visualized using locally estimated scatterplot smoothing (LOESS, implemented with the *ggplot2* package in R 4.2.2, which was used as a nonparametric tool for trend visualization rather than strict inferential modeling

due to the limited sample size) (Figure 2). Patterns in community β -diversity were visualized using non-metric multidimensional scaling (NMDS), calculated based on the Bray–Curtis distance matrix. Furthermore, permutation-based multivariate analysis of variance (PERMANOVA) was employed to test for significant differences in community composition between elevational zones. Concurrently, PERMDISP (permutation-based analysis of dispersion within groups) was used to assess the degree of variation in community composition within each elevational zone. This allowed distinction of whether elevation-based community differentiation stemmed from shifts in species composition centers or changes in intracommunity heterogeneity. To identify key species driving community differentiation, SIMPER (Similarity Percentage) analysis was employed to quantify each species' contribution to Bray–Curtis dissimilarity between communities, distinguishing whether differentiation was primarily driven by common or rare species. The abundance trends of two nationally protected and rare plants (*A. spinulosa* and *A. fokiensis*) selected based on national protection status and survey records were visualized through curve fitting. Because traditional correlation analyses are unreliable for rare species with patchy distributions and zero-inflated data across a limited sample size, we visually overlaid the occurrences of these species onto the NMDS ordination to demonstrate their placement within the community composition space. All data processing and statistical analyses

were conducted in the R 4.2.2 environment, with core functions relying on packages such as *vegan*, *ggplot2*, and *stats*.

3 | Results

3.1 | Characteristics of Community α -Diversity Variation Along the Elevational Gradient

The α -diversity indices for the tree layer exhibited a nonlinear trend with a mid-elevation peak along the elevational gradient (Figure 2). Within the tree layer, the Pielou's evenness index showed minimal variation along the elevational gradient, displaying an overall gradual decline (Figure 2a). The species richness first decreased, then increased, and finally declined gradually with increasing elevation, reaching relatively high levels at mid-elevation sites (Figure 2b). The Shannon–Wiener and Simpson indices remained relatively stable across the mid- to high-elevation range but exhibited greater fluctuations at low-elevation sites (Figure 2c,d). The α -diversity indices of the understory vegetation layer were generally higher than those of the tree layer, exhibiting distinct differences in trends and a pronounced “bimodal” pattern (Figure 2). The Pielou evenness, species richness, Shannon–Wiener, and Simpson indices of the understory vegetation layer were higher at low to mid-elevations, peaking at 400–600 m and 1000–1200 m, respectively. At mid-

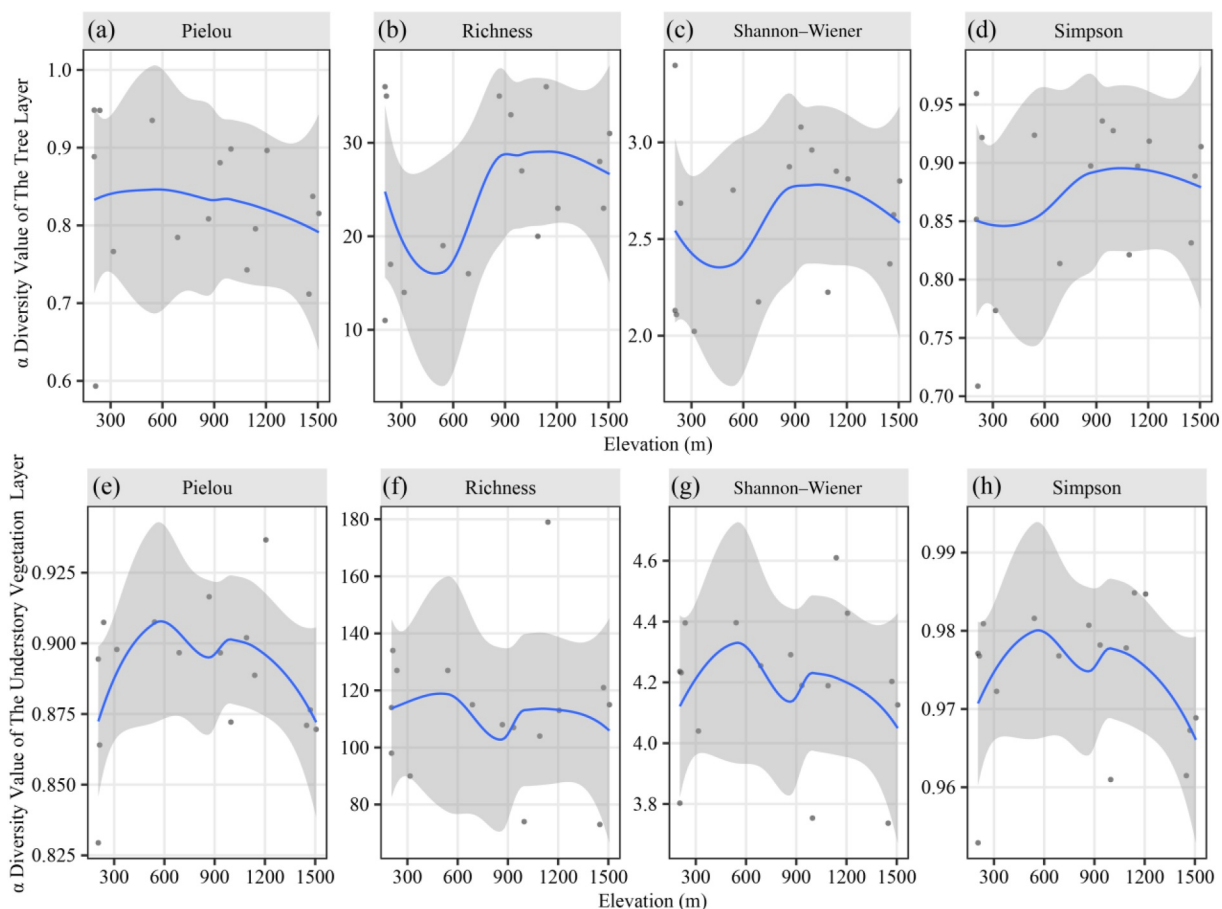


FIGURE 2 | α -Diversity indices for the tree layer and understory vegetation layer at different elevation sites. (a)–(d) Represent Pielou evenness, species richness, Shannon–Wiener index, and Simpson index for the tree layer, respectively; (e)–(h) represent Pielou evenness, species richness, Shannon–Wiener index, and Simpson index for the understory vegetation layer, respectively.

elevations, these indices exhibited fluctuating changes, first decreasing and then increasing (Figure 2e–h).

3.2 | Community Composition (β -Diversity) Differentiation Along the Elevational Gradient

Non-metric multidimensional scaling (NMDS) based on Bray–Curtis distance (Table S1) revealed distinct differentiation patterns in both the tree layer (stress = 0.13) and understory vegetation layer (stress = 0.11) across different elevational gradients within the sample plots (Figure 3). For the subsequent PERMANOVA and PERMDISP analyses, the continuous elevational gradient was discretized into three categories based on the vertical zonation of vegetation in the study area: low elevation (< 600 m), medium elevation (600–1000 m), and high elevation (> 1000 m). Within both the tree layer and understory vegetation layer, sites formed relatively independent distribution zones corresponding to these three elevation categories along both the NMDS1 and NMDS2 axes, indicating systematic changes in community composition across different elevational zones. Furthermore, overlaying the occurrences of the two nationally protected and rare ferns onto the NMDS ordination provided visual evidence of their habitat preferences: *A. spinulosa* occurred primarily in mid-elevation sites, whereas *A. fokiensis* was distributed across low- and high-elevation sites but absent from mid-elevation sites, suggesting differential habitat preferences along the elevational gradient (Figure 3a,b). PERMANOVA results further confirmed significant differences in community composition between elevational zones for both the tree layer ($R^2 = 0.26$, $p = 0.001$) and understory layer ($R^2 = 0.29$, $p = 0.001$), consistent with the information presented by confidence ellipses (Figure 3a,b). However, the confidence ellipses for understory vegetation samples from different elevational gradients showed relatively low overlap in the ordination space, indicating more pronounced segregation of community composition along the elevational gradient (Figure 3a,b). PERMDISP analysis indicated

that intragroup dispersion within different elevational zones did not reach significant differences for either the tree layer or understory vegetation layer (tree layer: $p = 0.63$, understory: $p = 0.81$). Combined with PERMANOVA results, this indicates significant differences in vegetation diversity between elevational zones, independent of intrazone plot heterogeneity.

3.3 | Species Contributions to Community Diversity

SIMPER analysis revealed that differences in community composition across elevational gradients were primarily driven by a few key species (Figure 4). In intergradient comparisons, top-ranked species accounted for a substantial proportion of the cumulative contribution to average Bray–Curtis dissimilarity, indicating that shifts in the abundance of these species were the main drivers of community β -diversity. Species with high contribution values exhibited marked abundance differences across elevational gradients, showing high dominance in some gradients while being significantly reduced or absent in others. Among the top 10 major contributing species in the tree layer, the primary contributors were *Cunninghamia lanceolata*, *Adinandra glischroloma*, *Castanopsis faberi*, *Cryptomeria japonica* var. *sinensis*, *Eurya loquaiana*, *Symplocos lucida*, *Rhododendron moulmianense*, *Eurya nitida*, *Mallotus paniculatus*, and *Cryptocarya chinensis*. *C. lanceolata* contributed more than twice as much as the other species (Figure 4a). The top 10 major contributing species in the understory vegetation layer were *Neolitsea chui*, *Eurya nitida*, *Saurauia tristyla*, *Blastus cochinchinensis*, *Schefflera delavayi*, *Heptapleurum minutistellatum*, *Ficus hirta*, *Castanopsis faberi*, *Microstegium fasciculatum*, and *Selaginella doederleinii*, with relatively small differences in contribution among species (Figure 4b). However, rare species did not appear among the top contributors, indicating that rare species have limited direct contribution to overall community β -diversity variation across elevational gradients. Instead,

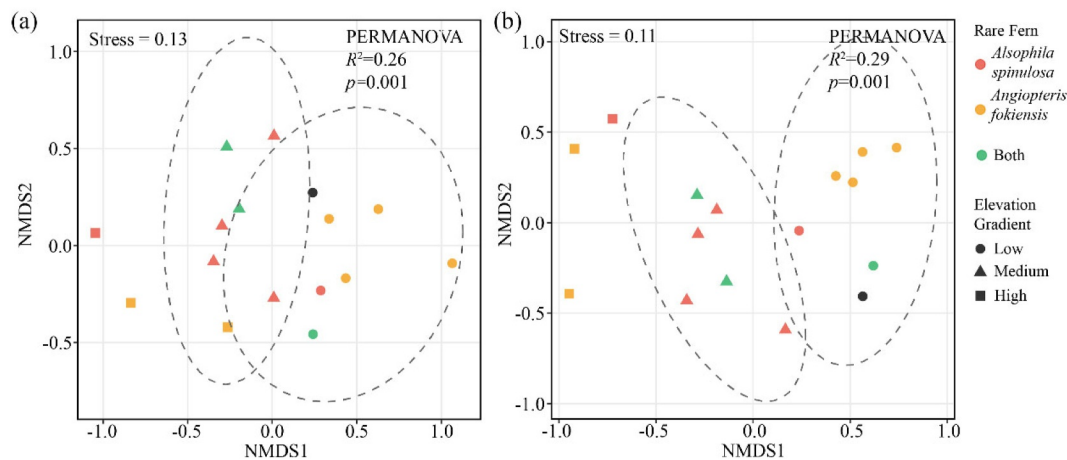


FIGURE 3 | NMDS ordination characteristics of β -diversity in the tree layer and understory vegetation layer communities at different elevational gradients. (a) and (b) Show the NMDS ordination plots for tree layer and understory vegetation layer plots, respectively. Colors indicate the occurrence of nationally protected and rare fern species: red for sites containing *Alsophila spinulosa*, yellow for sites containing *Angiopteris fokiensis*, green for sites containing both species, and black for sites where neither species was recorded. Symbol shapes represent elevational gradients: circles for low elevation, triangles for mid-elevation, and squares for high elevation. Dashed ellipses indicate the 95% confidence intervals for each elevational gradient plot in the ordination space; due to the limited number of high-elevation sites, the confidence ellipse for the high-elevation group is omitted. The stress value indicates the goodness-of-fit of the NMDS ordination.

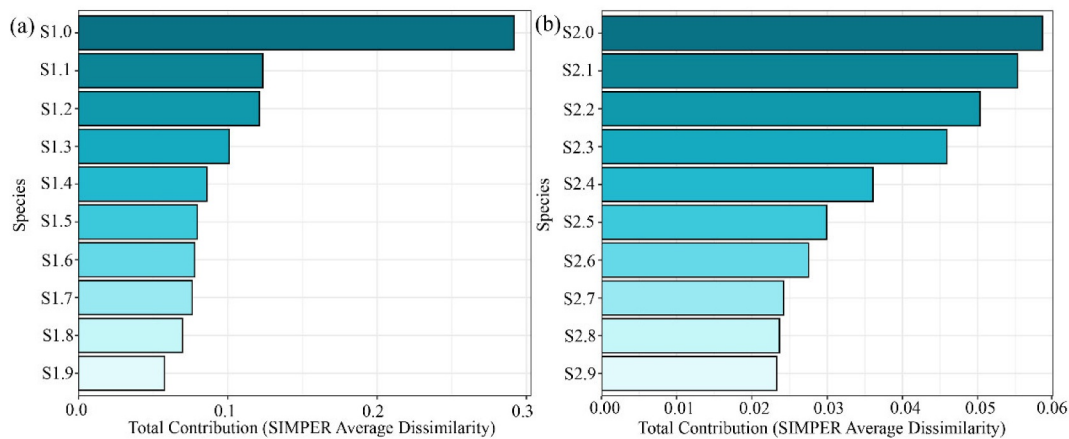


FIGURE 4 | Primary species contributing to β -diversity in tree layer and understory vegetation communities across elevational gradients. (a) Shows primary contributing species for tree layer differences, whereas (b) shows primary contributing species for understory vegetation layer differences. In the figures, S1.0–S1.9 represent the species *Cunninghamia lanceolata*, *Adinandra glischroloma*, *Castanopsis faberi*, *Cryptomeria japonica* var. *sinensis*, *Eurya loquaiana*, *Symplocos lucida*, *Rhododendron moulmainense*, *Eurya nitida*, *Mallotus paniculatus*, and *Cryptocarya chinensis*, respectively; S2.0–S2.9 correspond to *Neolitsea chui*, *Eurya nitida*, *Saurauia tristyla*, *Blastus cochinchinensis*, *Schefflera delavayi*, *Heptapleurum minutistellatum*, *Ficus hirta*, *Castanopsis faberi*, *Microstegium fasciculatum*, and *Selaginella doederleinii*, respectively.

community differences are primarily driven by changes in the abundance of relatively common species.

3.4 | Changes in the Number of Individuals of Rare Species Along Elevational Gradients

The response patterns of two nationally protected and rare species, *A. spinulosa* and *A. fokiensis*, along the elevational gradient showed distinct differences. Their population sizes exhibited pronounced nonlinear changes along the gradient, specifically a “single-peak” pattern and a “U-shaped” pattern, respectively (Figure 5). The number of *A. spinulosa* individuals reached higher levels in mid-elevation plots, whereas lower numbers were observed in low- and high-elevation plots; the species was not recorded in some plots (Figure 5a,c). In contrast, the distribution pattern of *A. fokiensis* differed from that of *A. spinulosa*. It was distributed in both low- and high-elevation sites, whereas relatively fewer individuals were recorded in mid-elevation sites (Figure 5b,c).

Given the limited sample size (16 plots) and the patchy distribution of these rare species, traditional parametric or nonparametric correlation analyses between their abundance and α -diversity indices are statistically unreliable (often yielding nonsignificant results due to excessive zero-inflation). However, as visually demonstrated in the NMDS ordination (Figure 3), the distinct spatial segregation of plots containing these ferns suggests that their distributions are more closely aligned with specific community composition and environmental pressures, particularly in the understory vegetation layer, rather than tracking overall community α -diversity.

4 | Discussion

Research reveals distinct patterns of diversity variation along the elevational gradient in the tree and understory layers of tropical mountain forests. Within the study area's elevational gradient, the species diversity index of the tree layer exhibited a

nonlinear trend with a mid-elevation peak, whereas the understory layer showed a pronounced bimodal distribution with overall diversity levels higher than those of the tree layer. These findings indicate that plant diversity at different vertical levels responds significantly differently to elevational gradients, with species richness and evenness of small plants in the understory layer generally exceeding those in the tree layer. Furthermore, we observed significant differentiation in community composition between the tree and understory layers along the elevational gradient, with understory species composition undergoing more pronounced turnover with elevation changes. NMDS ordination revealed distinct clusters of species composition among low-, mid-, and high-elevation sites. PERMANOVA analysis confirmed significant differentiation in both the tree layer ($R^2 = 0.26$) and understory layer ($R^2 = 0.29$). Conversely, PERMDISP analysis revealed no significant differences in community heterogeneity within individual elevational zones, supporting the conclusion that species turnover between elevational zones (rather than intrazonal variation) drives β -diversity differentiation. Collectively, biodiversity in south tropical mountain forests exhibits nonmonotonic changes along the elevational gradient, reflecting distinct nonlinear patterns at different layers and pronounced species turnover.

The findings of this study both align with and diverge from existing research on other mountain forest ecosystems. Overall, the nonlinear trend with a mid-elevation peak observed in the tree layer resembles the “single-peak” pattern of biodiversity along elevational gradients in many mountainous regions, characterized by a peak at mid elevations [25, 26]. This is typically attributed to lower elevations providing favorable temperature and moisture conditions supporting species richness, whereas harsher high-elevation environments reduce species numbers. Mid-elevations exhibit high diversity due to overlapping distributions of both low- and high-elevation species [27, 28]. However, significant variations exist across different mountain ranges and biological groups. “Single-peak” distributions are more common in mountains with large relative

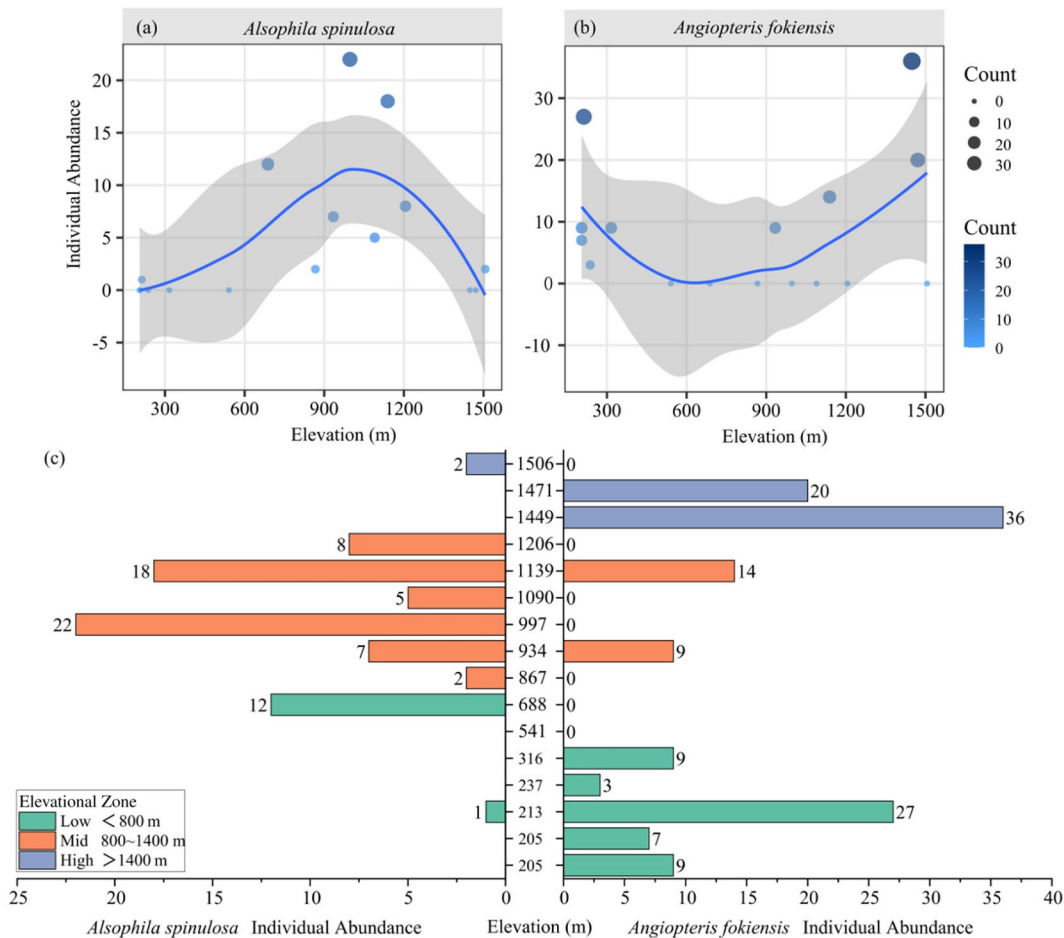


FIGURE 5 | The elevational distribution of *A. spinulosa* and *A. fokiensis*. (a) Shows the elevational distribution trend of *A. spinulosa*, (b) shows that of *A. fokiensis*, and (c) details the specific population distribution and differences between these two rare species across different elevations. Individual abundance represents the total number of individuals summed across all 20 m × 30 m standard plots within each sampling site.

height, whereas smaller elevation ranges or specific taxa may exhibit more diverse patterns [25]. For instance, studies in the cold-temperate mountains of Northeast China reveal that tree α -diversity decreases with altitude, whereas shrubs and herbs exhibit a V-shaped pattern of initial decline followed by increase [26]. The “double-peak” pattern observed in the understory vegetation layer in this study is also consistent with vegetation survey results from the southern slopes of the Tianshan Mountains in Xinjiang, where overall community diversity exhibited peaks at both medium and high elevations, specifically reaching diversity peaks in the mountain desert–grassland transition zone and alpine meadows, respectively [29]. Thus, the two peaks in understory α -diversity, low-to-medium and medium-to-high elevations, may reflect the species poverty of mid-elevation transitional zones, whereas low-elevation valleys and high-elevation forest gaps provide distinct suitable habitats. In this study, the number of species in the understory layer was significantly higher than that in the canopy layer, consistent with existing findings that the understory layer often contributes most to total species richness in forest communities. This further indicates that different vegetation life forms may exhibit strategic differences in resource and climate utilization, leading to variations in species diversity between the tree and understory layers.

The findings of this study may result from multiple ecological mechanisms acting in concert. However, it is crucial to note that because this study is a purely phytosociological survey without field-measured environmental data (e.g., soil nutrients, temperature, humidity, or light availability), the following mechanistic inferences represent hypothetical deductions based on the assumption of elevation as a proxy for environmental conditions (space-for-time substitution). Environmental filtering plays a dominant role in species composition across different elevational zones. As elevation increases, environmental stresses such as lower temperatures, poorer soils, and stronger winds intensify, enabling cold-tolerant, wind-resistant, and low-nutrient-tolerant species to survive and dominate [30, 31]. This may partly explain why coniferous species dominate the high-elevation tree layer, whereas low elevations predominantly feature thermophilic broadleaf species. This presumed environmental filtering effect may also occur in understory vegetation layers, resulting in high-elevation understories dominated by cold-tolerant, small-sized plants, whereas some low-elevation species become increasingly rare at higher elevations [32, 33]. Additionally, niche differentiation and competitive coexistence relationships may further shape elevational diversity patterns within the study area [34]. For instance, at low elevations, abundant heat and high productivity allow dominant species to

monopolize key resources through competition, resulting in greater fluctuations in species richness and lower evenness at these elevations [35, 36]. In the transitional mid-elevation zone, an “ecological transition stress belt” may exist, where lowland species gradually diminish, whereas alpine species have not yet extensively appeared, causing a temporary decline in total species numbers [37, 38]. As elevation increases further, although high-altitude environments are harsh, competition for understory resources diminishes. Specially adapted species (such as cold-tolerant shrubs and herbs) can occupy vacant ecological niches, allowing them to coexist and thereby restoring understory diversity [39, 40]. This explains the “bimodal” pattern observed in understory vegetation layers, where species richness is paradoxically lower in mid-elevation zones. As transitional zones between broadleaf and coniferous forests, mid-elevations experience drastic changes in light and moisture conditions. This may favor a few ecologically versatile species while reducing the presence of ecologically narrower low- and high-elevation species, ultimately lowering overall species richness. Canopy structure may also regulate understory diversity. For instance, dense tree canopies at low elevations may suppress understory plants via light shading, whereas at high elevations or in transitional communities, shorter and sparser trees allow more light to reach understory plants, allowing diversity to rebound [41–43]. This “canopy filtering” mechanism may partly explain the “bimodal” pattern observed in understory vegetation at low-to-mid and mid-to-high elevation transitions.

Furthermore, the significant differentiation in community composition is primarily driven by species turnover rather than niche loss, meaning each elevational zone possesses characteristic dominant species [29, 30]. Concurrently, SIMPER analysis indicates that differences between elevational communities are mainly driven by changes in the abundance of a few common species, with rare species not appearing among the primary contributors. Notably, in the tree layer, *C. lanceolata* contributed more than twice as much as any other species to β -diversity. As *C. lanceolata* is a major afforestation species in Southern China, its overwhelming contribution suggests that the forests in our study area have likely undergone substantial historical anthropogenic disturbance, such as afforestation or secondary succession after logging. Therefore, the community differentiation observed here cannot be attributed solely to natural elevational filtering; rather, it likely reflects an interaction between natural elevational gradients and human land-use history. This anthropogenic legacy may introduce confounding effects on the presumed “natural” elevational pattern, particularly in low- and mid-elevation zones where forestry activities are most intensive. This implies that the β -diversity pattern along the gradient primarily results from the turnover of widespread species, rather than the emergence or disappearance of rare species found only at single elevations. This aligns with the general pattern of mountain community change: The greater the elevation difference, the larger the species composition variation, and the higher the turnover rate of new species replacing existing ones [44]. Rare species, however, may thrive in the study area due to environmental pressures absorbed by other vegetation, exhibiting a distinct pattern of change along the elevational gradient. Their distribution shows no significant correlation with changes in vegetation diversity within the tree layer or understory vegetation layer.

Finally, this study holds significance for mountain forest conservation and biodiversity monitoring. On the one hand, the differing patterns of diversity change between the tree layer and understory vegetation layer underscore the need for conservation efforts to address multiple vertical levels within mountain ecosystems. Traditional conservation often focuses solely on tree layer composition, but our findings indicate that the understory layer exhibits more pronounced species turnover effects and bears a greater share of environmental pressures, warranting greater emphasis in conservation strategies [45]. Simultaneously, the marked differences in community composition across elevational zones indicate that each zone from low to high elevations harbors irreplaceable unique species assemblages. Therefore, comprehensive elevational gradient conservation is crucial for maintaining regional γ -diversity.

Although our study did not directly measure the impacts of climate change, the distinct vertical stratification patterns imply that understory microhabitats are particularly sensitive to environmental shifts [46, 47]. Additionally, this study provides data support for the distribution patterns of two nationally protected and rare ferns. *A. spinulosa* exhibits a peak distribution at mid-elevations, whereas *A. fokiensis* shows a U-shaped distribution, indicating differing tolerances to environmental stress and specific habitat requirements. Their population fluctuations showed no significant correlation with the tree layer or overall diversity but exhibited relatively stronger associations with the understory vegetation layer. Although not statistically significant, this suggests these ancient rare species’ distributions are more constrained by understory microenvironments, aligning with the environmental pressures faced by understory communities. Therefore, conservation practices must concurrently protect both the tree and understory layers to sustain these “living fossil” species [48, 49]. Additionally, given their heightened sensitivity to microenvironments, these rare species can serve as indicator species, reflecting the health of understory habitats. However, the highest elevation site in this study area was only 1500 m, and the spatial scope remains limited. Future research could validate and supplement these scientific findings at larger spatial scales and across more mountain ranges. Furthermore, integrating plot-scale environmental covariates (e.g., soil properties and light availability) and employing constrained ordination methods (e.g., RDA or CCA) would be essential to quantify the actual drivers of community differentiation and disentangle natural from anthropogenic influences. Integrating functional trait and phylogenetic diversity analyses could further explore the functional and evolutionary mechanisms underlying species turnover. In summary, this study enhances our understanding of tropical mountain forest diversity distribution along environmental gradients, underscores the importance of stratified research and integrated conservation, and provides a scientific basis for developing mountain biodiversity conservation strategies.

5 | Conclusion

This study, which investigated the elevational gradient in the tropical Yunkai Mountains forests of Southern China, found that both the tree layer and understory layer exhibited nonlinear changes in α -diversity, but the response patterns differed significantly between the two layers. Tree layer species richness reached a high level near the mid-elevation zone, whereas

understory diversity remained consistently higher than that of the tree layer, exhibiting a “bimodal” pattern with peaks at low-to-mid-elevation and mid-to-high-elevation zones. Concurrently, β -diversity in community composition exhibited pronounced differentiation along the elevational gradient, reflecting intense species turnover rather than simple nestedness relationships. This turnover was primarily driven by the replacement of widespread dominant species, notably including the afforestation species *C. lanceolata*, which highlights that historical anthropogenic disturbance interacts with natural elevational filtering to shape current community differentiation. Rare species contributed relatively little to overall community variation. However, narrowly distributed nationally protected and rare ferns such as *A. spinulosa* and *A. fokiensis* exhibited distinct elevational distribution patterns, indicating that these rare species require special attention in conservation practices. In summary, our findings underscore the critical role of forest vertical stratification in shaping elevational diversity patterns. Effective biodiversity conservation in tropical mountain forests must integrate complete elevational gradients with vertical stratification approaches, explicitly prioritizing the maintenance of understory microhabitats and acknowledging the legacy of historical land use within these ecosystems.

Author Contributions

Xu Li: conceptualization, investigation, writing – original draft, data curation, methodology, validation. **Zhipeng Li:** methodology, writing – review and editing, formal analysis, software, visualization. **Kunhong You:** investigation, data curation. **Yang Liu:** investigation, data curation. **Xialan Cheng:** investigation, data curation, resources. **Han Sheng:** investigation, data curation. **Shaohang Huang:** investigation, data curation. **Chushu Meng:** investigation, data curation. **Shu-Yi-Dan Zhou:** writing – review and editing. **Zhiyang Lie:** writing – review and editing, funding acquisition, project administration. **Juxiu Liu:** funding acquisition, writing – review and editing, project administration, supervision, resources.

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Ethics Statement

This study does not involve any research on animals or human subjects. Field surveys were approved and conducted in compliance with the relevant national laws and local regulations.

Consent

The authors have nothing to report.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available upon request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.

Table S1: Bray–Curtis distance indices at tree and understory layers.