

Postprint: Spatiotemporal Dynamics of Tree Layers in Forests along an Altitudinal Gradient in the Southern Gaoligong Mountains

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Abstract

Studying the spatiotemporal dynamics of community species composition and diversity is of great significance for revealing the distribution patterns of biodiversity and predicting trends of biodiversity change under global change scenarios. However, in mountain ecosystems, how species diversity and phylogenetic diversity of forest communities across different elevational gradients change over temporal scales remains unclear. This study examined 17 quadrats in a permanent monitoring transect of forest communities along an elevational gradient (960–2,878 m) on the east and west slopes of the southern Gaoligong Mountains, analyzing 9-year dynamic changes in species composition, species diversity, and phylogenetic diversity within the quadrats based on resurvey data of the tree layer (DBH \geq 5 cm) from 2004, 2008, and 2013. The results showed that: (1) Along the elevational gradient, species diversity exhibited a unimodal distribution pattern, phylogenetic diversity showed an increasing trend, and phylogenetic structure shifted from clustered to overdispersed or random. (2) At the temporal scale, no significant changes occurred in species diversity or phylogenetic diversity of the forest tree layer over the 9-year period. However, phylogenetic structure showed an increasingly clustered trend over time. (3) Across the elevational gradient, forest community quadrats in the low-elevation region of the east slope (960–1,381 m) exhibited significant species loss, with vegetation being completely replaced by cropland. The main species lost included *Terminalia chebula*, *Quercus acutissima*, *Pistacia weinmanniifolia*, *Hovenia acerba*, and *Ilex wattii*. Conversely, abundance-based β -diversity analysis indicated that species gains were concentrated in low-elevation quadrats on the west slope, with species showing significant increases in richness primarily including *Cyclobalanopsis oxyodon*, *Symplocos chinensis*, and *Taiwania cryptomerioides*. Accordingly, we speculate that the dynamic changes in community structure and diversity of the forest tree layer along the elevational gradient in

the Gaoligong Mountains are constrained by community succession and climate change at mid- and high elevations, while being primarily influenced by human activities at low elevations. These research results will deepen understanding of plant community dynamics in the subtropical evergreen broad-leaved forests of the Gaoligong Mountains and will also facilitate the development of targeted conservation strategies for the region.

Full Text

Spatiotemporal Dynamics of Forest Arbor Layer Along an Elevational Gradient in the Southern Gaoligong Mountains

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Abstract

Understanding the spatiotemporal dynamics of community species composition and diversity is crucial for revealing biodiversity distribution patterns and predicting biodiversity trends under global change scenarios. However, how forest community species diversity and phylogenetic diversity along different elevational gradients change over time remains unclear in mountain ecosystems. This study examined 17 permanent monitoring plots along an elevational gradient (960–2,878 m) on the eastern and western slopes of the southern Gaoligong Mountains. Based on resurvey data of the arbor layer (DBH \geq 5 cm) from

2004, 2008, and 2013, we analyzed the dynamics of species composition, species diversity, and phylogenetic diversity over a 9-year period. The results showed: (1) Species diversity exhibited a hump-shaped distribution pattern along the elevational gradient, while phylogenetic diversity showed an increasing trend, and phylogenetic structure shifted from clustered to overdispersed or random. (2) At the temporal scale, no significant changes occurred in either species diversity or phylogenetic diversity of the forest arbor layer during the 9-year period. However, phylogenetic structure became more clustered over time. (3) Along the elevational gradient, plots in the low-elevation region of the eastern slope (960–1,381 m) experienced significant species loss, with vegetation completely replaced by cropland. The main species lost included *Terminalia chebula*, *Quercus acutissima*, *Pistacia weinmanniifolia*, *Hovenia acerba*, and *Ilex wattii*. Conversely, abundance-based beta diversity analysis indicated that species gains concentrated in low-elevation plots on the western slope, with species showing significant richness increases primarily including *Cyclobalanopsis oxyodon*, *Symplocos chinensis*, and *Taiwania cryptomerioides*. We therefore speculate that dynamic changes in community structure and diversity of the arbor layer along the elevational gradient in the Gaoligong Mountains are constrained by community succession and climate change at mid- and high elevations, while low-elevation communities are mainly affected by human activities. These findings will enhance understanding of plant community dynamics in subtropical evergreen broadleaf forests of the Gaoligong Mountains and inform the development of targeted conservation strategies in the region.

Keywords: community dynamics, elevational gradient, Gaoligong Mountains, species diversity, phylogenetic diversity, spatiotemporal scale

Forests provide critical ecosystem functions and services globally, including carbon sequestration, climate regulation, and biodiversity conservation (Liang et al., 2016; Hisano et al., 2018). Under global change scenarios such as climate warming and human activities, forest ecosystem diversity is threatened, and forest community structure and diversity will undergo dramatic changes (Freeman et al., 2018; Esquivel-Muelbert et al., 2019; Salick et al., 2019). Studying forest community dynamics from the perspective of plant community species composition and diversity changes provides important theoretical value and practical guidance for forest ecosystem conservation and restoration (McDowell et al., 2020; Ding et al., 2021). Although the dynamic changes in forest community diversity and their underlying ecological mechanisms are important for forestry management and biodiversity conservation strategy formulation, long-term monitoring data from permanent plots are required to study community dynamics, and such data remain relatively scarce.

In mountain ecosystems, the distribution patterns of biodiversity along elevational gradients and their causes have long been focal issues for ecologists (Peters et al., 2019; Rahbek et al., 2019). Elevational diversity patterns are influenced by regional geological history, climate, energy, area, and human activities (An-

tonelli et al., 2018; Peters et al., 2019; Hu et al., 2020). Particularly since the Industrial Revolution, rapid population growth and land-use changes have caused large areas of primary vegetation in many low-elevation mountain regions to be replaced by farmland and cropland, drastically altering original mountain biodiversity distribution patterns (Guo et al., 2018). Consequently, elevational biodiversity distribution patterns are subject to combined effects of human activities and climate (Peters et al., 2019). Human activities and climate change can accelerate species vertical migration, alter distribution ranges, and even cause vegetation shifts (Zu and Wang, 2022). For example, on Chimborazo in the Americas, vegetation has moved upslope by an average of over 500 m in the past 200 years (Morueta-Holme et al., 2015); in the European Alps, more than a hundred plant species have migrated to higher elevations (Steinbauer et al., 2018; Rumpf et al., 2018); and over the past 70+ years, many plants in 29 mountain ecosystems in China have similarly shown upward elevational migration trends (Zu et al., 2021, 2023). Beyond species diversity, phylogenetic diversity incorporates information on evolutionary relationships and history among species, holding important applied value in community assembly mechanisms and biodiversity conservation (Webb et al., 2002; Luo et al., 2013; Liu et al., 2017). Although numerous studies have reported on phylogenetic structure and diversity of forest communities along elevational gradients (Qian et al., 2014; Xu et al., 2017; Luo et al., 2019a), how phylogenetic diversity changes over time along elevational gradients remains rarely reported and requires urgent research (Li D et al., 2020).

Subtropical evergreen broadleaf forests represent the most characteristic and important vegetation type in China's subtropical mountain ecosystems. As the main component of global evergreen broadleaf forests, they harbor the richest plant diversity and endemism and provide crucial ecosystem services (Editorial Committee of Vegetation of China, 1980; Song, 2013). The Gaoligong Mountains, oriented north-south, constitute a key biodiversity region in China, connecting three global biodiversity hotspots: the eastern Himalayas, the Hengduan Mountains, and the Indo-Burma region (Mittermeier, 2004; Liu et al., 2022), and serving as an important ecological security barrier in southwestern China (Luo et al., 2023). The Gaoligong Mountains host a complete vertical zonation along the elevational gradient, including monsoon evergreen broadleaf forests, semi-humid evergreen broadleaf forests, mid-montane humid evergreen broadleaf forests, and montane mossy dwarf forests (Li et al., 2000), making them a natural laboratory for studying elevational diversity patterns and dynamics of subtropical evergreen broadleaf forests. Previous studies have shown that seed plant species richness in the Gaoligong Mountains exhibits a hump-shaped distribution along the elevational gradient, associated with factors such as temperature, precipitation, and disturbance levels (Wang et al., 2007; Xu et al., 2008; Yue and Li, 2021). However, these studies were based on literature or single surveys that captured only a temporal snapshot of plant species diversity distribution patterns. Questions remain regarding how species composition, species diversity, and phylogenetic diversity of typical forest communities in the

region change spatiotemporally based on forest plot monitoring, and whether trends differ between slopes.

This study utilized permanent monitoring plots established along elevational gradients on the eastern and western slopes of the southern Gaoligong Mountains. Based on three systematic community surveys conducted in 2004, 2008, and 2013, we analyzed trends in species composition, species diversity, and phylogenetic diversity of the arbor layer ($DBH \geq 5$ cm) across different elevations, time periods, and slopes. We aimed to address three scientific questions: (1) What are the elevational distribution patterns of species and phylogenetic diversity of the forest arbor layer in the southern Gaoligong Mountains, and are these patterns consistent across different periods? (2) Have species and phylogenetic diversity changed significantly over time? (3) At the spatial scale, how does species composition change across different elevations and slopes, and which species contribute most to these changes? This study seeks to provide a theoretical basis for biodiversity conservation, ecosystem management, and vegetation restoration of subtropical evergreen broadleaf forests in the Gaoligong Mountains under global change scenarios.

1. Methods

1.1 Study Area and Plot Setup

The Gaoligong Mountains are located in southwestern China, primarily in western Yunnan Province, extending to southeastern Tibet Autonomous Region, forming the watershed between the Nujiang River and Irrawaddy River (Fig. 1 [Figure 1: see original paper]a). The administrative region mainly includes Yingjiang, Lianghe, Longling, and Tengchong counties in Yunnan Province, western parts of Longyang, Lushui, Fugong, and Gongshan, southern Chayu in Tibet Autonomous Region, and northern Kachin State in Myanmar, covering an area of 4.39×10^4 km² (Luo et al., 2023). Geological processes and river erosion have created dramatic elevational differences, with subtropical, temperate, and cold temperate climate zones distributed along the elevation. Climatically, the Gaoligong Mountains are primarily influenced by the Indian Ocean monsoon, exhibiting distinct wet and dry seasons: May–October as the rainy season and November–April as the dry season.

This study was conducted in the southern section of the Gaoligong Mountains, within the jurisdiction of the Baoshan Management and Protection Bureau of the Yunnan Gaoligongshan National Nature Reserve. The eastern slope is located in Longyang District, Baoshan City, managed by the Longyang Branch, while the western slope is in Tengchong City, Baoshan City, under the Tengchong Branch. In 2004, the Baoshan Management and Protection Bureau established 17 permanent monitoring plots along an elevational gradient along the Baihualing–Nangongfang–Linjiapu transect (Table 1 ; Fig. 1b). The eastern slope spans 960–2,878 m with 11 plots; the western slope spans 2,096–2,860 m with 6 plots. Each plot measured 400 m² (20 m × 20 m). Our forest plots rep-

resented typical vegetation types and elevational gradients in the study region (Table 1). Notably, four low-elevation plots on the eastern slope (E1–E4) were located in areas with intense human disturbance, dominated by remnant fragmented secondary forests with sparse species and individuals in the arbor layer (Table 1), but we included them in the monitoring system to track dynamics of species and individuals in these secondary forests.

1.2 Community Survey

In this study, the arbor layer in forest communities was defined as individuals with diameter at breast height (DBH) ≥ 5 cm, encompassing dominant tree species of typical regional vegetation types (Table 1). Surveys of tree species in the plots were conducted in 2004, 2008, and 2013. All trees with DBH ≥ 5 cm in each plot were tagged, numbered, and measured. Newly recruited individuals were tagged and surveyed during resurveys. Survey parameters included species, DBH, height, and crown width. All tree species and individuals recorded across the three surveys were compiled for subsequent analyses.

1.3 Species Diversity and Species Composition

We used species richness (S), Shannon-Wiener index (H) (Shannon, 1949), and Simpson index (D) (Simpson, 1949) to characterize species diversity.

Where: P_i is the proportion of individuals of species i relative to the total number of individuals in the plot; S represents the number of species in the plot. $H = -\sum_{i=1}^S P_i \ln P_i$

We used non-metric multidimensional scaling (NMDS) to analyze species composition within plots, employing abundance-based Bray-Curtis dissimilarity (Anderson et al., 2011), and presented ordination results using the first and second dimensions.

1.4 Phylogenetic Diversity

We constructed a phylogenetic tree for 83 woody plant species in the plots using the V.PhyloMaker package in R with Scenario 3, which adds species to families or genera based on their systematic positions (Jin and Qian, 2019). V.PhyloMaker integrates phylogenetic relationships of 74,533 vascular plant species globally. For species not included in the phylogeny, we randomly integrated them at the genus level into the phylogenetic tree. We selected three indices: Faith's phylogenetic diversity (PD), mean pairwise distance (MPD), and mean nearest taxonomic distance (MNTD). Faith's PD reflects the proportion of phylogenetic branch lengths of taxa within a community relative to all branches in the phylogeny (Faith, 1992); MPD reflects the average phylogenetic distance among species in a community; MNTD reflects the phylogenetic distance to the nearest neighbor (Webb et al., 2002). We standardized the three phylogenetic indices by comparing each community's observed phylogenetic diversity metrics against null models. Our null model randomized species

at the tips of the phylogenetic tree 999 times (Gotelli, 2000) to obtain SES.PD, SES.MPD, and SES.MNTD. $SES > 0$ indicates overdispersion, while $SES < 0$ indicates clustering (Webb et al., 2002). The calculation formula is as follows:

Where: obs represents the observed value; mean represents the mean of random simulations; sd represents the standard deviation of random simulations.

1.5 Data Analysis

To analyze elevational patterns of species and phylogenetic diversity across the three survey time points, we used generalized linear mixed models (GLME) based on the distribution characteristics of response variables. Species richness was modeled using Poisson distribution, while other response variables used Gaussian distribution (Luo et al., 2023). Elevation was set as a fixed effect, with elevation|slope as a random effect. Model parameters and explanatory power were calculated, where marginal R^2 includes only fixed effects and conditional R^2 includes both fixed and random effects (Nakagawa and Schielzeth, 2013). Because elevational biodiversity changes may be nonlinear, we fitted both linear and quadratic terms and defined the model with smaller AICc as superior.

To analyze temporal trends in species and phylogenetic diversity of forest arbor layers in the Gaoligong Mountains, we used paired t-tests to compare differences in species and phylogenetic diversity among the three time points. To explore spatial-scale trends in species composition changes across different elevations and slopes and identify the main contributing species, we applied the method of Legendre and Condit (2019) based on Temporal Beta Indices (TBI) and tested their significance. Specifically, this method compares species composition differences between T1 and T2 for each plot, comprising two components: B component (species losses) and C component (species gains). B and C components are further used to generate B-C plots. This method can test differences in B and C components for individual plots or across all plots. We compared differences among the three time points (2004, 2008, and 2013) using the TBI function and plot.TBI function in the `adespatial` package (Dray et al., 2019). All analyses were conducted in R 3.6.3 (The R Development Core Team, 2019).

2. Results

2.1 Elevational Patterns of Arbor Layer Species and Phylogenetic Diversity

A total of 83 arbor species with $DBH \geq 5$ cm were recorded across all plots. According to the APG IV system, these belonged to 54 genera and 30 families. Species diversity (species richness, Shannon index, and Simpson index) showed a hump-shaped distribution along the elevational gradient, with maximum diversity at mid-elevations (Fig. 2 [Figure 2: see original paper]). Comparisons against null models with randomized phylogenetic relationships revealed that standardized phylogenetic diversity (SES.PD, SES.MPD, SES.MNTD) in-

creased along the elevational gradient, with phylogenetic structure being clustered at low elevations and random or overdispersed at high elevations (Fig. 3 [Figure 3: see original paper]).

2.2 Temporal Changes in Species and Phylogenetic Diversity

At the temporal scale, paired t-test results indicated no significant changes in overall forest community species diversity or phylogenetic diversity across the three census years (Fig. 4 [Figure 4: see original paper]). However, phylogenetic structure became more clustered over time (Fig. 4).

Color gradients indicate different elevations (blue indicates low elevation and green indicates high elevation), NS indicates no significant differences based on t-tests ($P > 0.05$).

In 2004, 71 species with 1,205 individuals were recorded; in 2008, 76 species with 1,190 individuals; and in 2013, 76 species with 1,164 individuals. Species composition varied considerably across different slopes and elevations. Along the elevational gradient, four low-elevation plots on the eastern slope (960–1,381 m) exhibited significant complete species loss (Fig. 5 [Figure 5: see original paper]), with vegetation entirely replaced by cropland. Main species lost included *Quercus acutissima*, *Pistacia weinmanniifolia*, *Hovenia acerba*, and *Ilex watti* (Table 2). Conversely, abundance-based beta diversity analysis indicated that species gains concentrated in three low-elevation plots on the western slope (Fig. 5), with species showing significant richness increases primarily including *Cyclobalanopsis oxyodon*, *Symplocos chinensis*, and *Taiwania cryptomerioides* (Table 2).

Four plots in low elevations of eastern slope exhibit significant differences (* indicates significant differences).

3. Discussion

3.1 Elevational Patterns of Species and Phylogenetic Diversity

Numerous studies have shown that plant diversity along elevational gradients typically exhibits a hump-shaped distribution, with the peak located in the lower-middle portion of the mountain (Guo et al., 2013). However, climate change and human activities may alter this vertical distribution pattern of mountain plant diversity (Hisano et al., 2018; Peters et al., 2019). In this study, species diversity showed a hump-shaped pattern along the elevational gradient, inconsistent with patterns from primary forest surveys in the Gaoligong Mountains (monotonically decreasing) (Luo et al., 2023). We attribute this discrepancy to the larger elevational range included in our study, suggesting that strongly human-disturbed low-elevation plots may be the main reason for the hump-shaped pattern. Results from different survey periods indicate that the hump-shaped pattern of species diversity did not change significantly, suggesting that species composition and diversity in mid-elevation forest communities

remained relatively stable. Compared with species diversity, phylogenetic diversity incorporates evolutionary history and phylogenetic relationships among species, gaining wide application in community assembly and biodiversity conservation research (Faith, 1992; Donoghue, 2008; Cavender-Bares et al., 2009). Previous studies on tropical rainforest communities along elevational gradients in Malaysia showed that high-elevation communities may exhibit overdispersed phylogenetic structure due to trait convergence, while lowland and foothill communities show clustered phylogenetic structure (Culmsee and Leuschner, 2013). Similarly, our study found that high-elevation arbor layers showed overdispersed or random phylogenetic structure, results that do not support the tropical niche conservatism hypothesis (Wiens and Donoghue, 2004). This may be due to resource-use convergence leading to differentiation among high-elevation species or may be related to dispersal limitation. These findings also differ from results in northern Gaoligong Mountains showing phylogenetic structure shifting from overdispersed to clustered (Yue and Li, 2021). We speculate that human disturbance and the hot-dry environment in low-elevation valley regions may be the main causes of phylogenetic clustering, suggesting substantial differences in regional population density and climatic environmental factors between southern and northern Gaoligong Mountains.

3.2 Temporal Dynamics of Species and Phylogenetic Diversity

Long-term monitoring of forest plots at temporal scales is essential for understanding biodiversity changes, ecosystem function shifts, and effective forest ecosystem management (Liang et al., 2016). Meta-analysis results indicate that changes in forest cover at low elevations are key drivers altering plant elevational distributions (Guo et al., 2018). Similarly, our study found no significant changes in overall forest community species diversity or phylogenetic diversity. We attribute this to the large areas of intact primary subtropical evergreen broadleaf forest distributed at mid- and high elevations in the Gaoligong Mountains, which represent the most concentrated, intact, and typical region of subtropical evergreen broadleaf forest in China. Species composition in these mid- and high-elevation areas changed little over time, with relatively stable community structure likely constrained by natural successional processes, thus showing stable community composition overall. However, secondary forests or remnant fragmented forests outside protected areas, such as plots at 960–1,381 m on the eastern slope, experienced complete loss of arbor layer diversity due to land-use changes (cropland cultivation and cash crop planting) and frequent human activities (logging and tourism development) near villages. In contrast, species diversity on the western slope increased over time, likely due to both post-disturbance successional recovery and afforestation activities such as the Grain-for-Green program in low-elevation areas. Evidently, low-elevation forest communities on both slopes experienced strong human disturbance that directly altered species composition and diversity of the arbor layer. Notably, the Gaoligong Mountains Nature Reserve was established in 1983 and upgraded to a national nature reserve in 1986, after which logging and disturbance within the

reserve decreased and local conservation awareness gradually increased. Along with community succession, species composition and diversity changed little after 2008 even in low-elevation areas, suggesting that regional species diversity and ecosystem functions are undergoing active recovery and that overall community stability in the protected area has been further strengthened.

Temporal changes in phylogenetic diversity have been studied mainly in grassland ecosystems. For example, one study showed that persistent drought drove declines in phylogenetic diversity in American grasslands from 2000–2018 (Li D et al., 2020). However, no reports exist on temporal changes in phylogenetic diversity of forest communities, especially along elevational gradients. Our study confirmed that phylogenetic diversity of forest communities in the Gaoligong Mountains declined from 2004–2013, implying that species in communities became more closely related. However, whether the driving forces behind this decline are human activities, climate change, or other factors requires further investigation. Moreover, our study only included changes in the arbor layer from 2004–2013. How these forest communities have changed after 2013 requires analysis and in-depth discussion based on new survey data, representing an important focus for future research.

3.3 Changes in Species Composition Across Different Slopes and Elevations

In mountain ecosystems, slope aspect is often a key topographic factor influencing differences in plant composition and diversity distribution, with substantial potential differences in soil, moisture, heat, and light factors among aspects (Winkler et al., 2016; Dearborn and Danby, 2017). The north-south oriented Gaoligong Mountains are affected by the southwestern Indian Ocean monsoon (An, 2014), exhibiting typical foehn effects. The western slope generally receives higher precipitation than the eastern slope (Li et al., 2000), which may further drive compositional differences between slopes. For example, the Nushan Mountains act as a barrier, coupling monsoon-related precipitation and temperature changes to drive species differentiation of *Taxus wallichiana* between slopes, resulting in different species distributed on eastern and western slopes (Liu et al., 2013). Repeated cycles of such microevolutionary processes lead to differences in floristic composition among slopes. Our results showed substantial divergence in species composition between slopes, with higher species diversity on the western slope than the eastern slope at the same mid-elevation range. We speculate this may be related to greater precipitation on the western slope, which may support a larger species pool and reduce water stress within local communities, promoting greater species coexistence (Jiménez-Alfaro et al., 2018). Notably, due to land-use changes in low-elevation plots on the eastern slope, species typical of hot-dry valleys such as *Terminalia chebula*, *Quercus acutissima*, *Pistacia weinmanniifolia*, *Hovenia acerba*, and *Ilex wattii* disappeared from the arbor layer of fragmented secondary forests after 2008. These species require regional-scale attention and monitoring in future biodiversity conservation efforts. Conversely,

in low-elevation plots on the western slope, species showing significant richness increases included mainly *Cyclobalanopsis oxyodon*, *Symplocos chinensis*, and *Taiwania cryptomerioides*. The increased abundance of *Cyclobalanopsis oxyodon* and *Symplocos chinensis* may be associated with community successional processes, as both are dominant species in this successional stage; however, *Taiwania cryptomerioides* is artificially cultivated and represents human influence. Additionally, conservation and restoration measures for rare and endangered species such as *Manglietia insignis* and *Rhododendron protistum* var. *giganteum* in low-elevation areas on the western slope will benefit forest community nurturing and vegetation restoration in the region. Our study further found that mid- and high-elevation forest plots on both slopes showed overall species loss; the key biotic (e.g., interspecific competition) and abiotic (e.g., persistent drought, extreme weather) processes driving these changes require long-term monitoring research.

3.4 Implications for Mountain Biodiversity Conservation

Mountains are complex ecosystems that provide natural well-being for human society, cradle biodiversity, and harbor rich ecosystem services (Antonelli et al., 2018; Luo et al., 2019b; Hu et al., 2020). With intensifying human impacts on natural ecosystems and increasing extreme climate events, mountain biodiversity conservation faces enormous challenges. Currently, protected area coverage in low-elevation regions of Asian mountains is far below the 17% “Aichi Target 11” of the Convention on Biological Diversity (Elsen et al., 2018), and this deficiency will be further affected by elevation-dependent warming processes at global and regional scales (Pepin et al., 2015; Li B et al., 2020), particularly in low-elevation areas. In the Gaoligong Mountains, community composition and structure at mid- and high elevations within protected areas remained stable over time, indicating effective conservation. However, low-elevation areas with unique species composition and phylogenetic diversity, located outside protected areas, experienced complete vegetation transformation in less than 10 years, with four plots replaced by cropland, leading to substantial loss of biodiversity and ecosystem functions. In fact, across the Gaoligong Mountains and most mountains in Yunnan, current natural vegetation vertical distribution patterns often show a “pot-lid” shape, where high elevations retain remnant natural vegetation while low-elevation primary vegetation is largely replaced by cropland or plantations. This pattern is confirmed by large-scale studies showing that global mountain forest loss reached 7.1% between 2001–2018, concentrated mainly in low- and mid-elevation regions (<1,000 m) (He et al., 2023). We recommend establishing microreserves in low-elevation areas as an emergency measure to increase protected area coverage and enhance ecosystem integrity across entire mountain systems. Furthermore, the strategy of long-term community dynamics monitoring combined with multidimensional biodiversity indicators (e.g., species diversity and phylogenetic diversity) used in this study could be applied in other protected areas, with further inclusion of genetic diversity and functional diversity dimensions.

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References

- Ding H, Chen SF, Xu H, et al., 2022. Dynamics of arbor layer in the subtropical evergreen broad-leaved forest in the Wuyi Mountains, Fujian Province, southeastern China in 2013-2018. *Acta Ecologica Sinica*, 42(8): 3458-3469.
- Li H, Guo HJ, Dao ZL, 2000. *Flora of Gaoligong Mountain*. Beijing: Science Press.
- Liu J, Luo YH, Li DZ, et al., 2017. Evolution and maintenance mechanisms of plant diversity in the Qinghai-Tibet Plateau and adjacent regions: retrospect and prospect. *Biodiversity Science*, 25(2): 41-45.
- Luo YH, Liu J, Gao LM, et al., 2013. Applications and advances of DNA barcoding in ecological studies. *Plant Diversity and Resources*, 35(6): 761-768.
- Song YC, 2013. *Evergreen Broad-leaved Forests in China: Classification-Ecology-Conservation*. Beijing: Science Press.
- Wang ZH, Chen AP, Piao SL, et al., 2004. Pattern of species richness along an altitudinal gradient on Gaoligong Mountains, Southwest China. *Biodiversity Science*, 12(1): 82-88.
- Xu CD, Feng JM, Wang XP, et al., 2008. Vertical distribution patterns of plant species diversity in northern Mt. Gaoligong, Yunnan Province. *Chinese Journal of Ecology*, 27(3): 323-327.
- Editorial Committee of Vegetation of China, 1980. *Vegetation of China*. Beijing: Science Press.
- Zu K, Wang ZH, 2022. Research progress on the elevational distribution of mountain species in response to climate change. *Biodiversity Science*, 30(5): 21451.
- An ZS, 2014. *Late Cenozoic Climate Change in Asia: Loess, Monsoon and Monsoon-arid Environment Evolution*. Dordrecht: Springer.
- Anderson MJ, Crist TO, Chase JM, et al., 2011. Navigating the multiple meanings of beta diversity: a roadmap for the practicing ecologist. *Ecology Letters*, 14(1): 19-28.
- Antonelli A, Kissling WD, Flantua SG, et al., 2018. Geological and climatic influences on mountain biodiversity. *Nature Geoscience*, 11(10): 718-725.

- Cavender-Bares J, Kozak KH, Fine PV, et al., 2009. The merging of community ecology and phylogenetic biology. *Ecology Letters*, 12(7): 693-715.
- Culmsee H, Leuschner C, 2013. Consistent patterns of elevational change in tree taxonomic and phylogenetic diversity across Malesian mountain forests. *Journal of Biogeography*, 40(10): 1997-2010.
- Dearborn KD, Danby RK, 2017. Aspect and slope influence plant community composition more than elevation across forest-tundra ecotones in subarctic Canada. *Journal of Vegetation Science*, 28(3): 520-532.
- Donoghue MJ, 2008. A phylogenetic perspective on the distribution of plant diversity. *Proceedings of the National Academy of Sciences USA*, 105(Supplement 1): 11549-11555.
- Dray S, Bauman D, Blanchet G, et al., 2019. adespatial: Multivariate multiscale spatial analysis. R package version 0.3-3.
- Elsen PR, Monahan WB, Merenlender AM, 2018. Global patterns of protection of elevational gradients in mountain ranges. *Proceedings of the National Academy of Sciences USA*, 115(23): 6004-6009.
- Esquivel-Muelbert A, Baker TR, Dexter KG, et al., 2019. Compositional response of Amazon forests to climate change. *Global Change Biology*, 25(1): 39-56.
- Faith DP, 1992. Conservation evaluation and phylogenetic diversity. *Biological Conservation*, 61(1): 1-10.
- Freeman BG, Lee-Yaw JA, Sunday JM, et al., 2018. Expanding, shifting and shrinking: The impact of global warming on species' elevational distributions. *Global Ecology and Biogeography*, 27(11): 1268-1276.
- Gotelli NJ, 2000. Null model analysis of species co-occurrence patterns. *Ecology*, 81(9): 2606-2621.
- Guo F, Lenoir J, Bonebrake TC, 2018. Land-use change interacts with climate to determine elevational species redistribution. *Nature Communications*, 9(1): 1315.
- Guo Q, Kelt DA, Sun Z, et al., 2013. Global variation in elevational diversity patterns. *Scientific Reports*, 3: 3007.
- Hisano M, Searle EB, Chen HYH, 2018. Biodiversity as a solution to mitigate climate change impacts on the functioning of forest ecosystems. *Biological Reviews*, 93(1): 439-456.
- He X, Ziegler AD, Elsen PR, et al., 2023. Accelerating global mountain forest loss threatens biodiversity hotspots. *One Earth*, 6: 303-315.
- Hu A, Wang J, Sun H, et al., 2020. Mountain biodiversity and ecosystem functions: interplay between geology and contemporary environments. *ISME Journal*, 14(4): 931-944.

- Jiménez-Alfaro B, Girardello M, Chytrý M, et al., 2018. History and environment shape species pools and community diversity in European beech forests. *Nature Ecology & Evolution*, 2(3): 483-490.
- Jin Y, Qian H, 2019. V.PhyloMaker: an R package that can generate very large phylogenies for vascular plants. *Ecography*, 42(8): 1353-1359.
- Legendre P, Condit R, 2019. Spatial and temporal analysis of beta diversity in the Barro Colorado Island forest dynamics plot, Panama. *Forest Ecosystems*, 6(1): 1-11.
- Li B, Chen Y, Shi X, 2020. Does elevation dependent warming exist in high mountain Asia? *Environmental Research Letters*, 15(2): 024012.
- Li D, Olden JD, Lockwood JL, et al., 2020. Changes in taxonomic and phylogenetic diversity in the Anthropocene. *Proceedings of the Royal Society B: Biological Sciences*, 287(1929): 20200777.
- Liang J, Crowther TW, Picard N, et al., 2016. Positive biodiversity-productivity relationship predominant in global forests. *Science*, 354(6309): aaf8957.
- Liu J, Möller M, Provan J, et al., 2013. Geological and ecological factors drive cryptic speciation of yews in a biodiversity hotspot. *New Phytologist*, 199(4): 1093-1108.
- Liu J, Milne RI, Zhu GF, et al., 2022. Name and scale matters: clarifying the geography of Tibetan Plateau and adjacent mountain regions. *Global and Planetary Change*, 215: 103893.
- Luo YH, Cadotte MW, Burgess KS, et al., 2019a. Forest community assembly is driven by different strata-dependent mechanisms along an elevational gradient. *Journal of Biogeography*, 46(10): 2174-2187.
- Luo YH, Cadotte MW, Burgess KS, et al., 2019b. Greater than the sum of the parts: how the species composition in different forest strata influence ecosystem function. *Ecology Letters*, 22(9): 1449-1461.
- Luo YH, Ma LL, Seibold S, et al., 2023. The diversity of mycorrhiza-associated fungi and trees shapes subtropical mountain forest ecosystem functioning. *Journal of Biogeography*, 50(4): 715-728.
- McDowell NG, Allen CD, Anderson-Teixeira K, et al., 2020. Pervasive shifts in forest dynamics in a changing world. *Science*, 368(6494): eaaz9463.
- Mittermeier RA, Gil PR, Hoffman M, et al., 2004. *Hotspots Revisited: Earth's Biologically Richest and Most Endangered Terrestrial Ecoregions*. Chicago: University of Chicago Press.
- Morueta-Holme N, Engemann K, Sandoval-Acuña P, et al., 2015. Strong upslope shifts in Chimborazo's vegetation over two centuries since Humboldt. *Proceedings of the National Academy of Sciences USA*, 112(41): 12741-12745.

- Nakagawa S, Schielzeth H, 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 4(2): 133-142.
- Pepin N, Bradley RS, Diaz H, et al., 2015. Elevation-dependent warming in mountain regions of the world. *Nature Climate Change*, 5(5): 424-430.
- Peters MK, Hemp A, Appelhans T, et al., 2019. Climate-land-use interactions shape tropical mountain biodiversity and ecosystem functions. *Nature*, 568(7750): 88-92.
- Qian H, Hao Z, Zhang J, 2014. Phylogenetic structure and phylogenetic diversity of angiosperm assemblages in forests along an elevational gradient in Changbaishan, China. *Journal of Plant Ecology*, 7(2): 154-165.
- Rahbek C, Borregaard MK, Colwell RK, et al., 2019. Humboldt's enigma: What causes global patterns of mountain biodiversity? *Science*, 365(6458): 1108-1113.
- Rumpf SB, Hülber K, Klöner G, et al., 2018. Range dynamics of mountain plants decrease with elevation. *Proceedings of the National Academy of Sciences USA*, 115(8): 1848-1853.
- Salick J, Fang Z, Hart R, 2019. Rapid changes in eastern Himalayan alpine flora with climate change. *American Journal of Botany*, 106(4): 520-530.
- Shannon CE, 1949. Communication theory of secrecy systems. *Bell System Technical Journal*, 28(4): 656-715.
- Simpson EH, 1949. Measurement of diversity. *Nature*, 163(4148): 688.
- Steinbauer MJ, Grytnes JA, Jurasinski G, et al., 2018. Accelerated increase in plant species richness on mountain summits is linked to warming. *Nature*, 556(7700): 231-234.
- Wang Z, Tang Z, Fang J, 2007. Altitudinal patterns of seed plant richness in the Gaoligong Mountains, southeast Tibet, China. *Diversity and Distributions*, 13(6): 845-854.
- Webb CO, Ackerly DD, McPeck MA, et al., 2002. Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, 33(1): 475-505.
- Wiens JJ, Donoghue MJ, 2004. Historical biogeography, ecology and species richness. *Trends in Ecology & Evolution*, 19: 639-644.
- Winkler M, Lamprecht A, Steinbauer K, et al., 2016. The rich sides of mountain summits—a pan-European view on aspect preferences of alpine plants. *Journal of Biogeography*, 43(11): 2061-2071.
- Xu J, Chen Y, Zhang L, et al., 2017. Using phylogeny and functional traits for assessing community assembly along environmental gradients: A deterministic process driven by elevation. *Ecology and Evolution*, 7(14): 5056-5069.

Yue J, Li R, 2021. Phylogenetic relatedness of woody angiosperm assemblages and its environmental determinants along a subtropical elevational gradient in China. *Plant Diversity*, 43(2): 111-116.

Zu K, Wang Z, Zhu X, et al., 2021. Upward shift and elevational range contractions of subtropical mountain plants in response to climate change. *Science of the Total Environment*, 783: 146896.

Zu K, Lenoir J, Fang J, et al., 2023. Elevational shift in seed plant distributions in China's mountains over the last 70 years. *Global Ecology and Biogeography*, 32: 1098-1112.

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