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Ecological Processes

RESEARCH

Functional and phylogenetic structure of mammals along elevational gradients in the Central and East Himalayas

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Abstract

Background Mountain ecosystems are critical hotspots of global biodiversity, yet the dynamics of community assembly along their elevational gradients are not well understood. This gap is primarily due to the complexity of environmental and biotic interactions that influence species distribution and community structure. Although extensive research has been conducted on certain taxa, such as small mammals and bats, comprehensive studies encompassing entire mammal assemblages are lacking. Our research aims to bridge this gap by examining the taxonomic, phylogenetic, and functional diversity, as well as the assemblage structures of mammal communities across elevational gradients in the Central and East Himalayas, exploring how diverse ecological and evolutionary processes impact community assembly.

Methods We analyzed mammal elevational diversity patterns using species richness, functional diversity (FD), and phylogenetic diversity (PD). We compared the observed values of community structure, such as mean pairwise phylogenetic distance (MPD) and mean pairwise functional distance (MFD), with null-model corrected effect sizes to identify patterns and processes of community assembly. Using structural equation modeling and hierarchical partitioning, we investigated the relationships between climate, productivity, and various facets of diversity, describing the organization of each component across different elevations.

Results Taxonomic, functional, and phylogenetic diversity generally decreased with elevation but showed varied patterns such as mid-elevation peaks, low-elevation plateaus, or monotonic declines across different regions. Richness-controlled functional diversity increased towards mid-low elevations and decreased at higher elevations in both regions, whereas richness-controlled phylogenetic diversity lacked consistent patterns. Phylogenetic structures tended to cluster from mid to high elevations, indicating closer relationships than those observed in random communities, likely due to significant environmental turnover near tree lines. Functional structure showed greater clustering at high elevations and increased over-dispersion at lower elevations, suggesting that species are more functionally similar than expected at higher elevations and more diverse at lower elevations. Our results revealed that environmental factors, evolutionary histories, and trait-driven ecological processes collectively shape species richness along these gradients.

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Conclusions Our results showed incongruent community structures across phylogenetic and functional diversity. Generally, functional traits are closely linked to environmental conditions, reducing the chance of observing traits that are misaligned with their surroundings. Species with similar ecological roles or distinct evolutionary lineages often show convergent adaptations to highland environments. Additionally, our findings emphasize that community assembly varies with the biogeography and diversification history of individual mountain ranges, complicating the development of a generalized theory. Using multiple measures is important for accurate community structure assessments and effective conservation planning, as variable elevational patterns exist across different diversity dimensions.

Keywords Assemblage structure, Functional diversity, Himalaya mountains, Mammals, Phylogenetic diversity, Species richness

Background

Exploring elevational gradients offers a unique opportunity to uncover biodiversity patterns and community dynamics. The rapid environmental turnover from lower to higher elevations provides a natural laboratory to study how species composition, functional traits, and evolutionary relationships shift in response to varying environmental conditions. The elevational pattern of species richness is widely explored, often showing declines with elevation or mid-elevation peaks (Rahbek 1995; McCain 2005, 2007, 2009). However, species richness considers all species to be equally distinct, providing little information on the evolutionary makeup of the assemblage, how assemblages form, and the ecosystem functions they perform (Wilsey et al. 2005). In recent decades, indices integrating species' evolutionary histories or ecological functions, like phylogenetic (Faith 1992) and functional diversity (Petchey and Gaston 2002), have expanded the theoretical framework of biodiversity. This more comprehensive perspective on biodiversity could enhance comprehension of community assembly and the underlying mechanisms that shape it.

Research based on multidimensional interpretations of biodiversity has rapidly advanced (Pavoine and Bonsall 2011), yet uncertainties and controversies persist. Inconsistencies often arise among taxonomic, phylogenetic, and functional diversity patterns (Bässler et al. 2016; Kohli et al. 2021; Sun et al. 2020). Moreover, understanding the mechanisms that shape phylogenetic and functional diversity along these gradients proves more challenging than delineating those affecting species richness. Studies suggest that various climate and resource-related factors (e.g., productivity or resource abundance) influence phylogenetic or functional diversity across taxa (e.g., microorganism: Zhou et al. 2016; insect and bird: Laiolo et al. 2018; mammal: Sun et al. 2020; bird: Ding et al. 2021; Montaño-Centellas et al. 2021). For example, a global analysis of rodents revealed drought as a key factor in phylogenetic and functional diversity variation across regions (Kohli et al. 2022). Conversely, on a local scale, habitat-related factors (e.g., environmental heterogeneity and vegetation structural complexity) and primary productivity have been proposed as significant drivers of phylogenetic and functional diversity patterns in rodents (Sukma et al. 2019; Mortelliti and Brehm 2020; Sun et al. 2020).

Environmental gradients and biological interactions shape community assembly, resulting in phylogenetically and functionally distinct communities. Consequently, examining phylogenetic and functional structures could help to disentangle the relative importance of biotic and abiotic factors that shape communities. Originating from Darwin (1859), the species interactions–abiotic stress hypothesis posits that abiotic factors have a greater influence than biotic factors on the community in stressful environments, while biotic effects tend to dominate the process in more favorable regions (Louthan et al. 2015). Studies comparing functional and phylogenetic structures of communities with null models have suggested that low-elevation communities exhibit functional or phylogenetic over-dispersion due to competition, as functionally similar species cannot coexist; in contrast, high-elevation communities display greater clustering due to environmental filtering, where only species with specific traits can survive (Ding et al. 2021). However, community assembly might be more complex than initially anticipated, as recent findings show variations in these patterns and processes across different mountains and taxa. Two recent global-scale studies on birds emphasize the geographic variation in the interplay of phylogenetic and functional structure (Jarzyna et al. 2021; Montaño-Centellaset al. 2020). This variability is also evident in local-scale studies. For instance, tropical epiphytic ferns and frugivorous birds show clustering at both low and high elevations, driven by environmental conditions that select for specific traits (Kluge and Kessler 2011; Dehling et al. 2014). Convergent evolution may lead to trait clustering as species in different lineages evolve similar traits to adapt to environmental pressures, or limited lineage diversification in these environments might result in both trait and phylogenetic clustering. Thus, these complexities require more studies, particularly within a comparative framework (e.g., different regions of the same mountain system where local species share similar origins but experience different environmental influences), to assess the relative roles of environmental filtering and biotic competition in structuring communities along elevational gradients.

The Himalayas offer unique landscapes for exploring biodiversity patterns as it is one of the world's biodiversity hotspots. Further, this region is influenced by the Indian Ocean monsoon and high-pressure systems from the Qinghai-Tibet Plateau, forming a longitudinal climate gradient spanning the warm and humid east to the cool and dry west (Price et al. 2011; Hu et al. 2021). These climatic variations are likely to shape the assembly of communities in the area. For example, tropical mountains are expected to represent strong physiological filters for organisms (Janzen 1967). With extensive elevational and longitudinal gradients, the Himalayas provide abundant opportunities for specialization and niche partitioning, leading to significant spatial turnover in biodiversity (Hu et al. 2022).

It is important to note that relatively few studies on functional and phylogenetic diversity in mammals exist, and those that do, have emphasized specific groups such as non-volant small mammals and bats (e.g., non-volant small mammal: Dreiss et al. 2015; Kohli et al. 2021; Sun et al. 2020; Kohli et al. 2022; bat: Cisneros et al. 2014; Mancini et al. 2019; Bogoni et al. 2021). Here, our objective is to encompass the entire non-volant terrestrial mammal assemblage, including large-bodied species, for a comprehensive assessment of mammalian functional and phylogenetic diversity along the Himalayan elevational gradients. We also examined how different facets of diversity respond to environmental changes and how phylogenetic and functional components influence taxonomic diversity. Specifically, we addressed the following questions: (1) what are the elevational patterns of taxonomic, functional, and phylogenetic diversity of mammals across different mountain regions, and how do these patterns differ from one another? (2) What are the functional and phylogenetic structures of mammal communities, and what is the relative importance of ecological processes in structuring community assemblies along elevational gradients? How are climate and productivity linked with various facets of diversity, and how are these components organized and related to each other across different elevations?

Methods

Study areas

Our study spans the Himalayan longitudinal climate gradient, encompassing sites in both the Central and Eastern Himalayas. The Gyirong Valley (28° 15′–29° 0′ N, 85° 6′–85° 41′ E, abbreviated as Gyirong; Fig. 1a) is located in the Central Himalayas, while the Lebu Valley (26° 25′–28° 27′ N, 91° 28′–94° 22′ E, abbreviated as Lebu; Fig. 1b) lies in the East Himalayas (Figure S1; Hodges 2000). Gyirong experiences an annual average temperature of 0.45 °C (SD = 4.23) and precipitation of 423.58 mm (SD = 151.95), while Lebu has an annual average temperature of 3.63 °C (SD = 3.18) and precipitation of 530.16 mm (SD = 128.29) (climate data from WorldClim version 2.1; https://www.worldclim.org; see Figure S2 for monthly climate data). These climatic differences are influenced by their respective positions along the longitudinal gradient, with Gyirong situated in a drier and colder region and Lebu in a more humid and warmer region.

Vegetation along Gyirong's elevation includes evergreen broadleaved forest (1800–2500 m); coniferous and broad-leaf mixed forest (2500–3300 m); subalpine coniferous forest (3300–3900 m); alpine shrubs and meadows (3900–4700 m); alpine tundra with sparse herbs (4700–5400 m). In Lebu, it slightly differs: evergreen broadleaved forest (2300–2900 m); coniferous and broad-leaf mixed forest (2900–3400 m); subalpine coniferous forest (3400–3800 m); alpine shrubs and meadows (3800–4400 m); alpine meadow (4400–5000 m).

Sampling

We employed a standardized approach, using snap-traps and camera traps, to sample terrestrial mammals. We divided the entire elevational range into twelve 300-m elevational bands in Gyirong from 1800 to 5400 m a.s.l. and nine bands in Lebu from 2300 to 5000 m a.s.l. Sampling sites were chosen within undisturbed habitats. We did not sample higher elevations because of inaccessible topography and did not sample lower elevations because of the national boundary. With the Himalayan foothills typically starting around 1000 m a.s.l. (Hodges 2000), our sampling broadly covered the elevational gradient. This approach conforms to the typical standards of elevational gradient studies, which often encompass roughly 70% of the habitable extent (McCain 2005; Kohli et al. 2022).

For non-volant small mammals (shrews, rodents, and lagomorphs), we performed two replicated surveys during the wet season (Gyirong: May to June 2012, July to September 2013; Lebu: August to September 2018, May to June 2019). Each 300-m elevational band had five trapping sites (60 in Gyirong, 45 in Lebu; Fig. 1, Tables S1, S2)

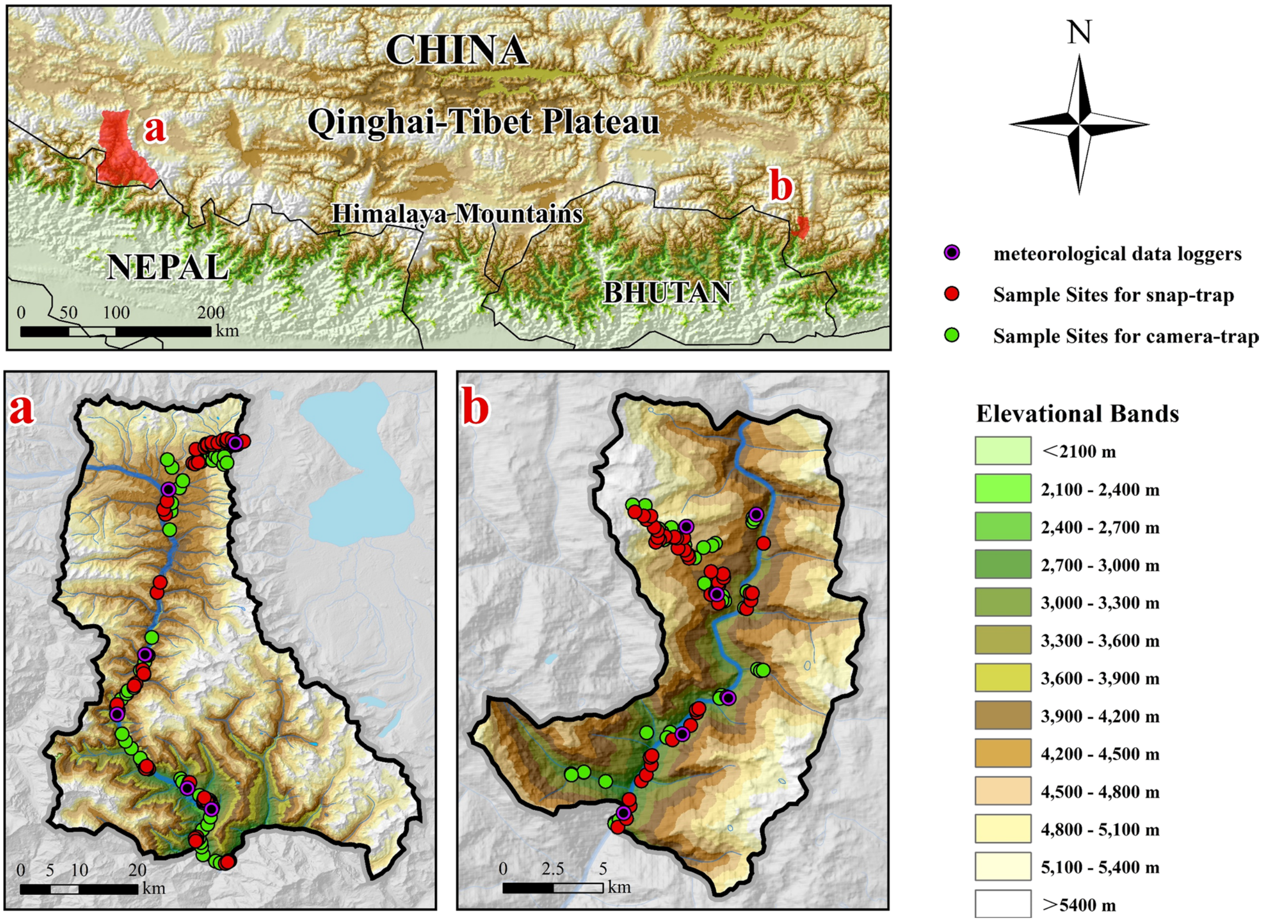

Fig. 1 Locations of **a** Gyirong Valley, Central Himalayas, and **b** Lebu Valley, East Himalayas

with 30 snap-traps placed 2 to 3 m apart. Traps operated for six consecutive days in early and late wet seasons, totaling 21,600 trap days in Gyirong and 16,200 in Lebu. Traps were baited with fried peanuts and ham (in equal proportions by weight). The sampling order for elevation bands was randomized to minimize temporal autocorrelation. Captured individuals were identified, measured, weighed, and preserved in 95% alcohol. Rare species were prepared as study skins, with their skulls cleaned and preserved. Specimens are stored at the Institute of Zoology, Chinese Academy of Sciences, and the Institute of Zoology, Guangdong Academy of Sciences (IZG).

We set five camera traps (EREAGLE®, E1b model) at each 300-m elevational band to sample large-bodied species from 2018 to 2020 (a total of 60 in Gyirong and 43 in Lebu; Fig. 1). Cameras were unbaited (active continuously) and strapped to a tree or stake 50 cm above the ground. Camera traps were positioned at least 500 m apart, and individual identification was performed for each captured animal. Records of the same individual appearing within a 30-min interval were considered as one record (Di Bitetti et al. 2006). These approaches prevent multiple counts of the same individual due to its movement, reducing the impact of spatial autocorrelation. In Lebu, only three camera traps were set at the highest elevational band due to the steep terrain. The effective deployment days for most cameras were more than 6 months. We specifically used camera data collected during the wet season from 90 consecutive deployment days for our subsequent analyses. This approach ensured a precise alignment with the sampling periods of snap traps. Additional details regarding camera trap sampling are available in Tables S3, S4.

Taxonomy of mammals followed Jiang et al. (2015). We used species accumulation and sample-based rarefaction curves to assess how well the species communities were sampled in each elevational band. A plateau in the species accumulation curve indicated sufficient sampling. We randomized the sample order 1000 times for each 300-m elevational band and obtained the sample-based rarefaction curves. The randomization was conducted by EstimateS 9.10 (https://purl.oclc.org/estimates).

Phylogeny and functional traits

For each elevational gradient, we downloaded 10,000 pseudo-posterior phylogenetic trees of mammals from vertlife.org (https://vertlife.org/) using the source of tree 'mammal birth–death node-dated completed tree' (Upham et al. 2019). We then computed a Maximum Clade Credibility tree using the R package *phangorn* (Schliep 2011) for Lebu and Gyirong (Figure S3). We tested for the phylogenetic signal of the continuous trait using Blomberg's K (Blomberg et al. 2003). A lower phylogenetic signal and less trait conservatism than expected from random evolution is indicated by a value of $K \leq 1$, whereas a higher degree of phylogenetic signal in trait data than expected from a Brownian motion of trait evolution is indicated by a value of $K > 1$. We tested for the phylogenetic signal of one group of categorical traits and three groups of binary traits using the δ statistic based on a Bayesian statistical framework proposed by Borges et al. (2019). The higher the δ-value the higher the degree of phylogenetic signal between a given tree and a trait. In general, Blomberg's K and δ statistics showed that the functional traits have significant phylogenetic signals (Table S6).

We selected a set of functional traits (Table 1) related to diet, foraging stratum, foraging time, and body mass to compute the functional diversity. Body mass is an informative trait associated with resource utilization; larger species typically require more resources and occupy higher trophic levels (Gaston and Blackburn 2008). Diet, foraging stratum, and foraging time reflect how species search for and utilize food resources. Trait data were sourced from Wilman et al. (2014). Diet and foraging stratum data are standardized, semiquantitative information about the relative importance of different categories translated from the verbal descriptions; for each category, the estimated percent relevance is recorded in 10% steps as integers from 0 to 10, with the values for all categories in a variable summing to 10 (i.e., 100%). Together with body mass (continuous) and foraging time (binary), this enables a finer distinction of species foraging ecology than typical categorical guild assignments allow (Table S5).

Diversity measures

We calculated taxonomic diversity (TD), functional diversity/richness (FD/FRic), and phylogenetic diversity (PD) for each 300-m elevational band. TD was measured as species richness by interpolating species' elevational ranges between their lowest and highest records and binning their occurrences into 300-m elevational bands (e.g., 1800–2099, 2100–2399 m a.s.l., etc.). This method is suitable for species in continuous habitats, as gaps in distribution are often due to inadequate sampling rather than true distribution gaps on a small spatial scale, especially when gaps are observed only for rare species (Rowe and Lidgard 2009). Given mammals' mobility and the continuous habitat along elevational gradients, interpolated richness was anticipated to provide a realistic measure.

PD was measured by Faith's phylogenetic diversity index (Faith 1992) using the function *pd* in the R package *picante* (Kembel et al. 2010). Faith's index was estimated as the sum of all branch lengths of the phylogeny connecting all species of a community (i.e., 300-m elevational band).

FD, based on Petchey and Gaston (2002), calculates the sum of branch lengths in the functional dendrogram for species within a community. We created the functional dendrogram of species by UPGMA clustering based on the functional distance matrix and calculated the dendrogram-based FD by the function *pd* in the R package *picante*. FRic (Villéger et al. 2008) measures the volume of a convex hull around all species within a community projected in multidimensional trait space. Pairwise functional distances were determined using Gower's distance (Gower 1966), and then the functional distance matrix dimensions were reduced through PCoA. The convex hull volume of functional spaces for community species was measured using the R package *FD* (Laliberté and Legendre 2010). PD and FD are tree-based metrics often used for comparison. Moreover, FD and FRic exhibited a strong correlation along elevational gradients (Lubu: $r = 0.98$, $P < 0.001$; Gyirong: $r = 0.95$, $P < 0.001$). Consequently, only FD was employed in subsequent analyses. Elevational patterns of FRic are presented in Figures S5–S7.

Table 1 Traits used to measure functional diversity of mammals

Trait type	Trait	Data type
Resource quantity	Body mass (g)	Continuous
Diet	Invertebrates, mammals, birds, reptiles, amphibians, fish, vertebrates (unknown), fruit, seed, other plant material and scavenge	Semiquantitative (integers 0–10, categories total 10)
Foraging stratum	Ground level (including aquatic foraging), scansorial, arboreal, aerial	Category
Foraging time	Nocturnal, crepuscular, diurnal	Binary

FD and PD are derived from information on species within an elevational band. To reduce the influence of species richness, we calculated the standardized effect size of PD and FD (SES.PD and SES.FD) as the richness-controlled diversity indicates in the R package *picante*. The null model was run by randomly selecting species 999 times from all the species recorded across the entire elevation gradient, keeping species richness constant in each band.

Phylogenetic and functional assemblage structure

We used the mean pairwise phylogenetic distance (MPD) and mean pairwise functional distance (MFD) to assess the variations in the phylogenetic and functional relatedness of mammal assemblage within each elevational band. MPD and MFD represent the average phylogenetic and functional distances between all taxon pairs within an assemblage, respectively (Webb et al. 2002). MPD and MFD are calculated as follows:

$$\text{MPD or MFD } = \frac{\Sigma_i^n \Sigma_j^n \delta_{i,j}}{n}, \tag{1}$$

where n is species richness in each band, $\delta_{i,j}$ is the pairwise phylogenetic or functional distance (Euclidean distance) between species i and species j. Large values of MPD and MFD indicate fewer phylogenetic and functional similarities between species within a community, respectively.

We investigated phylogenetic assemblage structure with the net relatedness index (NRI), which is calculated as the inverse of the standardized effect size of MPD between all species in the assemblage phylogeny (Webb et al. 2002). Here, the observed MPD value within each 300-m elevational band was compared against the values from 999 sets of randomized assemblages created by the tip-shuffling algorithm, with all species present along the elevational gradient as the source pool. This algorithm assumes that all species could colonize habitats across the gradient regardless of the influence of the biotic and abiotic factors. In each iteration, species richness was kept constant within each elevational band, but tip labels in functional or phylogenetic distance matrix were shuffled. We also calculated the net functional relatedness index (NFRI) as analogous to NRI, which the MFD standardized against null-model prediction as described above for the standardization of MPD to NRI. NRI and NFRI were calculated as follows:

$$\text{NRI or NFRI} = -1 \times \frac{\text{Dis}_{\text{obs}} - \text{Mean of Dis}_{\text{null}}}{\text{Standard deviation of Dis}_{\text{null}}}, \tag{2}$$

where Dis_{obs} is the observed value of MPD/MFD within each 300-m elevational band, Dis_{null} is the mean of MPD or MFD values from the 999 sets of randomized assemblages.

A negative NRI or NFRI value indicates phylogenetic or functional over-dispersion, where species are more distantly related or functionally different than expected by chance. Conversely, a positive value signifies phylogenetic or functional clustering, showing that species are more closely related or functionally similar than expected. A value of 0 denotes a random structure (Webb et al. 2002). Significant NRI or NFRI values are identified when the p-value (quantile of observed value versus null communities) is less than 0.05. The tip-shuffling algorithm randomizations were performed using the function 'ses.mpd' in R package *picante*.

Explanatory variables

To obtain the precise climate data in such fine-scale mountainous region, mean daily temperatures and accumulated precipitation were monitored by six sets of meteorological data loggers (HoBo Pro-RH/Temp, HoBo Pro-Precipitation/Temp) in Gyirong (at elevations of 2457, 2792, 3368, 3740, 4140, and 5230 m a.s.l.) from September 2015 to July 2016, and seven sets in Lebu (at elevations of 2440, 2822, 2914, 3311, 3499, 4219, and 4504 m a.s.l.) between August 2018 and 2019. Temperature and precipitation data were extended to all elevational bands using OLS regression and spatial interpolation in ArcGIS 10.2 (Figure S4). Principal component analyses were used to evaluate climate's overall influence on mammal communities, resulting in the first principal component (PC1) explaining 94.1% in Gyirong and 99.5% in Lebu of the temperature and precipitation variation. Temperature and precipitation are highly negatively correlated with PC1 in both Gyirong ($r = -0.970$, $p < 0.01$) and Lebu ($r = -0.973$, $p < 0.01$). The inverse of PC1 ($-1 \times \text{PC1}$) thus indicated a climate gradient from warm and wet to cold and dry with elevation increase, serving as a synthetic climate variable.

The Normalized Difference Vegetation Index (NDVI) was employed as a surrogate for net primary productivity (NPP). NDVI data (1-km^2 resolution) were obtained for January, April, July, and October spanning 10 consecutive years (2011–2019) from the Computer Network Information Center, Chinese Academy of Sciences (http://www.gscloud.cn). The value for each elevation band was calculated by averaging all grid cells within it.

The arrangement of communities and their biodiversity can be shaped by evolutionary history and trait-related ecological processes (Li et al. 2022). SES.PD/SES.FD and NRI/NFRI highlight distinct aspects of phylogenetic and functional information. SES.PD/SES.FD assesses the diversity of functional traits or phylogeny, whereas NRI/NFRI measures the degree of phylogenetic or functional similarity among species coexisting within the community. Principal components were computed using phylogenetic (SES.PD and NRI) and functional (SES.FD and NFRI) metrics, representing evolutionary histories and trait-related ecological processes. PC1, derived from phylogenetic metrics, explained 89.2% of the variation for SES.PD and NRI in Gyirong and 88.1% in Lebu. Both SES.PD and NRI exhibited strong correlations with PC1 (Gyirong: $r_{SES.PD} = 0.944$, $r_{NRI} = -0.944$, $p < 0.01$; Lebu: $r_{SES.PD} = 0.939$, $r_{NRI} = -0.939$, $p < 0.01$). Similarly, PC1 based on functional metrics explained 97.6% and 91.0% of the variability in Gyirong and Lebu respectively, with SES.FD and NFRI showing high correlations with PC1 (Gyirong: $r_{SES.FD} = -0.988$, $r_{NFRI} = 0.988$, $p < 0.01$; Lebu: $r_{SES.FD} = -0.954$, $r_{NFRI} = 0.954$, $p < 0.01$).

Statistical analysis

We standardized all variables to allow elevational patterns to be compared among different diversity measures and allow parameter estimates to be compared among predictors. We used generalized additive models to visualize the shape of diversity patterns (TD, PD, FD, SES.PD, SES.FD, MPD, and MFD) across elevation with the R package *mgcv* (Wood 2017). We allowed up to five dimensions of the smoothing function to prevent an over-parameterization of models (Laiolo et al. 2018). Original patterns are in Figures S5–S7.

The structural equation model (SEM), which defines causal relationships and mutually interconnected equations among variables (Grace 2006), was used to disentangle the direct and indirect effects between predictors and response variables by the R package *lavaan* (Rosseel 2012). Our models were constructed to demonstrate the relationship between environmental factors, evolutionary histories, trait-related ecological processes, and species richness (Fig. 4). Model fit was evaluated using the likelihood chi-square value (χ^2), where χ^2 *p*-values above 0.05 indicate a satisfactory fit.

Given the relatively limited sample sizes in our study (12 and 9 samples with 9 paths), we conducted supplementary analyses to validate and enhance the robustness of the SEM results. Bayesian estimation is less sensitive to small samples than traditional frequentist methods. We performed Bayesian structural equation modeling (BSEM) using the R package *brms* (Bürkner 2019), utilizing four chains with 2000 iterations each (1000 warm-up iterations). Convergence was evaluated using the potential scale reduction factor (Rhat), with a Rhat value of 1 indicating convergence. The Pareto-*k* diagnostic was conducted to confirm model acceptance using the R package *loo* (Vehtari et al. 2017), with the condition that all *k* estimates should be below 0.7. Additionally, we used hierarchical partitioning (Chevan and Sutherland 1991), a technique recognized for effectively addressing collinearity concerns, to discern the explanatory variables with the most substantial impact on the variance in the response variable. Lastly, we employed a Spatial Lag Model (SLM) to account for the potential spatial autocorrelation in our data, enabling us to evaluate its impact on the dependent variable.

Results

Diversity patterns

We documented a total of 56 mammal species: 50 in Gyirong, Central Himalayas, 28 in Lebu, East Himalayas, and 22 species shared between both sites (Figures S8–S9). Using snap-traps, we collected 735 small mammal individuals (identified to 22 species; we only included 18 species in our analysis because 4 unknown species lacked functional or phylogenetical information) in Gyirong, and 372 individuals (8 species) in Lebu. Camera traps captured 28 species in Gyirong and 20 in Lebu. Sample-based rarefaction curves for each 300-m elevational band reached an asymptote (Figures S10–S11), indicating sufficient sampling.

Taxonomic diversity displayed a low-elevation plateau pattern (denoted by a high plateau across lower elevations that declined monotonically towards higher elevations) in Gyirong and a monotonically decreasing pattern in Lebu. PD monotonically decreased with elevation in Gyirong but showed a high plateau across lower elevations with a small peak at the third elevational band from 2900 to 3200 m a.s.l. in Lebu. FD displayed a low-elevation plateau pattern in both sites (Fig. 2a, b). Richness-controlled phylogenetic diversity (SES.PD) showed a mid-valley pattern (lowest SES.PD appeared at the fifth and sixth elevational bands from 3000 to 3600 m a.s.l.) followed by a positive increase with elevation in the Gyirong and no distinguishable relationship with elevation ($R^2 = 0.027$, $P > 0.05$) in Lebu. Richness-controlled functional diversity (SES.FD) showed a low-elevation plateau pattern in Gyirong and a mid-peak pattern (peaking at the fifth elevational band from 3500 to 3800 m a.s.l.) in Lebu (Fig. 2c, d).

Phylogenetic and functional assemblage structure

MPD was higher in Gyirong (Central Himalayas) than in Lebu (East Himalayas). Both regions showed mid-valley patterns, with the lowest MPD at the sixth elevational band (3300 to 3600 m a.s.l.) in Gyirong, and the fifth band (3500 to 3800 m a.s.l.) in Lebu (Fig. 3a, b). MFD distribution was comparable between regions, characterized by low-elevation plateau patterns (Fig. 3e, f).

NRI clustered significantly ($P < 0.05$) in mid-elevations in both regions. In Gyirong (Central Himalayas), NRI increased in clustering from low to mid-elevations with

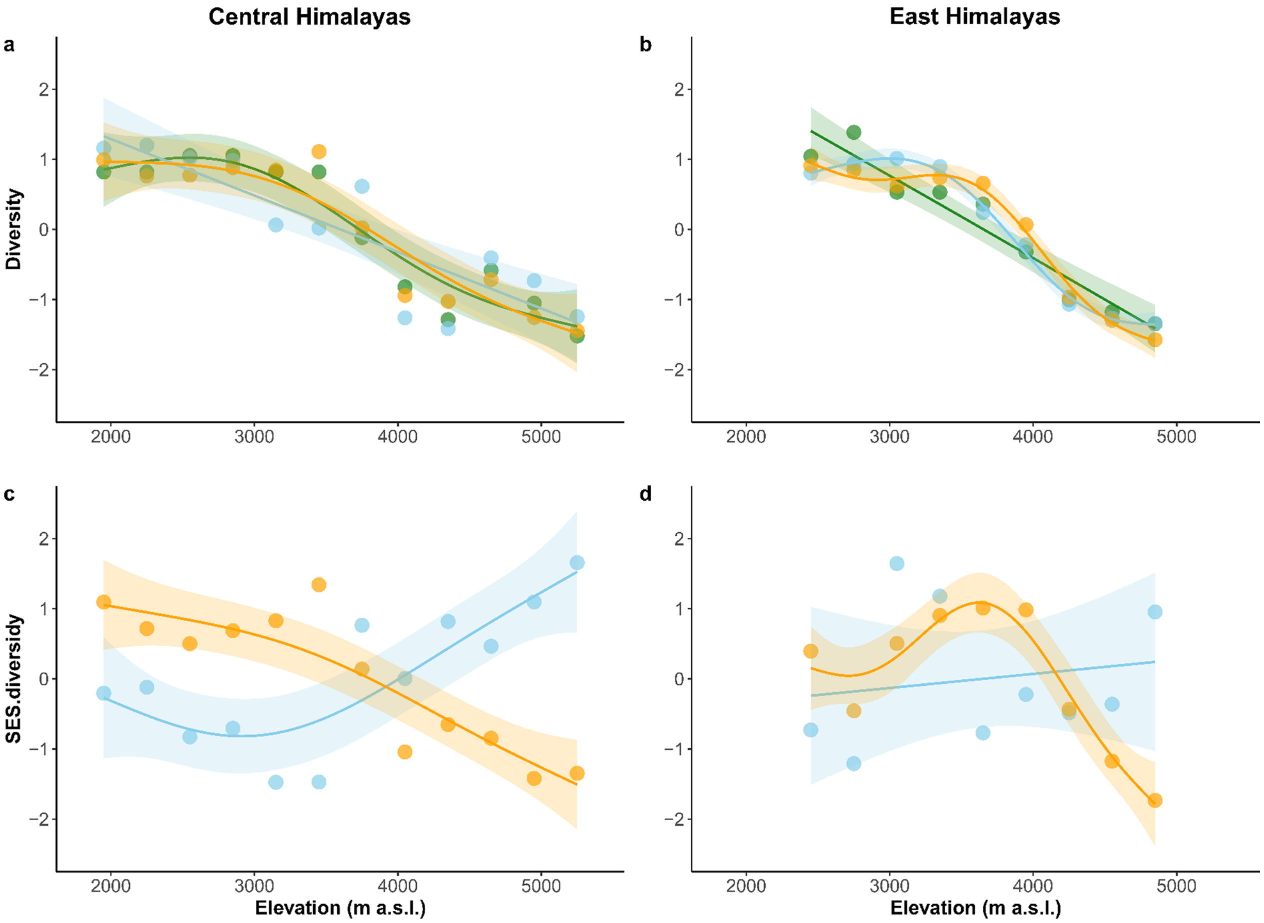

Fig. 2 Top row: elevational trends of mammal taxonomic diversity (green), phylogenetic diversity (blue), and functional diversity (orange). Bottom row: richness-controlled phylogenetic (SES.PD, blue) and functional diversity (SES.FD, orange). Patterns are shown along two elevational gradients in the Himalayas, China (Gyirong, Central Himalayas: **a**, **c**; Lebu, East Himalayas: **b**, **d**). All diversity values were standardized to zero mean and unit standard deviation for comparative purposes. Patterns predicted by generalized additive models (lines) and confidence intervals (shadows) are shown

significant clustering structure from 3000 to 3600 m a.s.l. after which there was a sudden drop with all values near zero (Fig. 3c). In Lebu (East Himalayas), NRI exhibited a relatively random pattern with elevation alternating between clustered and over-dispersed but with significant clustering from 3500 to 3800 m a.s.l. (Fig. 3d). NFRI demonstrated over-dispersion at low to mid-elevations (significantly over-dispersed from 2100 to 3300 m a.s.l. in Gyirong and from 2300 to 3500 m a.s.l. in Lebu), transitioning abruptly to clustering above 3600 m a.s.l. in both elevational gradients (significantly clustered from 3900 to 4200 m and 4800 to 5400 m a.s.l. in Gyirong, and from 4100 to 4700 m a.s.l. in Lebu; Fig. 3g, h).

Drivers of diversity

Our SEM demonstrated good fits ($P_{\chi^2} > 0.05$). In Gyirong (Central Himalayas), evolutionary history emerges as the sole significant direct explanatory variable for species richness, while the effects of other variables (climate and productivity) on species richness are entirely mediated indirectly through evolutionary history (Fig. 4a), with climate and productivity exhibiting similar indirect effects (Fig. 5). In Lebu (East Himalayas), multiple factors (climate, productivity, and evolutionary history) directly influence species richness, with climate showing the strongest effects (Figs. 4b and 5). In Gyirong, evolutionary history correlates with both climate and productivity, while in Lebu, it is not associated with either. In Gyirong, the trait-related ecological process connects directly to productivity and indirectly (via productivity) to climate (Fig. 4b), while in Lebu, it is solely related directly to climate (Fig. 4b).

The results from Bayesian Structural Equation Modeling (BSEM) and hierarchical partitioning were largely consistent with the trends observed in the conventional SEM. In Lebu, climate emerged as the most influential

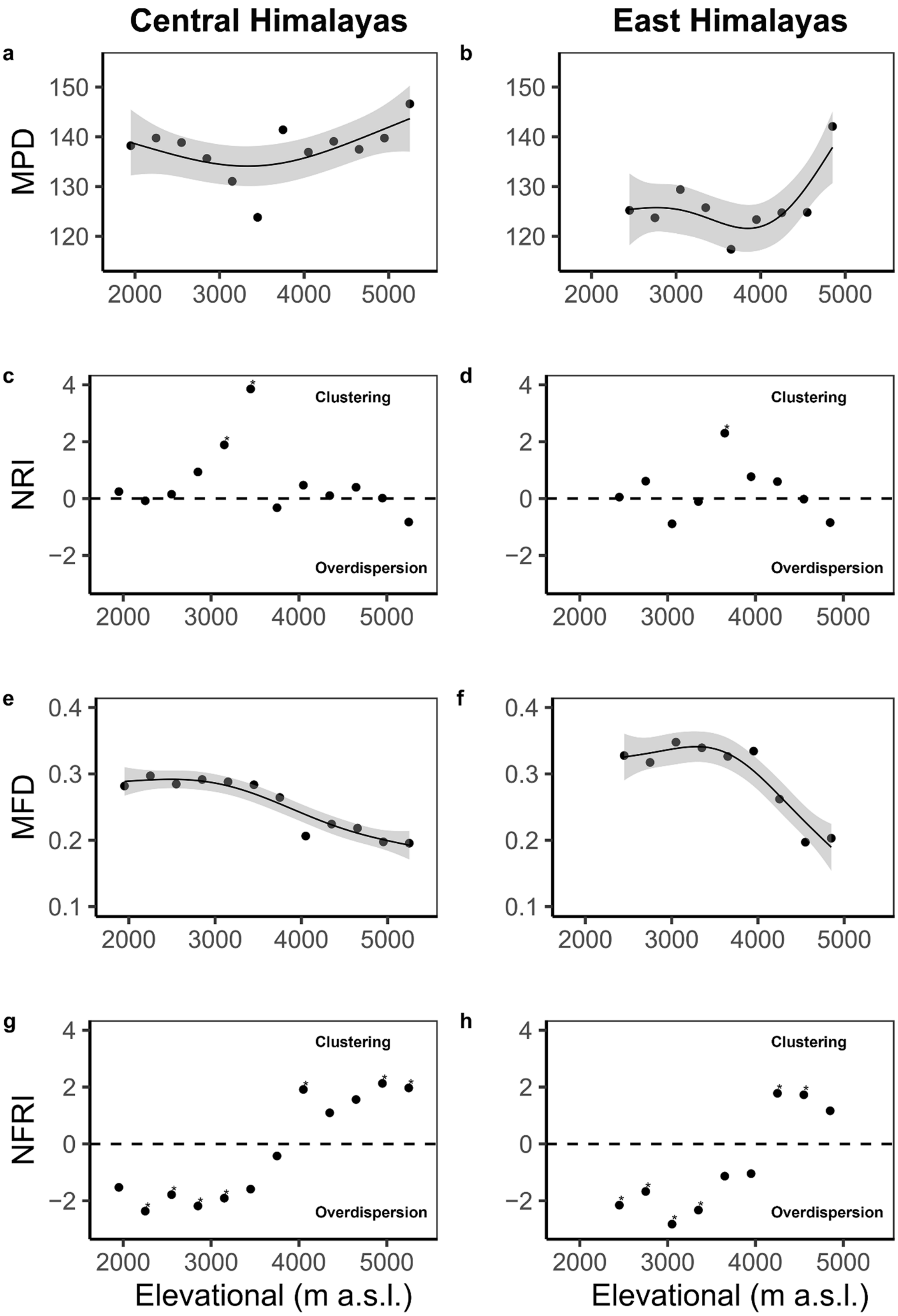

Fig. 3 Elevational patterns of the mean pairwise phylogenetic distance (MPD), mean pairwise functional distance (MFD), net relatedness index (NRI), and net functional relatedness index (NFRI) of mammals along two elevational gradients in the Himalayas (Gyirong, Central Himalayas: **a**, **c**, **e**, **g**; Lebu, East Himalayas: **b**, **d**, **f**, **h**). Patterns of MPD and MFD predicted by generalized additive models (black lines) and confidence intervals (gray shadows) are shown. The asterisk indicates clustered or overdispersion significantly at $P < 0.05$

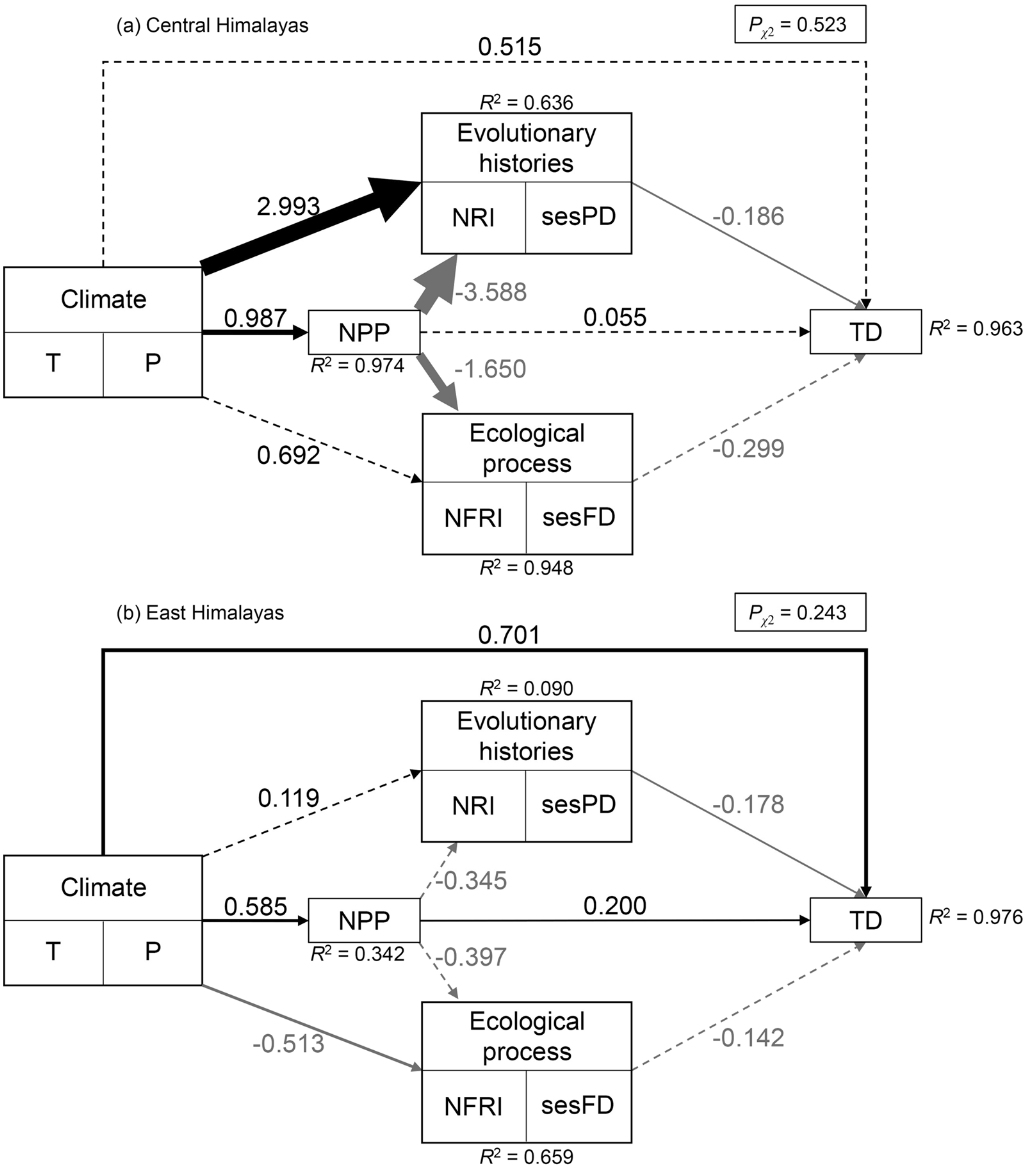

Fig. 4 Structural equation models linking climate (T: temperature; P: precipitation), net primary productivity (NPP), evolutionary histories (sesPD: richness-controlled phylogenetic diversity; NRI: net relatedness index), trait-related ecological processes (sesFD: richness-controlled functional diversity; NFRI: net functional relatedness index), and species richness (TD) in the **a** Central and **b** East Himalayas. Numbers near arrows indicate standardized path coefficients (width represents coefficient strength); black/grey arrows signify positive/negative relationships; solid lines are significant ($p < 0.05$), and dashed lines are not significant

factor, whereas none of the explanatory variables significantly account for species richness in Gyirong (Figures S12, S13). Hierarchical partitioning (Figure S14) showed that climate, productivity, and trait-related ecological processes each explained 26–28% of the independently explained variance in species richness, while evolutionary history explained 14% in Gyirong. In Lebu, climate accounted for over 46% of the independently explained variance, and productivity and trait-related ecological processes independently explained 21% and 25% of the variance, respectively, with evolutionary history contributing only 5%. Additionally, the spatial lag terms of the SLM were not significant in either region, suggesting that spatial dependence does not have a substantial impact on these variables, and the explanatory power of the variables was consistent with that in the aforementioned analyses (Table S9).

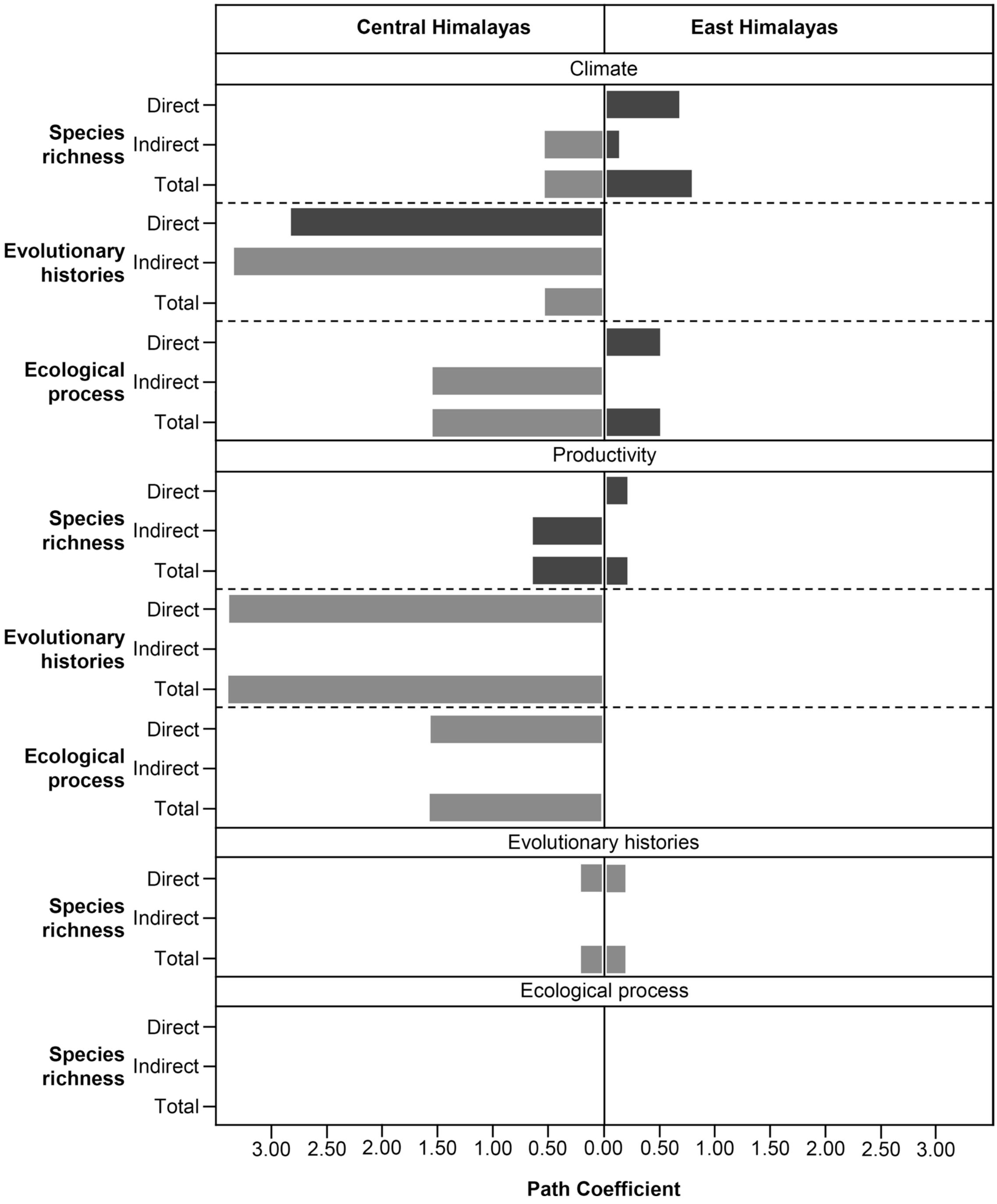

Fig. 5 Synthesis of direct, indirect, and total effects of variables over species richness, evolutionary histories, and trait-related ecological process obtained by structural equation models in Central and East Himalayas. Path coefficients represent standardized coefficients of significant paths, with black and grey indicating positive and negative relationships, respectively. Direct effects denote path coefficients when two variables solely link through a significant path. Indirect effects resulted from coefficients along significant paths with multiple arrows. The total effect of one variable on another was computed as the sum of its direct and indirect effects, encompassing all significant pathways connecting these variables

Discussion

Elevational patterns of mammal diversity

Previous studies examining mammal taxonomic diversity along elevation gradients have predominantly concentrated on bats and non-volant small mammals. Among these studies, approximately 50% to 90% reported a mid-peak and a declining pattern in bat and non-volant small mammal taxonomic diversity, respectively (McCain and Grytnes 2010). Few studies have explored the entire mammal assemblage along an elevational gradient; those that have done so only focused on taxonomic diversity showing mid-peak patterns of species richness in the Hengduan Mountains (Lan and Dunbar 2000) and the Himalayas (Hu et al. 2014, 2022). Here, we comprehensively sampled the terrestrial mammal community in Gyirong, Central Himalayas, and Lebu, East Himalayas, enabling an in-depth assessment of mammal diversity patterns across two extraordinary elevational gradients. We found a low-elevation plateau and a monotonically decreasing pattern of species richness along elevation in the Gyirong and Lebu, respectively. In a previous study, the elevational species richness pattern of non-volant small mammals in Gyirong was identified as a mid-peak pattern (Hu et al. 2017). However, after including large-bodied mammals in this study, the pattern for the entire non-volant terrestrial mammal community in Gyirong shifted to a low-elevation plateau pattern, indicating a weaker mid-domain effect. This shift is attributed to the broader elevational ranges of large-bodied mammal species (Figure S9). This observation aligns with theories suggesting that species with broader elevational ranges tend to be less constrained by geometric limitations (Colwell et al. 2004). The smaller area and the limited elevation range in Lebu may explain the distinct patterns of species richness observed there, in contrast to the more extensive elevational gradient and larger spatial area in Gyirong. Thus, the differences in mammalian diversity patterns observed between Gyirong and Lebu are not merely a reflection of variations in inherent biodiversity but also hint at broader ecological and geographical influences, such as varying mountain sizes, elevation ranges, or the amount of area per elevation band within each region.

The influence of the Indian Ocean monsoon is pronounced in the East Himalayas, leading to Lebu being warmer and more humid compared to the cooler and drier Gyirong in the Central Himalayas. In this context, Lebu serves as a transitional zone from temperate to subtropical climates, whereas Gyirong represents a typical temperate climate region. Notably, all observed diversity metrics (taxonomic, functional, and phylogenetic diversity) displayed a more rapid decline with increasing elevation in the Lebu compared to Gyirong (Table S7). This trend was corroborated by our subsequent analyses, which indicated climate as a more significant driver of species richness in Lebu, while evolutionary history played a more prominent role in Gyirong. These findings imply that environmental filtering may have a greater impact on assemblages in the more subtropical Lebu compared to temperate Gyirong. Greater climatic stability and productivity in tropical and sub-tropical regions may facilitate specialization and niche partitioning (Jocque et al. 2010), potentially supporting a higher proportion of specialists and species with smaller niches that are more sensitive to environmental changes (Fjeldså et al. 2012). Conversely, regions with more seasonality and lower productivity tend to contain more physiological and ecological generalist species (Dalsgaard et al. 2011). Our findings also align with Kohli et al. (2022), who showed that rodent diversity varies predictably from wet to dry mountains. These outcomes highlight the significance of accounting for regional climatic disparities when comparing elevational diversity patterns and their underlying drivers across different regions. While Kohli et al. (2022) identified significant differences in mountains globally across a wide aridity gradient, our study exhaustively sampled both dry and cool as well as wet and warm elevation gradients within a single mountain range. We examined various environmental factors and identified differences in elevational diversity patterns. These results emphasize the complexity of ecological processes and the importance of collaborative efforts between macroecological studies and comprehensive field research.

After controlling for species richness effects, we observed a mid-valley pattern in SES.PD in Gyirong, Central Himalayas (Fig. 2c). This observation is in line with a recent study that demonstrated a similar mid-valley pattern of SES.PD in birds from Gyirong (Ding et al. 2021). These findings imply that greater lineage diversity of mammals and birds emerged at both ends of the elevation gradient in Gyirong. Specifically, we found a disproportionately high level of SES.PD at high elevations, indicating that highland assemblages are comprised of distinct lineages, despite the relatively low species richness. The Mid Valley pattern observed here supports findings that lowland birds tend to represent older groups (Wu et al. 2014) and aligns with findings that high-elevation communities in the Himalayas are more distinct, with species sharing traits but having distinct evolutionary lineages (Shooner et al. 2018; Rana et al. 2019). Conversely, the erratic SES.PD pattern observed in Lebu, East Himalayas might arise from the relatively depleted species pool (28 species), although the numbers of species in each elevational band are comparable to those in Gyirong (Table S8). The interpretation of SES.PD as an ecological pattern or a statistical outcome can be challenging in communities with relatively low species richness owing to the possibility of a select few species having a disproportional influence on PD. In contrast, the SES.FD shows a similar pattern with observed functional diversity, suggesting that assemblages at high elevations have had functional differences filtered out, leaving only a subset of traits. This supports findings from both the Himalayas (e.g., bat: Chakravarty et al. 2021; birds: Ding et al. 2021) and other regions (e.g., small mammals: Sun et al. 2020; birds: Dehling et al. 2014; Hanz et al. 2019). The mid-peak or low-elevation plateau in SES.FD could result from overlapping ranges at mid-elevations among functionally different species—those adapted to lowland habitats (e.g., *Panthera pardus*, *Naemorhedus goral*, *Capricornis thar*, *Muntiacus vaginalis*) and those adapted to highland habitats (e.g., *Panthera uncia*, *Vulpes vulpes*, *Canis aureus*, *Pseudois nayaur*) (Figures S8, S9). Moreover, predator–prey interactions could also potentially influence diversity patterns (Ives et al. 2005). When predators follow their prey, it might enhance phylogenetic diversity but could have variable effects on functional diversity, potentially contributing to the observed discrepancies in indices. Overall, functional traits are likely closely associated with the environment, reducing the probability of the occurrence of functional traits that are out of place. Nevertheless, there is still a possibility that a few species with an unusual evolutionary history may appear at random elevations.

Our study also reveals contrasting trends in MPD and MFD. MPD showed mid-valley patterns with larger values beyond 4000 m a.s.l. (Fig. 3a, b) whereas MFD remained steady until 4000 m a.s.l., then drops rapidly (Fig. 3e, f). The rising MPD and declining MFD at higher elevations suggest that highland assemblages include phylogenetically distinct species with similar traits. This pattern occurs more frequently across taxa and regions than previously thought (Cadotte et al. 2019). Alternatively, within-clade competition for scarce resources in harsh environments may lead to competitive exclusion of close relatives, reducing overall phylogenetic diversity while increasing phylogenetic distances among species (Mayfield and Levine 2010). We observe steeper declines in species richness than in family and order richness, especially from mid to high elevations in both elevational gradients; interestingly, order richness increased with elevation in Gyirong, Central Himalayas and kept decreasing with elevation in Lebu, East Himalayas (Figure S15 and Table S8). Additionally, the decline in MFD at high elevations can be explained by the selection of specific traits that enhance survival in harsh environments.

Mechanisms of assemblage structure

We examined multiple metrics that when placed in context to elevation provide reinforcing evidence in support of processes such as abiotic filtering that influence assemblage structure (either phylogenetic or functional). In our system, mammal assemblages exhibited the highest phylogenetic clustering around 3600 m a.s.l. This clustering can be attributed to the rapid transition from forested environments to open habitats like alpine shrubs and meadows (the tree line situated approximately between 3600 and 4000 m a.s.l.), along with an overall reduction in climate suitability. Species from low-elevation lineages would face significant challenges in persisting or colonizing at these elevations due to the dramatic environmental turnover. Conversely, despite the harsher conditions above 4000 m a.s.l., this region is linked to the Qinghai-Tibet Plateau, where species adapted to high-elevation environments tend to evolve from distinct lineages (Shooner et al. 2018; Rana et al. 2019; Ding et al. 2021). As a result, the elevations around the tree line might harbor fewer coexisting lineages, leading to greater phylogenetic clustering compared to lower and higher elevations. Intriguingly, similar phylogenetic clustering patterns have been observed in other taxa at similar elevations within the Himalayas, despite varying evolutionary time scales and ecological needs (plants: Rana et al. 2019; Li et al. 2022; birds: Ding et al. 2021). This suggests that environmental filtering could exert a widespread influence across these elevational zones in the Himalayas.

As predicted, we observed patterns of over-dispersed functional assemblages in the lowlands and clustered assemblages in the highlands, which align closely with the species interactions–abiotic stress hypothesis. This trend is in line with a growing consensus across other mountain systems and taxa, where functional patterns are shaped by environmental filtering in highlands and interspecific competition and niche partitioning in lowlands (Bryant et al. 2008; Graham et al. 2009; Dehling et al. 2014; Dreiss et al. 2015; Hanz et al. 2019; Montaño-Centellas et al. 2020). These findings emphasize the pervasive impact of ecological and environmental processes in shaping assemblage structures across elevations in mountainous regions.

Factors influencing species richness

In Lebu, East Himalayas, species richness is influenced by multiple factors, with the effects of evolutionary histories and trait-related ecological processes being smaller compared to climate and productivity. These findings are in line with prior studies in the Himalayas, which have demonstrated that climate, productivity, or their interactive effects play a pivotal role in species distribution and assemblage structure (Elsen et al. 2017; Srinivasan et al. 2018; Pan et al. 2016; Hu et al. 2017, 2018, 2022).

In Gyirong, Central Himalayas, evolutionary history takes on a more significant role in driving species richness. Indeed, factors such as biogeography and the diversification history of individual mountain ranges have been revealed as important determinants in shaping biodiversity patterns (Su et al. 2020; Li et al. 2022). With the collision of the Indian plate and the Eurasian plate, species from both plates intermingled in the Central Himalayas. This mixing of species is expected to lead to greater phylogenetic dispersion in this area, owing to the distinct evolutionary histories of these two regions. Moreover, it is observed that lowland assemblages often encompass older lineages with longer periods of continuous evolution, contributing to greater phylogenetic diversity (Päckert et al. 2012; Wu et al. 2014). Conversely, in highland regions, species from different evolutionary origins with particular traits that facilitate survival in challenging environments during the uplift of the Qinghai-Tibet Plateau have led to phylogenetically distinct assemblages (Shooner et al. 2018). Thus, located in the Central Himalayas, Gyirong serves as a representative valley that connects the lowlands and the plateau, functioning as a biological corridor integrating fauna from distinct origins and evolutionary histories (Oriental vs. Palearctic). Notably, our study revealed higher MPD in Gyirong compared to Lebu.

Conclusions

Our study reveals that taxonomic, functional, and phylogenetic diversity exhibit different or even contrasting patterns and determinants across various mountain regions and elevations. Relying solely on species richness may inadvertently overlook the distinctive functions and evolutionary history inherent within a system, potentially hindering our understanding of community assembly and its underlying mechanisms. This gap may also pose challenges for the conservation of region's taxa when devising conservation strategies. Furthermore, our findings confirm the joint impact of environmental conditions, evolutionary histories, and trait-related ecological processes on species richness. However, the degree to which evolutionary histories and trait-related ecological processes shape species assembly relates to regional geological history, necessitating further research to uncover the underlying patterns of fundamental diversity.

Abbreviations

TD	Taxonomic diversity
FD	Functional diversity
Fric	Functional richness
PD	Phylogenetic diversity
SES.FD	Richness-controlled functional diversity
SES.PD	Richness-controlled phylogenetic diversity
MFD	Mean pairwise functional distance
MPD	Mean pairwise phylogenetic distance
NFRI	Net functional relatedness index
NRI	Net relatedness index
NDVI	The normalized difference vegetation index
NPP	Net primary productivity

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s13717-024-00547-z.

Supplementary Material 1.

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Author contributions

Y.H. and B.S. conceived the idea for this study and designed the research; Y.H., J.L., H.H. and Z.Z. conducted the fieldwork; Y.H., Z.D., and D.L. analyzed the data; Y.H. led the writing with assistance from B.S. and L.G. All authors contributed critically to the drafts and gave final approval for publication.

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Availability of data and materials

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Declarations

Ethics approval and consent to participate

Our research adhered to stringent ethical guidelines, undergoing a comprehensive ethical review by the Animal Experimental Ethical Inspection of IZG (No. GIZ20221202).

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing or conflict of interest.

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