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Multidimensional amphibian diversity and community structure along a 2 600 m elevational gradient on the eastern margin of the Qinghai-Tibetan Plateau

Xiao-Yi Wang^{1,2,4}, Mao-Jun Zhong¹, Jian Zhang³, Xing-Feng Si³, Sheng-Nan Yang¹, Jian-Ping Jiang¹, Jun-Hua Hu^{1,*}

¹ Chengdu Institute of Biology, Chinese Academy of Sciences, Chengdu, Sichuan 610041, China

² Key Laboratory of Bio-Resources and Eco-Environment of Ministry of Education, College of Life Sciences, Sichuan University, Chengdu, Sichuan 610065, China

³ Zhejiang Tiantong Forest Ecosystem National Observation and Research Station, School of Ecological and Environmental Sciences, East China Normal University, Shanghai 200241, China

⁴ University of Chinese Academy of Sciences, Beijing 100049, China

ABSTRACT

Mountain systems harbor an evolutionarily unique and exceptionally rich biodiversity, especially for amphibians. However, the associated elevational gradients and underlying mechanisms of amphibian diversity in most mountain systems remain poorly understood. Here, we explored amphibian phylogenetic and functional diversity along a 2 600 m elevational gradient on Mount Emei on the eastern margin of the Qinghai-Tibetan Plateau in southwestern China. We also assessed the relative importance of spatial (area) and environmental factors (temperature, precipitation, solar radiation, normalized difference vegetation index, and potential evapotranspiration) in shaping amphibian distribution and community structure. Results showed that the phylogenetic and functional diversities were unimodal with elevation, while the standardized effect size of phylogenetic and functional diversity increased linearly with elevation. Phylogenetic net relatedness, nearest taxon index, and functional net

relatedness index all showed a positive to negative trend with elevation, indicating a shift from clustering to overdispersion and suggesting a potential change in key processes from environmental filtering to competitive exclusion. Overall, our results illustrate the importance of deterministic processes in structuring amphibian communities in subtropical mountains, with the dominant role potentially switching with elevation. This study provides insights into the underlying assembly mechanisms of mountain amphibians, integrating multidimensional diversity.

Keywords: Community structure; Elevational gradient; Environmental filtering; Functional and phylogenetic diversity; Mountain systems

INTRODUCTION

Understanding the spatial patterns of biodiversity and the mechanisms driving them along geographical gradients is a fundamental question in ecology, biogeography, and

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*Corresponding author, E-mail: hujh@cib.ac.cn

conservation biology (Gaston, 2000; MacArthur, 1984; Sutherland et al., 2013). Mountain systems harbor an evolutionarily unique and exceptionally large portion of global biodiversity, with high environmental heterogeneity across space and time (Elsen & Tingley, 2015; Körner, 2000; Perrigo et al., 2020; Rahbek et al., 2019). Along elevational gradients in mountain systems, environmental conditions often vary over a small spatial range, leading to markedly different habitats and climatic zones over short geographical distances (Perrigo et al., 2020). Elevational gradients therefore offer an excellent opportunity to evaluate biodiversity patterns and community assembly (Körner, 2000; McCain & Grytnes, 2010). The elevation-diversity relationship is one of the most frequently documented diversity-environment relationships but remains controversial (Graham et al., 2014; Nogués-Bravo et al., 2008). There is a lack of coincident characterizations of biodiversity along elevation with little agreement on the mechanisms behind them or the spatial scales at which these mechanisms operate (Jarzyna et al., 2021; Laiolo et al., 2018).

Along elevational gradients, higher elevations are generally colder and less productive (Körner, 2000; Perrigo et al., 2020). Accordingly, elevational patterns of species richness often show a decrease with elevation or peak at mid-elevation (McCain & Grytnes, 2010; Peters et al., 2016). The increasing harshness of climatic conditions at higher elevations (e.g., decreasing temperature, increasing temperature fluctuations) and decreasing food resources and habitat complexity are likely explanations for the decreasing patterns of species richness (Chamberlain et al., 2016; McCain, 2007). The decrease in species richness in high-elevation communities may also be caused by strong abiotic filtering, thereby limiting the ability of species to colonize or persevere in such environments (Montaño-Centellas et al., 2021).

Furthermore, investigating species-specific functional traits and evolutionary history can provide complementary approaches to characterize the mechanisms responsible for community assembly along elevational gradients (Graham et al., 2014; Jarzyna et al., 2021). Functional traits related to behavioral, morphological, and physiological strategies and adaptations differentially reflect the ability of species to use resources and capture ecological requirements (Coyle et al., 2014). Therefore, the functional traits of species communities associated with different environmental conditions across biogeographical gradients can reflect both environmental filtering and ecological adaptations, and further influence ecosystem functioning (Violle et al., 2014). Phylogenetic relatedness is based on the time since divergence from a common ancestor and is used as a proxy for ecological differences among species (Faith, 1992). Therefore, integrating functional diversity (FD; Tilman, 2001), and phylogenetic diversity (PD; Faith, 1992) may help to detect and untangle the extent to which different processes are driving elevational patterns of community assembly (Coyle et al., 2014; Graham et al., 2014). Compared with species richness patterns, fewer studies have explored the drivers of elevational patterns of FD and PD, although a growing number of studies have recently been completed across taxa (e.g., Graham et al., 2009; Jiang et al., 2018; Zhang et al., 2021). Notably, a decline in both FD and PD is often detected with

elevation (Dehling et al., 2014; Hanz et al., 2019). However, consensus about the generality of elevational patterns and the importance of deterministic processes underlying biodiversity patterns in montane systems remains elusive (Du et al., 2021; Jarzyna et al., 2021; Montaño-Centellas et al., 2020; Mori et al., 2013).

Under the classic community assembly theory, two main deterministic processes, i.e., environmental filtering and biological interactions (mainly competitive exclusion causing limiting similarity; Cavender-Bares et al., 2009), are hypothesized to shape spatial variation in diversity and community structure (Montaño-Centellas et al., 2021; Webb et al., 2002). A community where species are functionally more similar to each other than in null models (clustering) can often be attributed to environmental filtering, where specific environmental conditions (mainly related to physiological tolerance, habitat affinity, or resource requirements) allow species with a certain set of traits to co-exist (Webb et al., 2002). In contrast, communities with functionally different species (overdispersion) are often considered to be the consequence of interspecific competition (when a species may have a competitive or adaptive advantage over other species), leading to either competitive exclusion or character displacement (Kluge & Kessler, 2011; Mayfield & Levine, 2010). Therefore, interspecific competition may lead to a community pattern of phylogenetic overdispersion (Webb et al., 2002). However, it may also lead to phylogenetic clustering if certain clades have stronger competitiveness than others (Mayfield & Levine, 2010). Furthermore, it is suggested that environmental filtering may be an important community driver under harsh conditions (e.g., lower temperatures and productivity), while competitive exclusion dominates under benign conditions (stress-dominance hypothesis; Coyle et al., 2014). Thus, it is reasonable that phylogenetic and functional structures change from overdispersed communities at lower elevations to clustered communities with increasing elevation (Figure 1A) (Graham et al., 2009; Hanz et al., 2019). However, community assembly processes with elevation are likely to be complex and show different trends, including clustering at mid elevations and overdispersion at low and high elevations (Jarzyna et al., 2021), or may exhibit a single process (Montaño-Centellas et al., 2020). When investigating phylogenetic and functional structures of communities, there could be an offset between two processes along elevational gradients (e.g., weakened environmental filtering with strengthened competition; Figure 1B) (Du et al., 2021; Jiang et al., 2018).

Amphibians provide an ideal system to explore the spatial patterns and ecological mechanisms driving communities (Buckley & Jetz, 2007; Wells, 2007). Their highly permeable skin, unshelled eggs, and low dispersal ability make them highly sensitive to environmental perturbations and geographic isolation, and they can face strong interspecific competition under limited resources (Wells, 2007). Elevational patterns of amphibian diversity have been documented in many mountain systems (e.g., Khatiwada et al., 2019; Naniwadekar & Vasudevan, 2007; Wang et al., 2020). Contemporary and historical ecological factors have been considered as filters acting on multidimensional amphibian

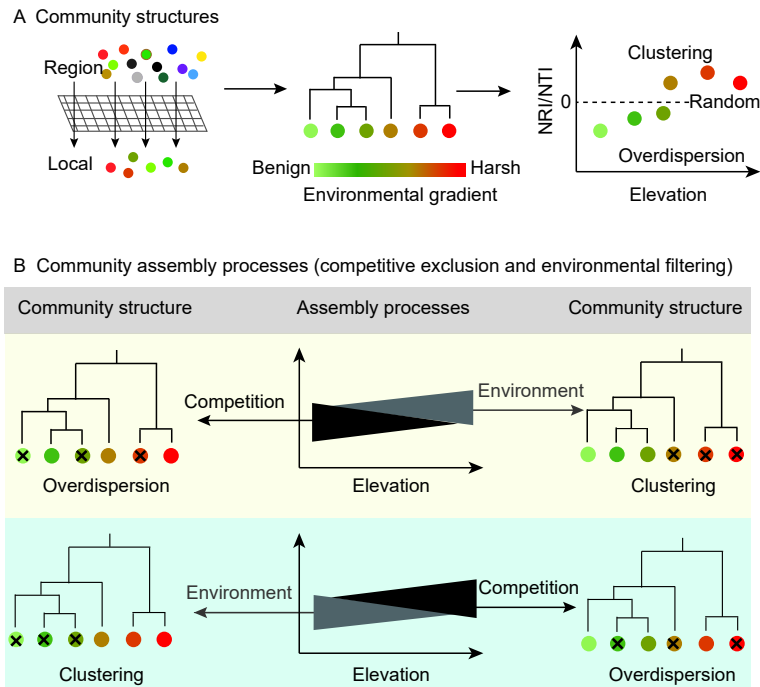


Figure 1 Conceptual framework for inferring community structures and assembly processes along elevational gradients

A: Hypothetical communities and three potential community structures are illustrated. NRI and NTI are net relatedness index and nearest taxon index, respectively. NRI or NTI > 0 indicates phylogenetic or functional clustering; NRI or NTI < 0 indicates phylogenetic or functional overdispersion; NRI or NTI = 0 indicates random structure. B: Inferring community assembly processes from phylogenetic niche conservatism hypothesis: clustering communities are driven by environmental filtering and overdispersed communities are driven by competitive exclusion along the elevational gradient. Although environmental filtering in harsh conditions (e.g., lower temperatures and productivity) may be an important driver shaping communities and competitive exclusion dominates in benign conditions, community assembly processes along the elevational gradient are actually more complex and often contain an offset process. Long triangle represents variation in strength of environmental filtering and competitive exclusion along the elevational gradient.

diversity patterns (i.e., species richness, FD, and PD) at different spatial scales (e.g., Fritz & Rahbek, 2012; Khatiwada et al., 2019; Ochoa-Ochoa et al., 2019; Tsianou & Kallimanis, 2020). However, studies integrating multidimensional amphibian diversity along elevational gradients are still scarce regarding assessment of the ecological mechanisms driving community assembly.

Here, we explored the potential drivers of diversity distribution and community structure for amphibians along a 2600 m elevational gradient on Mount Emei on the eastern margin of the Qinghai-Tibetan Plateau in southwestern China. A hump-shaped pattern of amphibian richness along the elevational gradient has been reported for this mountain previously (Wang et al., 2020). Specifically, based on earlier findings, we investigated how PD, FD, and community structure varied along the elevational gradient, and examined the relative importance of spatial and environmental variables in shaping multidimensional diversity (i.e., species richness, PD, and FD) and community structure of amphibians.

MATERIALS AND METHODS

Study area and species data

This study was carried out on Mount Emei (N29°16'–29°43', E103°10'–103°37'), located in the transition zone between the Qinghai-Tibetan Plateau and Sichuan Basin in southwestern

China (Figure 2A), with an elevational gradient of 500–3 099 m a.s.l. (Figure 2B). This mountain is in the interior “Rainy Zone of West China” and is characterized by a humid subtropical monsoon climate, with abundant rainfall during the May–September period and in the middle and high mountain areas (Tang, 2006). Average annual temperature drops from 17 °C to 3 °C with increasing elevation. Situated at the junction between tropical and temperate zonation types, Mount Emei harbors remnants of native subtropical primary forest (Tang, 2006), and shows discernible vertical vegetation types along the elevational gradient (from low to high): i.e., evergreen broad-leaved forest, evergreen and deciduous broad-leaved mixed forest, and coniferous forest (Li & Shi, 2007). Unique geomorphological factors, varied landscapes, and complex habitats support an exceptionally rich biodiversity, especially endemic and rare species (Li & Shi, 2007; Zhao & Chen, 1980). However, as part of the well-known Natural and Cultural World Heritage site (i.e., Mount Emei Scenic Area), ongoing mass tourism and increasing human-nature conflicts threaten the sustainable survival and conservation of amphibians on Mount Emei.

A complete 2 600 m elevational gradient was sampled from 500 m to 3 099 m a.s.l. Information on taxonomy, species composition, and elevational distribution of amphibians was integrated with field records from this study and the Chengdu Institute of Biology (CIB), Chinese Academy of Sciences

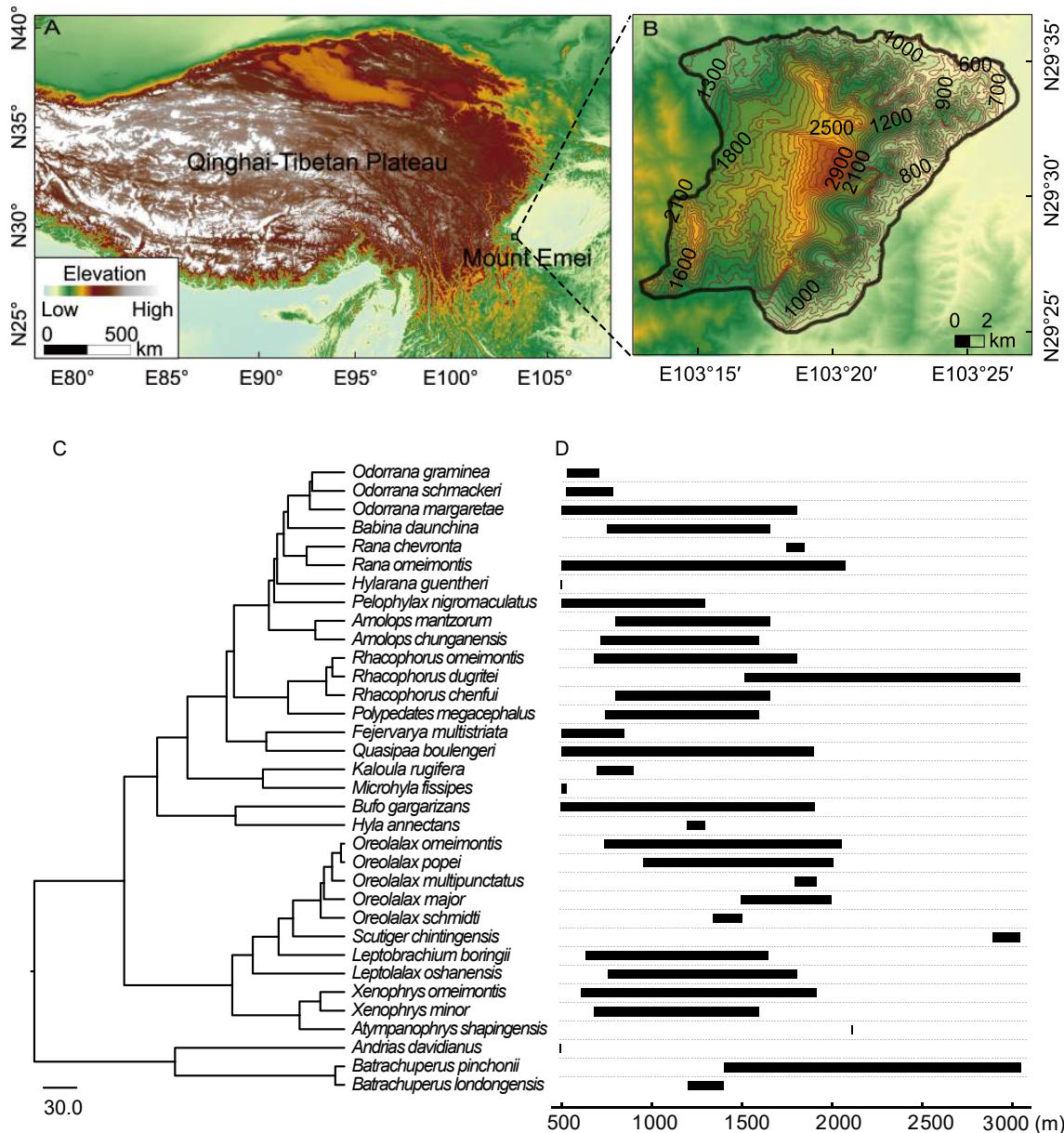


Figure 2 Location (A) and elevational overview of Mount Emei (B); phylogenetic tree reconstruction (C) and elevational range size (D) of amphibians on Mount Emei, southwestern China

(CAS), previous literature (Fei et al., 1976; Liu, 1950; Zhao et al., 2018), and museum specimens from the Herpetological Museum, CIB, CAS. During the breeding season (May–July) in 2017 and 2018, we conducted 23 line transects and three sampling points covering terrestrial and aquatic habitats along the elevational gradient to survey amphibians (Supplementary Table S1). These transects and sampling points belong to the BEST (Biodiversity along Elevational gradients: Shifts and Transitions) research network (<https://best-mountains.org>). All transects were 200 m long and 5 m wide. Surveyors (at least two people) systematically searched for adult individuals using an electric torch at a relatively steady pace (about 2.0 km/h) after sunset each (rainless) night, with the locations of observed individuals recorded by GPS (Wang et al., 2020).

To understand the degree of variability in amphibian

diversity on Mount Emei, we divided elevation into 13 elevational bands at 200 m intervals, which are considered reasonable and effectual intervals when testing diversity-elevation relationships across different taxa, including amphibians (Hu et al., 2011). We defined the elevational ranges of 500–1 299 m, 1 300–2 099 m, and 2 100–3 099 m a.s.l. as low, mid, and high elevations, respectively, due to the vegetation types (see also Wang et al., 2020). Overall, we documented 35 amphibian species belonging to 22 genera and nine families. For each species, the elevational distribution was considered to cover a continuous range between the minimum and maximum documented elevations (Wang et al., 2020). We also compiled lists of co-occurring species for each elevational band (Supplementary Table S2).

Functional traits and dendrogram

For functional traits, we used species-level amphibian traits linked to morphology, reproduction, mobility mode, and resource use to assess FD (Ochoa-Ochoa et al., 2019; Zhao et al., 2018). We characterized nine functional traits for the amphibian species on Mount Emei (except for *Amolops granulatus*, without elevational information; for details see Supplementary Tables S3, S4). The categorical attributes were treated as binary traits (0 or 1) (Li et al., 2019). We obtained these traits from previous literature (Chen et al., 2019; Fei et al., 2006, 2009a, 2009b), field observations, and our measurements. We measured the morphological traits of 2 270 individuals (mean±SE=67±14 per species) covering both male and female individuals with electronic digital calipers (YB5001B, Kraftwelle Company, China) from the Herpetological Museum, CIB, CAS. The mean value of each morphological trait of each species was used for analysis. All specimens were deposited in the CIB/CAS Herpetological Museum.

We used Gower's distance to compute pairwise functional distances between species (Gower, 1966). We then constructed a functional dendrogram of amphibian species using the complete linkage method based on the functional distance matrix (Supplementary Figure S1) using the function "pd" in the R package *picante* (Kembel et al., 2010).

Phylogenetic tree reconstruction

To estimate the phylogenetic relatedness of species in communities, we constructed a species-level phylogenetic tree (except for *A. granulatus*) (Figure 2C, D). We downloaded the distribution of 5000 phylogenies for species on Mount Emei from the global phylogeny of amphibians (Jetz & Pyron, 2018). We then sampled 5000 pseudo-posterior distributions and constructed a maximum clade credibility tree with mean node heights using TreeAnnotator v1.8.3 (Drummond & Rambaut, 2007). The resulting consensus phylogeny was used for subsequent phylogenetic analyses.

Phylogenetic signals are defined as the statistical dependence among species trait values that link their phylogenetic relatedness, with strong phylogenetic signals equated with signs of niche or evolutionary conservatism (Fritz & Purvis, 2010). We used the statistic D (Fritz & Purvis, 2010) and Pagel's λ values (Pagel, 1999) based on the Brownian motion model to test the phylogenetic signals of selected traits. If D approaches 0 or $\lambda=1$, a trait is distributed as expected under the Brownian motion model of evolution (i.e., conserved trait evolution); a value of $D<0$ suggests that a trait is highly clustered, and $\lambda=0-1$ suggests that the effect of phylogeny on trait is weaker than expected; and a value of $D\geq 1$ or $\lambda=0$ indicates that the trait is randomly distributed (i.e., no signal) or overdispersed on the phylogenetic tree. Most selected traits had significant phylogenetic signals, indicating strong phylogenetic niche conservatism (Supplementary Table S5).

Quantification of diversity and community structure

We calculated PD and FD using the "pd" function in the R package *picante* (Kembel et al., 2010). PD was measured as the minimum total branch length connecting all species within

the community to the root of the phylogenetic tree (Faith, 1992). FD was considered as the sum of branch lengths of the functional dendrogram (Petchey & Gaston, 2002). These two tree-based richness metrics are correlated with species richness as they sum across species (Petchey & Gaston, 2002; Webb et al., 2002). Indeed, we identified significant relationships among amphibian species richness, FD, and PD on Mount Emei via Pearson's correlation tests ($r>0.9$). Therefore, to evaluate the contribution of the phylogenetic relationship to PD after controlling for species richness, we calculated the standardized effect size of PD (SES.PD) using the "sespd" function in the R package *picante* (Kembel et al., 2010):

$$\text{SES.PD} = \frac{\text{PD}_{\text{observed}} - \text{mean}(\text{PD}_{\text{random}})}{\text{sdPD}_{\text{random}}} \quad (1)$$

where $\text{PD}_{\text{observed}}$ is the observed PD in a community, $\text{PD}_{\text{random}}$ is the mean PD in null communities, and $\text{sdPD}_{\text{random}}$ is the standard deviation of PD in null communities. We also calculated SES.FD based on the functional dendrogram using the same procedure. To guarantee the statistical requirements and likely cover species with different dispersal capacities, we generated all null distributions for each community by randomly sampling species in an elevational band and its adjacent six elevational bands (i.e., adjacent three at higher and lower elevations) 999 times, maintaining the species richness constant in each community (Jarzyna et al., 2021).

To measure the degree of both phylogenetic and functional relatedness among co-occurring species for each community, we calculated the net relatedness index (NRI) and the nearest taxon index (NTI) using the "mpd" and "mntd" functions in the R package *picante* (Kembel et al., 2010). NRI measures phylogenetic relatedness among taxa and quantifies overall taxa on a phylogenetic tree at a deep level:

$$\text{NRI} = -1 \times \frac{\text{MPD}_{\text{observed}} - \text{mean}(\text{MPD}_{\text{random}})}{\text{sdMPD}_{\text{random}}} \quad (2)$$

where $\text{MPD}_{\text{observed}}$ is the observed mean phylogenetic or functional distance between all taxon pairs in the community, $\text{MPD}_{\text{random}}$ is the mean phylogenetic or functional distance from 999 randomizations, and $\text{sdMPD}_{\text{random}}$ is the standard deviation of $\text{MPD}_{\text{random}}$ (Webb et al., 2002). NTI measures phylogenetic relatedness of each taxon and quantifies the extent of terminal clustering within a tree at a shallower level, and was calculated using the same procedure, except replacing MPD with the mean nearest taxon distance (MNTD) (Webb et al., 2002):

$$\text{NTI} = -1 \times \frac{\text{MNTD}_{\text{observed}} - \text{mean}(\text{MNTD}_{\text{random}})}{\text{sdMNTD}_{\text{random}}} \quad (3)$$

Negative and positive values of NRI and NTI suggest overdispersion and clustering, respectively (Webb et al., 2002). If the absolute values of NRI or $\text{NTI}>1.96$, the community structure is significantly overdispersed or clustered relating to the random communities generated from the species pool ($\alpha=0.05$). According to the magnitude of the deviations between observed values and expectations from null models, the strength of the processes acting upon

communities can be inferred (Webb et al., 2002): clustering communities are driven by environmental filtering and overdispersed communities by competitive exclusion.

Spatial and environmental predictors

We considered area as the spatial driver of amphibian diversity (Khatiwada et al., 2019; Peters et al., 2016). We calculated the area of each 200 m elevational band using SRTM digital elevation data (<https://srtm.csi.cgiar.org/srtmdata/>) at a spatial resolution of approximately 90×90 m using the cylindrical equal-area (world) projection with ArcGIS v9.2 (ESRI, Redland, USA).

We compiled a set of climatic variables from WorldClim 2.0 at a spatial resolution of 30 arc-seconds (Supplementary Table S6) (Fick & Hijmans, 2017). We measured the values in each 200 m band by averaging all grid cells within the elevational band in ArcGIS v9.2 (ESRI, Redland, USA). To avoid high collinearity among variables, we examined correlations among temperature variables and excluded certain variables using Pearson's correlation tests ($|r| > 0.75$) and likewise for precipitation variables (Supplementary Figure S2). We retained three temperature variables and one precipitation variable, including mean monthly temperature range, temperature annual range, temperature seasonality and annual precipitation. Temperature is considered a strong predictor of energy availability for organisms (Peters et al., 2016). Annual precipitation includes direct and indirect effects of water on species richness and distribution (Hawkins et al., 2003). The normalized difference vegetation index (NDVI), which is a proxy of primary productivity and food availability (Verschuyl et al., 2008), was obtained from the Resource and Environment Science and Data Center (<http://www.resdc.cn/>); potential evapotranspiration relating to heat and light inputs in the environment (Hawkins et al., 2003) and solar radiation, which can influence life-history strategies, locomotor performance, and physiological function (Bancroft et al., 2007; Wang et al., 2019), were obtained from CHELSA v1.2 (Karger et al., 2017; <https://chelsa-climate.org/>). These variables change markedly along the elevational gradient (Supplementary Figure S3) and can influence the physiology and survival of amphibian species (Buckley & Jetz, 2007; Hu & Jiang, 2018; Wells, 2007).

Statistical analyses

We performed first-, second-, and third-order polynomial regressions to assess the linear, quadratic, and cubic patterns of multidimensional diversity along elevation, respectively. We selected the best fitting models according to the lowest corrected Akaike information criterion (AIC_c) value (Anderson, 2008) using the package *MuMIn* (Bartoń, 2020).

We conducted simple ordinary least squares (OLS) regression to examine potential associations between each predictor and diversity and community structure. To compare regression coefficients, we standardized all dependent and independent variables (SD=1 and mean=0) before regression analysis. In addition, we performed multiple regression analyses to explore the multivariate explanatory power of the predictors in shaping elevational diversity patterns and community structure. We selected the best model from 255

models based on the lowest AIC_c value. If $\Delta AIC_c < 2$, we used the model-averaging method to assess the relative importance of the predictor variables (Burnham & Anderson, 2002). All analyses were performed in R v3.6.2 (R Core Team, 2019).

RESULTS

Elevational patterns of PD, FD, and community structure

Along the elevational gradient, PD, FD, and their SES values were significantly correlated with elevation (Figure 3; Supplementary Table S7). Both PD and FD displayed similar, asymmetric, unimodal patterns with an abrupt decline after 2 100 m a.s.l. (Figure 3A, B). The observed diversities were higher at low (500–1 299 m a.s.l.) and mid elevations (1 300–2 099 m a.s.l.) than at high elevations (2 100–3 099 m a.s.l.). Polynomial regression showed that the diversity patterns well fit a cubic function with elevation rather than simple linear or quadratic regression (Figure 3A, B; Supplementary Table S7). Both SES.PD and SES.FD showed increasing trends with elevation (Figure 3C, D; Supplementary Table S7), indicating that communities at low and mid elevations had higher PD and FD but lower SES.PD and SES.FD compared with that at high elevations.

Most selected traits exhibited strong phylogenetic signals (Supplementary Table S5). We found clustered communities at low elevations and overdispersed communities at high elevations, as most phylogenetic NRI and NTI values at low elevations were greater than zero, indicating phylogenetic clustering, and all phylogenetic NRI and NTI values at high elevations were less than zero, indicating phylogenetic overdispersion (Figure 4A, B). At mid elevations, phylogenetic NTI, but not phylogenetic NRI, showed an obvious decreasing trend (Figure 4A, B). Functional NRI values at low and mid elevations were greater than zero, while values at high elevations were less than zero, indicating functional clustering at low and mid elevations and overdispersion at high elevations (Figure 4C). Several NRI and NTI values were less

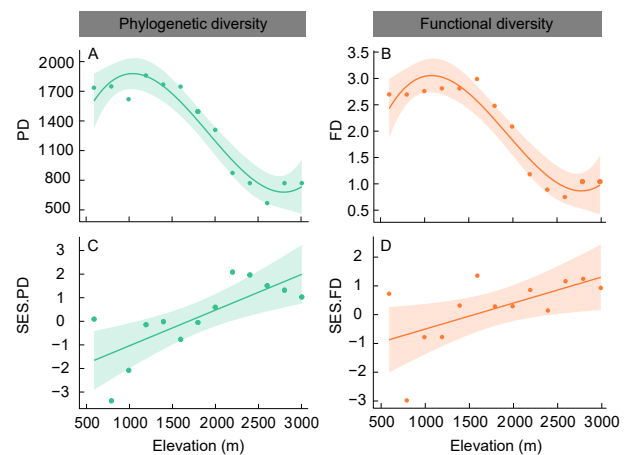


Figure 3 Diversity patterns of amphibians along the elevational gradient

A: Phylogenetic diversity (PD); B: Functional diversity (FD); C: Standardized effect size of PD (SES.PD); D: SES.FD. Shaded areas show 95% confidence intervals

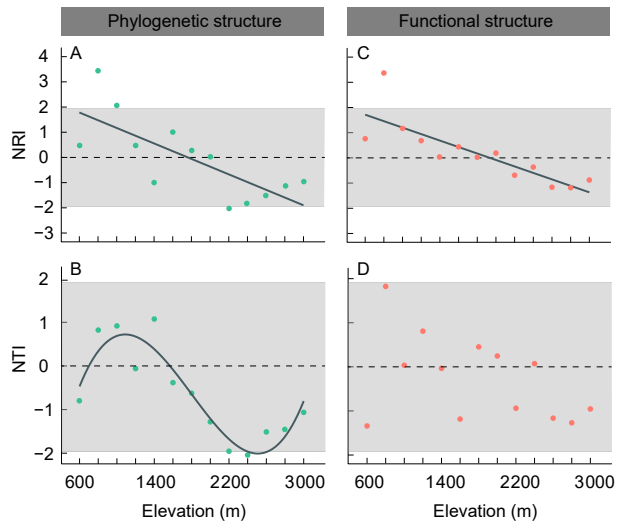


Figure 4 Phylogenetic and functional structures of amphibian communities along the elevational gradient

A: Phylogenetic net relatedness index (NRI); B: Phylogenetic nearest taxon index (NTI); C: Functional NRI; D: Functional NTI. Shaded areas show range between -1.96 and 1.96 . Solid lines indicate trend of NRI and NTI along the elevational gradient (for more details see Supplementary Table S7).

than -1.96 or greater than 1.96 (Figure 4), indicating that these communities could be significantly overdispersed or clustered. Overall, along the elevational gradient, both phylogenetic and functional NRI values showed a decreasing trend, while a unimodal pattern was detected for phylogenetic NTI (Figure 4A–C), thus indicating a potential transformation of community structure from clustering to overdispersion.

Drivers of amphibian diversity and community structure

We found positive relationships among six predictors (i.e., area, potential evapotranspiration, solar radiation, temperature seasonality, temperature annual range, and precipitation) and species richness, PD, and FD. Potential evapotranspiration, solar radiation, temperature seasonality, and precipitation were negatively correlated with SES.PD, whereas potential evapotranspiration and precipitation were negatively correlated with SES.FD. There was a negative relationship between mean monthly temperature range and PD, but a positive relationship with SES.PD and SES.FD (Table 1). Potential evapotranspiration, solar radiation, temperature seasonality, and precipitation positively affected phylogenetic NRI, phylogenetic NTI, and functional NRI, while mean monthly temperature range had the opposite effect on these three metrics (Table 1).

Multiple regression analyses showed that spatial and environmental predictors had different explanatory power for amphibian multidimensional diversities and community structures (Table 2; Supplementary Table S8). Solar radiation, potential evapotranspiration, temperature, and precipitation factors played important roles in shaping species richness, FD, and PD. Moreover, mean monthly temperature range, temperature seasonality (positively), NDVI, area, temperature annual range, and annual precipitation (negatively) jointly structured the SES.PD pattern. In contrast, NDVI and

temperature range were important explanatory variables for SES.FD. Spatial and environmental predictors jointly but with different explanatory power shaped the NRI and NTI patterns (Table 2; Supplementary Table S8).

DISCUSSION

Our study combined three dimensions of diversity (i.e., species richness, FD, and PD) and various predictors (spatial and environmental factors) to analyze changes in amphibian diversity, community structures, and underlying drivers along an extensive elevational gradient on the eastern margin of the Qinghai-Tibetan Plateau in southwestern China. Our results revealed that multidimensional diversity and community structure of amphibians on Mount Emei displayed different patterns. We found strong relationships between predictors and multidimensional diversity and community structure. Furthermore, we inferred that the dominant role of deterministic processes potentially changed with elevation from environmental filtering to competitive exclusion.

We provided a much-needed joint evaluation of multidimensional amphibian diversity along an elevational gradient. Even elevational diversity patterns across different mountains vary greatly, amphibian diversity is generally expected to decrease with elevation or show a unimodal pattern (Khatiwada et al., 2019; Naniwadekar & Vasudevan, 2007; Peters et al., 2016). As amphibians are highly sensitive to environmental stress and particularly vulnerable to perturbations (Wells, 2007), communities at higher elevations may show lower diversity than lowland communities, as observed on Mount Emei (McCain & Grytnes, 2010; Wang et al., 2020; Wells, 2007). Similar to species richness (Wang et al., 2020), FD and PD also showed unimodal patterns with elevation on Mount Emei (Figure 3A, B; Supplementary Table S7). These unimodal patterns are likely to be affected by species richness due to their positive relationships. Both FD and PD vary with elevation across different taxa in different mountain regions, with declining (Dehling et al., 2014; Hanz et al., 2019), hump-shaped (Ding et al., 2021), and increasing patterns detected (Montaño-Centellas et al., 2020), thus highlighting the uniqueness of each mountain system. In the current study, compared with the expected values from null models, we identified a negative to positive tendency for SES.PD and SES.FD (Figure 3), suggesting that PD and FD become increasingly higher than expected regardless of the levels of species diversity. From a functional perspective, the functional traits of species mainly represent the range of activities that organisms are engaged in within the community and ecosystem (Petchey & Gaston, 2002). The richness-controlled FD (SES.FD) showed an increasing pattern on Mount Emei, suggesting increased functional differences or a small number of more versatile species at higher elevations than expected to tolerate intense competition and/or harsher environments. For example, aquatic and arboreal (i.e., *Rhacophorus omeimontis*) species occurred more frequently at higher elevations compared to lowland communities, which were mainly composed of semi-aquatic and terrestrial species (Supplementary Table S2). Communities with lower FD at low elevations are considered less prone to lose species with

Table 1 Influences of each spatial and environmental variable on multidimensional diversity and community structures based on simple ordinary least squares (OLS) regression analyses

Multidimensional metrics	Area	NDVI	Potential evapotranspiration	Solar radiation	Mean monthly temperature range	Temperature seasonality	Temperature annual range	Annual precipitation
Species richness (SR)								
Coefficient	0.637	-0.118	0.865	0.651	-0.545	0.901	0.598	0.780
R ²	0.401	0.014	0.748	0.424	0.297	0.812	0.357	0.608
P	0.020	0.701	<0.001	0.016	0.054	<0.001	0.031	0.002
Phylogenetic diversity (PD)								
Coefficient	0.605	-0.185	0.894	0.699	-0.577	0.922	0.592	0.818
R ²	0.366	0.034	0.799	0.489	0.332	0.850	0.351	0.669
P	0.028	0.545	<0.001	0.008	0.039	<0.001	0.033	<0.001
Functional diversity (FD)								
Coefficient	0.637	-0.147	0.862	0.673	-0.529	0.905	0.614	0.784
R ²	0.406	0.022	0.756	0.454	0.280	0.819	0.377	0.615
P	0.019	0.632	<0.001	0.011	0.063	<0.001	0.026	0.002
SES.PD								
Coefficient	-0.338	0.274	-0.753	-0.724	0.679	-0.691	-0.250	-0.762
R ²	0.114	0.075	0.567	0.529	0.460	0.477	0.062	0.581
P	0.259	0.366	0.003	0.005	0.011	0.009	0.411	0.002
SES.FD								
Coefficient	-0.264	0.104	-0.598	-0.523	0.557	-0.550	-0.183	-0.611
R ²	0.069	0.011	0.357	0.273	0.310	0.302	0.034	0.373
P	0.384	0.735	0.031	0.067	0.048	0.052	0.550	0.027
Phylogenetic NRI								
Coefficient	0.320	-0.291	0.748	0.752	-0.657	0.678	0.252	0.762
R ²	0.102	0.084	0.559	0.566	0.432	0.460	0.064	0.581
P	0.286	0.336	0.003	0.003	0.015	0.011	0.405	0.002
Phylogenetic NTI								
Coefficient	0.395	-0.258	0.712	0.619	-0.655	0.683	0.257	0.703
R ²	0.156	0.066	0.507	0.383	0.429	0.466	0.066	0.495
P	0.181	0.396	0.006	0.024	0.015	0.010	0.400	0.007
Functional NRI								
Coefficient	0.317	-0.249	0.823	0.760	-0.682	0.766	0.328	0.823
R ²	0.101	0.062	0.678	0.577	0.465	0.586	0.108	0.678
P	0.291	0.413	<0.001	0.003	0.010	0.002	0.274	<0.001
Functional NTI								
Coefficient	0.514	0.228	0.445	0.232	-0.241	0.496	0.384	0.378
R ²	0.265	0.052	0.198	0.054	0.058	0.246	0.148	0.143
P	0.072	0.454	0.128	0.446	0.428	0.085	0.195	0.203

Negative relationships are indicated by (-). The level of significance is $P < 0.05$. SES: Standardized effect size; NRI: Net relatedness index; NTI: Nearest taxon index; NDVI: Normalized difference vegetation index.

extreme traits (Santillán et al., 2019), probably because these communities are generally more clustered and functionally similar owing to environmental filtering. In reverse, overdispersed communities at higher elevations are more prone to lose species with extreme traits (Santillán et al., 2019), emphasizing the need for conservation at high elevations. Moreover, because many lineages do not show substantial radiation (Fritz & Rahbek, 2012) and the proportion of species with existing recently diverged relatives is unexpectedly high, species-rich regions at low elevations have relatively low SES.PD. These points underline the importance of integrating phylogenetic and functional information to better understand elevational patterns of amphibian diversity.

Community structures and potential mechanisms may be inconsistent across mountains (Montaño-Centellas et al., 2020), and many studies show a decline in FD and PD with a change from an overdispersed to clustered community along single elevational gradients (Dehling et al., 2014; Graham et al., 2009; Hanz et al., 2019; Mori et al., 2013). In our study, however, we found an interesting pattern with clustered structures in lowland communities versus overdispersed structures in highland communities, despite differences between phylogenetic and functional NRI and NTI (Figure 4). According to the classic framework of community assembly (Figure 1) and the significant phylogenetic signals, environmental filtering (e.g., mean monthly temperature range

Table 2 Influences of spatial and environmental variables on multidimensional biodiversity and community structures

Multidimensional metrics	Coefficient of the best model								R ² _{adj}
	Area	NDVI	Potential evapotranspiration	Solar radiation	Mean monthly temperature range	Temperature seasonality	Temperature annual range	Annual precipitation	
Species richness (SR)				1.924	-4.764		3.131	-6.085	0.941
Phylogenetic diversity (PD)				2.186	-1.989	3.585		-6.114	0.956
Functional diversity (FD)				2.656	-2.048	3.908		-6.926	0.960
SES.PD		-0.963			1.482				0.868
SES.FD		-2.363			-2.440		1.862		0.891
Phylogenetic NRI		1.660		2.006			-0.819		0.727
Phylogenetic NTI	1.025				-1.881			-1.126	0.726
Functional NRI		1.430	-3.871					5.369	0.857
Functional NTI		1.412			-1.419				0.662

Best model selection for multiple regressions is based on lowest AICc. Negative relationships are indicated by (-). SES: Standardized effect size; NRI: Net relatedness index; NTI: Nearest taxon index; NDVI: Normalized difference vegetation index.

and potential evapotranspiration) may act as the main process determining clustered structures at low elevations and competitive exclusion may have the strongest effect at high elevations on Mount Emei. This transformation suggests that competition is strengthened toward the mountain peak. This could be due to the diminished availability of habitats and resources at high elevations, with shrinking area and increasing harshness (Supplementary Figure S3), leading to limited resources and increasing interspecific competition. Notably, the low dispersal ability and similar microhabitat requirements (e.g., strong reliance on humid environments) of amphibian species may strengthen interspecific competition under limited resources toward high elevations (Montaño-Centellas et al., 2020; Wells, 2007). For example, most species (e.g., *Oreolalax* species) on Mount Emei would compete for aquatic habitats for eggs and larva under harsh environments (Supplementary Table S4). It is worth noting that NRI and NTI, which measure different facets of community structure, may cause different phylogenetic and functional structure patterns (Webb et al., 2002). Thus, we need to pay attention to differences in assessments of community structure and assembly processes from the metrics themselves.

Amphibians at higher elevations may experience greater environmental harshness than those living at lower elevations, since harshness varies markedly with elevation on Mount Emei. Different diversity-environment relationships have been found across mountains, and interpretations based on different geographic scales, taxa, and biogeographic regions vary considerably (e.g., Du et al., 2021; Naniwadekar & Vasudevan, 2007; Song et al., 2020). Area greatly influences species distribution, with larger areas able to provide more suitable habitats and thus more species (Rahbek, 1997). Regional area can be considered as a proxy of competition as it represents average resource availability (Zhang et al., 2015). In the current study, the area of each elevational band had a positive effect on species richness, PD, FD, and several community metrics, indirectly suggesting the effect of competitive exclusion on amphibian diversity. Productivity, climate, and their interactions are considered strong predictors for shaping biodiversity patterns (Hawkins et al., 2003). Our study reconfirmed that productivity and climatic factor

interactions shaped multidimensional diversity and community structures at the local scale. In this study, different dimensional diversity patterns were influenced by different ambient conditions (climatic and energy-related variables), thus highlighting the importance of environmental filtering in structuring amphibian communities (Tables 1, 2). The community assembly mechanisms we inferred from Mount Emei contradict the stress dominance hypothesis (Coyle et al., 2014; Swenson & Enquist, 2007) and the traditional view that environmental filtering dominates community structures at high elevations (Kraft et al., 2007; Webb et al., 2002). One possible reason for this inconsistency may be that human interference at densely populated scenic spots and tourist activity at low elevations indirectly strengthen environmental filtering. The amphibian communities on Mount Emei are under different degrees of environmental impact at different elevations, even those communities governed by competitive exclusion, indicating that community assembly is complex and environmental factors are important for shaping diversity and species co-existence. Both climate change and anthropogenic disturbance exacerbate shifts in distribution range, abundance, and genetic diversity of natural populations (Elsen & Tingley, 2015; Hu et al., 2019; Luo et al., 2021), and further studies on changes in amphibian diversity and community on Mount Emei under global change are needed to gain deeper insight into the assembly processes. In mountainous regions, however, the unique topography, complex landscapes, and rapid microenvironment changes make it difficult to characterize all climatic factors and thus regular long-term monitoring is needed in the future (Rahbek et al., 2019).

Our study has several limitations. Although multidimensional richness-based diversity metrics from presence-absence data were used in this study, other metrics (e.g., evenness, which is the regularity of spacing of species in functional trait space and phylogeny) (Pavoine & Bonsall, 2011), other methods (e.g., convex hull and kernel density hypervolumes) (Mammola et al., 2021), and different null models should be included to better understand elevational biodiversity patterns and assembly (Miller et al., 2017). Second, how evolutionary (e.g., *in situ* speciation and character displacement or convergent evolution) and geological processes (e.g., geological changes inferred from the ecological background

and history) drive elevational amphibian diversity should be further explored (Fritz & Rahbek, 2012). Additionally, deterministic (e.g., environmental filtering and competitive exclusion) and stochastic processes (e.g., colonization, extinction, and ecological drift) can simultaneously drive community structure (Chase, 2010), with inconsistent importance among these forces. Moreover, due to the methodological limitations in randomization approaches, stochastic processes remain difficult to be distinguished from the offset between deterministic niche-based processes (Du et al., 2021). Given this, more controlled experiments or manipulations in further studies are required to evaluate the relative importance of these processes.

In conclusion, our study illustrated that the combination of diversity metrics and multiple predictors provided deep insight into the mechanisms that shape amphibian distribution and community structure along an extensive elevational gradient in southwestern China. We also revealed a change in community structure with elevation, with a potential switch from environmental filtering to competitive exclusion with elevation. Furthermore, our results confirmed the predictive power of spatial and environmental variables in explaining elevational biodiversity patterns and community structure. Our findings authenticate the importance of considering multidimensional diversity simultaneously when assessing assembly mechanisms.

SCIENTIFIC FIELD SURVEY PERMISSION INFORMATION

Permission for field surveys was granted by the Mount Emei Scenic Area Management Committee.

SUPPLEMENTARY DATA

Supplementary data to this article can be found online.

COMPETING INTERESTS

The authors declare that they have no competing interests.

AUTHORS' CONTRIBUTIONS

X.Y.W. and J.H.H. conceived and designed the study; X.Y.W., M.J.Z., and J.H.H. analyzed the data with assistance from J.Z. and X.F.S.; X.Y.W. and J.H.H. wrote the article with assistance from M.J.Z., J.Z., X.F.S., S.N.Y., and J.P.J. All authors read and approved the final version of the manuscript.

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