

Letter to the editor

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Spatiotemporal patterns of anuran functional diversity in temperate montane forests

Functional diversity is an integrative approach to better understand biodiversity across space and time. In the present study, we investigated the spatiotemporal patterns (i.e., elevation and season) and environmental determinants of anuran functional diversity on Tianping Mountain, northwest Hunan, China. Specifically, 10 transects were established from low (300 m a.s.l.) to high (1 492 m a.s.l.) elevations, and anuran communities were sampled in spring, early summer, midsummer, and autumn in 2017. Four functional diversity indices were computed for each transect in each season using ecomorphological functional traits. Our results demonstrated that these indices had contrasting responses to increasing elevations. However, they did not differ significantly among seasons in terms of temporal patterns. Interestingly, the unique spatiotemporal functional diversity patterns were impacted by distinct environmental variables, such as leaf litter cover, water temperature, number of trees, and water conductivity.

Exploring the spatiotemporal patterns of biodiversity is central to modern ecology, particularly in regard to species distribution characteristics, species coexistence mechanisms, and community assembly rules (Fu et al., 2006; Khatiwada et al., 2019). Spatial patterns of biodiversity can be assessed along latitudinal/elevational gradients (Zhu et al., 2020) or between different landscape types (e.g., agricultural, forest, and urban areas) (Figueiredo et al., 2019). Temporal patterns of biodiversity are usually assessed annually or seasonally in accordance with the time scales of focus (Lepš et al., 2019; Tonkin et al., 2017). However, most previous studies have only explored species richness despite the fact that biodiversity is a concept that contains multiple facets (e.g., functional diversity and phylogenetic diversity) (Gaston, 1996).

Species richness can only reflect limited information about biodiversity (Gotelli & Colwell, 2011). This is because the ecological roles of species are not equivalent across

ecosystems (Zhao et al., 2018). Instead, their functional characteristics, rather than their taxonomic identity, drive their biotic interactions (predation and competition) (Zhao et al., 2019). Therefore, in recent decades, an increasing number of studies have focused on functional diversity of communities, which is considered a more integrative approach for better understanding biodiversity across space and time (Eskildsen et al., 2015). For instance, Peña-Joya et al. (2020) identified seasonal differences between taxonomic and functional diversity in lizards distributed in the Sierra El Cuale, western Mexico, with higher values in the rainy and dry seasons, respectively. In terms of amphibian communities, functional diversity can differ significantly by land use (i.e., forest, tobacco, and suburban). For example, Pereyra et al. (2018) reported higher functional diversity for amphibians in suburban areas of Argentina. However, many previous studies have been conducted in tropical regions, and empirical studies are needed in temperate regions to understand the general spatiotemporal patterns of amphibian functional diversity in montane forests.

Environmental variables can affect amphibian species distribution and abundance, and act as constraints for the occupation of traits in functional space (Eskildsen et al., 2015; Ochoa-Ochoa et al., 2020). Specifically, as ectotherms, amphibian species distribution is first determined by climatic factors (e.g., air temperature and precipitation) (Enriquez-Urzelai et al., 2019; Lourenco-de-Moraes et al., 2014, 2019). In addition, species with greater thermal tolerance can exhibit wider elevational distribution (Khatiwada et al., 2020). Therefore, different amphibian assemblages may be related to the distinct occupation of trait space, which is associated with changes in functional richness. Moreover, climatic factors can also control amphibian seasonal migration (e.g., breeding and hibernation) (Fei & Ye, 2016; Snyder & Weathers, 1975),

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causing fluctuations in species abundance, which may induce cascading effects on the evenness of trait distribution. In amphibian habitats, microhabitat features (e.g., leaf litter cover, canopy cover, shrub cover, and number of trees) (de Oliveira et al., 2017; Urbina-Cardona et al., 2006; Yang et al., 2019) are important, not only reflecting habitat heterogeneity, to some extent, but also acting as potential filters of species distribution, especially for functional specialists (Raxworthy et al., 2008; Villacampa et al., 2019). Consequently, differences in microhabitat characteristics among habitats may be consistent with changes in species with extreme traits in functional space. Although several theories have been reported, empirical studies on the mechanisms by which environmental variables determine amphibian functional diversity are still limited, especially in temperate regions.

Using a multi-trait approach incorporating intraspecific trait variability (i.e., each species was divided into two distinct functional entities: juvenile and adult), we quantified the spatiotemporal patterns and environmental determinants of anuran functional diversity in temperate montane forests. Specifically, we: (1) assessed the spatial patterns of anuran functional diversity along an elevational gradient; (2) tested the temporal patterns of anuran functional diversity among seasons (i.e., spring, early summer, midsummer, and autumn); and (3) explored the microhabitat environmental factors that determine anuran functional diversity. Based on previous studies (e.g., Zhu et al. (2020), Sun et al. (2021)), we predict that anuran functional diversity will decrease continuously along an elevational gradient. We also predict that anuran functional diversity will differ significantly among seasons. Moreover, as environmental variables can affect species composition (occurrence and abundance), which exhibits distinct occupation of trait space, we predict that microhabitat features, such as water temperature, number of trees, canopy cover, shrub cover, leaf litter cover, and leaf litter depth, will play important roles in determining functional diversity of anuran communities.

During the four sampling events, 14 anuran species belonging to six families were recorded (Supplementary Table S1). Overall, *Amolops ricketti*, *Paramegophrys liui*, *Paa boulengeri*, and *Leptobranchium boringii* were the dominant species, while *Fejervarya multistriata* and *Feirana quadranus* were the rarest species. The amphibian assemblages in each transect differed across the four seasons (see Zhu et al. (2020) for more details). The species were subsequently divided into 18 functional entities (Supplementary Table S1). In total, morphological traits were measured for 456 individuals and each functional entity was measured for 25.3 ± 29.6 individuals (mean \pm standard deviation (SD)).

Values of functional diversity indices are presented as mean \pm SD, followed by the range. When incorporating the data from the four samplings together, transect functional richness (FRic) was 0.298 ± 0.179 (0.025–0.617), and showed a significant inverse bell shape in response to increasing elevation (Figure 1A; Table 1). Functional evenness (FEve) was 0.347 ± 0.141 (0.064–0.522) and exhibited a significant hump-shape relationship with increasing elevation (Figure 1A; Table 1). In addition, functional divergence (FDiv; 0.843 ± 0.086 ; 0.700–0.982) and functional specialization

(FSpe; 0.350 ± 0.093 ; 0.175–0.526) increased significantly along the elevational gradient (Figure 1A; Table 1). At the temporal scale, the functional diversity indices of the transects could not be calculated for October as they did not contain sufficient functional entities. For the other three months, however, no significant differences were found for the four indices ($P > 0.05$).

For the best generalized linear model (GLM), water temperature and number of trees had significant effects on functional evenness. Functional divergence was significantly affected by water temperature, canopy cover, shrub cover, leaf litter depth, and water conductivity. Functional specialization was significantly impacted by number of trees, shrub cover, leaf litter cover, and water conductivity. However, there was no significant relationship between functional richness and microhabitat variables (Supplementary Table S2). Hierarchical partitioning analyses indicated that leaf litter cover was the most important contributor to functional richness (28.31%), followed by shrub cover (22.10%). Water temperature (38.14%) contributed the most to functional evenness, followed by number of trees (32.91%). Functional divergence variation was mainly explained by canopy cover (38.34%), water conductivity (21.94%), and water temperature (19.63%). Functional specialization variation was predominantly contributed to by water temperature (25.31%) and water conductivity (19.92%) (Figure 1B).

We explored the spatiotemporal patterns of anuran functional diversity, as well as their microhabitat determinants on Tianping Mountain in northwest Hunan, China. Overall, our results indicated that all four selected functional diversity indices exhibited significant responses along the elevational gradient. Specifically, there was an inverse bell shape relationship between FRic and elevation, in contrast with our previous study showing that anuran species richness increased significantly with elevation (Zhu et al., 2020). This suggests that although fewer species were detected along the low-elevation transects, they exhibited specific functional traits (e.g., adult *Hyla gongshanensis* and adult *F. multistriata*). This may be due to the fact that they lived in farmland close to the low-elevation transects, and were functional specialists compared with the mountain stream species (Zhao et al., 2018). FEve had a significant hump-shape response to increasing elevation, indicating that the distribution of relative biomass of the functional entities in functional space was more regular in the mid-elevation transects. This is not surprising, as our previous study indicated that one or two large-bodied dominant species usually exist at low (e.g., *A. ricketti* and *Odorrana schmackeri*) and high elevations (e.g., *P. boulengeri* and *L. boringii*), accounting for a high percentage of total biomass in the transects (Zhu et al., 2020). Interestingly, FDiv and FSpe increased significantly with elevation, providing evidence that functional generalists (i.e., adult *Megophrys sangzhiensis* and adult *Fejervarya multistriata*) were gradually replaced by functional specialists (i.e., adult *L. boringii* and juvenile *P. boulengeri*) from low to high elevational transects. This accords with the unique community assembly process observed along the elevational gradient in the study area (Zhu et al., 2020). It also explains why functional specialists were not abundant in the low-elevation transects (e.g., *F.*

Table 1 Models used to test responses of anuran functional diversity indices to elevational gradient

Response variable	Source of variation	df	Estimate (SE)	t	P	R ²
FRic	Elevation	7	-0.003 (0.001)	-2.669	0.032	0.57
	Elevation ²	7	<0.001 (<0.001)	2.793	0.027	
	Intercept	7	1.403 (0.001)	3.020	0.019	
FEve	Elevation	7	0.003 (0.18)	2.713	0.030	0.54
	Elevation ²	7	<0.001 (<0.001)	-2.614	0.035	
	Intercept	7	-0.729 (0.379)	-1.909	0.098	
FDiv	Elevation	8	<0.001 (<0.001)	2.576	0.033	0.45
	Intercept	8	0.691 (0.063)	10.949	< 0.001	
FSpe	Elevation	8	<0.001 (<0.001)	4.345	0.002	0.70
	Intercept	8	0.146 (0.050)	2.894	0.020	

FRic: Functional richness; FEve: Functional evenness; FDiv: Functional divergence; FSpe: Functional specialization. Elevation and Elevation² indicate linear and quadratic terms in regression models, respectively. Significant effects are indicated in bold.

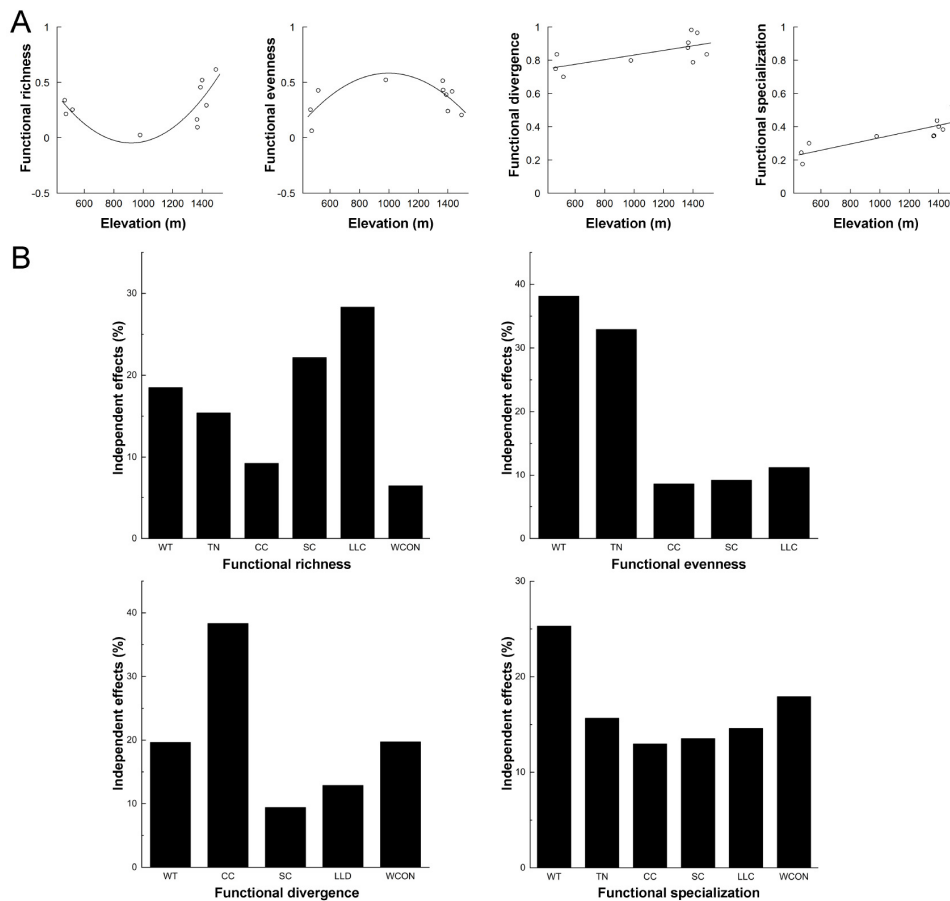


Figure 1 Spatiotemporal patterns of anuran functional diversity in temperate montane forests

A: Relationships between anuran functional diversity indices and elevations on Tianping Mountain; B: Hierarchical partitioning showing independent contribution of selected environmental variables to variation in different functional diversity indices. Abbreviations of microhabitat variables are: WT: Water temperature; TN: Number of trees; CC: Canopy cover; SC: Shrub cover; LLC: Leaf litter cover; LLD: Leaf litter depth; WCON: Water conductivity.

multistriata). However, as a limited number of transects were used in the present study, more transects should be added (particularly at mid-elevations, 978–1 388 m a.s.l.) in future research to verify our conclusions.

In terms of temporal scale, no significant differences were found in the four indices among seasons, supporting the

claims that different seasons can play equally important roles for anurans (Gardner et al., 2007). Indeed, different anuran species can exhibit very different abundances along the same transects in accordance with their seasonal migration behavior, which is regulated by the characteristic ecological conditions of each season (Fei et al., 2009, 2012; Snyder &

Weathers, 1975). For instance, *L. boringii* usually breeds between February and April, *Paramegophrys liui* breeds from April to July, and *O. schmackeri* and *M. sangzhiensis* breed from June to August (Fei et al., 2009, 2012). In addition, our results also reflect, to some extent, the adaptation of species to minimize interspecific competition for resources between functionally similar species (Shimadzu et al., 2013). For instance, *A. chunganensis* was a dominant species in August, while functionally similar species *A. ricketti* was more abundant in October. Indeed, this can be attributed to the life history traits of these two species. Specifically, *A. chunganensis* usually lives in forests, and only appears near streams to spawn during the breeding season. In contrast, *A. ricketti* lives along the same streams throughout the whole year (Fei et al., 2012). Therefore, *A. ricketti* can compensate for the contribution of *A. chunganensis* to the functional diversity indices along the transects.

Based on the GLMs and hierarchical partitioning results, microhabitat variables significantly impacted anuran functional diversity. Specifically, FRic was positively correlated with water temperature, number of trees, and leaf litter cover, although these effects were not significant. FEve was mainly determined by water temperature and number of trees, but the correlations between them were negative. These results were consistent with previous studies showing that transects with warm temperature, more trees, and higher percentage of leaf litter cover can support more species with diverse traits (Khatiwada et al., 2019). However, these species were not evenly distributed along the transects in terms of relative biomass, which may be determined by their ecological niche breadth. In addition, our results suggested that transects with more trees and a higher percentage of leaf litter cover, but lower water temperature and conductivity usually exhibited higher FDiv and FSpe. Indeed, most such transects were located at high elevations, which contained greater and more diverse vegetation. Therefore, more functional specialists, such as adult *L. boringii*, juvenile and adult *P. boulengeri*, adult *Paramegophrys liui*, and adult *O. margaretae*, inhabited these transects. This was because habitats with higher leaf litter cover were ideal breeding sites for these species (Fei et al., 2009, 2012). Furthermore, as habitats with more diverse and dense vegetation harbor greater insect abundance (Thompson et al., 2014), these transects were also ideal foraging sites for these functional specialists. This balance between prey (insects) and predators (anuran) can also increase the resilience of mountain forest ecosystems (Bellone et al., 2017).

In conclusion, the present study demonstrated that spatiotemporal patterns of anuran functional diversity in Tianping Mountain were influenced by microhabitat variables. Our results provide important information for local amphibian conservation activities (e.g., functional specialists and high-elevation mountainous streams). However, more studies on other mountains are still needed to demonstrate the general patterns of anuran functional diversity, and to explore how these patterns can affect food webs and ecosystem functioning in temperate montane forests. Furthermore, our study indicated the existence of unique community assembly processes in mountain-dwelling amphibians, and future study

could better explain these processes by incorporating phylogenetic signals. More importantly, as functional diversity indices are more sensitive than those based on taxonomic approaches, they can provide early warning signals of disturbance impacts in montane forests.

SCIENTIFIC FIELD SURVEY PERMISSION INFORMATION

Permission for field surveys in Hunan Province was approved by the Management Office of Badagongshan Nature Reserve (No. BDGSR201204001). Animal collection and measurement protocols were approved by the Animal Care and Use Committee of the Chengdu Institute of Biology, China (No. CIB2010031015).

SUPPLEMENTARY DATA

Supplementary data to this article can be found online.

COMPETING INTERESTS

The authors declare that they have no competing interests.

AUTHORS' CONTRIBUTIONS

T.Z. conceived and designed the study. Z.J.S., W.B.Z., W.Z., C.L.Z., C.L.L., B.Z., D.X., W.B.F., and T.Z. collected the data. Z.J.S., W.B.Z., and T.Z. analyzed the data and wrote the first draft of the manuscript. C.L.Z., W.B.Z., S.Q.S., and J.P.J. commented on the manuscript. All authors read and approved the final version of the manuscript.

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