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Letter to the editor
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Applying zeta diversity to understand species turnover patterns of small mammals in the Mountains of Southwest China

DEAR EDITOR,

Mountainous regions are generally characterized by high species turnover, yet studies applying novel conceptual frameworks to analyze the spatial structure and organization of montane biota along elevational gradients remain scarce. Based on the zeta diversity framework — a novel turnover metric that focuses on average number of species shared across sites — and a comprehensive presence-absence dataset of small mammals collected from 22 elevational gradients in the Mountains of Southwest China (MSC), we compared zeta diversity patterns (i.e., zeta decline, retention rate) across low-, mid-, and high-elevation zones and between insectivores and glires, which differ in dispersal ability and functional traits. We tested two hypotheses regarding the drivers of mammalian species turnover, i.e., elevation zone and dispersal ability. We also explored the drivers of species turnover by calculating zeta decay and comparing zeta decline under different normalizations (Sørensen- and Simpson-equivalent) and sample selection schemes (all combinations (ALL) and non-directional nearest-neighbors (NON)). The ALL scheme considers random selection of site combinations and does not take into account the spatial location of sites. As for the NON scheme, the spatial location of sites is taken into account. Results showed that community assemblages in the high-elevation zone exhibited the highest (complete) turnover rate. Furthermore, insectivores demonstrated a higher species turnover rate than glires. Geographic distance had a marked effect on species turnover, especially for the high-elevation zone and insectivore assemblages. In conclusion, both landscape structure and species dispersal ability played crucial roles in driving species turnover patterns of small mammals in the MSC. Furthermore, zeta diversity metrics provide a useful tool for understanding the mechanisms of spatial turnover patterns in montane biota.

Understanding the patterns and drivers of species turnover along spatial gradients (e.g., elevational gradients) is a fundamental issue in ecology and biogeography (Baselga, 2010; Hui & McGeoch, 2014). Mountain ecosystems and elevational gradients are excellent systems for studying biodiversity patterns and their underlying mechanisms (Brown, 2001; Körner, 2000). In mountainous regions, geographic isolation tends to increase with elevation, regardless of the shape of the mountain range (Elsen & Tingley, 2015). Low-elevation habitats have better spatial connectivity, while species in mid- and high-elevation habitats need to disperse farther to reach another suitable habitat. Additionally, mid- and high-elevation species are generally restricted to a particular elevation zone due to habitat heterogeneity (e.g., topography and climate) in different zones. Hence, compared to low-elevation zones, community assemblages in mid- and high-elevation zones are more isolated and likely composed of more mountain-endemic species (Brown, 2001), resulting in higher species turnover in the mid- and high-elevation assemblages.

Non-volant small mammals (hereafter “small mammals”) constitute excellent model species for studying community assembly and compositional turnover due to their relatively high species diversity, low dispersal ability, and narrow niche breadth, which facilitate community dissimilarity. As the two major small mammal taxa, glires (Rodentia and Lagomorpha) and insectivores (Eulipotyphla) differ substantially in body size, metabolic rate, diet, and habitat requirements (Gliwicz & Taylor, 2002; Wen et al., 2022b). Although both taxa are species-rich, glires exhibit enhanced dispersal capabilities compared to insectivores due to their larger body sizes. Furthermore, with lower habitat diversity, insectivores typically show smaller home ranges compared to glires, leading to more habitat generalists (Santini et al., 2013). Thus, montane glires and insectivores are likely to exhibit different spatial turnover patterns driven by differences in dispersal abilities and functional traits.

Zeta diversity (ζ_i) represents an innovative diversity metric designed to capture the average number of species shared across different sites (Hui & McGeoch, 2014). Zeta diversity overcomes many of the limitations of existing approaches for measuring compositional turnover, especially for multi-site, cross-scale assemblage patterns. The application value of zeta diversity has been demonstrated in multiple empirical studies related to conservation (McGeoch et al., 2019; Wen et al., 2022a).

Utilizing the zeta diversity framework and small mammal occurrence data collected from 22 elevational gradients, we

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analyzed the turnover patterns of non-volant small mammals in the MSC and tested two hypotheses regarding mammalian community assembly.

(1) Elevation zone hypothesis: The degree of population isolation tends to increase with elevation. High-elevation assemblages are more likely to consist of endemic species and less likely to share species compared to low-elevation assemblages. Therefore, we predict that community assemblages in the high-elevation zone will display a more pronounced turnover pattern than those in the low- and mid-elevation zones.

(2) Dispersal ability hypothesis: Given that glires possess enhanced dispersal abilities and are adaptable to a broader variety of habitat types, we predict that insectivores, irrespective of the elevation zone, will exhibit a higher turnover rate in comparison to glires.

Based on an extensive literature review, we collated a presence-absence dataset of small mammals across 22 elevational gradients in the MSC (Supplementary Figure S1). In total, 93 small mammal species (glires: 59 species; insectivores: 34 species) were included, with 67, 73, and 62 species in the low-, mid-, and high-elevation zones, respectively.

We compared three zeta diversity metrics among the three elevation zones (i.e., low-, mid-, and high-elevation) and the two taxonomic groups (i.e., glires and insectivores) across all elevation zones: i.e., zeta decline, retention rate based on the zeta ratio, and zeta decay over space (Hui & McGeoch, 2014; McGeoch et al., 2019). In addition, we used different sample selection schemes (i.e., ALL and NON) and zeta values (i.e., raw, Sørensen- and Simpson-equivalent) to calculate zeta decline (McGeoch et al., 2019). Further details on data sources and statistical analyses are provided in the Supplementary Materials.

Across the 22 examined elevational gradients, distinct patterns of zeta diversity decline were observed in the low-, mid-, and high-elevation zones. Specifically, the low-elevation zone showed the slowest decline, followed by the mid-elevation zone, while the high-elevation zone showed the steepest decline (Figure 1A). As expected, a slower decline was observed for the NON scheme compared to the ALL scheme, likely due to the increased probability of neighboring sites sharing species (Supplementary Figure S2A, C, E). Additional analyses using normalized zeta values revealed that for the mid- and high-elevation zones, a slightly steeper decline was observed when employing the Sørensen index to measure zeta diversity decline, although the difference between the Sørensen and Simpson results was non-significant (Supplementary Figure S2D, F). Conversely, for the low-elevation zone, zeta decline was significantly steeper when measured by Sørensen analysis than by Simpson analysis (Supplementary Figure S2B). The retention curves associated with the low- and mid-elevation zones were characterized by an asymptotic shape at higher orders (Figure 1B). In contrast, the retention rate curve for the high-elevation zone demonstrated a modal shape, with the zeta ratio increasing steadily to ζ_9 and then declining to zero at ζ_{20} (Figure 1B; Supplementary Table S1).

When divided into insectivores and glires, the two small mammal groups showed different patterns of zeta diversity decline across all elevation zones. Generally, glires showed a slower zeta diversity decline compared to insectivores (Figure 1C). Zeta decline was also slightly slower under the NON scheme than under the ALL scheme and stabilized at lower orders (insectivores at ζ_{10} and glires at ζ_{19}) (Supplementary Figure S3A, C). Confidence intervals for the decline under different schemes overlapped for most orders. Normalized zeta decline was also slightly steeper when measured using the Sørensen index than the Simpson index, although the difference was non-significant (Supplementary Figure S3B, D). The retention rate curve for the insectivores was modal, with the zeta ratio starting to decrease at ζ_5 and declining to zero at ζ_{15} (Figure 1D; Supplementary Table S1). In contrast, the retention rate curve for the glires demonstrated a sharp initial increase in the first three orders, followed by an asymptotic pattern for the higher orders (beyond ζ_9) (Figure 1D; Supplementary Table S1). Notably, the species retention rate for glires was consistently higher than that for insectivores.

The regression slopes for the distance decay curves across the three elevation zones were statistically significant within the range of ζ_2 to ζ_5 (Supplementary Table S2). With the increase in geographic distance, the zeta values of ζ_2 to ζ_5 showed a downward trend in all three elevation zones (Figure 1E–G). As the order increased, the slope of the decay curve became smaller (Supplementary Table S2). For the same orders across the three elevation zones, the decay curve slope was most pronounced in the high-elevation zone, followed by the mid-elevation zone, and was least pronounced in the low-elevation zone (Supplementary Table S2).

The insectivores and glires exhibited similar distance decay patterns across all elevation zones. For insectivores, zeta values decreased with distance from ζ_2 to ζ_5, with distance decay being more pronounced at lower orders (Figure 1H, I). For glires, zeta values demonstrated a stronger decay from ζ_2 to ζ_3. At the same order, the decay curve of insectivores showed a steeper slope compared to that of glires (Supplementary Table S2).

Based on zeta diversity pattern analysis, our results delineated the elevational pattern of species turnover for small mammals in the MSC. Consistent with the elevation zone hypothesis, community assemblages in the high-elevation zone showed the highest species turnover. The modal retention curve for the high-elevation zone also implied complete species replacement at high zeta orders (beyond ζ_{20}) (Figure 1B) (McGeoch et al., 2019). Although the different sample selection scheme results indicated that spatial proximity of sites was less influential on compositional change in the three elevation zones (Supplementary Figure S2), the distance decay patterns of zeta diversity indicated that the structure of the high-elevation assemblage was much more dependent on distance between sites (Figure 1E–G). Notably, comparing zeta decline between the Sørensen- and Simpson-equivalent normalizations (Supplementary Figure S2) showed that the nestedness component had a considerable impact on small mammal communities in the low-elevation zone.

The distance between the source and sink regions of species increases with elevation due to the influence of topography-driven isolation, thus hindering species dispersal among suitable habitat patches. Furthermore, the diversity of habitat types in the MSC (Supplementary Figure S4) and restriction of species to different elevation zones, possibly due to environmental filtering and competitive exclusion, can also promote isolation. Thus, both potential mechanisms (i.e., niche and dispersal processes) may contribute to the rapid compositional turnover of small mammals in the high-elevation zone.

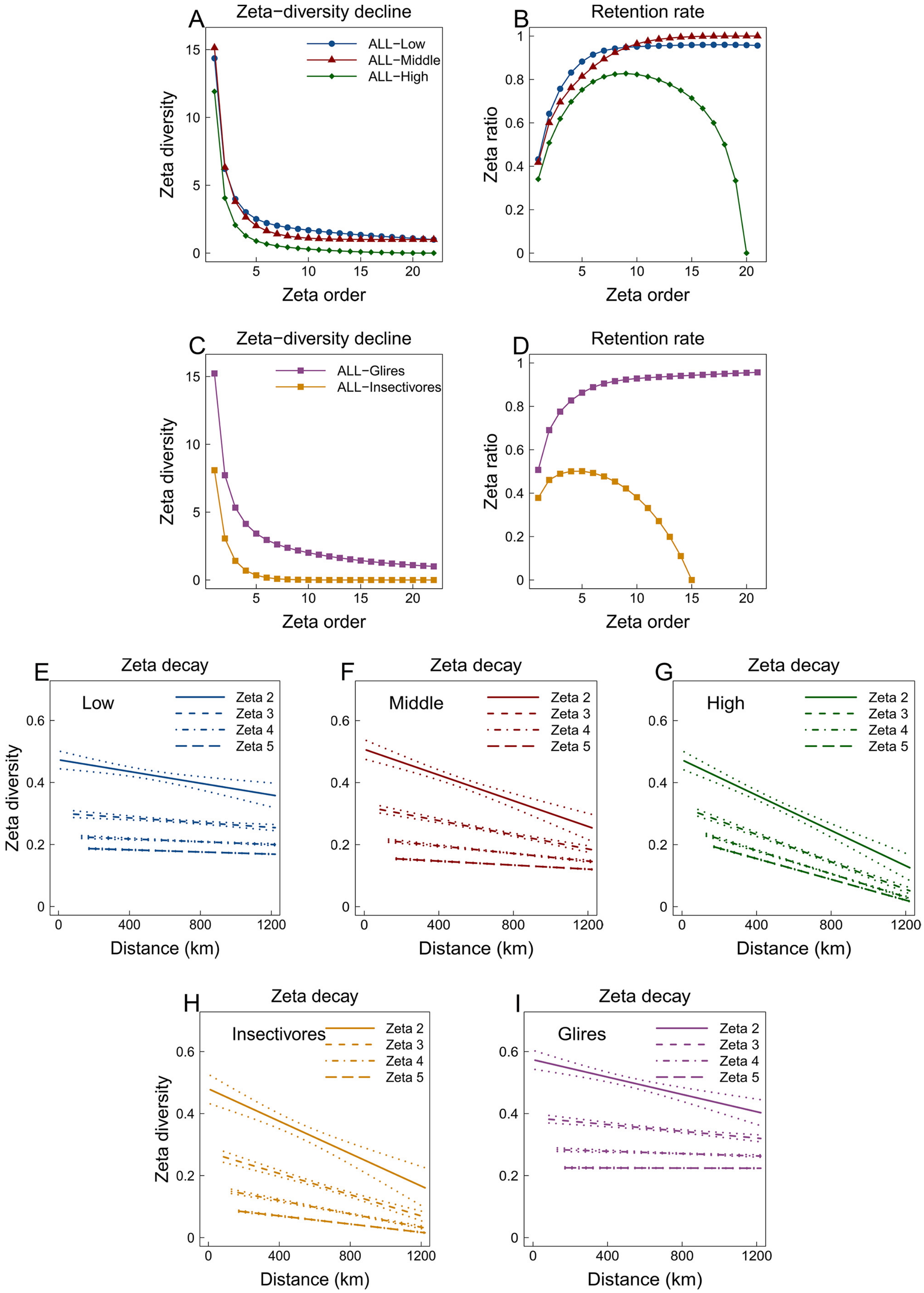

Figure 1 Zeta diversity patterns of non-volant small mammals in the MSC

A, B: Zeta diversity decline (A) and retention rate (B) curves for small mammals at low- (*n*=67), mid- (*n*=73), and high-elevation zones (*n*=62) across 22 elevational gradients (analysis was conducted using ALL-sample selection scheme and raw zeta values). C, D: Zeta diversity decline (C) and retention rate (D) curves for glires (*n*=59) and insectivores (*n*=34) for all elevation zones across 22 elevational gradients (analysis was conducted using ALL-sample selection scheme and raw zeta values). E–G: Distance decay curves of zeta diversity (Sørensen-equivalent) for zeta orders 2–5 of small mammal communities at low- (E), mid- (F), and high-elevation zones (G). Dashed lines indicate 95% confidence intervals. H, I: Distance decay curves of zeta diversity (Sørensen-equivalent) for zeta orders 2–5 for glire (H) and insectivore communities (I) at all elevation zones. Dashed lines indicate 95% confidence intervals.

In the current study, zeta diversity patterns of glires and insectivores were also compared. These two mammalian groups are characterized by different dispersal abilities and functional traits, including body size, diet, and habitat requirements (Gliwicz & Taylor, 2002; Wen et al., 2022b). Our results were consistent with the dispersal ability hypothesis, with the insectivores exhibiting a higher species turnover than glires, as well as complete species replacement at higher zeta orders (beyond ζ_{15}) and greater susceptibility to changes in distance between sites (Figure 1H, I). Our findings also indicated that the replacement component is a primary driver of species turnover pattern for both glires and insectivores in the MSC.

Given their less vagile nature, insectivore assemblages within mountainous regions are more profoundly impacted by isolation than glires. The pronounced habitat heterogeneity of mountain ecosystems can also confine insectivores, as habitat specialists, to fragmented habitats (Santini et al., 2013). Accordingly, our results provide evidence supporting the hypothesis that both dispersal mechanisms and niche processes have collectively contributed to the turnover patterns of small mammals in the MSC. Furthermore, our findings also suggest that, due to a greater propensity for isolation caused by geographical barriers, dispersal mechanisms may exert a more pronounced influence on the community assembly of insectivores (Wen et al., 2022b).

Using zeta diversity, a novel turnover metric, we explored the species turnover patterns of small mammals across 22 elevational gradients in the MSC. The increasing trend in mammalian species turnover in the high-elevation zone revealed the profound effect of landscape configuration on turnover patterns of montane species. Furthermore, the distinct patterns of zeta diversity observed between the glires and insectivores emphasized the key role of species dispersal ability in driving turnover patterns in mountainous regions. Analysis of distance decay in zeta diversity further underscored the importance of spatial distance in driving species turnover in the MSC, especially for species in the high-elevation zone and habitat specialists with poor dispersal ability (i.e., insectivores). Considering the limitations of this study (e.g., specific environmental drivers of turnover were not evaluated) and to provide recommendations for biological conservation efforts, we propose that future studies should explore critical environmental and geographic factors that drive species turnover of small mammals in the MSC and other mountain systems, e.g., multi-site generalized dissimilarity modeling (McGeoch et al., 2019).

SUPPLEMENTARY DATA

Supplementary data to this article can be found online.

COMPETING INTERESTS

The authors declare that they have no competing interests.

AUTHORS' CONTRIBUTIONS

J.Z.K., Z.X.W., and Q.S.Y. conceived and designed the study. J.Z.K. and Z.X.W. analyzed the data with assistance from M.Q.W. J.Z.K. and Z.X.W. wrote the manuscript with assistance from A.F., T.T., and L.X. All authors read and approved the final version of the manuscript.

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