Spatial Heterogeneity of Climate Fluctuations Shapes Ecological Processes and Community Dynamics in Riverine Invertebrates Across a Landscape

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Conflict of Interest

The authors declare no conflict of interest.

Author Contributions

XL, QL, QC, MCC, and VHR drafted the article and conceptualized the project. XL and MCC devised the research methodology. XL, JW and MCC conducted data processing and analysis. All authors reviewed and revised the article.

Data availability statement

The data that supports the findings of this study are available in the supporting information Data S4 at https://onlinelibrary.wiley.com/doi/10.1111/jbi.13913.

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Abstract

Climate fluctuations exhibit spatial heterogeneity in influencing ecological processes and community dynamics. However, the mechanisms underlying these impacts on biodiversity remain largely unexplored. This study investigates how spatial variations in climate fluctuations affect the relative significance of ecological processes shaping invertebrate community dynamics across 15 rivers in the European Iberian Peninsula over 21 years. Spatial shifts in community dynamics were driven by a combination of deterministic (climatic filtering) and stochastic (temporal variability) processes. Notably, the dominance of deterministic versus stochastic processes showed an elevation-dependent pattern characterized by a single peak. Analyzing community dynamics across different elevations provides a foundational basis for predicting and mitigating the biodiversity impacts of climate change, guiding effective conservation strategies.

Keywords: climatic fluctuation, community dynamics, temporal beta diversity, elevation patterns, stochastic processes, deterministic processes

1 Introduction

Overwhelming evidence suggests an unprecedented decline in global biodiversity and the vital ecosystem services it delivers [1]. This trend is particularly pronounced for species facing varied fates due to adaptations in their life histories, morphology, and physiology amidst the complexities of a changing global environment. For instance, species inhabiting high-altitude or latitude regions often struggle to adapt to shifting climatic conditions [2]. Spatial heterogeneity within landscapes is crucial for understanding how diverse biological communities respond to both anthropogenic and natural environmental changes through various ecological processes.

Spatial variations in climatic fluctuations are pivotal in shaping the geographic distribution of community dynamics. For instance, the influence of climate variability on community dynamics has been extensively documented [3-5]. Moreover, with climate fluctuations intensifying at higher latitudes and elevations [6], disparities in community dynamics may arise due to geographical distinctions. Existing research has predominantly focused on two main areas: the spatial patterns of climate fluctuations [7,8] and the impacts of these fluctuations on biogeographic patterns and community dynamics [5,9,10]. However, the interaction between spatial patterns of climate variability and the geographic distribution of community dynamics remains largely unexplored from a mechanistic perspective involving ecological processes.

The importance of ecological processes is integral to understanding the underlying mechanisms that result in the resulting spatial patterns in community dynamics. Deterministic processes are typically associated with environmental and biological

filtration, whereas stochastic processes are more commonly linked to probability distributions and ecological drift [11-13]. For instance, the relative importance of ecological processes undergoes a transformation with community succession. Over time, there is a shift from stochastic to deterministic processes, which become the dominant forces shaping community composition [12,14]. Additionally, different time scales influence the relative importance of ecological processes. Some studies have indicated that deterministic processes tend to prevail over longer time scales, influencing community dynamics [15,16].

This study represents a pioneering effort to investigate the intricate relationship between spatial climate fluctuations and community dynamics from a mechanistic standpoint rooted in ecological processes. We conducted an analysis of ecological processes influencing community dynamics using extensive long-term data on benthic macroinvertebrates from a geographically expansive and continuously monitored area (Fig. 1). Our primary hypothesis examined whether heightened climate fluctuations, particularly in higher elevations, significantly influence the geographical patterns observed in community dynamics. Furthermore, we assessed how changes in elevation might modify the relative contributions of stochastic and deterministic processes driving biological community dynamics.

2 Materials and Methods

2.1 Study area and Macroinvertebrate data

The benthic macroinvertebrate data used in this study were originally collected and analyzed by Cañedo-Argüelles, et al. [17] from 15 rivers located in the northeastern

part of the Iberian Peninsula in Spain. This region is characterized by a Mediterranean climate, with annual precipitation ranging from 500 to 1400 mm and mean annual temperatures between 7 and 15°C. According to the Assessment Criteria of Mediterranean Rivers [18], the human pressures in the studied river reaches are assessed as relatively low.

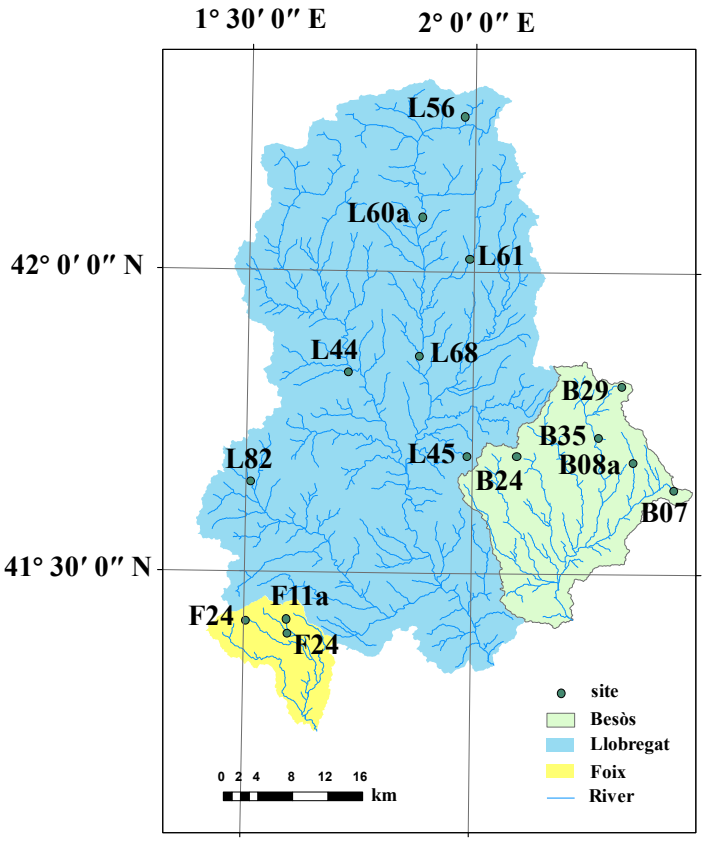

Figure 1. Sampling sites in the Iberian Peninsula studied by Cañedo-Argüelles, et al. [17]

2.2 Climate variables and Time variables

In addition to the biological data analyzed by Cañedo-Argüelles, et al. [17], which focused on the spatial variation of community structure, we incorporated additional variables from diverse sources to explore various aspects. Elevation data and monthly

climatic variables such as mean minimum temperature, mean maximum temperature, and total precipitation were sourced from the WorldClim 2 database [19] for each sampling site over the period spanning 1997 to 2017. These data were further processed using the "biovars" function within the R package "dismo" [20] to derive 19 physical and climatic variables, including annual precipitation, mean annual temperature, minimum temperature of the coldest month, and maximum temperature of the hottest month (see Appendix S1 for details).

Temporal variables were generated to represent stochastic processes in time (e.g., ecological drift) using the asymmetric eigenvector map (AEM) method, which is a filtering approach to model the effects produced by directed processes (e.g., time) [21]. Studies of time-series dynamics often necessitate logical consistency, which posits that a previous point in time will have an effect on a later point in time. Consequently, the AEM approach represents the optimal methodology for such studies [22]. The sampling times of each sample point were sorted, placed in the same frame, and the AEMs are computed in such a way that each sampling time point corresponds to the corresponding AEM. In calculating the AEM, the sampling time interval was employed to determine the weights. The formula was as follows:

$$Weight = 1 - (d / d\max)^2 \quad [1]$$

In this context, the notation "d" represents the sampling time interval, while "dmax" denotes the maximum value of the sampling time interval. Given a sample size of n, the AEM produces a total of n-1 positive eigenroots, with no negative eigenroots.

The eigenfunctions can be divided into two sets of variables with positive and negative temporal correlation [23]. Based on the Moran I coefficients, we selected positively correlated AEMs [21], as detailed in Appendix S1. The AEMs were computed with the "aem.time" function from the "adespatial" package [24].

2.3 Data analysis

The objective of this study was to examine how climate fluctuations vary with altitude. To this end, the temporal dynamics of the altitudinal patterns of total monthly precipitation, mean monthly minimum temperature, and mean monthly maximum temperature were examined. Additionally, the coefficients of variation (CVs) of total monthly precipitation, mean monthly minimum temperature, and mean monthly maximum temperature were calculated and their variation with altitude was explored. The test is performed using the generalized additive model (GAM).

The GAM model was employed to investigate elevation patterns in species richness across sample sites over a 21-year period. Subsequently, the presence and absence data were utilized to calculate three distance matrices for each sample point based on the Jaccard coefficient of variation. These matrices represent temporal beta diversity (Btotal), its decomposed species substitution (Brepl), and richness difference (Brich). The distance matrices were obtained using the "BAT" package in R, as outlined by Cardoso [25]. Subsequently, the GAM model was employed to investigate the elevation patterns of temporal beta diversity and its components, with the relative importance of the different components of temporal beta diversity then calculated. The Wilcoxon test was employed to ascertain which of the components of temporal beta

diversity (Brep and Brich) was the primary driver.

To validate how elevational change in the relative significance of stochastic and deterministic processes can drive the shift of community dynamics, we employed generalized dissimilarity models (GDMs) to estimate temporal beta diversity and its components, while accounting for climatic and temporal variables [26,27]. GDMs transform environmental variables through an iterative maximum likelihood fitting process with the objective of identifying the optimal fit between environmental discrepancies and community differences [28].

The GDM assumes that biome variance increases monotonically with environmental variance and employs a link function to transform linear predictors in order to adjust for the nonlinear relationship between the two [28]. The GDM model fit is constrained by the number of i-spline basis functions, with a default value of three i-splines [29]. We conducted variance decomposition at each sample point to assess the rate of explanation of temporal beta diversity and its components by climatic and temporal variables. This was accomplished using the the "gdm.partition.deviance" function in the R package "gdm" [28,30]. Then, the GAMs were employed to investigate the relationship between the ratio of pure explanatory rates of climatic and temporal variables and elevation, with the objective of identifying patterns of elevation on the various ecological processes that shape community dynamics.

3 Results

3.1. Climatic fluctuations

We computed the total monthly precipitation and the average monthly minimum- and maximum- temperatures in relation to elevation, and found that precipitation gradually increases with elevation through the GAM model, and that both minimum and maximum temperatures diminish with rising elevation (Fig. 2a, 2d, 2g). When calculating the coefficient of variation (CV) for precipitation, minimum temperature, and maximum temperature over the study period, we found a decrease in precipitation fluctuation with increasing altitude, but that the fluctuation of minimum and maximum temperature increased gradually (Fig. 2b, 2e, 2h). The results indicated that the frequency of extreme weather events (precipitation, minimum and maximum temperatures), although different at different altitudes, did not show a clear altitudinal pattern (Fig. 2c, 2f, 2i). For the definition and frequency of extreme events, see Appendix S3 for details: Table S2, and further statistical information on the GAM model, please refer to Appendix S3.

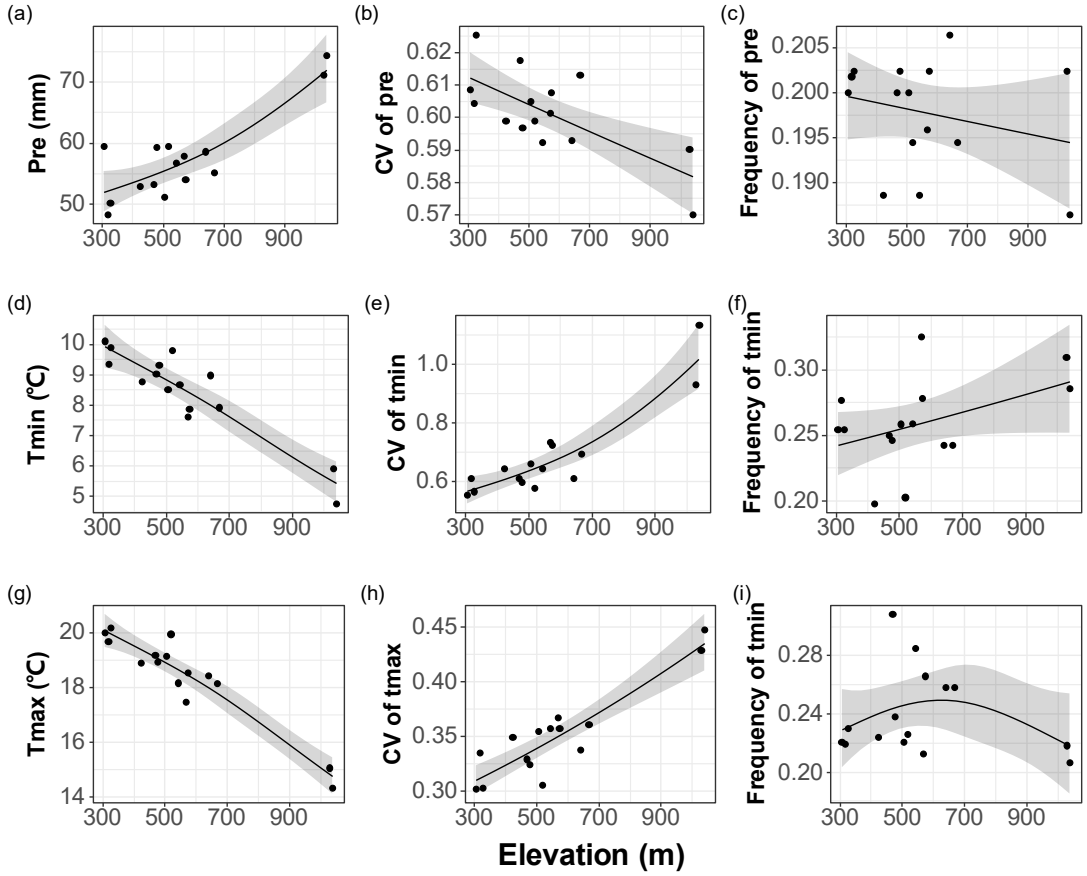

Figure 2. Elevation patterns of (a) monthly total precipitation, (b) the variability of monthly total precipitation, (c) the frequency of monthly total precipitation, (d) monthly mean minimum temperature, (e) the variability of monthly mean minimum temperature, (f) the frequency of monthly mean minimum temperature, (g) monthly mean maximum temperature, (h) the variability of monthly mean maximum temperature, (i) the frequency of monthly mean maximum temperature.

3.2 Biotic dynamics

Using generalized additive modeling (GAM), species richness followed a bimodal pattern with elevation over the study period (Fig. 3a). The temporal beta diversity (Btoal)

gradually decreased with increasing elevation, but its components Brepl and Brich did not show a clear or regular change with elevation (Fig. 3b, 3c, 3d). Species turnover (Brepl) was significantly higher than richness difference (Brich) when a wilcoxon test for Brepl and Brich was performed. This result suggested that species turnover dominated the temporal beta diversity in the region (Refer to Appendix S3 for further details).

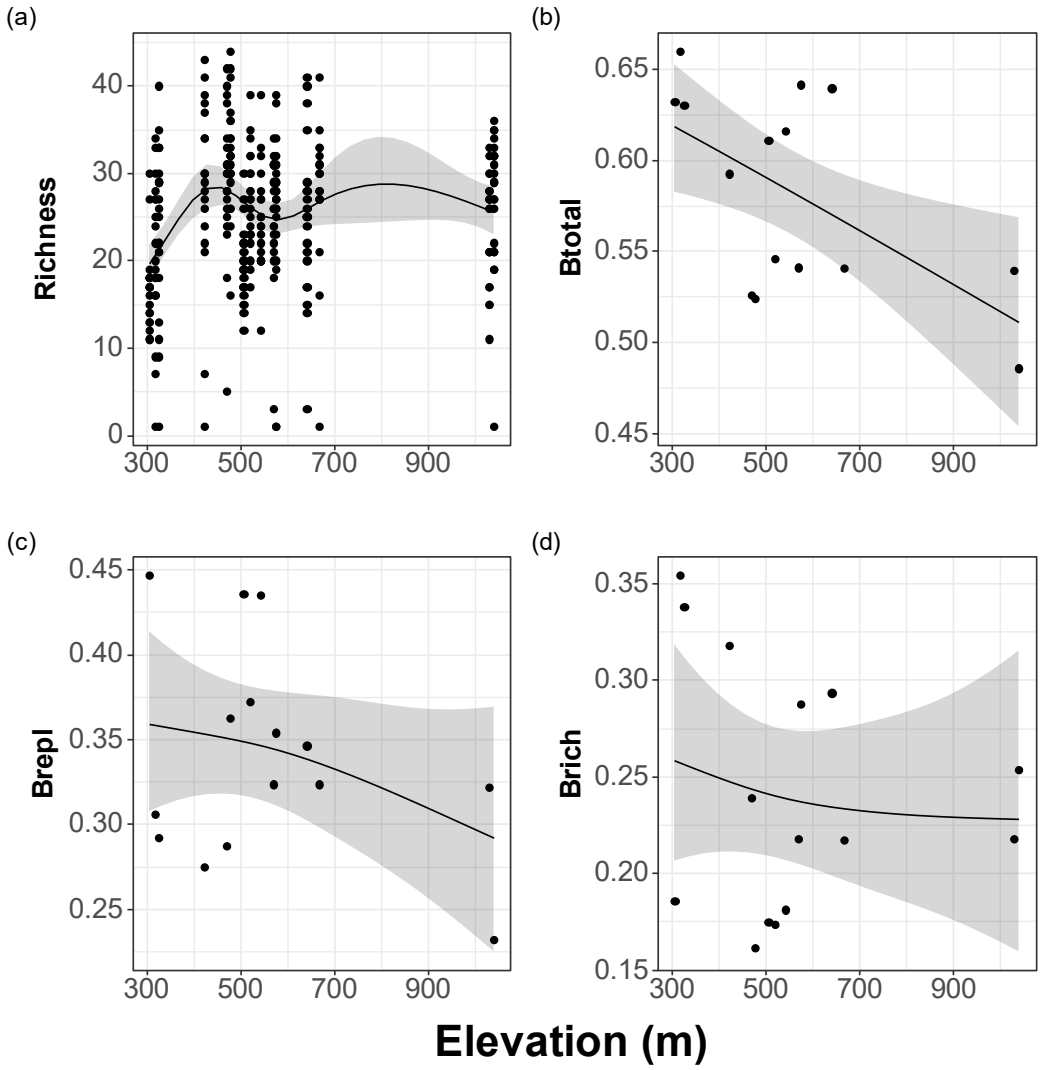

Figure 3. Elevation patterns of (a) Richness, (b) temporal beta diversity (Btotal), (c) species

replacement (Brepl), and (d) richness difference in temporal beta diversity (Brich).

3.3 Ecological processes

The GDM model's explanatory power for temporal beta diversity and its components (Brepl and Brich) had notable variation across sample points. We discovered that for temporal beta diversity and its components (Brepl and Brich), AEM was usually more important than the climate variable during the study period. The ratio of climate to AEM for Btotal exhibits a unimodal pattern of increasing and then decreasing. In contrast, the ratios for Brepl and Brich do not demonstrate a clear elevation pattern (Fig. 4a, 4b, 4c). See Appendix S2 for further details.

We conducted a separate analysis of the changes in the relative importance of climate and AEM with elevation. Our findings revealed that for Btotal, the importance of climate exhibited a single-peaked pattern of increasing and then decreasing with elevation. In contrast, for Brepl and Brich, there was no clear pattern of elevation in the importance of climate (Fig. 4d, 4e, 4f). In contrast, for Brepl, the relative importance of AEM exhibited an elevation pattern of decreasing and then increasing. In contrast, for Btotal and Brich, the relative importance of AEM underwent a change, yet there was no discernible elevation pattern (Fig. 4g, 4h, 4i).

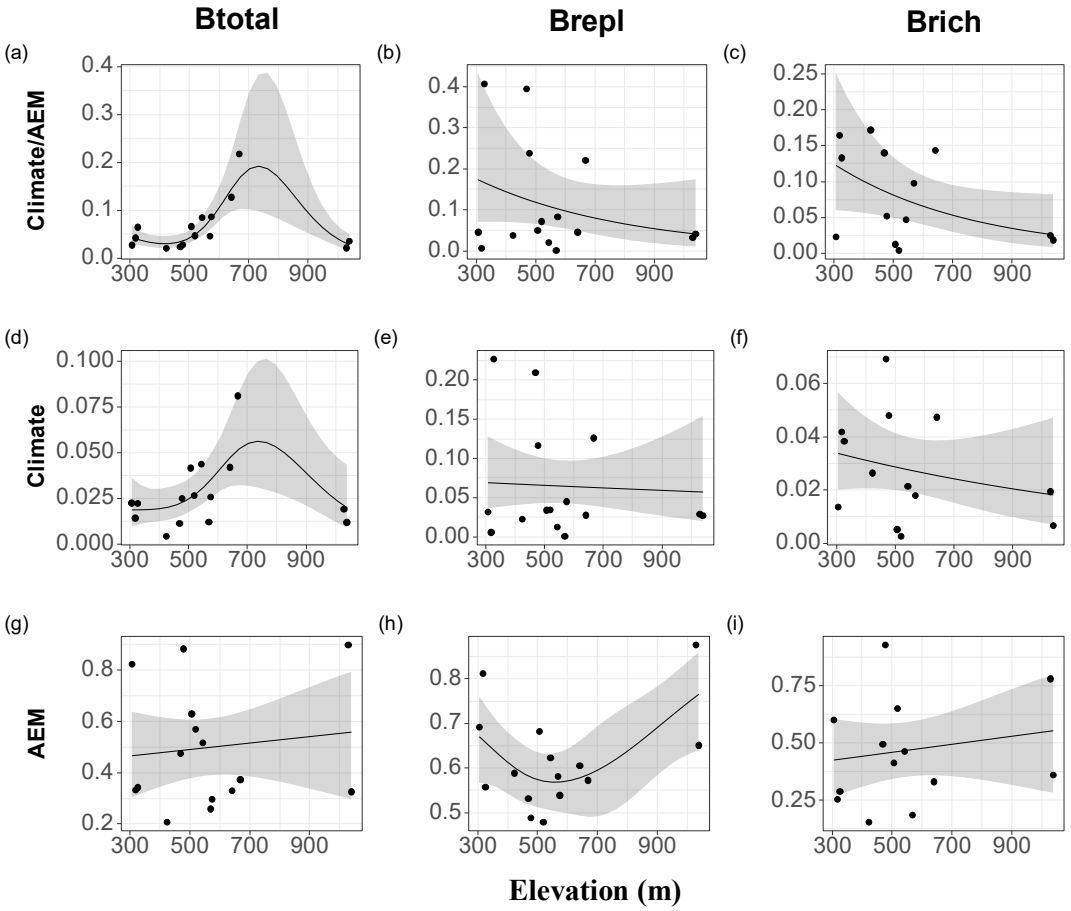

Figure 4. Elevation patterns of the relative importance of different ecological processes driving (a) temporal beta diversity (Btotal), (b) species replacement in temporal beta diversity (Brepl), and (c) richness difference in temporal beta diversity (Brich). Elevation patterns of the relative importance of climate driving (d) Btotal, (e) Brepl, and (f) Brich. Elevation patterns of the relative importance of AEM driving (g) Btotal, (h) Brepl, and (i) Brich.

4 Discussion

We examined the association between the spatial pattern of climate fluctuations and the geographic pattern of community dynamics to attempt to explore the influence of elevation and the relative importance of deterministic and stochastic processes in community dynamics. Our hypothesis that climate fluctuations increase with altitude is partially confirmed. The results show that temperature fluctuation increases with elevation, but that the elevation pattern of precipitation fluctuation is in the opposite direction. We also found that the main influence on community dynamics was determined by stochastic processes, and the importance of deterministic versus stochastic processes exhibited a single-peak pattern with elevation.

4.1 Spatial variation of community dynamics

Temporal beta diversity gradually declined with increasing elevation, suggesting that macroinvertebrate community fluctuations gradually decreased and community stability increased. A growing body of evidence suggested that as species richness increased, the community became more stable, which is an example of the "portfolio effect", where the stability of the community increases with diversity. This finding has been extensively supported by studies of the diversity-stability ratio (DSR) of ecosystems [31]. For instance, with increasing species richness, the temporal synchronization of populations in a community diminishes, indicating that the community became more resistant to fluctuations and became more stable [32]. However, our findings revealed a bimodal pattern of species richness, with no

discernible trend of increase with elevation. Elevational patterns of species richness demonstrated a diverse pattern as the study taxa and study area changed. However, differences in elevational gradients in this study precluded a complete demonstration of the bimodal pattern. The discrepancy in the results may be attributed to the influence of species abundance. Communities with greater abundance generally have fewer fluctuations in the community, and the distribution of population-abundance heterogeneity also impacts DSR [33,34].

The results of this study indicated that temporal beta diversity was primarily driven by species replacement, which is consistent with previous findings [35-37]. The frequent turnover of macroinvertebrate species may be attributed to the high temporal heterogeneity of the climate at the study site. Climate clearly played a crucial role in the worldwide distribution of biodiversity [38]. The region's pronounced environmental fluctuations have introduced novel temporal ecological niches for macroinvertebrates, thereby promoting local species survival and facilitating species turnover [36,37,39]. The rapid turnover observed among macroinvertebrates often coincided with changes in rare taxa [40-42], which are particularly sensitive and vulnerable to environmental fluctuations [43,44]. The frequency of species occurrence during the study period is detailed in Appendix S1. Additionally, macroinvertebrates possess unique life history responses and evolutionary strategies that allow them to exploit these temporal ecological niches, potentially leading to significant species turnover [37].

4.2 Inconsistent ecological processes across the landscape

The results revealed a single peak pattern regarding the relative importance of deterministic and stochastic processes in the community dynamics that we observed in our study area. With regard to total temporal beta diversity (Btotal), the significance of deterministic processes undergoes a process of increasing and then decreasing importance. In relation to the turnover component of the main driver of temporal beta diversity (Brepl), the significance of stochastic processes exhibited a decreasing and then increasing trend. This results may be closely related to climate fluctuations, which, when within the tolerance range of organisms, filter species more and more strongly as they are enhanced, leading to stronger and stronger effects on biotic communities [45]. Once a certain threshold is surpassed, heightened climatic fluctuations result in species mortality, thereby resetting the community and introducing stochastic processes such as stochastic colonization, which further underscores the importance of stochastic processes [46]. Our study suggested that stochastic and deterministic processes jointly influenced macroinvertebrate community dynamics. We found that stochastic processes were the main drivers of community dynamics. Whereas ecological niche theory highlights the influence of environmental filtering and species interactions on communities [47], this study supports the neutral theory. In our study, the time variable was the predominant factor driving the elevational patterns of macroinvertebrate community dynamics, this may be related to the scale of our study. Deterministic processes played an increasingly essential role as the scale of the study increased, as documented by the spatial and temporal distribution of biodiversity [48,49]. Our findings indicated that for Btotal, the ratio of deterministic to stochastic processes

305 followed a single-peaked model, similar to the behavior of the deterministic process.

306 The stochastic variables (AEMs in Appendix 1) were linked to stochastic
307 ecological processes that include fluctuations in species abundance and richness among
308 other characteristics. Temporary variation in species abundance can result in the
309 generation of temporal stochastic processes by failure to detect rare species.
310 Alternatively, sample sites with high total species numbers (temporal γ-diversity)
311 throughout the study period were less likely to collect rare species and those rare species
312 may not always be detected. However, our results suggested that the relative importance
313 of deterministic and stochastic processes in macroinvertebrate community dynamics
314 exhibited a single-peak pattern. This result was not surprising because biodiversity
315 elevational patterns vary greatly worldwide.

316 Frequent extreme climate events, such as droughts affecting our rivers, have
317 resulted in stochastic patterns of species extinction and colonization, albeit tempered
318 by ecosystem resilience. The frequency, intensity, and periodicity of these events,
319 including floods and droughts, significantly influence community dynamics [50]. These
320 disturbances disrupt macroinvertebrate communities from returning to their optimal
321 ecological niches, thereby reducing interspecific competition. Consequently, these
322 disruptions may manifest as an amplification of stochastic processes, obscuring their
323 spatial and temporal patterns. Community dynamics often exhibit temporal lags, where
324 gains or losses projected in a given year are influenced by the community's preceding
325 status. For example, population losses during unfavorable years may be compensated
326 by gains in more favorable periods, thereby altering expected community dynamics

[47].

5 Conclusions

Amid the current era of heightened global climate variability, analyzing the spatial trends of these fluctuations can offer valuable insights into the worldwide distribution of biodiversity, such as migrations to higher elevations in search of refuges. We believe that continued investigations will establish a solid theoretical basis for predicting the geographic spread of community dynamics influenced by diverse ecological processes amidst ongoing global transformations. Consequently, long-term biomonitoring remains essential, particularly in regions vulnerable to climatic variability, such as mountainous areas. Our findings emphasize the importance of distinguishing between temporal community dynamics and observed spatial variations to enhance local biodiversity management and conservation efforts across diverse landscapes.

For instance, shifts in community dynamics are intricately linked to changes in the frequency, intensity, and periodicity of extreme events, which exhibit spatial differentiation, including variations with elevation. Thus, further exploration of seasonal and cyclical fluctuations in climatic patterns could significantly enhance the predictability and effectiveness of regional conservation strategies through the implementation of locally tailored practices for biodiversity protection.

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