



Article

Environmental Factors Shape the Differences in Biodiversity-Area Relationships in Riverine Macroinvertebrates of Two Rivers in the Tibetan Plateau in China

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Abstract: The species-area relationship (SAR) is a well-established, globally recognized ecological pattern, and research on SAR has expanded to include the phylogenetic diversity-area relationship (PDAR). However, this research has generally been limited to terrestrial systems. Using data on freshwater macroinvertebrates, the log–log form of the SAR and PDAR power models were compared between the Lhasa River and the Niyang River on the Tibetan Plateau in China. The study reveals that there is a significant difference in the slopes of SAR and PDAR between the two rivers, with the Lhasa River having a considerably higher slope. The beta diversity calculations in these two basins support this pattern, with the Lhasa River exhibiting significantly higher numbers of species and greater total phylogenetic beta diversity than the Niyang River. Regarding species replacement, the turnover component was the primary driver of both species and phylogenetic beta diversity in both rivers. These differences in the beta diversity components were mainly driven by dispersal constraints because spatial distance had a large effect on total beta diversity and turnover fractions. In addition, the nestedness component was more affected by climate and land cover, indicating that highland rivers are subject to the threats of anthropogenic disturbance and climate change. Therefore, spatial factors play a crucial role in determining the distribution of passively dispersed benthic organisms as the scale of change in rivers increases from local to regional effects.

Keywords: headwater; macroinvertebrate; phylogenetic diversity; species-area relationships; phylogenetic diversity-area relationships; beta diversity



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1. Introduction

The study of species-area relationships (SARs) is closely linked to the study of the processes responsible for the generation, maintenance, protection, and loss of biodiversity. Exploration of patterns of biodiversity and their underlying mechanisms has been a central theme of research in ecology and biogeography [1,2]. The analysis of SAR has advanced our understanding of the mechanisms that drive the spatial scaling of species richness. SAR is commonly described by the power model, $S = c A^z$ [3], which is log–log-transformed for statistical utility $\log S = \log c + z \log A$. In general, z is the slope of the regression equation (i.e., the rate at which species richness increases as area increases) [4]. Because z values can indicate complex overall changes in community composition [5,6], they can be used to compare how community composition varies with scale in different regions and how they respond to environmental conditions. However, SAR may not be the optimal solution for elucidating patterns of spatial diversity, but it can serve as a first step in explaining differences in community structure across spatial scales.

As ecologists increasingly recognize that species richness is only one aspect of diversity, the study of SAR has been expanded to include phylogenetic diversity-area relationships (PDARs) [7,8]. Taxonomic diversity assumes that all species in a community are evolutionarily independent and ecologically equivalent [9]. However, this assumption is one-sided and ignores the fact that species are products of complex ecological and evolutionary processes [10]. Even if the number and richness of species increase or decrease, this may or may not affect the phylogenetic structure. Therefore, the incorporation of the phylogenetic diversity-area relationship into a study can be used to examine changes in the phylogenetic composition of species assemblages that occur as the area increases [11]. Moreover, phylogenetic diversity (PD) is more closely related to functional diversity [12,13]. The study of phylogenetic diversity-area relationships can provide information on the differential and complementary responses of species to environmental gradients. Larger z values indicate that phylogenetic diversity increases with area, possibly as a result of dispersal limitation or environmental filtering of certain clades. In contrast, lower z values indicate that most clades are present at smaller spatial scales. Therefore, relatively few clades are added as the area increases [6]. However, PDAR has been studied mostly in terrestrial systems [14–16] and rarely in freshwater investigations.

The biological significance of two parameters (c and z) for SAR models has attracted the interest of biogeographers and ecologists [15,17,18]. As c is the expected species per unit area, it can be considered a measure of α -diversity [4]. The z value is typically used by some authors as a measure of β -diversity [19–22]. However, the relationship between z values and β -diversity is controversial, in part because of the diverse definitions of β -diversity [4,23]. This article aims to clarify the biological significance of the z value by calculating beta diversity using the Sørensen index [24]. Beta diversity represents two distinct phenomena: turnover and nestedness [24]. Turnover implies the replacement of some species by others [25]. Contrary to turnover, nestedness of species assemblages refers to the fact that the biotas of sites with smaller numbers of species are subsets of the biotas at richer sites [26].

Beta diversity models help to reveal the processes that structure ecological communities. Deterministic processes based on ecological niche theory and stochastic processes based on neutrality theory are generally considered to be the two main ecological processes of community assembly [27]. According to the relative significance of the two processes, β -diversity should be related to environmental variability (i.e., habitat environmental conditions) and/or geographic proximity (dispersal constraints) [28,29]. The former implies that habitats with different environmental conditions have different community assemblages, and that the greater the environmental variability, the greater the resulting β -diversity. The latter suggests that if spatial variation in species composition is the result of spatiotemporal limitations on dispersal, then beta diversity should correlate more strongly with geographic distance than with environmental dissimilarity per se [30]. Likewise, there are differences in the relative importance of the ecological processes that drive the mechanisms underlying SAR. The relative importance of the mechanisms generating SAR can vary with increasing scales of dispersal (acting at small to intermediate scales), habitat diversity (mainly at intermediate scales), and speciation (mainly at the largest scales) [31–33].

Habitat types in SAR studies in freshwater SARs have mostly focused on lakes [34,35], ponds [36], and wetlands [37], and the taxonomic focus of the studies is more on fishes [38] than other aquatic organisms. In streams and rivers, fewer SAR studies are focused on taxonomic diversity [18]. The parameters of the log–log form of SAR can be influenced by both habitat characteristics and the biological characteristics of the organisms that are present [18]. Streams and rivers are among the most threatened ecosystems in the world [39] and therefore should be the subject of additional studies on this topic. Benthic macroinvertebrates, which are ecologically very important for stream biodiversity, should also not be overlooked as study organisms because they provide important ecological functions, including the transfer of nutrients and energy through the food web [40].

Unlike other freshwater organisms such as fish and algae, macroinvertebrates are highly sensitive to anthropogenic disturbance, and their community composition is strongly influenced by changes in river habitat and water quality. Consequently, they are often used to assess river ecological health and biodiversity [41–44]. Furthermore, spatial and temporal changes in benthic-macroinvertebrate species diversity represent the integration of ecological and evolutionary processes operating at different spatiotemporal scales [45]. Because of their wide range of habitats and life history strategies, benthic macroinvertebrates may be especially useful in elucidating the mechanisms that influence the spatial distribution of species.

To our knowledge, this is the first study to compare SAR and PDAR in riverine benthic macroinvertebrates. The objective of this study was to examine the impact of the area of different watersheds on the species and phylogenetic diversity of benthic macroinvertebrates. Our research questions examine (1) whether the slopes of the log–log form of the power SAR model of species richness and phylogenetic diversity differed between two rivers and (2) how spatial factors and environmental conditions in the two rivers affect the estimation of species richness and phylogenetic diversity.

2. Materials and Methods

2.1. Study Areas

This study was conducted in the Lhasa River and the Niyang River, two major tributaries of the Yalutsangpo River basin located along the southwest boundary of the Tibetan Plateau in China (Figure 1). The Yalutsangpo River has five tributaries, each with watersheds larger than 10,000 km². The Tibetan Plateau, often referred to as “The World’s Third Pole”, serves as a barrier area that is of ecological significance because it contains a unique high-altitude aquatic habitat with a distinct biota. Tibetan rivers have garnered increasing attention because of their ecosystem structure and function, which is susceptible to anthropogenic interference [46–48] and has high sensitivity to global climate change [49,50].

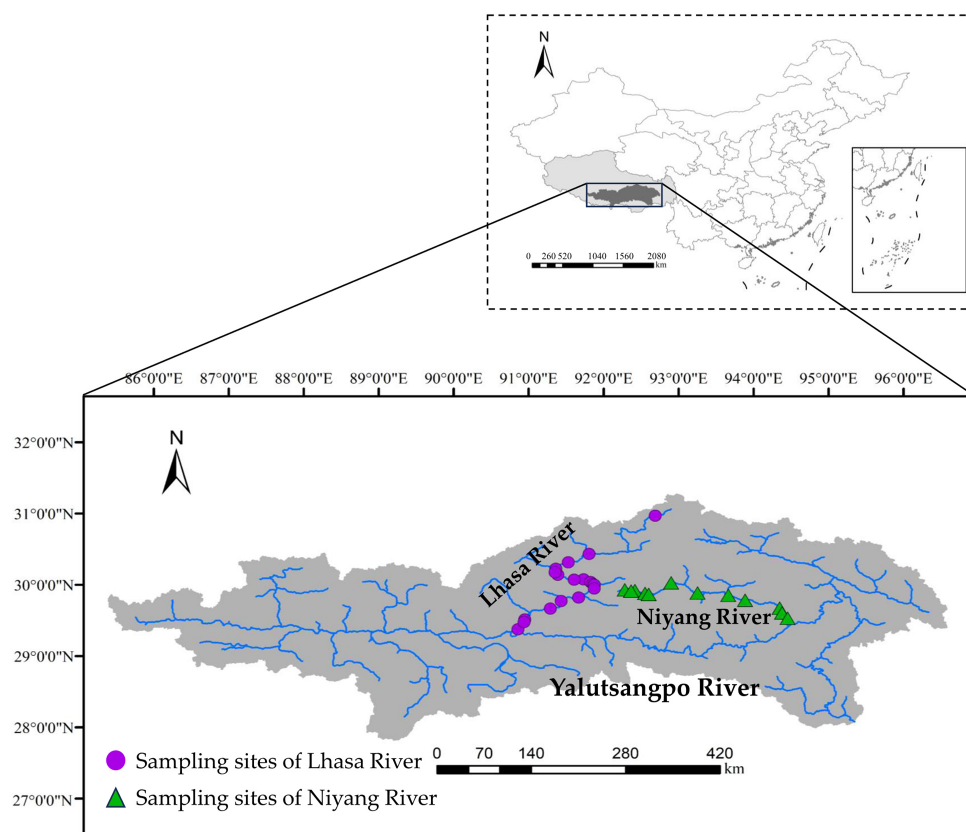


Figure 1. Sampling sites in the Lhasa River and the Niyang River in China.

The Lhasa River (29°20′–31°15′ N, 90°05′–93°20′ E), on the southwestern Tibetan Plateau and the left bank of the middle reaches of the Yalutsangpo River, is the largest tributary of the Yalutsangpo River. The average altitude of the Lhasa River is ~4812 m, with a total length of 551 km and a basin area of about 32,588 km², and it flows from northeast to southwest. Affected by factors related to the terrain, such as the Mira Mountains in the east, it is difficult for the humid water vapor of the Indian Ocean to reach the Lhasa River Basin. Consequently, the area belongs to the plateau temperate semi-arid monsoon climate zone, with an average annual temperature of ~5.3 °C and annual precipitation of ~460 mm [51,52].

The Niyang River (28°29′–30°30′ N, 92°10′–94°35′ E) is located in southeastern Tibet, i.e., the left bank of the middle and lower reaches of the Yalutsangpo River, with an average elevation of ~3274 m, a total length of 309 km, and a watershed area of about 17,535 km². It flows from northwest to southeast. The Niyang River originates from the glacial Lake Cuomuliangla, west of the Mila Mountains. The Niyang River is affected by the cold stream in the north and the warm stream of the Indian Ocean. This region belongs to the plateau humid temperate climate zone [53], with an average annual temperature of ~8.5 °C and an annual precipitation of ~1295 mm [54]. It primarily receives replenishment from precipitation, the melting of snow and glaciers, and underground water sources [53,54]. The Niyang River Basin is prone to many natural disasters, such as mudslides and floods.

Eighteen sampling sites were located in the Lhasa River and twelve sampling sites in the Niyang River (Figure 1). Sampling sites were distributed along the mainstem channel from upstream to downstream in both rivers. We used spatial scales within the entire drainage area upstream from a certain sampling site. The drainage area upstream of each sampling site was generated within ArcGIS by generating flow-direction and flow-accumulation grids from DEM data.

2.2. Data Information

We searched science databases for benthic macroinvertebrate records of the Lhasa and Niyang rivers. In all databases, we used the following search keywords: “aquatic insect*” or “benthic macroinvertebrate*” or “macroinvertebrate*” and “Yalutsangpo River*” or “Yarlung Zangbo River*” or “Yarlung Zangbo-Brahmaputra River*” or “Yarlung Zangbo*” or “Niyang River*” or “Lhasa River*” or “Palong Zangpo River*” or “Tibet Plateau*”. This resulted in discovering a total of 30 articles. In the 30 articles, we searched for study area and study species, resulting in 7 relevant research papers (including 2 articles in Chinese) [55–61] from which species inventories could be extracted for specific sample sites. We obtained benthic macroinvertebrate presence/absence data from tables, appendices, and associated databases cited. A complete list of included studies is presented in Supplementary Table S1. To account for differences in sampling effort and identification, reported abundances of all taxa were summarized at the highest possible taxonomic resolution for each reported sampling event, typically at the family level or higher (e.g., order, class, or phylum) [62,63]. This process systematizes the inventory of local species and their corresponding taxonomic levels but excluded synonyms of species reported.

Because of the absence of available phylogenetic trees for benthic macroinvertebrates of the Yalutsangpo River, we assessed phylogenetic diversity using path lengths between pairs of related species via standard Linnaean taxonomic ranks [12,64]. The position of species in taxonomic trees is often used as a powerful proxy for phylogenetic diversity studies [65–67]. This approach responds to their topological position in evolutionary trees and is closely related to diversity estimates based on temporally calibrated phylogenetic relationships [65,67].

2.3. Spatial and Environmental Factors

We used a method based on asymmetric eigenvector mapping (AEM) [68] to model the spatial process that was based on the upstream area above the sampling sites, which resulted in the generation of a series of spatial eigenvectors. AEM considers directionality, which can more accurately capture diffusion processes along the channel [69,70]. To perform

AEM, we first constructed a site-by-edge binary matrix based on the relative coordinates of the actual sample points in space and the directionality of their previous connections. Second, we assigned weights to each of the above edges based on the actual distance between the sample points (in this study, mainly the river distance between the sample points), which was further used to generate spatial eigenvectors through the R package “adespatial” [71]. We selected eigenvectors with positive spatial correlation as measured by Moran’s I statistic. Four positive spatial correlation eigenvectors were retained for the Lhasa River and designated as Vector 1 (V1), Vector 2 (V2), Vector 3 (V3), and Vector 4 (V4). The Niyang River also retains 4 positive spatial correlation eigenvectors which are Vector 1 (V1), Vector 2 (V2), Vector 3 (V3), and Vector 9 (V9).

We analyzed climate and land use data that can be linked to and used as indicators of hydrological factors (e.g., water quality and flow measurements) from the hydrological data available in all the articles because land use changes have been shown to cause changes in stream chemical processes, hydrology, geomorphology, and stream biology [72]. Temperature and precipitation are also closely related to climate and can affect streamflow and water temperature [73]. Climate data for each of the river site locations were extracted from the WorldClim database, which contains 19 bioclimatic datasets with long-term average temperature and precipitation data for the years 1970 to 2000 [74]. We used 11 temperature factors and 8 precipitation factors (specific information is in Supplementary Table S2). Land-cover information was obtained from the National Tibetan Plateau Science Data Center. We used 30 m surface coverage remote sensing images of the Tibetan Plateau to calculate land-cover information by delineating the watershed upstream of each sampling site [75]. Ten main types of land-use information were parsed for further analysis, i.e., farmland, forest, grassland, shrub, wetland, open water, tundra, urbanization, bare ground, and glacier (all measured in %).

2.4. Data Analysis

For PD, we used the R package “vegan” to calculate the interspecific classification distance [76]. Subsequently, this classification distance matrix was subjected to hierarchical clustering using the R package “stats” to generate a Linnaeus classification tree. For each river, we used the dendrogram to calculate the PD metric (including tree roots) using the “picante” R package [77].

We estimated the SAR and PDAR using the power (log–log) SAR model. The model uses the formula $\log S = \log c + z \log A$, where S can be either species richness (SR) or phylogenetic diversity (PD). We fitted a linear regression to the Lhasa River and the Niyang River separately. We used log₁₀-transformed species richness or PD as the response variable and log₁₀-transformed drainage area as the predictor at sampling sites. The power model was selected because it has been demonstrated to be the most widely used model with the best performance [3,78–81]. The model’s parameters also enable comparisons between studies and further biogeographic analysis [15,17]. Furthermore, because our objective was to compare the Lhasa River and the Niyang River species diversity-area relationships (SAR and PDAR), we used the simplest power law model to facilitate comparisons between the Lhasa and Niyang River species to test the difference between the z values of SAR and PDAR for the Lhasa River and the Niyang River species. Additionally, we used analysis of covariance (ANCOVA) to perform homogeneity tests, specifically examining the regression slopes between the two rivers.

We used the Sørensen dissimilarity coefficient to represent taxonomic and phylogenetic diversities (β_{sor}) and their turnover (β_{sim}) and nestedness (β_{sne}) components [24]. First, we calculated $SR\beta$ ($Sr\beta_{sor}$, $SR\beta_{sim}$, and $Sr\beta_{sne}$) based on the presence/absence data by using the R package “betapart” [82]. Second, we generated 3 phylogenetic dissimilarity matrices using taxonomic information of macroinvertebrates. The “betapart” package calculates phylogenetic beta diversities based on a taxonomic tree. To achieve this, the path to the root of the tree must be included in the calculations. Therefore, the R package “vegan” was used to calculate the interspecific taxonomic distances before the matrix was calculated.

Subsequently, the taxonomic distance matrix was subjected to a hierarchical clustering procedure using the R package “stats” to produce the Linnean taxonomic tree. Third, we obtained three $Pd\beta$ indices ($Pd\beta_{sor}$, $Pd\beta_{sim}$, and $Pd\beta_{sne}$) based on the aforementioned phylogenetic tree using the R package “betapart”. MNTD (mean nearest taxon distance) and MPD (mean pairwise distance) were calculated to delineate the differentiation among taxa within two communities. They are measures of phylogenetic beta diversity. We further tested for differences in mean $SR\beta$, $Pd\beta$, βMPD , and $\beta MNTD$ between the Lhasa River and the Niyang River using Wilcoxon rank-sum tests.

We used the generalized dissimilarity model (GDM) to investigate how environmental and spatial factors affect the spatiotemporal variations of benthic macroinvertebrate β -diversity. Compared with traditional linear models, this approach can better explain the nonlinear relationship between β -diversity and environmental and/or spatial variables [83]. Before determining the fit of GDMs and to avoid the effects of multicollinearity, the redundancy of the environmental variables was assessed using the R package “Hmisc” [84], and highly correlated (Spearman $\rho_2 > 0.7$) environmental variables were removed.

3. Results

3.1. Macroinvertebrate Community Composition

We found information on organisms from 4 phyla, 8 classes, 17 orders and 55 families in the two rivers (in Supplementary Table S1). There were 3 phyla, 6 classes, 13 orders, and 30 families in the Lhasa River, while there were 4 phyla, 8 classes, 14 orders and 46 families in the Niyang River.

3.2. Species- and Phylogenetic Diversity-Area Relationships

The log-transformed power law models of species richness and phylogenetic diversity were different between the Lhasa River and the Niyang River (Figure 2; Supplementary Table S3). Cumulative species richness in the Lhasa River increased from 9 to 30, and cumulative phylogenetic diversity increased from 220 to 638, with a concomitant increase in area (from 3632 to 11,315 km²). The Niyang River increased in cumulative species richness from 15 to 47 and cumulative phylogenetic diversity from 332 to 981, with an increase in watershed area (from 26 to 5219 km²). For both SAR and PDAR, the z values of the Lhasa River were significantly higher than those of the Niyang River (0.916 vs. 0.166 for SAR; 0.851 vs. 0.155 for PDAR). ANCOVA analyses showed that SAR and PDAR were significantly different between the two rivers ($p < 0.001$).

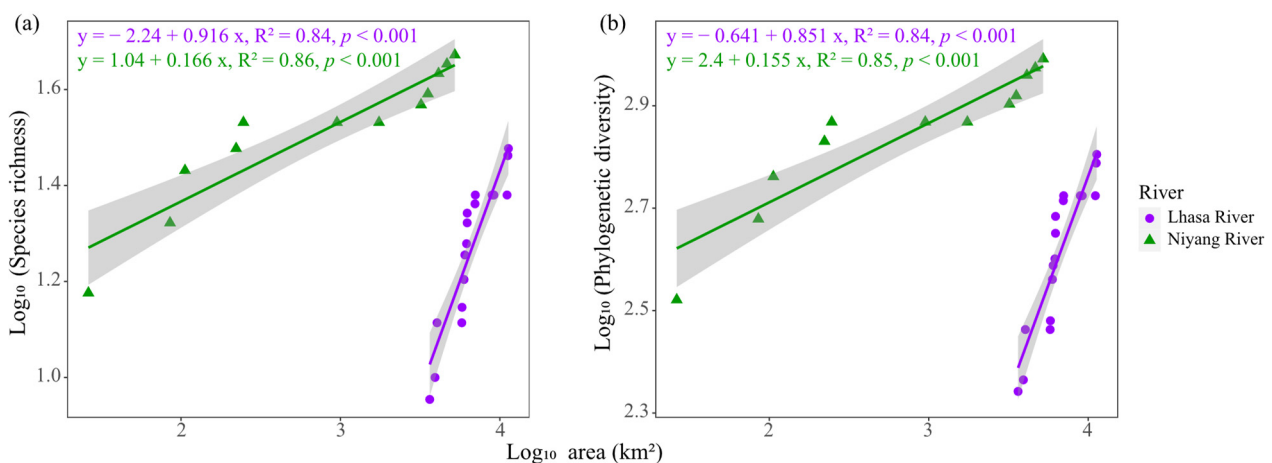


Figure 2. (a) Species- and (b) phylogenetic diversity-area relationships of Lhasa River and Niyang River in China. The shaded area indicates standard errors for the fitted values.

3.3. β -Diversity Values

Average values of species and phylogenetic β -diversity of benthic macroinvertebrates varied considerably between the two basins of the Lhasa River and the Niyang

River (Table 1; Figure 3). Macroinvertebrate assemblages in the Lhasa River and Niyang River showed greater variation in taxonomic composition (0.784 and 0.599, respectively) than they did in phylogenetic structure (0.587 and 0.499, respectively) among sites. The two dimensions of beta diversity in the Lhasa River and the Niyang River were mainly driven by turnover components. In the Lhasa River, the ratio of the turnover components to the total taxonomic and phylogenetic beta diversity was 88% and 75%, respectively. In the Niyang River, the ratio of the turnover components to the total taxonomic and phylogenetic beta diversity was 89% and 85%, respectively. In contrast, the contribution of nestedness components to overall beta diversity was relatively low. Specifically, in the Lhasa River and the Niyang River, the rates of species nestedness were 12% and 11%, while the rates of lineages were 25% and 15%, respectively.

Table 1. Macroinvertebrate β -diversity and its components (mean values) in Lhasa River and Niyang River.

	Lhasa River		Niyang River	
	Species	Phylogenetic	Species	Phylogenetic
Bsor	0.784 (100%)	0.587 (100%)	0.599 (100%)	0.499 (100%)
Bsim	0.688 (88%)	0.443 (75%)	0.534 (89%)	0.423 (85%)
Bsne	0.096 (12%)	0.144 (25%)	0.065 (11%)	0.076 (15%)

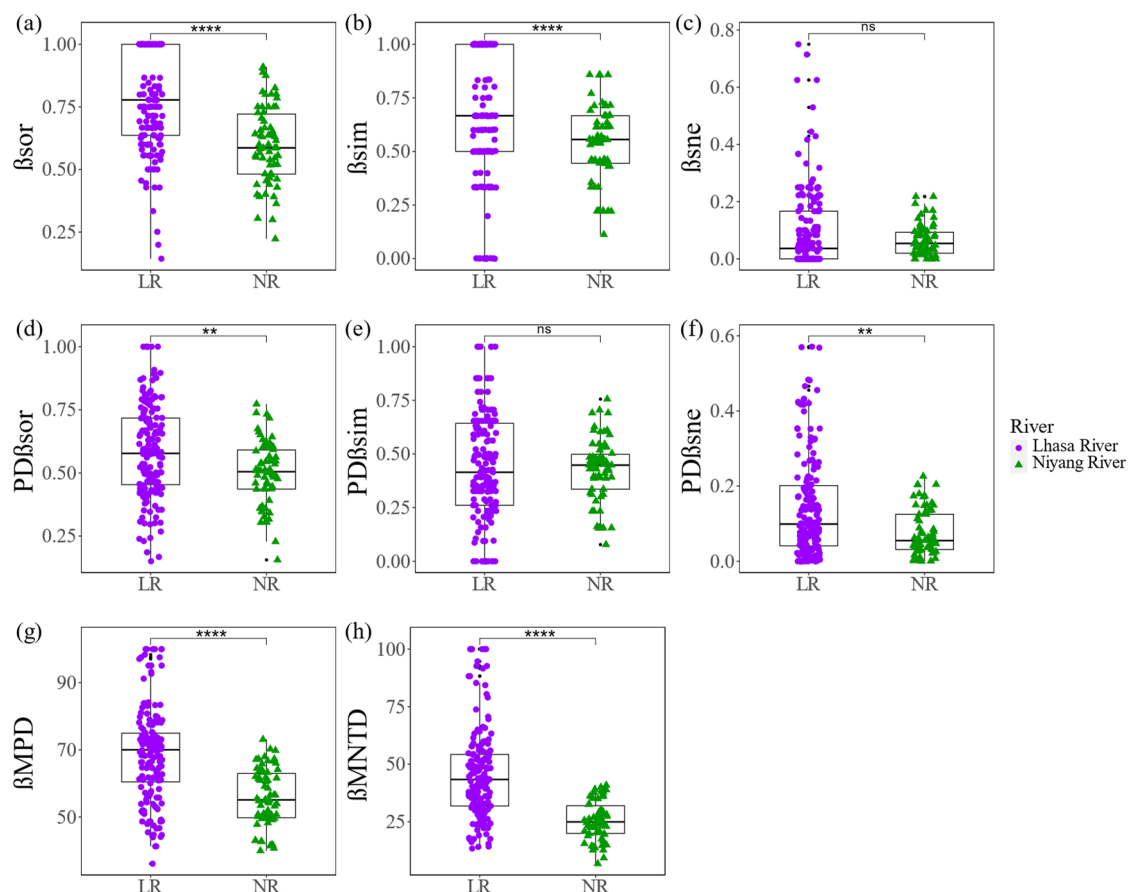


Figure 3. Benthic macroinvertebrate taxonomic ($Sr\beta_{sor}$, $Sr\beta_{sim}$, and $Sr\beta_{sne}$; (a–c)) and phylogenetic β -diversity components ($Pd\beta_{sor}$, $Pd\beta_{sim}$, $Pd\beta_{sne}$, β_{MPTD} , and β_{MNTD} ; (d–h)) in the Lhasa River and Niyang River basin. Notes: ns: $p > 0.05$; **: $p \leq 0.01$; ****: $p \leq 0.0001$.

Observed species total β -diversity ($Sr\beta_{sor}$) was significantly higher in the Lhasa River (mean $Sr\beta_{sor} = 0.784$) than in the Niyang River (mean $Sr\beta_{sor} = 0.599$) (Wilcoxon test

$p < 0.001$). Species turnover ($SR\beta_{sim}$) was significantly higher in the Lhasa River (mean $SR\beta_{sim} = 0.688$) than in the Niyang River (mean $SR\beta_{sim} = 0.534$) (Wilcoxon test $p < 0.001$), but species nestedness components were not significantly different between the Lhasa River and Niyang River. Observed total phylogenetic β -diversity ($Pd\beta_{sor}$) was significantly higher in the Lhasa River (mean $Pd\beta_{sor} = 0.587$) than in the Niyang River (mean $Pd\beta_{sor} = 0.499$) (Wilcoxon test $p < 0.01$), and the phylogenetic nestedness components ($Pd\beta_{sne}$) were significantly higher in the Lhasa River (mean $Pd\beta_{sne} = 0.144$) than in the Niyang River (mean $Pd\beta_{sne} = 0.076$) (Wilcoxon test $p < 0.01$). The phylogenetic turnover components were not significantly different between the Lhasa River and the Niyang River. Phylogenetic heterogeneity between the two watersheds was likewise significantly different. The mean of all observed phylogenetic distances between occurrences in the two communities was significantly higher in the Lhasa River (mean $\beta MPD = 68.747$) than in the Niyang River (mean $\beta MPD = 55.779$) (Wilcoxon test $p < 0.001$). The mean of phylogenetic distances between closely related species in the two communities was significantly higher in the Lhasa River (mean $\beta MNTD = 45.767$) than in the Niyang River (mean $\beta MNTD = 25.621$) (Wilcoxon test $p < 0.001$).

3.4. Key Drivers of Beta Diversity and Its Components

Generally, different sets of variables were considered to have important effects on the values of $SR\beta$ and $PD\beta$ of benthic macroinvertebrate community structure (Table 2; Figure 4). Five spatial factors (elevation, V1, V2, V3, and V4), seven climatic factors (AMT, MDR, TS, TAR, AP, PWM, and PS), and six land-use factors (farmland, woodland, shrubland, open water, urbanization, and glacier) were selected in the Lhasa River as the key factors for benthic communities. Five spatial factors (elevation, V1, V2, V3, and V9), six climatic factors (AMT, MDR, ISO, AP, PDM, and PDQ), and four land-use factors (farmland, open water, urbanization, and glacier) were selected as key factors for benthic communities in the Niyang River. The generalized dissimilarity models showed that the variation of beta diversity explained by the selected factors ranged from 12.29% to 28.26% in the Lhasa River and from 16.3 to 28.75% in the Niyang River.

Table 2. Statistical results of the generalized dissimilarity models for benthic macroinvertebrate communities in the Lhasa River and Niyang River basin using two types of eigenfunction-based models.

Position	Metrics	Pure Spatial	Pure Climatic	Pure Land Cover	Shared
Lhasa River	$Sr\beta_{sor}$	22.15	1.6	0	1.25
	$SR\beta_{sim}$	23.99	1.76	0	1.16
	$Sr\beta_{sne}$	1.71	2.79	3.21	2.52
	$Pd\beta_{sor}$	22.82	1.65	0.6	2.08
	$Pd\beta_{sim}$	20.69	1.58	0.05	1.58
	$Pd\beta_{sne}$	1.77	4.43	3.51	1.27
Niyang River	$Sr\beta_{sor}$	8.11	3.48	0.07	5.89
	$SR\beta_{sim}$	9.17	1.86	0.41	6.85
	$Sr\beta_{sne}$	10.62	2.2	1.09	0.24
	$Pd\beta_{sor}$	3.68	3.74	0.14	2.2
	$Pd\beta_{sim}$	4.95	4.22	0.15	3.35
	$Pd\beta_{sne}$	5.18	3.67	15.09	0.99

Spatial factors had a greater effect than climate on total beta diversity and turnover components of beta diversity of species and phylogenetic diversity in the Lhasa River and Niyang River. Land-cover factors had minimal or almost no effect. For the nestedness components of β -diversity, climate, and land cover had a greater effect than spatial factors on species and phylogenetic diversity in the Lhasa River. In the Niyang River, spatial factors had a greater effect on species than climate and land cover, while land cover had a greater effect on phylogenetic diversity than spatial factors. Climate had the least effect.

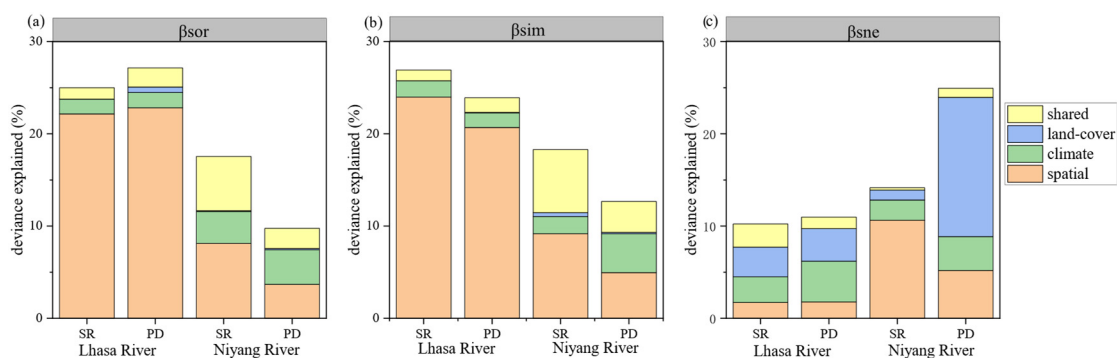


Figure 4. Color-coded presentation of the relative role of spatial, climatic, and land-cover factors in structuring benthic macroinvertebrate communities' taxonomic and phylogenetic β -diversity phenomena (a) and their turnover, (b) and their nestedness (c) components in Lhasa River and Niyang River. Variations in each β -diversity phenomenon comprise four parts: pure spatial effects, pure climatic effects, pure land-cover effects, and their shared effects.

4. Discussion

Cumulative SAR and PDAR were both significantly positively correlated in the Lhasa River and the Niyang River, with steeper slopes for species and lineages being found in the Lhasa River. The significant difference in slopes indicated that species richness increased faster in the Lhasa River than in the Niyang River as the watershed area increased in size and scale. Phylogenetic diversity-area relationships provided additional information to that found using the traditional SAR values.

Phylogenetic diversity-area relationships, like observed SAR, differed between the Lhasa River and the Niyang River. This suggests that the Lhasa River and the Niyang River species respond differently to processes that influence the PD of their assemblages. This suggests that, as the watershed area increases, phylogenetic diversity in the Lhasa River is increasing faster than in the Niyang River, and the phylogenetic structure of the Lhasa River is more diverse than that of the Niyang River.

Our results showed that the total β -diversity of both species and phylogeny in the Lhasa River was significantly higher than that in the Niyang River. This suggests that the species and lineages among the sample sites in the Lhasa River differed from those in the Niyang River. Species β -diversity in the Lhasa River and the Niyang River differed significantly mainly in the turnover component, and the SR β_{sim} was significantly higher in the Lhasa River than in the Niyang River. The significant difference in the SR β_{sim} suggests that the Lhasa River has a higher turnover of species and that species are more heterogeneously distributed among the sample sites. This is also evident in that the SAR slope is steeper in the Lhasa River and that species richness changes more rapidly with increasing scale.

The results of the Lhasa and Niyang River analyses indicate that species distributions are strongly influenced by spatial distance. Changes in species composition can be caused by dispersal constraints imposed by the distance per se [85], which highlights the critical influence of neutral processes that construct communities [86]. In addition, spatial distance is often associated with differences in environmental variables that are also responsible for species composition turnover [87,88].

The phylogenetic β -diversity of the Lhasa River and the Niyang River differed significantly mainly in the nestedness components, and the Pd β_{sne} of the Lhasa River being significantly higher than that of the Niyang River. The significant difference in the Pd β_{sne} suggests that the variation in the formation/disappearance of lineage branches caused by the increase or decrease in taxa of a small number in the Lhasa River was higher than that in the Niyang River. The observed value of the Pd β_{sne} explains why the slope of the PDAR of the Lhasa River was significantly higher than that of the Niyang River. Comparing the phylogenetic heterogeneity between the Lhasa River and the Niyang River, the β MPD and

the β MNTD in the Lhasa River were significantly higher than those values in the Niyang River. There were greater differences in species and phylogenetic compositions between the Lhasa River communities. Specifically, the species in the Lhasa River were found to be more distantly related compared to the Niyang River, which had more closely related species.

Analyses of the nestedness components of phylogenetic diversity in the two catchments examined indicate a high degree of land use and climate effects between them. This may be related to wider changes geographically in that Tibet is severely affected by climate change and is currently experiencing among the fastest increases in mean temperature outside the northern and southern poles [89]. Consequently, the region is experiencing rapid changes in natural vegetation, human land use [90], permafrost degradation, glacier shrinkage and/or disappearance, and changes in river hydrology [91,92].

Glacier retreat promotes the upstream dispersal of downstream taxa, with the ultimate extinction of specialists, leading to increase nestedness in assemblage components [93–95]. This could have a significant effect on the Niyang River, as it receives some of its water from melting glaciers [96]. In addition, human pressures can reduce species turnover by reducing the distribution of small-range species and expanding the distribution of large-range species [97].

Significant land conversion has already taken place in the Lhasa River Basin. Over 90% of the original grasslands and sparse vegetation have been converted to urban areas near Lhasa City, construction of large hydropower stations in the middle reaches, and afforestation projects in the river floodplains [49,98]. Habitat conversion may lead to a high proportion of species loss in a small number of sites within a region, which can result in increased nestedness assemblages.

We found that $SR\beta$ and $PD\beta$ of benthic macroinvertebrates in the Lhasa River and the Niyang River were mainly determined by turnover. This result is consistent with studies in alpine streams [55]. This suggests that the turnover of species and lineages may play a more important role in the variation of the composition of benthic macroinvertebrates in the two basins than the net loss (or gain) from the nestedness of species and lineages. Total species β was significantly higher than total phylogenetic β for all benthic macroinvertebrates, suggesting that phylogeny tends to be redundant when species turnover occurs between communities. The dominant turnover of $SR\beta$ and $PD\beta$ may be related to the larger environmental gradient in which the Lhasa and Niyang Rivers are situated. The rivers studied, being located on the Tibetan Plateau, have large elevation gradients, complex river morphology, and topographic heterogeneity. These factors may lead to strong dispersal constraints and biogeographic effects [99,100] that support rapid species and lineage turnover.

In our study results, the spatial factor of distance explains a higher proportion of the total beta, as well as the turnover component, of the Lhasa and Niyang Rivers. The concept of metacommunities indicates that communities are typically connected through dispersal [2]. Several studies have demonstrated that spatial factors are linked to the dispersal processes of organisms and are crucial in determining the patterns of benthic macroinvertebrate communities at large scales [8,49,101,102]. Furthermore, dispersal constraints may facilitate the formation of new species over evolutionary timeframes by hindering gene flow between populations in separate streams. This, in turn, may promote increases in β -diversity [86]. However, the three sets of predictor variables (space, climate, and land cover) had relatively low explanatory rates in that residuals ranged from 71.25% to 87.71%, indicating that community changes may be influenced by various unconsidered variables, such as biotic interactions, sedimentation, and topography [103–105].

5. Conclusions

Our findings highlight that variations in species turnover and phylogenetic diversity can be driven by dispersal constraints and unique geographic features. These results provide possible strategies for conserving rivers with complex ecosystem structures. For example, advocating for contemporary conservation strategies aimed at preserving diverse

habitat assemblages, such as those found in the Tibetan Plateau, can help safeguard the unique ecological features and species diversity present in these regions. Because the Lhasa River and the Niyang River have positive slopes for SAR and PDAR, high total beta diversity and major turnover components, both rivers have high species and phylogenetic heterogeneity. This suggests that most of the sample sites in the two rivers had relatively unique species assemblages and phylogenetic structures, and that the diverse habitats of the two watersheds are appropriate targets for conservation efforts [106]. Spatial factors are important drivers of species distributions of passively dispersed benthic macroinvertebrates. Species in our study area and throughout the Tibetan Plateau are limited by dispersal and geographic barriers, which can result in an uneven distribution of species within the catchment.

The spatial prioritization of river conservation sites is currently an area of active research. In this study, the loss or gain of biodiversity within communities was linked to climate. Because the headwaters of highland rivers are glacier-fed and contain unique species, the impact of climate change on glacier-endemic species is likely to be greater. Therefore, the headwaters of these two watersheds should be prioritized for conservation efforts. Finally, it is important to consider the impact of land use practices that result in habitat fragmentation on biodiversity when deciding on the most appropriate environmental management approaches to use.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/w16060882/s1>, Table S1: Taxonomic information of macroinvertebrate species; Table S2: Climatic variables of the Lhasa River and the Niyang River; Table S3: Slopes of SARs and PDARs for the Lhasa River and the Niyang River.

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