



# The role of environmental conditions, climatic factors and spatial processes in driving multiple facets of stream macroinvertebrate beta diversity in a climatically heterogeneous mountain region

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## ABSTRACT

There is a growing recognition that examining patterns of ecological communities and their underlying determinants is not only feasible based on taxonomic data, but also functional and phylogenetic approaches. This is because these additional facets can enhance the understanding of the relative contribution of multiple processes in shaping biodiversity. However, few studies have focused on multifaceted beta diversities in lotic macroinvertebrates, especially when considering driving factors operating at multiple spatial scales. Here, we examined the spatial patterns of multi-faceted (i.e., taxonomic, functional and phylogenetic) beta diversity and their components (i.e., turnover and nestedness) of macroinvertebrates in 50 sites in 10 streams situated in the north and south slope of the Qinling Mountains, the geographical dividing line of Northern and Southern China. We found that the streams draining the north slope showed significantly lower values of beta diversity based on all three facets than the streams draining the south slope. Such north-to-south increases of beta diversity were caused by the distinct climatic and local environmental conditions between the sides of the mountain range. Moreover, spatial variables generally played the most important role in structuring all facets and components of beta diversity, followed by local environmental and climatic variables, whereas catchment variables were less important. Despite the similar results of relative contribution of explanatory variables on each beta diversity facet, the details of community-environment relationships (e.g., important explanatory variables and explanatory power) were distinct among different diversity facets and their components. In conclusion, measuring functional and phylogenetic beta diversity provides complementary information to traditional taxonomic approach. Therefore, an integrative approach embracing multiple facets of diversity can better reveal the mechanisms shaping biodiversity, which is essential in assessing and valuing aquatic ecosystems for biodiversity management and conservation.

## 1. Introduction

Understanding the driving mechanisms of biodiversity variation has long been one of the hot topics in ecology and biogeography. Traditionally, a large number of studies based on species identities have been conducted to examine variation in community composition in specific regions throughout the world (Bo et al., 2020; Leibold et al., 2004; Magurran, 2013). However, the shortcomings of species-based approaches have been recognized recently, as they treat species as

equivalent units and neglect the differences in evolutionary relationships and functional traits between species (Flynn et al., 2011; Magurran, 2013; Saito et al., 2015). Therefore, an increasing number of recent studies have examined ecological communities in the light of multiple facets of biodiversity, i.e., using taxonomic, functional and phylogenetic approaches (D'agata et al., 2014; Heino and Tolonen, 2017; Li et al., 2020; Sobral et al., 2016). Integrating functional and phylogenetic information into community ecology frameworks provides valuable additional information on the roles of ecological and evolutionary

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processes in shaping community composition (Safi et al., 2011; Winter et al., 2009).

Functional diversity is a measure involving the value and range of species traits that influence their performance and that affect ecosystem functioning (Mason et al., 2005; Villéger et al., 2008). Because the effects of environmental filtering on species are mediated by traits (i.e., biological, ecological and morpho-behavioral characteristics), it is generally assumed that functional diversity shows a stronger association with environmental variations compared with taxonomic diversity (Diaz and Cabido, 2001; Verberk et al., 2013). Distinguishing the effects of multiple scales of driving forces (e.g., local environmental conditions, landscape features and climatic factors) on functional trait composition can enhance our understanding of the assembly mechanisms of biotic communities (Lindholm et al., 2020; McGill et al., 2006).

The importance of phylogenetic diversity is also increasingly highlighted in current biodiversity research, as it represents the evolutionary history of species coexisting within a community and reflects the diversity of a complex set of intrinsic (e.g., morphological, physiological and reproductive) and extrinsic (e.g., behavioral, growth and environmental tolerance) traits (Graham and Fine, 2008; Webb et al., 2002). As species identities within a community largely depend on evolutionary history, characterizing phylogenetic diversity can be used to identify the adaptations of species in a community to generate new evolutionary responses to cope with changing environmental conditions (Morlon et al., 2011; Ricklefs, 1987). Furthermore, considering that species traits may be conserved across the phylogeny, phylogenetic diversity has been regarded as an overall proxy measure of the functional characteristics of ecological communities and can thus account for unmeasured functional diversity (Sol et al., 2017; Winter et al., 2013).

Beta diversity, measuring the heterogeneity in community composition between localities, has gradually evolved to be a central issue in biodiversity studies (Anderson et al., 2011; Whittaker, 1972). Recently, ecologists proposed that partitioning overall beta diversity into the turnover and nestedness-resultant components can further reveal driving mechanisms of biodiversity patterns across large spatial and temporal scales (Baselga, 2010; Carvalho et al., 2012; Podani and Schmera, 2011). The turnover component reflects the species replacement linked to environmental filtering, as well as spatial and historical constraints (Qian et al., 2005), whereas the nestedness-resultant component derives from the non-random process of species loss (or gain) along environmental gradients (Gaston and Blackburn, 2000). Despite the earlier studies of beta diversity focused on the taxonomic dimension, beta diversity patterns can also be measured based on functional and phylogenetic data (Cardoso et al., 2014). According to evidence from some recent studies, phylogenetic and functional diversities were usually not coincident with taxonomic diversity and the three facets of beta diversity also responded to distinct ecological drivers (Cai et al., 2019; Heino and Tolonen, 2017; Rocha et al., 2018). For instance, Heino and Tolonen (2017) found that taxonomic beta diversity of boreal lake macroinvertebrates was driven by environmental variation and spatial distance, whereas functional and phylogenetic composition were only weakly related to environmental variation.

Riverine networks are hierarchically structured systems and, hence, lotic biodiversity patterns are generally structured by multi-scale spatial (i.e., local environmental conditions, catchment features and climatic condition) and temporal features (Poff et al., 2010; Townsend et al., 2003). Many previous studies have shown that (1) at local scale, water chemistry (e.g., nutrient concentrations) and physical (e.g., current velocity, substrate) conditions were important in structuring stream biodiversity patterns (Beisel et al., 2000; Jiang et al., 2010); (2) at catchment scale, land cover and land use characteristics, have been demonstrated to be correlated with lotic communities (Allan, 2004; Townsend et al., 2003); (3) at regional scale, climatic factors (e.g., temperature and rainfall) also have a significant influence on lotic biodiversity (Lawrence et al., 2010; Miserendino et al., 2018). In addition, according to the metacommunity concept (Leibold et al., 2004),

spatial processes and environmental conditions jointly affect community composition (Heino et al., 2015), as environmental filters can only act once individuals have been able to disperse to a new location (Kärnä et al., 2015). However, surprisingly few studies have simultaneously examined the relative importance of multi-scale environmental (i.e., local environmental, catchment and climatic) features and spatial variables for beta diversity patterns of lotic macroinvertebrates based on all the three facets (Rocha et al., 2018).

In the present study, we selected 50 sites in 10 streams situated in the north and south slope of the Qinling Mountains, aiming to (1) compare the patterns of multi-faceted beta diversity (i.e., taxonomic, functional and phylogenetic) and their components (i.e., turnover and nestedness) of stream macroinvertebrates between the north slope and the south slope; (2) disentangle the relative contribution of multi-scale environmental (i.e., local environmental, catchment and climatic) factors and spatial variables in shaping multiple facets of beta diversity of stream macroinvertebrates. These streams were located at the geographical boundary between northern China and southern China, thus providing an ideal opportunity to understand the mechanisms of biodiversity maintenance in a subtropical biodiversity hotspot. We specifically tested the following hypotheses: (1) the beta diversity patterns would be distinct between the north slope and the south slope streams, due to significant physicochemical and climatic differences between these sides of the mountains. Particularly, we expected a higher level of beta diversity based on all three facets in the south slope streams than in the north slope streams. (2) Local environmental, catchment and climatic variables, as well as spatial variables should contribute importantly but differently to variations in different facets of beta diversity. Specifically, functional and phylogenetic beta diversity should be less affected by spatial factors (Heino and Tolonen, 2017), but should be more influenced by environmental variables, due to the trait-environment relationships (Poff et al., 2010).

## 2. Materials and methods

### 2.1. Study area and macroinvertebrate sampling

This study was based on a dataset collected from 50 mountainous stream sites (i.e., 10 streams  $\times$  5 sites per stream) respectively situated in the north and south sides of the Qinling Mountains, the geographical boundary between northern China and southern China and the watershed between the Yangtze River and the Yellow River (Fig. 1). As the geographical dividing line of northern China and southern China, the Qinling Mountains have long been considered among the biodiversity hotspots in the world and have thus attracted continuing attention by ecologists (Tang et al., 2006; Zhang, 1979). There were five streams located in the Weihe River (the largest tributary of the Yellow River) Basin and five streams in the Hanjiang River (the largest tributary of Yangtze River) Basin, respectively. The five streams (i.e., Luofu, Shidi, Bahe, Heihe, Shitou) of the Weihe River Basin (WRB) are situated in the northern Qinling Mountains and experience a semi-humid temperate monsoon environment, whereas the remaining five streams (i.e., Xushui, Jinshui, Yuehe, Xunhe, Jiqian Rivers) of the Hanjiang River Basin (HRB) located in the south slope of Qinling Mountains and experience a humid subtropical monsoonal environment. At each stream, five mainstem sites were selected based on the following criterion: they should represent different habitat conditions and broadly evenly distributed from upstream to downstream of stream.

Macroinvertebrates were sampled during April and May in 2018 from the 50 sites in the 10 streams. At each site, we took five quantitative samples using a Surber net (0.09 m<sup>2</sup>, net mesh size 450  $\mu$ m), separately from most typical habitats along a river reach of ca. 100 m. The typical habitats usually comprised riffles and pools at each sampling reach, and represented principal substrate conditions (e.g., cobbles, boulders and pebbles). Specimens were hand-picked from the sediment on a white porcelain plate, and were later stored and preserved in 70%

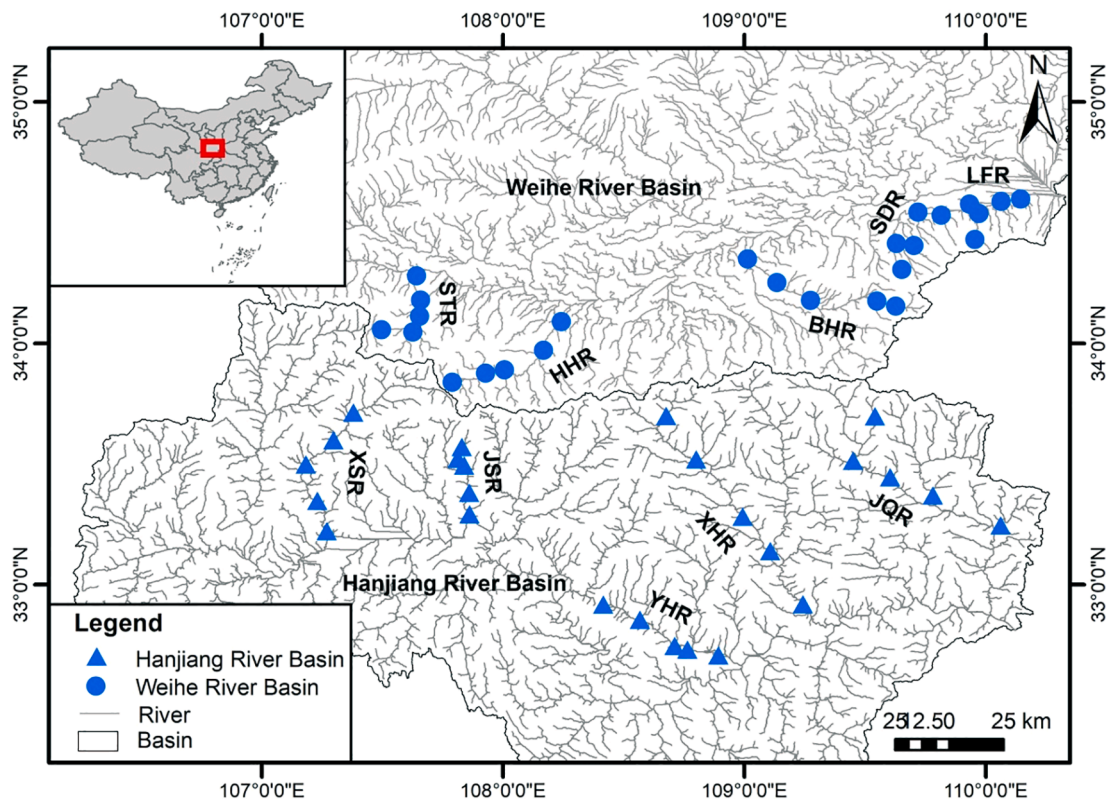


Fig. 1. Location of the streams and the sampling sites in the Weihe and Hanjiang Rivers Basins. XSR-Xushui River, JSR-Jinshui River, YHR-Yuehe River, XHR-Xunhe River, JQR-Jiqian River, LFR-Luofu River, SDR-Shidi River, BHR-Bahe River, HHR-Heihe River, STR-Shitou River.

ethanol. Macroinvertebrates were identified to the lowest taxonomic level (usually genus or species) where possible in the laboratory, according to the relevant references (Brinkhurst, 1986; Dudgeon, 1999; Epler, 2001; Morse et al., 1994; Zhou et al., 2003) and then counted.

## 2.2. Macroinvertebrate trait and taxonomic information

We selected 13 functional traits for macroinvertebrates species: voltinism, occurrence in drift, maximum crawling rate, swimming ability, attachment, armoring, shape, respiration, size at maturity, rheophily, thermal preference, habit, and trophic habit. These traits have been proved to be key traits responding sensitively to various environmental gradients in the studied region (Li et al., 2019). The trait information of macroinvertebrate species were obtained mainly from published literature sources (Morse et al., 1994; Poff et al., 2006; Usseglio-Polatera et al., 2000), and then the 13 trait groups were divided into 43 categories (Supplementary files: Table S1).

Due to the absence of true phylogenetic data for all macroinvertebrate taxa, we used taxonomic distance based on the path lengths in the Linnean taxonomic trees as a proxy for true phylogeny. This approach has been used in many macroinvertebrate studies involving phylogenetic diversity (e.g. Heino and Tolonen, 2017; Li et al., 2020; Rocha et al., 2018). This taxonomic tree included six taxonomic levels: species, genus, family, order, class, and phylum. Taxonomic information for each higher taxon was checked using an online database (www.fauna-europea.org).

## 2.3. Local environmental variables

At each site surveyed, a set of local physical and chemical variables were measured after macroinvertebrate sampling. Water temperature (WT), pH, dissolved oxygen (DO), electrical conductivity (Cond) and total dissolved solids (TDS) were measured using a multi-parameter

water quality sonde (YSI 556Pro). Water depth and current velocity (measured in the middle of the sampling location with a FP111 flowmeter) were averaged from 7 to 10 equal cross-stream transect along a 100 m reach. Turbidity was measured in nephelometric turbidity unit using portable turbidity Orbeco-Hellige 996 m. Water samples were collected to quantify the total amounts of nitrogen (TN), ammonium ( $\text{NH}_4\text{-N}$ ), nitrate ( $\text{NO}_3\text{-N}$ ), nitrite ( $\text{NO}_2\text{-N}$ ), total phosphorus (TP) and Chlorophyll *a* (*Chl-a*) in the laboratory, according to the standard Chinese analytical methods (Huang et al., 1999).

## 2.4. Catchment variables

We measured catchment-scale land use variables, i.e. the percentages of seven different land use types (forest, agriculture, shrub, grassland, urbanization, open water, and "others") at each site using Arc GIS 10.3. We delineated the sub-watershed of each site using the soil and water assessment tool (SWAT) based on a 30 m resolution digital elevation model (DEM, <http://www.cnrc.cn/>). The outputs were converted to a catchment polygon for each sampling site, which included the entire drainage area upstream of the site. For each sub-watershed, land use data used included available remote sensing images of Landsat images, Sentinel 2 and ASTER. Then the images were then interpreted and expressed as percentage of seven principal land use types.

## 2.5. Climatic variables

We used elevation and long-term temperature and precipitation data extracted from the WorldClim database (resolution ~ 1 km) as climatic factors in the present study. Following the bioclim framework proposed by Hijmans et al. (2005), the long-term climatic information were subsequently processed into 19 bioclimatic (including 11 temperature and 8 precipitation) variables.

## 2.6. Spatial variables

The spatial variables were obtained by means of an eigenfunction analysis using principal coordinates of neighbor matrices (PCNM, [Borcard and Legendre, 2002](#)) based on horizontal overland (Euclidean) distances among sites. We had to rely on Euclidean overland distances because the two main river basins are not connected by watercourses. Also, in many previous stream studies, the results based on overland and watercourses distances have been similar for macroinvertebrate communities (e.g. [Kärnä et al., 2015](#)). The PCNM represents the spatial configuration of sample units using principal coordinates of a truncated (nearest neighbors only) among sites distance matrix and the principal coordinates with positive eigenvalues were retained as spatial variables in the subsequent analyses ([Gilbert and Bennett, 2010](#)). PCNMs with high eigenvalues represent small-scale geographical/spatial patterns, and low eigenvalues represent broad-scale geographical/spatial patterns in species distributions. We used the “pcnm” function from the *vegan* software package in R ([R Development Core team, 2020](#)) to generate the spatial PCNM axes, and retained 28 PCNM axes (PCNM1–PCNM28) with positive eigenvalues.

## 2.7. Data analysis

### 2.7.1. Calculation of different facets of beta diversity

We calculated three facets of total beta diversity (i.e., taxonomic, functional and phylogenetic) of macroinvertebrate assemblages, each decomposed into the turnover and nestedness-resultant components. The turnover component accounts for dissimilarity immune to nestedness-resultant richness variation between assemblages, while the nestedness reflects dissimilarity caused by nestedness-resultant richness differences between assemblages ([Baselga, 2010, 2012](#)).

Firstly, we generated three dissimilarity matrices based on macroinvertebrate species-by-site data using the function “beta.pair” in the R package *betapart* ([Baselga et al., 2018](#)). This function produces three dissimilarity matrices: overall dissimilarity (Sorensen index, beta.sor), turnover (Simpson index, beta.sim) and nestedness (beta.sne).

Secondly, we calculated three functional dissimilarity matrices based on trait data according to the method proposed by [Villéger et al. \(2013\)](#). Before calculating these functional dissimilarity matrices, we calculate trait distances between taxa with the Gower distance ([Gower, 1971](#)) using the function “gowdis” in package *FD* ([Laliberté et al., 2014](#)), and generated principal coordinates analysis (PCoA) trait vectors using the function “cmdscale” from the package *stats*. The first two PCoA vectors were used in the calculation of convex hull volumes shaping any two communities in functional space. The Mantel test showed a high correlation ( $r = 0.89$ ,  $p < 0.001$ ) between the Euclidean distances based on the first two PCoA components and the overall Gower distance matrix. Then, three functional dissimilarity matrices (i.e., functional Sorensen, Simpson and nested-resultant) were obtained using the function “functional.beta.pair” from the R package *betapart* ([Baselga et al., 2018](#)).

Thirdly, we generated three phylogenetic dissimilarity matrices as functional beta diversity, but now based on taxonomic information as proxy for phylogeny. Before calculating phylogenetic beta diversity, between-species taxonomic distance was calculated using the function “taxa2dist” in the package *vegan* ([Oksanen et al., 2019](#)). Further, the species-by-species distance matrix was used to calculate phylogenetic vectors based on the function “cmdscale” from the package *stats*. Similar to calculation of functional beta diversity, the first two phylogenetic PCoA vectors were used. The Euclidean distance matrix based on the two PCoA vectors was also strongly correlated with the original taxonomic distance matrix (Mantel  $r = 0.84$ ,  $p < 0.001$ ). Finally, three phylogenetic dissimilarity matrices (i.e. phylogenetic Sorensen, Simpson and nested-resultant) were produced based on the PCoA components and the site-by-species matrix using the function “functional.beta.pair”.

### 2.7.2. Statistical analysis

We first examined the relationships between dissimilarities based on different beta diversity facets (i.e., taxonomic, functional and phylogenetic) using Pearson coefficient-based Mantel tests on 999 permutations ([Nekola and White, 1999](#)). Permutational analysis of variance (PERMANOVA) (PERMANOVA, [Anderson, 2014](#)) was applied to test the differences of community structure among the two regions (north slope vs. south slope) and among streams (10 streams) based on the different facets and their components. In addition, permutational analysis of multivariate dispersions (PERMDISP, [Anderson, 2006](#)) was carried out to examine whether the multifaceted community compositional heterogeneity varied between the two regions. Both the statistical testing in the context of PERMANOVA and PERMDISP analyses were performed using a permutations test with 999 iterations.

Finally, we utilized distance-based redundancy analysis (dbRDA) ([Legendre and Anderson, 1999](#)) and associated variation partitioning procedures ([Legendre and Legendre, 1998](#)) to examine the relationships between different biological dissimilarities and the four sets of explanatory variables (i.e., local environmental, catchment, climatic and spatial variables). Prior to dbRDA, highly correlated independent variables (Pearson’s  $r > 0.80$ ) from each set of explanatory variables were removed, and the remaining ones were  $\log(x + 1)$  transformed if they violated normality assumption. Forward selection procedure was conducted to select the final sets of local environmental, catchment, climatic and spatial variables using the function “ordiR2step” (999 permutations) in the R package *vegan*. Variation partitioning was utilized to reveal pure and shared effects of different sets of explanatory variables to variation in each beta diversity facet and component. The dbRDA and variation partitioning were run using the function “capscale” and function “varpart” in the R package *vegan*, respectively. All analyses were conducted in R ([R Development Core team, 2020](#)).

## 3. Results

Local environmental, catchment and climatic variables exhibited considerable variation across the 50 stream sites ([Table 1](#)). For local environmental variables, the stream sites in the south slope showed significantly higher values of conductivity, pH, total nitrogen and nitrate but lower values of water temperature, turbidity and ammonium than sites in the north slope. The catchment variables differed slightly between the two groups of sites, with higher percentage of urban, grassland and others sites in the north slope ([Table 1](#)). Most climatic variables showed significant differences between the two site groups. In general, the sites in the north slope had lower values of temperature- and precipitation-related factors ([Table 1](#)).

Average between-site dissimilarities of macroinvertebrate assemblages varied considerably among the three facets across the studied streams ([Table S2](#)). For taxonomic beta diversity, the mean pairwise dissimilarities were 0.774 (SD = 0.144) for the Sorensen index, 0.662 (SD = 0.185) for the Simpson index, and 0.112 (SD = 0.110) for the nestedness-resultant index. The mean relative contribution of the turnover and nestedness-resultant components to overall dissimilarity was 85.0% and 15.0%, respectively ([Table S2](#)). For the functional and phylogenetic beta diversity, overall dissimilarity and its two components were much lower than species-based diversity, with mean values  $< 0.4$  for three indices of functional facet and  $< 0.2$  for phylogenetic facet ([Table S2](#)). Moreover, unlike the dominance of the turnover component over nestedness for taxonomic beta diversity, the functional and phylogenetic overall dissimilarities (Beta.sor) were both mainly contributed by the nestedness-resultant components (Beta.sne), which accounted for 65.7% and 88.0% of functional and phylogenetic overall dissimilarities, respectively ([Table S2](#)). Taxonomic, functional, and phylogenetic pairwise dissimilarities were often significantly, yet typically weakly correlated ([Fig. 2](#)). The Mantel correlations between taxonomic dissimilarities and functional dissimilarities were moderate (Mantel  $r$  range from 0.377 to 0.551, [Fig. 2 a-c](#)), but the other

**Table 1**

Mean values ± SD of local environmental, catchment and climatic variables in the studies stream sites. Results of independent-sample t-tests between sites in the Weihe River Basin (WRB) and the Hanjiang River Basin (HRB) are also shown. Those p-values < 0.05 are bolded. N.S. = not significant. \* denotes variables entered into the db-RDA models.

	WRB	HRB	t	P
<b>Local environmental</b>				
* Water temperature (°C)	15.5 ± 3.5	17.5 ± 4.6	<b>-1.988</b>	<b>0.040</b>
* Current velocity (m/s)	0.71 ± 0.32	0.54 ± 0.43	1.638	N.S.
* Water depth (m)	0.19 ± 0.03	0.18 ± 0.04	1.117	N.S.
* Dissolved oxygen (mg/L)	9.25 ± 0.53	9.15 ± 1.02	0.423	N.S.
* pH	8.14 ± 0.40	7.60 ± 0.20	<b>5.950</b>	<b>&lt;</b>
* Conductivity (µs/cm)	334.9 ± 268.2	179.1 ± 69.2	<b>2.813</b>	<b>0.009</b>
* Turbidity (NTU)	11.81 ± 13.40	38.63 ± 50.80	<b>-2.553</b>	<b>0.017</b>
Total nitrogen (mg/L)	3.289 ± 1.234	2.245 ± 0.440	<b>3.822</b>	<b>0.001</b>
* Ammonium (mg/L)	0.711 ± 0.446	0.988 ± 0.349	<b>-2.451</b>	<b>0.018</b>
* Nitrate (mg/L)	2.160 ± 1.117	0.870 ± 0.503	<b>5.266</b>	<b>&lt;</b>
* Nitrite (mg/L)	0.122 ± 0.152	0.081 ± 0.062	1.244	N.S.
* Total phosphorus (mg/L)	0.036 ± 0.028	0.028 ± 0.032	0.988	N.S.
* Chlorophyll a (mg/L)	6.174 ± 7.286	5.231 ± 3.372	0.587	N.S.
<b>Catchment</b>				
* % Agriculture	13.4 ± 16.2	12.2 ± 12.0	0.298	N.S.
* % Forest	59.2 ± 15.2	60.4 ± 14.9	-0.288	N.S.
* % Urban	0.7 ± 0.8	0.2 ± 0.2	<b>3.009</b>	<b>0.006</b>
* % Shrub	20.9 ± 9.2	25.4 ± 7.2	-1.921	N.S.
* % Grassland	2.8 ± 3.5	0.5 ± 0.5	<b>3.252</b>	<b>0.003</b>
* % Water	0.2 ± 0.2	0.3 ± 0.2	0.346	N.S.
* % Others	2.7 ± 3.3	1.0 ± 1.0	<b>2.504</b>	<b>0.016</b>
<b>Climatic</b>				
Altitude	618.5 ± 312.4	563.2 ± 267.7	0.671	N.S.
* Annual Mean Temperature	12.0 ± 1.9	13.3 ± 1.9	<b>-2.363</b>	<b>0.022</b>
Mean Diurnal Range	10.4 ± 0.8	9.6 ± 0.5	<b>4.729</b>	<b>&lt;</b>
* Isothermality	29.6 ± 1.3	30.2 ± 1.5	-1.393	N.S.
Temperature Seasonality	912.6 ± 73.0	816.9 ± 38.3	<b>5.803</b>	<b>&lt;</b>
Max Temperature of Warmest Month	28.8 ± 3.1	28.5 ± 2.3	0.424	N.S.
* Min Temperature of Coldest Month	-6.7 ± 0.8	-3.3 ± 1.8	<b>-8.564</b>	<b>&lt;</b>
* Temperature Annual Range	35.5 ± 2.7	31.7 ± 1.0	<b>6.561</b>	<b>&lt;</b>
Mean Temperature of Wettest Quarter	6.1 ± 1.7	7.3 ± 1.8	-0.643	N.S.
Mean Temperature of Driest Quarter	0.4 ± 1.2	3.0 ± 1.6	<b>-6.559</b>	<b>&lt;</b>
Mean Temperature of Warmest Quarter	21.7 ± 2.6	22.2 ± 2.4	-0.300	N.S.
Mean Temperature of Coldest Quarter	0.4 ± 1.2	3.0 ± 1.6	<b>-6.559</b>	<b>&lt;</b>
* Annual Precipitation	651.7 ± 51.1	813.2 ± 50.5	<b>-11.23</b>	<b>&lt;</b>
Precipitation of Wettest Month	116.3 ± 10.1	147.0 ± 8.7	<b>-11.54</b>	<b>&lt;</b>
Precipitation of Driest Month	6.1 ± 1.4	7.3 ± 1.5	<b>-2.924</b>	<b>0.005</b>
* Precipitation Seasonality	71.5 ± 2.2	71.1 ± 3.1	0.510	N.S.
Precipitation of Wettest Quarter	322.8 ± 28.5	392.6 ± 21.1	<b>-9.837</b>	<b>&lt;</b>
* Precipitation of Driest Quarter	22.8 ± 3.2	28.2 ± 5.1	<b>-4.485</b>	<b>&lt;</b>
			<b>-11.04</b>	<b>0.001</b>

**Table 1 (continued)**

	WRB	HRB	t	P
Precipitation of Warmest Quarter	279.5 ± 23.1	348.3 ± 20.9		<b>&lt;</b>
Precipitation of Coldest Quarter	22.8 ± 3.2	28.2 ± 5.1	<b>-4.485</b>	<b>&lt;</b>
				<b>0.001</b>

correlations were quite low ( $r < 0.260$ ).

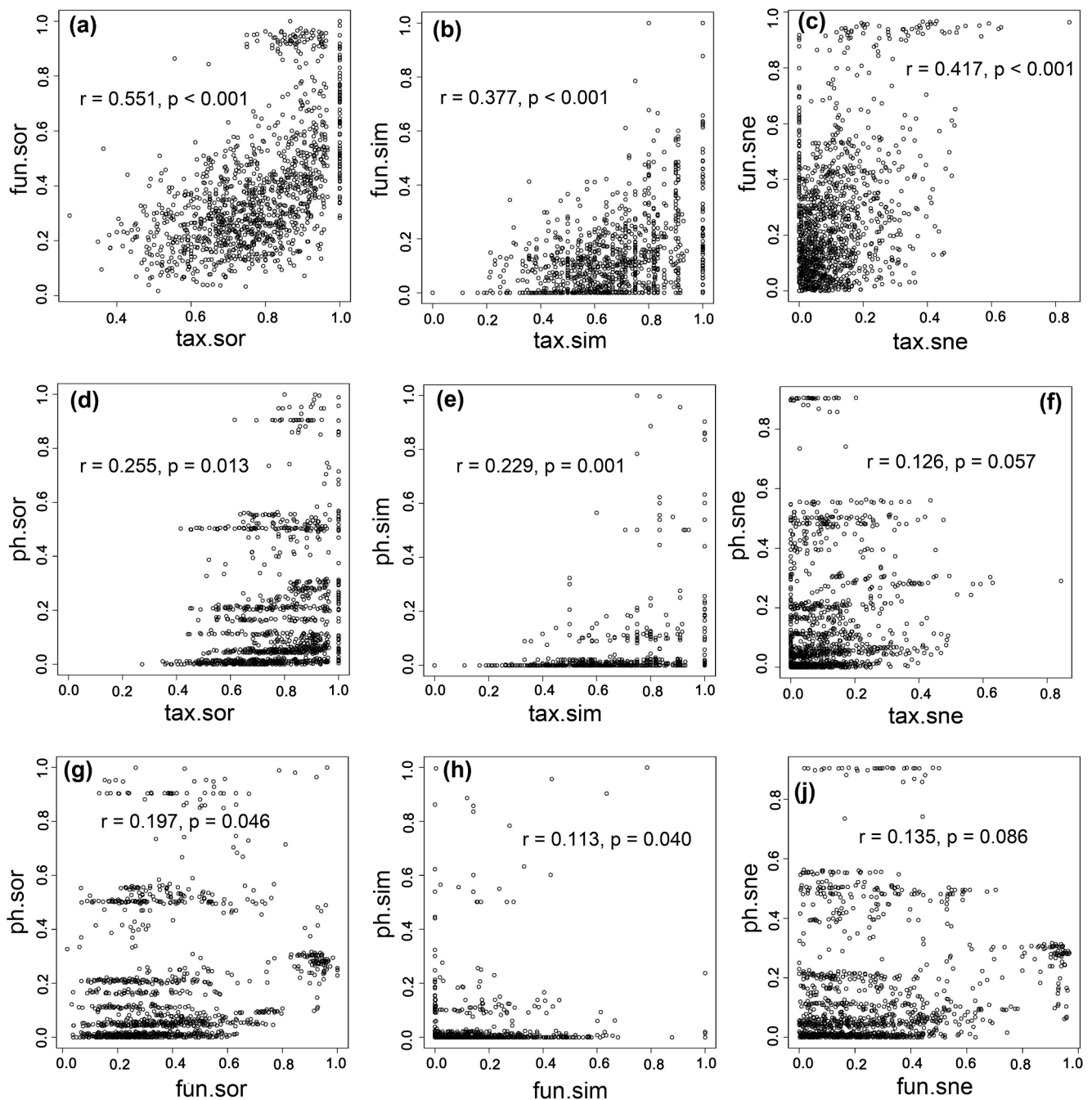
PERMANOVA indicated that macroinvertebrate communities differed significantly between the two regions (north slope vs. south slope) and among streams for taxonomic composition (all  $p < 0.05$  for taxonomic beta diversity and its two components) (Table 2). However, for functional and phylogenetic compositions, the effects of regions and streams were generally not significant ( $p > 0.05$ ), except being significant sources of variation for functional overall dissimilarity (fun.sor) and the nestedness-resultant component (fun.sne) (Table 2).

According to PERMDISP, we detected significant or marginally significant differences of taxonomic and functional community heterogeneity (overall beta diversity and its two components) between streams in the north slope and the south slope (Table 3). Specifically, south slope communities were more heterogeneous (with higher average distance to the group centroid) than north slope communities from both taxonomic and functional perspectives. Nevertheless, for phylogenetic beta diversity, average distance to the group centroid for the overall dissimilarity and the two components did not differ significantly between the north slope and the south slope (Table 3). We also directly compared the values of the three facets of pairwise beta diversity between the north slope streams and the south slope streams. The northern streams usually showed significantly lower diversity than the southern streams for most pairwise dissimilarities, expect for taxonomic turnover, phylogenetic overall dissimilarity and nestedness (Supplementary files, Fig. S1). In general, the functional and taxonomic dissimilarities showed larger differences between northern and southern streams compared with phylogenetic dissimilarities.

According to the results of dbRDA, different sets of variables were selected for each component of dissimilarity (i.e. Beta.sor, Beta.sim and Beta.sne) among three diversity facets. Variables in the local, catchment, climate and spatial sets were all selected as key factors in the forward selection procedure. At the local environmental scale, the selected significant variables mostly denoted variation in current velocity, water temperature and water chemistry (e.g. NO<sub>3</sub>-N, conductivity). Among the catchment variables, variation in urban and forest cover were typically included in the set of key variables. For the climatic variables, those related to variation in temperature and precipitation were typically included in the models. Among spatial variables, the first 8 PCNM filters (i.e., denoting relatively broad-scale spatial variation) were usually identified as important in structuring taxonomic, functional and phylogenetic beta diversity (see more details of the significant variables and adjusted R<sup>2</sup> values in the forward selection in Tables S3–S5).

Variation partitioning revealed that local environmental conditions, catchment land-use, climatic factors and spatial variables all played important roles in structuring beta diversity patterns, but their relative contributions varied among the three diversity (i.e., taxonomic, functional and phylogenetic) facets (Fig. 3). The total amount of explained variations in the three facets of beta diversity and their components ranged from 17% to 52%. For the taxonomic beta diversity, the total variation explained by the models was 38% for Beta.sor, 52% for Beta.sim, and 44% for Beta.sne, respectively (Fig. 3a, d, h). For functional beta diversity, the total variation explained including all predictors was 24% for Beta.sor, 21% for Beta.sim, and 31% for Beta.sne, respectively (Fig. 3b, e, i). Models including all predictor variables explained 17%, 51%, and 20% of variation in phylogenetic Beta.sor, Beta.sim and Beta.sne, respectively (Fig. 3c, f, j).

For the unique fractions, the unique contributions of spatial (statistically significant in all 9 models, range from 5% to 18%), local



**Fig. 2.** Correlations between different facets (i.e., taxonomic, functional, and phylogenetic) dissimilarity matrices. Pearson correlation ( $r$ ) and significance ( $p$  value) of Mantel tests are also given.

environmental (statistically significant in 8 models, range from 2% to 20%) and climatic (statistically significant in 7 models, range from 6% to 17%) variables generally accounted for the considerably large fractions of variation explained in the three facets of beta diversity and their components (Fig. 3). Among the 9 variation partitioning models, 6 dissimilarities, including taxonomic Beta.sim, all 3 functional dissimilarities and phylogenetic Beta.sor and Beta.sne were best explained by pure effects of spatial variables, 2 dissimilarities (taxonomic Beta.sor and phylogenetic Beta.sim) were best explained by local environmental variables, and 1 dissimilarity matrix (taxonomic Beta.sne) was best explained by climatic variables (Fig. 3). Catchment variables explained minor, but statistically significant fractions of variation in taxonomic Beta.sor and taxonomic Beta.sne. For the fractions representing shared effects (i.e., variation explained by  $> 2$  sets of variables), the shared

fraction jointly explained by local environmental, climatic and spatial variables were large in the models of three taxonomic dissimilarities, and functional Beta.sor and Beta.sne, while other shared fractions were generally small.

#### 4. Discussion

We found high total taxonomic beta diversity of macroinvertebrates ( $>75\%$  dissimilarity on average) among the stream sites surveyed, but quite low average values of the total functional ( $<40\%$  dissimilarity) and total phylogenetic ( $<20\%$  dissimilarity) beta diversity. This suggests that although the taxonomic composition of macroinvertebrate assemblages is highly different among the stream sites, the functional and phylogenetic compositions vary little between most site pairs. Such a

**Table 2**

Results of permutational analysis of variance (PERMANOVA) for testing average differences in the macroinvertebrate communities between the regions (north slope vs south slope) and between the 10 streams, based on the three beta diversity facets (i.e., taxonomic, functional and phylogenetic). P-values < 0.05 are bolded.

Source	df	SS	MS	Pseudo-F	P(perm)
Tax.sor					
Region	1	19,562	19,562	7.106	<b>0.001</b>
Stream	9	62,192	6910.2	3.088	<b>0.001</b>
Tax.sim					
Region	1	24,089	24,089	12.604	<b>0.001</b>
Stream	9	55,048	6116.4	4.025	<b>0.001</b>
Tax.sne					
Region	1	13,875	13,875	3.650	<b>0.001</b>
Stream	9	42,725	4747.3	1.236	<b>0.016</b>
Fun.sor					
Region	1	2811.6	2811.6	2.970	<b>0.011</b>
Stream	9	15,548	1727.5	2.113	<b>0.002</b>
Fun.sim					
Region	1	390.36	390.36	2.321	0.308
Stream	9	143.68	15.964	0.077	0.816
Fun.sne					
Region	1	1250.8	1250.8	2.032	0.181
Stream	9	12,030	1336.7	2.848	<b>0.007</b>
Ph.sor					
Region	1	485.7	485.7	1.122	0.362
Stream	9	2626.3	291.81	0.626	0.942
Ph.sim					
Region	1	519.56	519.56	10.607	0.178
Stream	9	43,241	4804.5	1.005	0.464
Ph.sne					
Region	1	3544.8	3544.8	0.939	0.683
Stream	9	31,287	3476.3	0.906	0.813

**Table 3**

Permutational analysis of multivariate dispersions (PERMDISP) showing average values and SE of distances to the group centroid based on the three beta diversity facets (i.e., taxonomic, functional and phylogenetic) between streams in the north slope and the south slope.

	Average	SE	Model Stats
Tax.sor			
North	44.304	2.346	F = 7.441, p = <b>0.019</b>
South	52.511	1.925	
Tax.sim			
North	35.815	2.876	F = 2.707, p = 0.111
South	41.919	2.389	
Tax.sne			
North	61.366	1.182	F = 2.164, p = 0.141
South	58.852	1.235	
Fun.sor			
North	20.710	1.755	F = 5.819, p = <b>0.041</b>
South	30.940	3.861	
Fun.sim			
North	6.620	1.115	F = 1.580, p = 0.143
South	9.950	2.364	
Fun.sne			
North	14.532	1.732	F = 5.789, p = <b>0.044</b>
South	24.282	3.664	
Ph.sor			
North	12.135	2.759	F = 0.118, p = 0.833
South	13.698	3.614	
Ph.sim			
North	2.902	1.306	F = 0.939, p = 0.507
South	5.055	1.797	
Ph.sne			
North	14.078	3.346	F = 0.308, p = 0.759
South	11.942	1.904	

finding is in accordance with a few similar macroinvertebrate studies (Heino and Tolonen, 2017; Rocha et al., 2019), which also reported much lower functional and phylogenetic dissimilarities compared with taxonomic dissimilarity. In most of studied sites, taxa from functionally

and phylogenetically distant classes, e.g., aquatic insects (Insecta), crustaceans (Malacostraca), worms (Oligochaeta) and free-living flatworms (Turbellaria), generally occurred together. Thus, a large proportion of functional traits and branch lengths of the phylogenetic tree were shared among different sites, resulting in low levels of functional and phylogenetic dissimilarities between sites, on average. In contrast to the dominance of taxonomic turnover over taxonomic nestedness-resultant component, functional and phylogenetic beta diversities were mainly contributed by the nestedness-resultant component (both > 65%), indicating a strong difference in functional and phylogenetic richness (Villéger et al., 2013; Zhang et al., 2019). The minor macroinvertebrate classes, e.g., leeches (Hirudinea), snails (Gastropoda), mussels (Bivalvia), and mites (Arachnida) only occurred at a part of sampling sites, leading to the higher nestedness-resultant than turnover component both for the functional and phylogenetic facets.

In addition, we found quite weak correlations between different dimensions of beta diversity, suggesting that taxonomic, functional and phylogenetic beta diversity offer distinct information of variation in community composition (Heino and Tolonen, 2017). Such results highlight the need of measuring functional and phylogenetic diversity in biodiversity studies, as they provide complementary information to that provided by taxonomy only (Devictor et al., 2010).

The streams in the north slope of Qinling Mountain (WRB) showed lower values of beta diversity based on all three facets compared with the south slope streams (HRB). For lotic macroinvertebrates, climatic factors generally exert indirect effects via influencing in-stream water physico-chemistry and hydrology. For instance, changes in air temperature could influence the life history features and spatio-temporal distribution of aquatic organisms indirectly through their effect on water temperature (Li et al., 2012). Similarly, variation in precipitation significantly affects flow regimes in rivers and streams, which may further regulate the composition of lotic communities (Doretto et al., 2020; Piano et al., 2020; Rocha et al., 2018). Therefore, the distinct beta diversities between the streams in the north slope and the streams in the south slope can be attributed to their significantly different climatic and local environmental conditions.

We found that spatial variables were generally the most important in structuring the three facets of beta diversity and their components, followed by local environmental and climatic variables, whereas catchment variables were less important. Our findings are slightly different from a recent lotic macroinvertebrate study in boreal streams (Rocha et al., 2018), which highlighted that local environmental factors were the most important, followed by spatial variables, for macroinvertebrate communities. The differences may be due to the distinct climatic patterns, geomorphic features and environmental conditions between the two studied regions (i.e., boreal in Rocha et al.'s study vs subtropical in this study). Due to the harsh environmental conditions and ice age history, boreal streams usually tend to support more common taxa with high dispersal ability, which lead to a stronger effect of environmental filtering than spatial process (Heino et al., 2018; Siqueira et al., 2020). In contrast, in the studied streams located at transitional zone between warm temperate and subtropics, there were more rare species with low abundance and poor dispersal ability (Li et al., 2020), resulting in a greater influence of dispersal limitation (i.e., spatial process) than environmental filtering. In addition, the Qinling Mountains, as the geographical dividing line of northern China and southern China, are a large barrier for the spread of species and thus influence ecological communities (Tang et al., 2006; Zhang, 1979). The riverine networks in mountainous and hilly regions provide many unique niches for the macroinvertebrate species, but simultaneously limit the free dispersal of species across sites. As a result, the distribution ranges of relic species and evolutionarily young species are relatively small in this region, forming specific species composition and phylogenetic structure in some sub-regions or habitat types (Zhang, 1979). In a few recent studies, spatial factors (e.g., those related to dispersal limitation) played an important role in structuring not only species composition but also trait

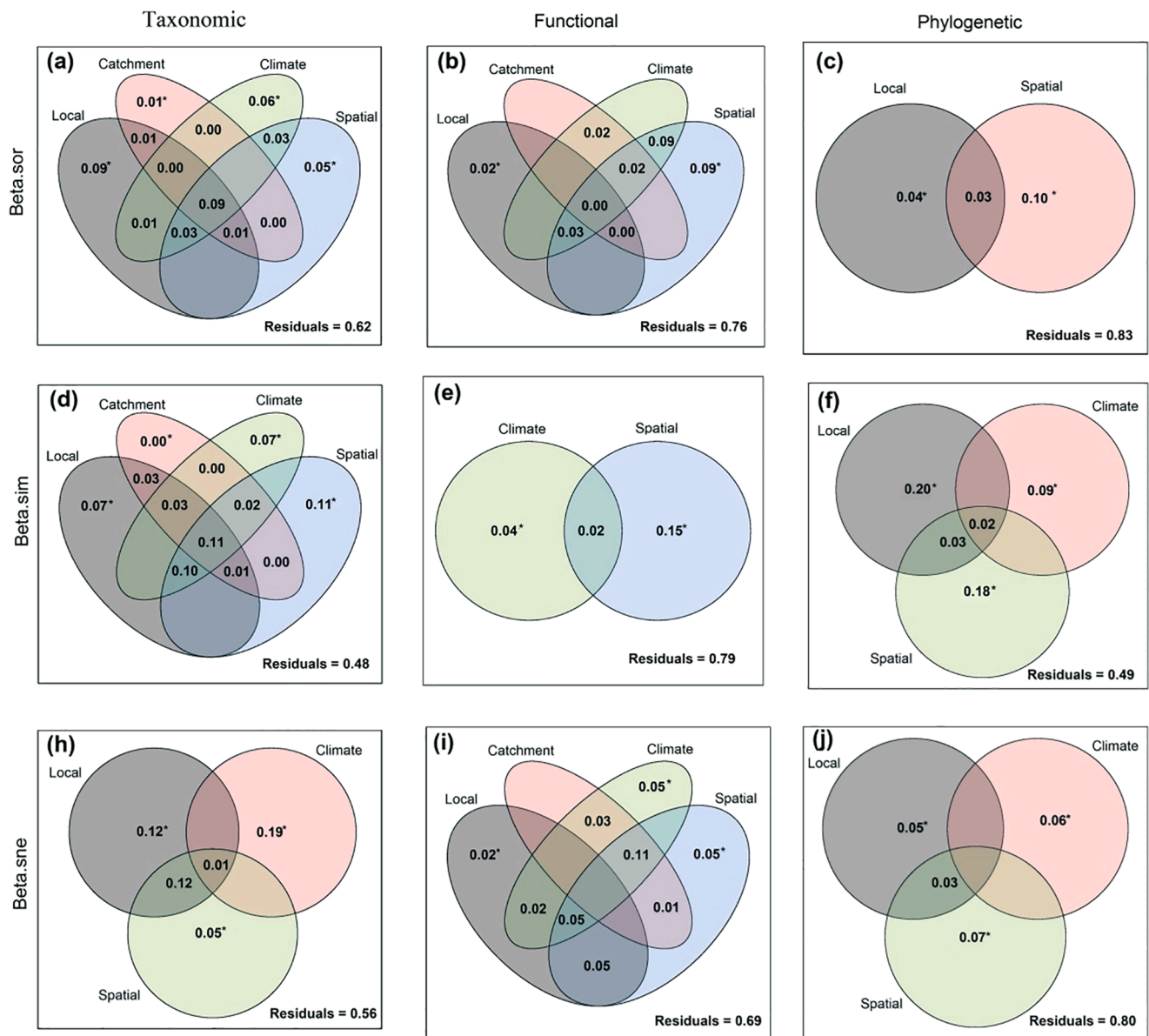


Fig. 3. Results of variation partitioning based Venn diagrams, showing taxonomic, functional and phylogenetic facets of beta diversity variation explained by unique and joint effects of local, catchment, climate, and spatial variables. The explained variation is based on adjusted  $R^2$  (\* denotes  $p < 0.05$ ). Abbreviations: Beta.sor, Sorensen; Beta.sim, Simpson; Beta.sne, nestedness-resultant.

and phylogenetic structure at relatively broad spatial scales (Heino and Tolonen, 2017; Li et al., 2020). Therefore, considering the regional geomorphology and geographical extent encompassing the studied streams, it is not surprising that dispersal limitation significantly affects taxonomic identities, functional traits and evolutionary histories exhibited by species in macroinvertebrate communities.

Unlike we expected, environmental variables did not play a more important role than spatial factors in shaping functional and phylogenetic beta diversities. This result is somewhat surprising, as it is generally recognized that functional and phylogenetic community compositions are better associated with local environmental variables compared with community composition (Sol et al., 2017; Villéger et al., 2008; Winter et al., 2013). A possible reason is that we measured a limited number of local environmental variables and thus may ignore some potentially important environmental variables in this study, such as substrate type, litter quality and quantity (Death and Collier, 2010), as well as predation pressure (Reice, 1991). Furthermore, regarding functional and phylogenetic community compositions, most

combinations of functional traits and evolutionary histories are represented by at least one taxon in each stream site, resulting in low variation in functional beta diversity and thus rather weak relationships with environmental differences among streams (see also Heino and Tolonen, 2017). In addition, our studied sites were all located at the mainstem of each stream, which also may lead to a higher contribution of spatial variables on driving macroinvertebrate assemblages.

Compared to spatial, local environmental and climatic variables, we found that catchment variables were at best weak correlates of the three facets of beta diversity and their components. This result is somewhat surprising, as many studies have emphasized the significant effects of land use on in-stream local environmental conditions and subsequently on macroinvertebrate assemblages (Allan, 2004; Jiang et al., 2017). Even though the catchment features measured did not strongly affect macroinvertebrate beta diversity, it should be noticed that some important local environmental factors (e.g., nutrient concentration and conductivity) explaining the variation in the three facets of beta diversity are often affected by land use (Allan, 2004). Thus, we strongly



recommend including them in future research on the determinants of lotic biodiversity.

## 5. Conclusion

Examining multiple facets and components of beta diversity is becoming an important topic in biodiversity research, as this approach can provide complementary information about community assembly mechanisms (Sobral et al., 2016; Villéger et al., 2013). In the present study, we found weak correlations between taxonomic, functional and phylogenetic dissimilarities (for overall beta diversity, as well as turnover and nestedness-resultant components) of stream macroinvertebrates, highlighting the necessity of measuring multiple facets of diversity for efficient biodiversity assessment and conservation planning. From the north slope (warm-temperate zone) of the Qinling Mountain to the south slope (north subtropics), we observed significant increases of the three facets of beta diversity, possibly due to the different local physicochemical and climatic conditions between the north and south slope streams. All facets of macroinvertebrate beta diversity were best explained by spatial variables, followed by local environmental conditions and climatic variables, whereas catchment variables were less important in driving beta diversity of macroinvertebrate communities. In summary, analyzing taxonomic, functional and phylogenetic facets of beta diversity provides important perspectives, which cannot be showed if only taxonomic composition is considered (Cai et al., 2019). This is because the distributions of species and ecological communities are driven by multiple evolutionary and ecological processes operating at multiple spatial and temporal scales (Morlon et al., 2011). Given the complexity of community assembly mechanisms, we recommend that an integrative approach embracing multiple facets of diversity is essential in biodiversity assessment and conservation work, as such an approach can complement traditional strategies focusing on taxonomic composition and generate better understanding of environmental determinants and spatial patterning of biodiversity.

## CRedit authorship contribution statement

**Xiaoming Jiang:** Conceptualization, Formal analysis, Methodology, Visualization, Supervision, Writing - original draft, Writing - review & editing. **Baozhu Pan:** Data curation, Supervision. **Wanxiang Jiang:** Data curation, Investigation. **Yiming Hou:** Data curation, Investigation. **Haiqiang Yang:** Data curation. **Penghui Zhu:** Investigation. **Jani Heino:** Writing - original draft, Writing - review & editing.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

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