



Original research article

## River network position mediates dispersal connectivity and environmental filtering in shaping benthic communities

Jiacheng Zhou<sup>a,b</sup>, Zhibin Song<sup>c,d</sup>, Jiancheng Hu<sup>e</sup>, Lu Tan<sup>a</sup>, Danny Chun Pong Lau<sup>f</sup>,  
Tao Tang<sup>a,b,\*</sup> 

<sup>a</sup> Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan 430072, China

<sup>b</sup> University of Chinese Academy of Sciences, Beijing 100049, China

<sup>c</sup> College of Hydrology and Water Resources, Hohai University, Nanjing 210098, China

<sup>d</sup> China Institute of Water Resource and Hydropower Research, Beijing 100038, China

<sup>e</sup> School of Environmental Science and Engineering, Hubei Polytechnic University, Huangshi 435003, China

<sup>f</sup> Department of Aquatic Sciences and Assessment, Swedish University of Agricultural Sciences, Uppsala 75007, Sweden



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## ABSTRACT

Understanding how river network position (RNP) shapes biodiversity patterns is critical for unraveling metacommunity assembly mechanisms in riverine ecosystems. However, the influence of RNP on the replacement and nestedness components of beta diversity remains underexplored. Here, we examined benthic macroinvertebrates and diatoms across six tributaries of the upper Jinsha River on the Tibetan Plateau, China. RNP was quantified using river order, upstream drainage area and three graph-theoretical metrics: betweenness, closeness and Harary centrality. Beta diversity was assessed using Local Contributions to Beta Diversity (LCBD), with three indices calculated:  $LCBD_{Total}$  (overall compositional uniqueness),  $LCBD_{Rep}$  (species replacement) and  $LCBD_{Nes}$  (species nestedness). Our results revealed that  $LCBD_{Total}$  and  $LCBD_{Rep}$  of benthic macroinvertebrates and diatoms decreased as betweenness centrality increased, while  $LCBD_{Nes}$  remained unaffected. Moreover, environmental variables including water depth and flow velocity also significantly influenced  $LCBD_{Total}$  and  $LCBD_{Rep}$ . Turbidity significantly affected  $LCBD_{Total}$  of both macroinvertebrates and diatoms, whereas total nitrogen affected only  $LCBD_{Total}$  of diatoms. We further found that the joint effects of betweenness centrality and important environmental variables on  $LCBD_{Total}$  and  $LCBD_{Rep}$  exceeded their independent effects, indicating that RNP captures not only spatial configuration but also underlying environmental variation along the river network. Additionally, river sites with low betweenness centrality,  $< 800$  for diatoms and  $< 1710$  for benthic macroinvertebrates, emerged as critical nodes structuring community composition. Our findings highlight that RNP simultaneously governs metacommunity assembly through dispersal connectivity and habitat filtering, thereby underscoring the need to integrate network topology into strategies for conserving biodiversity in dendritic river systems.

\* Corresponding author at: Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan 430072, China.

E-mail addresses: [zhoujiacheng@ihb.ac.cn](mailto:zhoujiacheng@ihb.ac.cn) (J. Zhou), [240201010015@hhu.edu.cn](mailto:240201010015@hhu.edu.cn) (Z. Song), [hujiancheng@hbpu.edu.cn](mailto:hujiancheng@hbpu.edu.cn) (J. Hu), [tanlu@ihb.ac.cn](mailto:tanlu@ihb.ac.cn) (L. Tan), [danny.lau@slu.se](mailto:danny.lau@slu.se) (D.C.P. Lau), [tangtao@ihb.ac.cn](mailto:tangtao@ihb.ac.cn) (T. Tang).

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## 1. Introduction

River network position (RNP) refers to the spatial location of a given river reach within the dendritic river network. It influences habitat connectivity as well as dispersal pathways of aquatic organisms, thereby shaping metacommunity structure (Brown and Swan, 2010, Gansfort and Traunspurger, 2019, Henriques-Silva et al., 2019, Schmera et al., 2018). Elucidating how RNP shapes the distribution of lotic organisms not only improves our understanding of the drivers of freshwater biodiversity, but also provides critical insights for effective conservation and management strategies (Altermatt, 2013, Patrick et al., 2021, Tonkin et al., 2018). Consequently, research on RNP's ecological effects has increased substantially in recent decades.

Our understanding of how RNP influences lotic organisms has been built largely upon simple, linear metrics—notably river order and upstream drainage area (Carvalho et al., 2021, Jacquet et al., 2022, Jyrkankallio-Mikkola et al., 2018, Schweizer and Jager, 2011, Stearman et al., 2019, Swan and Brown, 2017). These metrics frame rivers as longitudinal continua from headwaters to downstream reaches (Altermatt et al., 2020, Vannote et al., 1980), capturing gradients in ecosystem size and dispersal potential. Low-order streams, with small upstream drainage areas, are typically narrow, shallow and hydrologically isolated, thereby constraining both longitudinal and lateral dispersal (Baguette et al., 2013, Heino et al., 2015, Olden et al., 2001). In contrast, high-order rivers typically form wider and more interconnected channels, promoting organismal dispersal across broader spatial extents (Carvajal-Quintero et al., 2019).

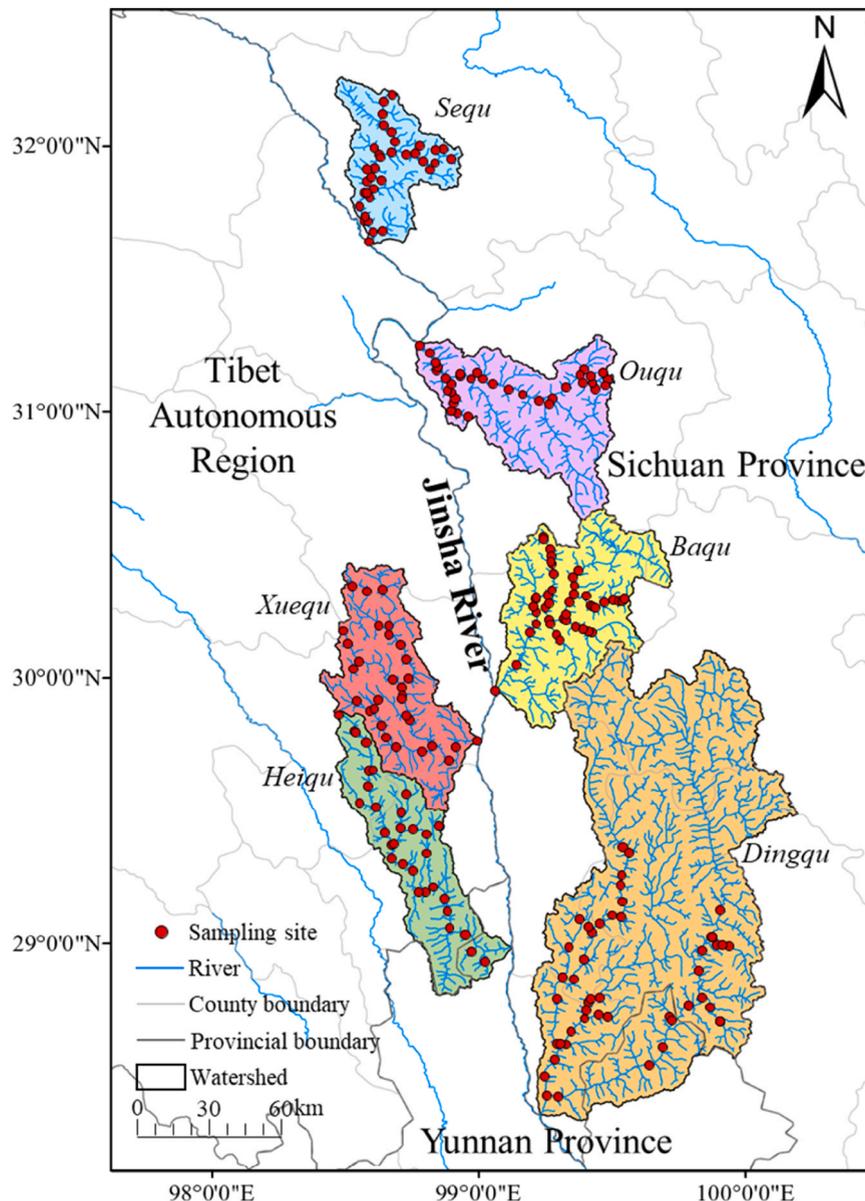


Fig. 1. Positions of the sampling sites in the river network.

However, river networks are not merely linear systems. Their branching, hierarchical topology, the very structure of connections and confluences, is expected to profoundly shape the spatial arrangement of aquatic communities (Chaput-Bardy et al., 2017, Quesada-Alvarado et al., 2023). Although recent years have seen growing interest in how network topology influences biological distributions, most empirical work remains focused on fish species with strong active dispersal abilities (Borges et al., 2020, Borthagaray et al., 2020, Henriques-Silva et al., 2019, Lee et al., 2022a). For other aquatic taxa, particularly those with different dispersal modes or weaker mobility, studies are still notably scarce.

Previous research on biodiversity across river networks has predominantly examined variation in species richness and overall composition (i.e.,  $\beta$ -diversity) along positional gradients (Hitt and Angermeier, 2011, Stearman et al., 2019, Tan et al., 2021). Less clear, however, is how the underlying components of beta diversity, i.e., species replacement and nestedness, respond to river network position. Replacement occurs when species are substituted from one site to another, reflecting ecological replacement, whereas nestedness arises when poorer communities constitute subsets of richer ones (Baselga, 2010, Soininen et al., 2018). In dendritic river networks, these two components are expected to respond differently to spatial connectivity and dispersal processes. Headwaters and other peripheral reaches, often isolated and poorly connected, should limit species exchange, promoting beta diversity dominated by replacement (Heino et al., 2015). In contrast, central and downstream reaches benefit from greater hydrological connectivity, facilitating dispersal and the accumulation of species from upstream sources. Such conditions are expected to enhance the role of nestedness (Jamoneau et al., 2018). Despite these theoretical expectations, empirical tests examining how river network position shapes the replacement and nestedness components of  $\beta$ -diversity remain limited.

RNP has commonly been treated as a spatial proxy for connectivity and dispersal limitation among reaches in most studies (Turunen and Snåre, 2025, Swan and Brown, 2017). Yet RNP reflects more than dispersal potential; it also systematically structures heterogeneity in physicochemical conditions across river networks (Hui et al., 2023). Headwater reaches, typically located at the periphery of river networks, are weakly connected and therefore tend to exhibit pronounced variability in environmental parameters such as temperature, chemistry, and substrate among sites (Clarke et al., 2008, Gothe et al., 2014, Meyer et al., 2007). In contrast, downstream reaches occupy more central positions where enhanced connectivity promotes the accumulation and longitudinal transport of materials, leading to increasingly homogeneous physicochemical conditions (Funk et al., 2023). We therefore hypothesize that RNP shapes local biodiversity through a dual pathway: by governing both organismal dispersal and in-stream environmental conditions. This integrated mechanism, however, awaits explicit empirical testing.

In the present study, we examined the effects of RNP on benthic macroinvertebrates and attached diatoms across six adjacent rivers in the Tibetan Plateau of China. Both groups of lotic organisms exhibit contrasting dispersal strategies, with macroinvertebrates dispersing through both aerial and aquatic pathways, whereas diatoms rely on passive dispersal by water flow (He et al., 2020, Vanormelingen et al., 2008). RNP for each site was quantified using metrics including river order (RO), upstream drainage area (UDA), betweenness centrality (BC), closeness centrality (CC) and Harary centrality (HC). The following three hypotheses are to be tested: (H1) Topological metrics are more effective RNP indicators than simpler metrics of RO and UDA, as topological metrics have a stronger influence on benthic macroinvertebrates and diatoms. (H2) The replacement component of beta diversity in benthic macroinvertebrates and diatoms decreases as RNP metrics increase, whereas the nestedness component increases. (H3) Joint effects of RNP and environmental variables explain more variation in beta diversity of benthic macroinvertebrates and diatoms than either factor alone. In addition, due to the passive dispersal of diatoms, we expect the independent effect of RNP to be stronger for diatoms than for macroinvertebrates.

## 2. Materials and methods

### 2.1. Study area and sampling design

The study area is located in the southeastern margin of the Tibetan Plateau, China (28°20'20"–32°13'55" N, 98°25'25"–100°10'32" E; Fig. 1), with elevation ranging from 2040.36 to 4670.28 m. The average annual temperature ranges from –4.79–12.97 °C and rivers are typically ice covered from November to March (Wang et al., 2022). Annual precipitation varies from 546.51 to 818.44 mm, with approximately 75 % occurring between June and September. This region is characterized by highly heterogeneous topography of towering mountains, deep valleys and canyons, which strongly influence vegetation distribution and support unique biomes and high levels of biodiversity (Zhou et al., 2022). The vegetation is dominated by plateau meadows that harbor a rich array of rare plant and animal species (Chen et al., 2020). Often referred to as the “Third Pole of the World”, the area has a low population density and minimal human disturbance. Consequently, the rivers remain in a near-pristine state with high longitudinal connectivity, offering a

**Table 1**  
Mainstream length and drainage area of the surveyed rivers.

River name	Mainstream length (km)	Drainage area (km <sup>2</sup> )
Dingqu	222	12163
Baqu	144	3250
Heiqu	144	2608
Xuequ	111	2672
Ouqu	120	2841
Sequ	94	1624

unique natural laboratory for studying the relationship between RNP and lotic biodiversity patterns.

We surveyed 223 sites across six tributaries of the Jinsha River, the headwater of the Yangtze River, in September of 2020, 2021 and 2022 (Fig. 1). The six surveyed rivers, including Dingqu, Baqu, Heiqu, Xuequ, Ouqu and Sequ, range from 94 to 222 km in length, with watershed areas varying between 1624 and 12163 km<sup>2</sup> (Table 1). The six rivers were selected to represent a broad gradient of environmental and spatial conditions, including variations in watershed area, flow rates and habitat types. By considering these rivers as replicates, we aim to draw regionally generalized insights into the relationship between river network position and biodiversity patterns.

## 2.2. Benthic macroinvertebrates and diatoms data

Benthic macroinvertebrates were collected using a Surber sampler with 420 μm mesh and a sampling area of 0.09 m<sup>2</sup>. Wadeable sites were sampled across the whole river section, while non-wadeable sites were sampled in near-shore locations with water depths less than 0.5 m. At each site, five replicates were randomly collected within a 100 m longitudinal reach. All specimens from the replicates were subsequently pooled into a single sample container to represent the site-level assemblage with the addition of 95 % ethanol solution for fixation in the field. In the laboratory, macroinvertebrate samples were identified and sorted under a 40 × dissecting microscope with reference to taxonomic literature (Merritt et al. 2019, Morse et al., 1994, Zhou et al., 2003). Most macroinvertebrates were identified to the genus level, while Chironomidae was identified to the subfamily level. Macroinvertebrate names were verified and updated using FADA database (<http://fada.biodiversity.be>). Finally, density (ind./m<sup>2</sup>) was calculated for each taxon appeared in each sampling site.

At the same sites, 15 natural substrates were collected randomly from five micro-habitats to obtain attached diatom samples. Most samples were collected from cobbles, with a few samples from soft sediments where no coarse substrates were available (USEPA, 2007). We used a circular lid with the radius of 2.7 cm to fix the sampling area and attached diatoms were brushed using a scrubbing brush and washed several times with stream water (Liu et al., 2023). All algal slurry from the 15 substrates was collected into one container and the slurry was volumed to 550 mL. Algal samples were fixed with 4 % formalin in the field. After brought back to the laboratory, subsample was acid-cleaned to make permanent diatom slides (Tang et al., 2016). For each permanent diatom slide, at least 600 valves were identified and counted under a 1000 × oil immersion lens. Diatoms were identified to species level based on taxonomic references (Hu and Wei, 2006, Krammer, 2000, Krammer, 2002, Krammer, 2003, Lange-Bertalot et al., 2001, Li and Qi, 2010, Li and Qi, 2014, Qi, 1995, Shi, 2004). Species names were verified and updated using AlgaeBase (<https://www.algaebase.org>). Finally, relative abundance data was calculated for each taxon appeared in each sampling site.

Different levels of taxonomic resolution were applied to the two biological assemblages analyzed in this study. For benthic macroinvertebrates, genus-level identification is widely regarded as sufficient for ecological assessments because it generally preserves the key response patterns to environmental gradients (Heino and Soininen, 2007). In contrast, diatom responses are often highly species-specific, with even closely related taxa displaying distinct tolerances to nutrient enrichment, pH, salinity, or other physico-chemical stressors (He et al., 2020). Therefore, species-level identification was employed for diatoms in this study to ensure the accuracy and robustness of our analyses. Previous cross-taxon diversity studies have also adopted such mixed-resolution approaches (Castillejo et al., 2024, Kurthen et al., 2020).

## 2.3. River network position metrics

The five river network metrics were extracted from a 30-m resolution digital elevation model obtained from the Geospatial Data Cloud (<https://www.gscloud.cn>). To ensure consistency in spatial resolution across all study basins, river networks were extracted in ArcGIS 10.3 using a uniform flow accumulation threshold (Flow Accumulation > 5000) applied via the Con function in the Raster Calculator. This operation assigns a value of 1 to cells with a flow accumulation greater than 5000, while leaving all other cells as NoData, thereby delineating the main river channels. RNP metrics were then calculated for each sampling site based on the extracted river networks. These metrics included: (1) river order (RO), assigned following Strahler's (1957) hierarchical stream ordering method, and (2) upstream drainage area (UDA), defined as the total catchment area upstream of the sampling site. Both RO and UDA were calculated using the stream order and watershed analysis modules within the Hydrology / Spatial Analyst tools in ArcGIS 10.3 (ESRI, 2014).

To quantify the topological characteristics of each sampling site within its respective river network, three additional graph theory-based metrics were calculated. These metrics describe node positions from complementary dimensions of network structure (Lee et al., 2022b). Each river network was conceptualized as a spatial graph in which the upstream and downstream termini of each river segment were defined as nodes, and all sampling sites were likewise incorporated as nodes. The resulting spatial graph was represented as a directed adjacency matrix, enabling topological analysis. Edge weights in the network were assigned according to the waterway distance between nodes, following the weighting formula of Henriques-Silva et al. (2019):

$$\text{Weight} = 1 - (d_{ij}/d_{\max})^3,$$

where  $d_{ij}$  represents the waterway distance between nodes  $i$  and  $j$ ,  $d_{\max}$  is the maximum waterway distance within river networks. Subsequently, a two-dimensional adjacency matrix was constructed, in which each element represented the presence and weight of a directed edge between two nodes. If a directed edge existed from node  $i$  to node  $j$ , the corresponding matrix element was assigned the computed weight ( $\text{matrix}[i][j] = \text{Weight}$ ); otherwise, it was set to zero. Based on this framework, three topological metrics were

computed to quantify network connectivity and structural properties of the river networks: (1) Betweenness centrality (BC) quantifies the number of shortest paths between all node pairs that pass through a given node along the direction of water flow, reflecting its role as a “stepping-stone” in the network (Rayfield et al., 2011). BC has value range from 0 to infinity, with 0 indicating that the node is located at a headwater and therefore does not mediate connectivity within the network. Higher BC values indicate that a node lies on a larger number of shortest paths. (2) Closeness centrality (CC) is defined as the reciprocal of the sum of shortest-path distances from a target node to all other nodes along the flow direction. It reflects the proximity from a given node to all others along flow direction, representing the relative proximity of that node to the rest of the network (Rayfield et al., 2011). CC values range between 0 and 1, where values approaching 0 indicate that the node is far from other nodes, whereas values approaching 1 indicate that the node is in close proximity to all other nodes and thus highly accessible within the network. (3) Harary centrality (HC) is defined as the reciprocal of the shortest-path distance along the flow direction to the most distant node in the graph, reflecting the accessibility of a site to the most remote nodes within the system (Hage and Harary, 1995). HC values range from close to 0–1, where values near 0 indicate that the node is highly distant from the farthest site, whereas values closer to 1 suggest that the node is relatively close to all other sites, including the most remote ones, and thus occupies a more accessible position in the network. These network topology metrics were calculated in R (Version 4.4.1) using the “igraph” package (Csardi and Nepusz, 2006).

#### 2.4. Environmental variables

Prior to biological sampling, concentrations of dissolved oxygen (DO), conductivity and turbidity of river water were measured using a water quality analyzer (YSI ProPlus) at each site. In addition, approximately 100 mL of river water was collected into a pre-cleaned polyethylene bottle and acidified to  $\text{pH} < 2$  with concentrated sulphuric acid in the field. After brought back to the laboratory, water samples were used to measure concentrations of total nitrogen (TN), total phosphorus (TP) and chemical oxygen demand by potassium permanganate ( $\text{COD}_{\text{Mn}}$ ) with a continuous flow water quality analyzer (SAN++, Skalar) (Chinese NEPA, 2002). Water depths and current velocities were measured where benthic macroinvertebrates and diatoms were sampled, and the average water depth and flow velocity were thereafter calculated for each sampling site.

#### 2.5. Data analyses

Prior to statistical analysis, all RNP metrics were normalized to a 0–1 scale using the 5th and 95th percentiles as reference bounds, thereby ensuring comparability across metrics. Environmental variables were  $\log_{10}(x + 1)$ -transformed to reduce skewness and limit the leverage of outliers. To reduce collinearity, pairwise correlations among RNP metrics and among environmental variables were assessed separately, and metrics/variables with Pearson  $r > 0.7$  were excluded from subsequent analysis.

To evaluate the compositional uniqueness of macroinvertebrate and diatom assemblages at each sampling site within the respective river networks, we employed Local Contributions to Beta Diversity (LCBD) as a measure of site-specific beta diversity (Legendre and De Cáceres, 2013). Three complementary indices were computed: (1)  $\text{LCBD}_{\text{Total}}$ , representing overall compositional uniqueness, (2)  $\text{LCBD}_{\text{Rep}}$ , reflecting uniqueness due to species replacement, and (3)  $\text{LCBD}_{\text{Nes}}$ , indicating uniqueness attributable to nestedness patterns (Legendre, 2014). All indices were calculated using the framework proposed by Baselga (2010), (2013).

We used generalized additive mixed models (GAMMs), with river identity treated as a random factor, to explore the effects of RNP metrics and environmental variables on each LCBD index, respectively. Predictors demonstrating statistical significance ( $p < 0.05$ ) were retained, and their partial effects were examined. Additional GAMMs were fitted using retained RNP metrics and environmental variables as predictors to evaluate the independent and joint effects of RNP and local environmental conditions on community compositional uniqueness. To quantify and compare the relative contributions of RNP metrics and environmental variables to the LCBD indices, three separate GAMMs were constructed: (1) including only RNP metrics, (2) including only environmental variables, and (3) including both predictor sets. The marginal  $R^2$  of fixed effects was used to quantify the explained variance by each model. The unique contribution of RNP metrics was calculated as the difference in marginal  $R^2$  between the full model and the model including only environmental variables, whereas the unique contribution of environmental variables was obtained as the difference between the full model and the model including only RNP metrics. The shared contribution was estimated as the variance jointly explained by both predictor sets, calculated by subtracting the unique contributions from the total explained variance of the full model. The remaining variance was considered unexplained (Peres-Neto et al., 2006, Nakagawa, 2014). Additionally, to identify important river network positions requiring conservation, we assessed the statistical significance of each site’s contribution to beta diversity (LCBD) of benthic macroinvertebrates and diatoms for each river by performing random and independent permutations of the community matrix (Legendre and De Cáceres, 2013). Sites with  $p < 0.05$  were considered significant contributors. Important RNP metrics at significant sites were summarized using boxplots, and the upper whisker was adopted to delineate priority conservation sites, providing a consistent and broadly applicable criterion that minimizes the influence of outliers caused by anomalous or transient conditions. Following McGill et al. (1978), the upper whisker of each boxplot was defined as the maximum value that does not exceed 1.5 times the interquartile range above the 75th percentile:

$$\text{Upper whisker} = \max(x_i \leq Q_3 + 1.5 \times (Q_3 - Q_1))$$

where  $Q_1$  and  $Q_3$  represent the 25th and 75th percentiles, respectively.

All statistical analyses were conducted in R version 4.4.1. The “adespatial” package was used to obtain replacement and nestedness components and calculate LCBD indices (Dray et al., 2024). The GAMMs were performed with the “gam4” package (Wood and

Scheipl, 2025). Partial effects were calculated by the “ggeffects” package (Lüdtke, 2018).

### 3. Results

#### 3.1. River network position metrics and environmental variables

The five RNP metrics displayed wide value ranges, indicating diverse topological positions of sampling sites within the river networks (Table 2). River order ranged from 1 to 5, with a mean value of 3. Upstream drainage area varied from  $1.05 \times 10^4$ – $1.18 \times 10^4$  km<sup>2</sup>. Betweenness centrality also showed high variability, ranging from 8 to 34,900, with a mean value of 3279. In contrast, closeness centrality and Harary centrality both ranged between 0 and 1, with low mean values (0.024 and 0.015, respectively). The correlations among the five RNP metrics indicated that river order, upstream drainage area and betweenness centrality were strongly correlated ( $r = 0.61$ – $0.67$ ), whereas closeness centrality and Harary centrality showed weak correlations with the other metrics ( $|r| < 0.35$ ) (Fig. 2). Overall, all pairwise correlations remained below the commonly accepted threshold for collinearity ( $|r| < 0.7$ ).

Water quality was in good condition for most sites, according to the Chinese Environmental Quality Standard for Surface Water (State Environmental Protection Administration, 2002) (Table 2). The mean COD<sub>Mn</sub> concentration met the Class I standard, while mean TN, TP, and DO concentrations corresponded to the Class II standard. The mean conductivity (176.8 μS/cm) and turbidity (20.7 NTU) were also low. Flow velocity and water depth ranged from 0.02 to 1.03 m/s and 0.07–0.34 m among sites, respectively (Table 2).

#### 3.2. Important RNP metrics and environment variables to spatial patterns of benthic macroinvertebrates and diatoms

In total, 119 benthic macroinvertebrate taxa were identified in the six rivers, belonging to 7 classes, 15 orders, and 67 families. Among them, 112 taxa were aquatic arthropods, constituting the dominant group in terms of taxonomic richness. Site-specific richness ranged from 4 to 44 taxa, with an average number of 19 taxa per site. *Baetis* sp. was the dominant taxon, with relative abundance exceeding 5 % in all six rivers and even exceeding 20 % in the Heiqu, Xuequ, and Sequ rivers. Other taxa with relative abundance above 5 % in at least two rivers included *Epeorus* sp., *Cheumatopsyche* sp., *Hydropsyche* sp. and *Stenopsyche* sp.

A total of 326 diatom species were identified in the six rivers, belonging to 2 classes, 19 orders, and 24 families. The number of species ranged from 3 to 68, with an average number of 33 species per site. *Achnanthes minutissima* was the dominant species, with relative abundance surpassing 5 % in the six rivers and accounting for over 40 % in the Ouqu and Sequ rivers. Other species with relative abundance above 5 % in at least two rivers included *Achnanthes biasolettiana*, *Encyonema ventricosum*, *Achnantheidium rivulare* and *Reimeria sinuata*.

Among the RNP metrics, only betweenness centrality was significantly and negatively associated with LCBD<sub>Total</sub> and LCBD<sub>Rep</sub> for both macroinvertebrates and diatoms (Table 3, Fig. 3). Regarding environmental variables, water depth was negatively related to LCBD<sub>Total</sub> and LCBD<sub>Rep</sub> in both groups, whereas flow velocity showed a positive relationship. TN positively affected LCBD<sub>Total</sub> in diatoms only, while turbidity had significant negative effects on LCBD<sub>Total</sub> in both macroinvertebrates and diatoms (Table 3, Fig. 3). By comparison, LCBD<sub>Nes</sub> in both macroinvertebrates and diatoms showed no significant associations with any RNP metric or environmental variable. Notably, betweenness centrality was also significantly related to key environmental gradients, being positively associated with water depth and turbidity but negatively with flow velocity (Table 4, Fig. 4).

For macroinvertebrates, the joint effects of betweenness centrality and environmental variables explained the largest proportion of variance in LCBD<sub>Total</sub> (25.1 %) and LCBD<sub>Rep</sub> (12.0 %). In comparison, environmental variables alone accounted for 6.4 % and 8.0 % of the variance, respectively, whereas betweenness centrality alone explained only 1.3 % and 1.6 %. A similar pattern was observed for

**Table 2**

Mean and range of river network metrics and environmental variables across sampling sites. COD<sub>Mn</sub>: Chemical oxygen demand by potassium permanganate, DO: Dissolved oxygen, TN: Total nitrogen, TP: Total phosphorus.

	Mean	Range
<b>River network position metrics</b>		
River order	3	1–5
Upstream drainage area (km <sup>2</sup> )	865.65	$1.05$ – $1.18 \times 10^4$
Betweenness centrality	3279	$8$ – $3.49 \times 10^4$
Closeness centrality	0.024	$2.50 \times 10^{-4}$ –1
Harary centrality	0.015	0.005–0.030
<b>Environmental variables</b>		
COD <sub>Mn</sub> (mg/L)	1.60	0.26–8.11
Conductivity (μS/cm)	176.8	21.5–473.4
DO (mg/L)	7.29	5.82–8.26
Flow velocity (m/s)	0.46	0.02–1.03
TN (mg/L)	0.21	0.04–1.07
TP (mg/L)	0.03	0.004–0.42
Turbidity (NTU)	20.7	0.1–233.1
Water depth (m)	0.20	0.07–0.34

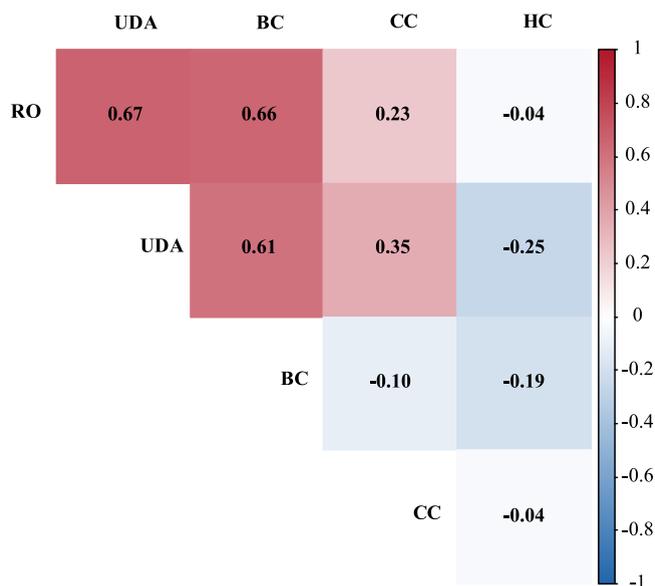


Fig. 2. Pearson correlation matrix of river network position metrics. RO: River order, UDA: Upstream drainage area, BC: Betweenness centrality, CC: Closeness centrality, HC: Harary centrality.

Table 3

Summary statistics for predictors in the GAMMs for  $LCBD_{Total}$ ,  $LCBD_{Rep}$  and  $LCBD_{Nes}$  of benthic macroinvertebrates and diatoms. RO: River order, UDA: Upstream drainage area, BC: Betweenness centrality, CC: Closeness centrality, HC: Harary centrality,  $COD_{Mn}$ : Chemical oxygen demand by potassium permanganate, DO: Dissolved oxygen, TN: Total nitrogen, TP: Total phosphorus,  $LCBD_{Total}$ : Local contribution to beta diversity,  $LCBD_{Rep}$ : Local contribution to beta diversity driven by replacement,  $LCBD_{Nes}$ : Local contribution to beta diversity driven by nestedness.

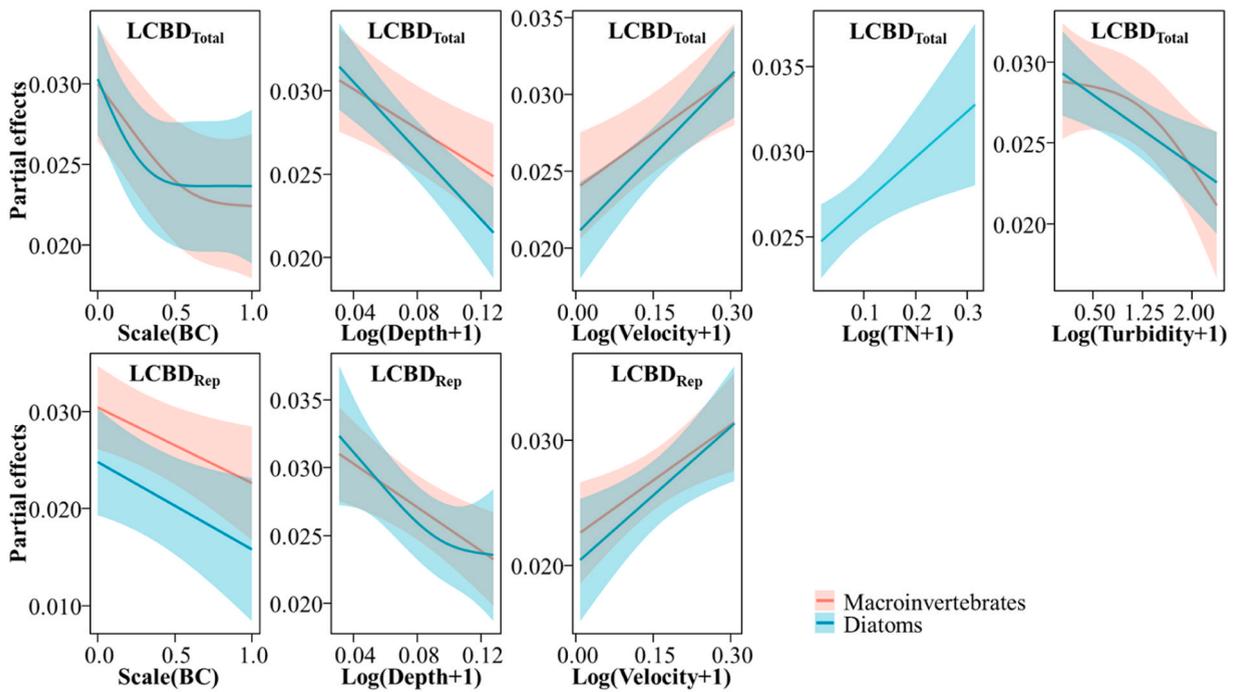
Predictors	Macroinvertebrates			Diatoms		
	$LCBD_{Total}$ p-value	$LCBD_{Rep}$ p-value	$LCBD_{Nes}$ p-value	$LCBD_{Total}$ p-value	$LCBD_{Rep}$ p-value	$LCBD_{Nes}$ p-value
<b>River network metrics</b>						
RO	0.101	0.593	0.176	0.402	0.688	0.079
UDA	0.175	0.682	0.694	0.675	0.157	0.641
BC	< 0.001	0.018	0.240	0.001	0.033	0.725
CC	0.470	0.605	0.505	0.239	0.582	0.374
HC	0.873	0.329	0.475	0.298	0.785	0.206
<b>Environmental variables</b>						
$COD_{Mn}$	0.100	0.804	0.152	0.405	0.183	0.067
Conductivity	0.348	0.077	0.468	0.327	0.460	0.311
DO	0.779	0.673	0.302	0.167	0.091	0.120
Flow velocity	0.001	0.006	0.261	< 0.001	0.006	0.669
TN	0.571	0.069	0.965	0.006	0.266	0.102
TP	0.670	0.085	0.261	0.333	0.443	0.074
Turbidity	0.002	0.059	0.136	0.004	0.215	0.053
Water depth	0.002	0.003	0.218	< 0.001	0.010	0.234

diatoms, with joint effects explaining 20.3 % of the variance in  $LCBD_{Total}$  and 10.7 % in  $LCBD_{Rep}$ . Environmental variables alone explained 19.0 % and 5.6 %, while betweenness centrality alone contributed 1.4 % and 2.8 %, respectively (Fig. 5).

### 3.3. Important river network positions identification

We found that sites with betweenness centrality (BC) values below 1710 and 800 made significant contributions to beta diversity ( $LCBD$ ) for benthic macroinvertebrates and diatoms, respectively (Fig. 6). Across the six rivers, river segments with  $BC < 800$  (i.e., red segments) had total lengths ranging from 240.7 to 462.6 km, whereas segments with  $BC < 1710$  (i.e., red and blue segments) ranged from 283.5 to 541.5 km. These segments were primarily distributed in first to third order streams (Fig. 7).

Although threshold values differed between benthic macroinvertebrates and diatoms, the spatial patterns of segments were broadly consistent among rivers, with most segments occurring in peripheral and branching of the river networks rather than in central mainstem positions.

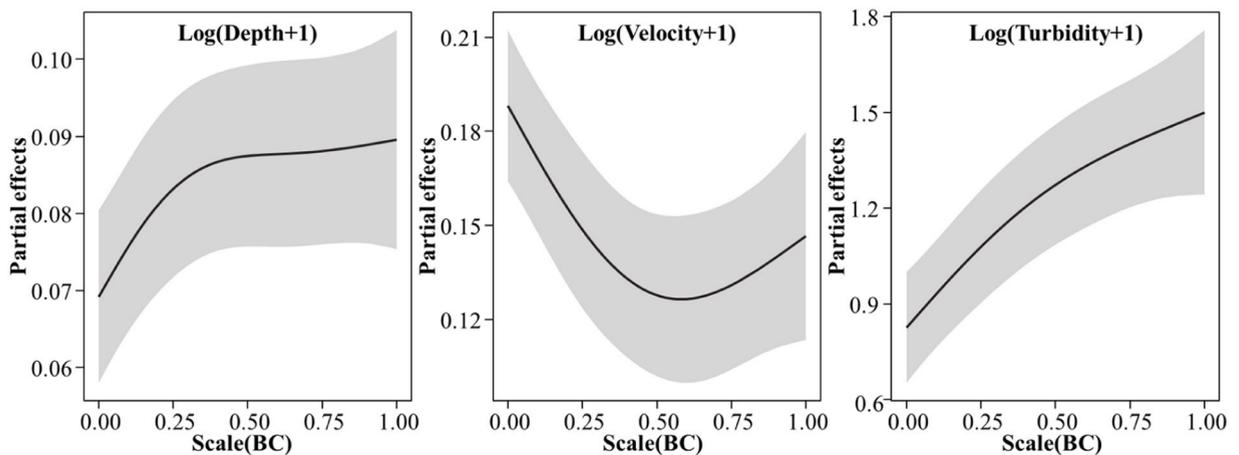


**Fig. 3.** The figure shows partial effects of river network position metrics and environmental variables on  $LCBD_{Total}$  and  $LCBD_{Rep}$  from the Generalized Additive Mixed Models (GAMMs). Solid lines depict fitted responses, with shaded areas representing 95 % confidence intervals. Red and green lines correspond to macroinvertebrates and diatoms, respectively. BC: Betweenness centrality, Depth: Water depth, Velocity: Flow velocity, TN: Total nitrogen,  $LCBD_{Total}$ : Local contribution to beta diversity,  $LCBD_{Rep}$ : Local contribution to beta diversity driven by replacement.

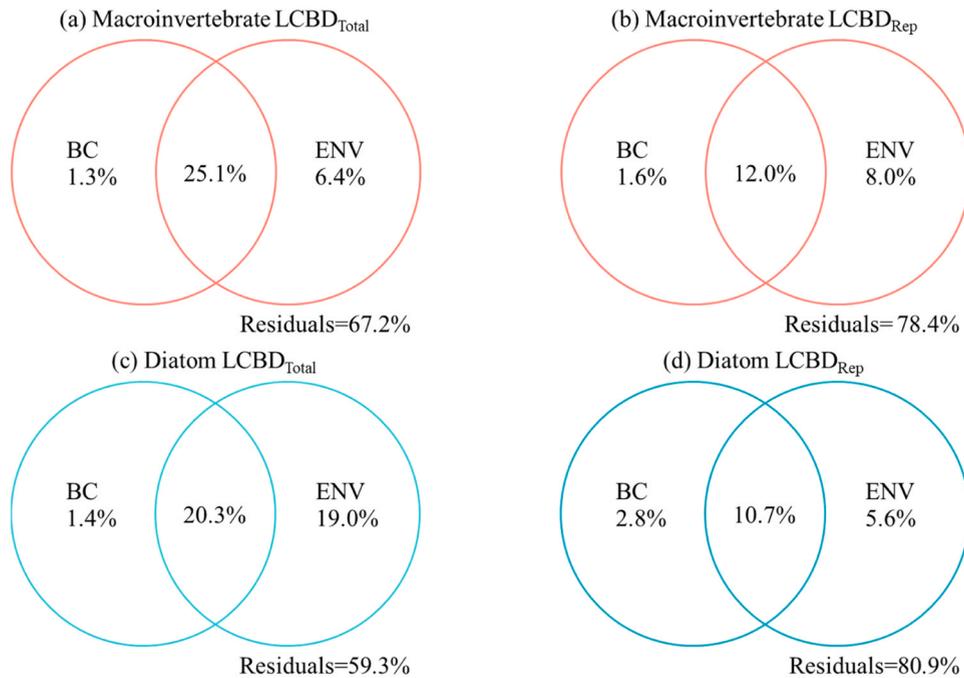
**Table 4**

Relationships between environmental variables and betweenness centrality, with effective degrees of freedom (edf) and significance (p-value) from the GAMMs.

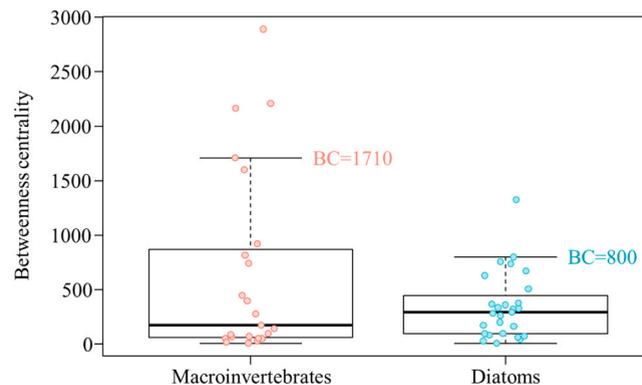
Variables	Metric	edf	p-value
Water depth	Betweenness centrality	2.414	< 0.001
Flow velocity	Betweenness centrality	2.458	< 0.001
Total Nitrogen	Betweenness centrality	1.000	0.583
Turbidity	Betweenness centrality	1.833	< 0.001



**Fig. 4.** The figure shows partial effects of river network position metrics on environmental variables from the Generalized Additive Mixed Models (GAMMs). Solid lines depict fitted responses, with shaded areas representing 95 % confidence intervals. BC: Betweenness centrality, Depth: Water depth, Velocity: Flow velocity.



**Fig. 5.** Relative contributions of environmental variables (ENV) and betweenness centrality (BC) to  $LCBD_{Total}$  and  $LCBD_{Rep}$ . Percentages indicate the proportion of variation explained by each component.  $LCBD_{Total}$ : Local contribution to beta diversity,  $LCBD_{Rep}$ : Local contribution to beta diversity driven by replacement.



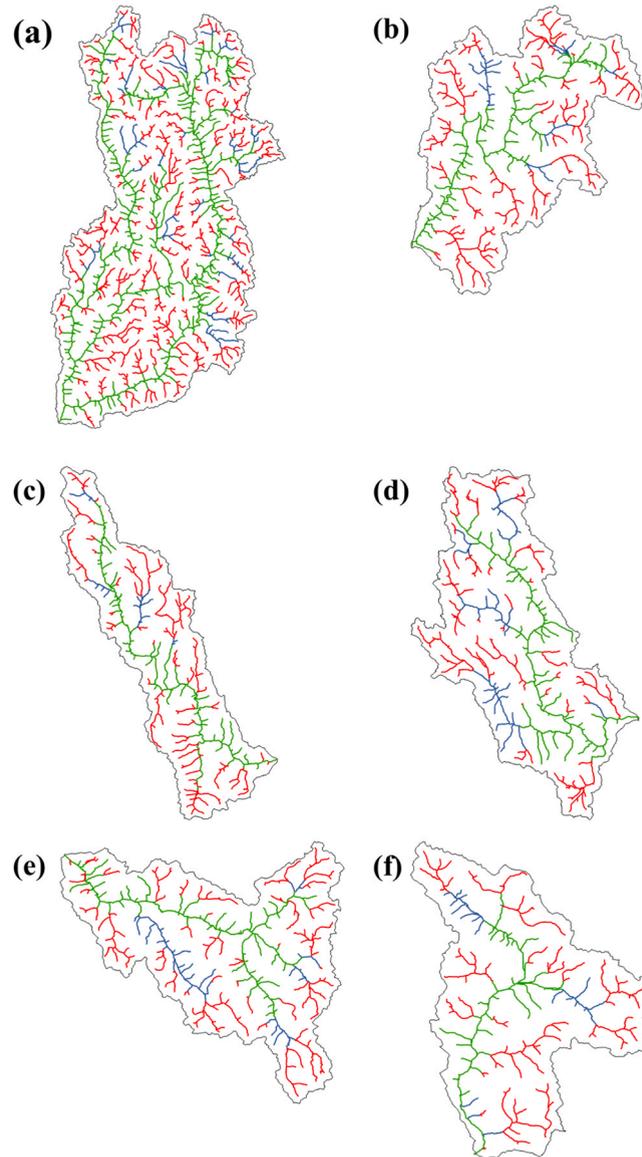
**Fig. 6.** Boxplots of betweenness centrality for sites sampled for macroinvertebrates and diatoms. BC: Betweenness centrality.

#### 4. Discussions

Our study revealed the effects of RNP and environmental variables on the LCBD indices of benthic macroinvertebrates and diatoms in the upper Jinsha River. Among the RNP metrics, only betweenness centrality showed significant effects on  $LCBD_{Total}$  and  $LCBD_{Rep}$ . Specifically,  $LCBD_{Total}$  and  $LCBD_{Rep}$  of both benthic macroinvertebrates and diatoms declined significantly with increasing betweenness centrality, whereas  $LCBD_{Nes}$  was not significantly related to betweenness centrality. Notably, betweenness centrality exhibited synergistic interactions with environmental factors and their combined effects exceeded the explanatory power of either factor alone.

##### 4.1. Ecological significance of betweenness centrality

We found that among RNP metrics examined, only betweenness centrality was significantly associated with the beta diversity of both benthic macroinvertebrates and diatoms. This finding supports our first hypothesis and underscores the key role of network topology in shaping community structure. By quantifying how frequently a node acts as a bridge along the shortest paths connecting other nodes, betweenness centrality reflects its potential to facilitate hydrological and biological exchanges across the river network



**Fig. 7.** River network segments classified by betweenness centrality thresholds: red (<800), blue (800–1710), and green (>1710). (a): Dingqu, (b): Baqu, (c): Heiqu, (d): Xuequ, (e): Ouqu, (f): Sequ.

(Altermatt, 2013). Previous studies have also shown that betweenness centrality reflects connectivity constraints and bridge effects in spatially structured networks, thereby regulating dispersal pathways and biological exchanges among sites and, in turn, shaping biodiversity patterns (Borges et al., 2020, Lee et al., 2022a). Notably, the relatively strong correlations observed between betweenness centrality and other RNP metrics—such as river order and upstream drainage area—suggest that betweenness centrality also integrates their spatial and hydrological information.

In dendritic river networks, the influence of betweenness centrality on biodiversity extends beyond dispersal processes to include its effects on local environmental conditions. Sites with high betweenness centrality tend to occupy central positions within dendritic river networks, connecting multiple tributaries and thereby facilitating organism dispersal and the transport of waterborne materials. In contrast, sites with low betweenness centrality values are typically peripheral and weakly connected, where limited connectivity maintains higher environmental heterogeneity and strengthens the influence of environmental filtering and dispersal limitation on local community composition (Gothe et al., 2014, Jyrkankallio-Mikkola et al., 2018). These patterns suggest that betweenness centrality links network structure with both dispersal processes and environmental heterogeneity, explaining its strong association with biodiversity.

#### 4.2. The Influence of betweenness centrality on $LCBD_{Total}$ and $LCBD_{Rep}$ of both macroinvertebrates and diatoms

We found that  $LCBD_{Total}$  and  $LCBD_{Rep}$  of macroinvertebrates and diatoms declined with increasing BC, whereas BC had no significant effect on  $LCBD_{Nes}$  (Table 3, Fig. 3). This pattern partially supports our second hypothesis, in that the replacement component of beta diversity in benthic macroinvertebrates and diatoms decreases as RNP metrics increase. The absence of a significant relationship between  $LCBD_{Nes}$  and RNP metrics suggests that species nestedness does not increase toward more connected network positions. Instead, the observed decline in  $LCBD_{Total}$  and  $LCBD_{Rep}$  suggests that species replacement is the dominant process structuring communities along the river network. This pattern may arise because in these high-elevation rivers, strong environmental heterogeneity combined with harsh climatic conditions may constrain the establishment of dispersing species, thereby limiting the homogenizing effects of dispersal and reinforcing environmentally driven species replacement. Similar patterns have been reported in other dendritic and metacommunity systems. For diatom assemblages, Jamoneau et al. (2018) found that total beta diversity and its replacement component were higher in upstream reaches than in mid- and downstream reaches, with beta diversity primarily driven by species replacement rather than nestedness. Meta-analytical evidence from Soinin et al. (2018) further supports this interpretation, showing that species replacement is generally more sensitive than nestedness to environmental gradients and dispersal limitation. Likewise, for stream macroinvertebrates, Li et al. (2023) demonstrated that species replacement dominates beta diversity in streams of the Tibetan Plateau.

We further observed that water depth was negatively related to  $LCBD_{Total}$  and  $LCBD_{Rep}$  in both macroinvertebrates and diatoms, whereas flow velocity showed a positive relationship. TN positively affected  $LCBD_{Total}$  in diatoms only, while turbidity had significant negative effects on  $LCBD_{Total}$  in both macroinvertebrates and diatoms. Notably, as betweenness centrality increases, water depth and turbidity increase, while flow velocity decreases. However, betweenness centrality showed no significant relationship with TN (Table 4, Fig. 4). This divergence likely reflects differences in the drivers behind these variables: depth, turbidity, and flow velocity are strongly shaped by network topology, whereas TN is primarily controlled by exogenous nutrient inputs from anthropogenic activities such as agricultural fertilization and livestock grazing (Heasley et al., 2019, Lin et al., 2021). Sites with low betweenness centrality were typically located in shallow headwater streams, characterized by clear water, high flow velocity, and coarse substrates dominated by large cobbles (Gothe et al., 2014, Richardson, 2019). These environmental characteristics promote the development of diverse microhabitats that support divergent assemblages, thereby increasing community uniqueness (Astorga et al., 2014, Zhu et al., 2023). These findings are consistent with previous studies showing that higher substrate heterogeneity promotes beta diversity in benthic communities (Astorga et al., 2014, Gething et al., 2020, Mathers et al., 2024). In contrast, sites with high betweenness centrality were generally situated in midstream or mainstem reaches, characterized by greater depth, slower flow, and higher turbidity. Increased depth and turbidity reduce light penetration, promote finer sediment deposition, which together lead to habitat homogenization and more similar communities across sites (McGoff et al., 2013, Strecker and Brittain, 2017). When integrating these results with the observed influence of betweenness centrality, a clear pattern emerges: as betweenness centrality increases, water depth and turbidity also increase, while flow velocity decreases, ultimately leading to a reduction in LCBD. This pattern provides support for our third hypothesis that RNP acts not merely as a spatial factor but also indirectly shapes community composition through its influence on environmental conditions. Moreover, due to the passive dispersal of diatoms, the independent effect of RNP was indeed stronger for diatoms than for macroinvertebrates, further confirming our expectations (Fig. 5).

#### 4.3. Implications for conservation and management

Current biodiversity conservation strategies often emphasize protecting river segments that harbor rare species or exceptionally high biodiversity (Hill et al., 2021). However, given the limited resources for conservation and restoration, it is generally impractical to safeguard a large number of river segments across extensive landscapes (Hermoso et al., 2011, Linke et al., 2011). Therefore, a robust evaluation of the conservation value of individual river segments is essential to maximize biodiversity protection under constrained budgets. In this context, identifying sites whose community uniqueness disproportionately contributes to regional biodiversity provides an evidence-based framework for prioritizing conservation and management actions effectively. We found that sites with betweenness centrality below 1710 and 800 showed significant contributions to beta diversity for benthic macroinvertebrates and diatoms, respectively. This difference can be attributed to the distinct dispersal traits and environmental sensitivities of the two groups. Diatoms rely on passive hydrological dispersal. As betweenness centrality increases, central nodes function as confluence hubs that efficiently mix diatom communities from multiple upstream tributaries and facilitate their downstream drift, thereby rapidly reducing community uniqueness. In contrast, benthic macroinvertebrates possess a certain degree of active dispersal through adult flight and are more sensitive to environmental gradients (Heino et al., 2013). These traits allow their community uniqueness to persist across a wider range of betweenness centrality values before homogenization becomes dominant.

Translating these site level patterns into management relevant spatial units, we propose a hierarchical conservation framework. First, segments with low betweenness centrality ( $BC < 800$ ) provide unique habitat conditions that sustain high community uniqueness for both benthic macroinvertebrates and diatoms. These areas warrant the highest level of protection, with management focusing on preserving environmental heterogeneity, including natural variations in water depth, flow velocity, and substrate composition, while strictly avoiding human-induced alterations such as channelization, excessive sediment input, or riparian vegetation removal. Second, river segments with betweenness centrality values between 800 and 1710 serve as critical ecological connectors. For diatoms, community homogenization may already be underway, but for macroinvertebrates, these segments remain important contributors to beta diversity. Management should aim to maintain or enhance habitat heterogeneity and natural hydrological connectivity, for example through riparian buffer restoration and regulation of sediment inputs.

It is important to note that the specific betweenness centrality thresholds identified in this study are not universally applicable, as they depend on river network structure and spatial resolution. However, the methodological approach is broadly transferable. Future studies should therefore apply the same analytical framework linking network position metrics to community uniqueness and beta diversity, while recalibrating threshold values according to network structure, environmental gradients and biodiversity responses.

#### 4.4. Limitations and future perspectives

Several limitations of this study should be acknowledged. First, although we examined benthic macroinvertebrates and attached diatoms, other taxonomic groups with different dispersal modes, such as fish, plankton, or microorganisms, may respond differently to RNP. Second, our analyses focused on species-based beta diversity and did not consider functional trait composition or functional beta diversity, which may exhibit distinct responses to network structure and dispersal processes. Third, the lack of temporal replication limits our ability to assess how these patterns vary across seasons or hydrological conditions. Future studies incorporating multiple regions, a broader range of taxonomic groups, functional trait dimensions and temporal replication will be essential to further evaluate the generality of our findings.

## 5. Conclusion

LCBD indices of both benthic macroinvertebrates and diatoms were primarily associated with betweenness centrality, while environmental variables including water depth, flow velocity, turbidity and total nitrogen also played a critical role. It is worth noting that betweenness centrality interacted synergistically with environmental variables, indicating that RNP not only captures spatial dispersal across the river network, but also reflects environmental variation. In addition, we suggest that preserving environmental heterogeneity at sites below key betweenness centrality values is critical for maintaining species diversity in dendritic freshwater systems.

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## CRedit authorship contribution statement

**Tao Tang:** Writing – review & editing, Project administration, Methodology, Funding acquisition, Conceptualization. **Danny Chun Pong Lau:** Writing – review & editing. **Zhibin Song:** Writing – review & editing, Investigation. **Jiacheng Zhou:** Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Lu Tan:** Resources, Investigation. **Jiancheng Hu:** Writing – review & editing, Investigation.

## 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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## Data availability

Data will be made available on request.

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