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Response Mechanisms of Passive Biotic Communities to Changes in River Connectivity

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Rapid urban development has led to the anthropogenic disruption of natural river connectivity, posing unprecedented threats to aquatic biological communities. Understanding how river connectivity influences the structure of these communities is crucial, particularly in urban mountainous regions where this topic remains underexplored. Here, we assessed river connectivity in the Mother River of Beijing, one of the world's largest megacities, and analyzed its effects on the biodiversity, dominant species, and biomass of benthic fauna, zooplankton, phytoplankton, and fungi. Our results showed that the river connectivity index (RCI) ranged from 0.0003 to 0.3978, with higher connectivity observed in the middle reaches of the river. RCI values were distinctly categorized into 2 types: high connectivity and low connectivity. Organisms at different trophic levels exhibited varying responses to river connectivity, with the composition of dominant benthic species differing by 62.5% between connectivity conditions, a higher variation than that observed in other taxa. Notably, diatom richness displayed significant spatial heterogeneity and was strongly negatively correlated with RCI. Our findings demonstrate that river connectivity exerts taxon-specific effects across multiple trophic levels, underscoring the need to consider both faunal diversity gains and potential diatom losses when designing urban river restoration and conservation strategies.

Introduction

River ecosystems, rich in biodiversity, are vital to global biogeochemical cycles and deliver essential ecosystem services to human societies [1]. However, population growth, economic expansion, rising energy demands, and climate change are accelerating the degradation of river systems, placing them among the most at-risk ecosystems globally [2]. A key factor in sustaining river ecosystem health is connectivity, the unimpeded movement of water, sediment, and organisms through channel networks. Nevertheless, rapid urbanization, along with human activities such as dam construction, channelization, culvert installation, and the expansion of impervious surfaces, increasingly compromises river connectivity by disrupting flow dynamics, altering channel morphology, and impeding sediment transport on a global scale [3]. For instance, only 37% of rivers over 1,000 km in length remain uninterrupted along their full course [4]. This loss of connectivity not only undermines biogeochemical cycles and the movement of organic and inorganic materials but also has far-reaching impacts on the composition and dynamics of biological communities [5].

To assess river connectivity for conservation and restoration efforts, structural indicators such as the dendritic connectivity index (DCI) and the integral index of connectivity (IIC) have been widely applied [6,7]. While these metrics effectively quantify river fragmentation, they primarily rely on river length as a proxy for habitat availability [8]. This approach has limitations, as it assumes that all river segments along a longitudinal gradient are ecologically equivalent, failing to account for ecological differences between them [6]. Structural connectivity refers to the physical arrangement and continuity of river habitats, whereas functional connectivity emphasizes the actual movement, dispersal, and exchange of organisms and materials across this structure. A comprehensive understanding of river connectivity requires the integration of both structural and functional connectivity. Functional indicators are essential to link physical fragmentation with biological consequences. Functional connectivity considers biological transport and dispersal mechanisms, providing a more holistic view of connectivity's ecological impacts [9]. By combining physical and ecological connectivity and addressing the needs of different biological groups, researchers can more accurately quantify connectivity loss, identify biodiversity patterns, and strengthen the scientific foundation for river restoration efforts. However, a critical next step is to translate these connectivity metrics into ecological consequences for different organisms. In particular, understanding how river connectivity influences the dispersal and persistence of biological communities provides an essential link between hydrological processes and biodiversity outcomes.

The global decline in river connectivity has led hydrologists and ecologists to investigate how biological communities are sustained and how organisms respond to hydrologic processes [10]. For many aquatic organisms, passive dispersal is a key mode of migration [11]. In this study, passive communities refer to organisms that lack active movement capacity and are

mainly transported by hydrological processes, including benthic fauna, zooplankton, phytoplankton, and fungi. This distinguishes them from active dispersers such as fish, which rely on swimming ability to move between habitats. Species such as benthic invertebrates, fish, aquatic plants, and stream-associated amphibians rely on river corridors to move between habitats. When connectivity is lost, species become isolated, leading to increased inbreeding, reduced genetic diversity, and limited migration and resource access. Maintaining river connectivity is therefore essential for population persistence [12]. For example, disrupted connectivity prevents fish from migrating between foraging and breeding areas, threatening the survival of freshwater fish species worldwide [13]. Although ecological research has made substantial progress in understanding these impacts [5,14], most studies have focused on top predators, often neglecting the consequences of disrupted connectivity on organisms at lower trophic levels.

Understanding how river connectivity influences biological community structure across trophic levels is essential for the preservation and restoration of river ecosystems. Lower trophic-level organisms, including benthic invertebrates, zooplankton, phytoplankton, and microorganisms, play fundamental roles in biogeochemical cycling and ecosystem function. By processing nutrients in the water column, these organisms support elevated trophic levels through food web interactions [15]. Reductions in the abundance of primary producers and decomposers can trigger cascading trophic effects, ultimately affecting ecosystem stability. However, most studies investigating aquatic community dynamics have primarily examined environmental factors such as water physicochemical properties (e.g., dissolved oxygen, temperature, pH, and flow rate) [16], nutrient levels (e.g., nitrogen and phosphorus) [17,18], climate change [19], and anthropogenic pressures (e.g., pesticide contamination and dam construction) [20,21]. Limited research has explicitly considered river connectivity as a critical driver of community structure. Disruptions to connectivity fragment habitats, hinder species migration, and alter hydrological conditions, further affecting species distributions, community composition, and ecological function across trophic levels [22]. Although some studies have explored the impact of connectivity on basal trophic levels, they often focus on a single community type and lack a systematic examination of interactions across trophic levels [23]. Thus, a comprehensive investigation of how river connectivity shapes community structure and ecological function at different trophic levels remains an urgent research need. Addressing this knowledge gap is critical for designing effective conservation and restoration strategies for river ecosystems.

To bridge this gap, this study focuses on the "Mother River" of Beijing, which is experiencing a loss of river connectivity, as a model system to quantify river connectivity using spatial maps and habitat suitability models. We investigate the relationships between river connectivity and key biological groups, including primary producers (phytoplankton), primary consumers (zooplankton and benthic fauna), and decomposers (fungi). Specifically, this study aims to (a) accurately quantify river connectivity in the mountain gorge section of the Yongding River, (b) identify dominant populations under different connectivity conditions, and (c) analyze the impacts of river connectivity on biodiversity and biomass at different trophic levels. The findings of this study will contribute to quantify the ecological consequences of river fragmentation and provide a solid theoretical foundation for biodiversity conservation and river habitat restoration.

Materials and Methods

Study area

The Yongding River is known as the "Mother River" of China's capital. However, with the acceleration of industrialization and urbanization, Yongding River is facing serious challenges, including excessive extraction of water resources, diminishing environmental carrying capacity, water quality degradation, and river fragmentation, which severely limits the healthy economic and social development of the Beijing–Tianjin–Hebei region. The river exhibits a meandering course with an average gradient of 3%, and the main channel width varies considerably, ranging from 80 to 750 m. The surrounding land use primarily consists of cropland, orchards, forested land, grassland, residential areas, transportation infrastructure, water bodies, hydraulic facilities, and other land types. In recent years, researchers have started to focus on the ecological issues of the Yongding River. Earlier studies integrated field monitoring and modeling to assess water quality, hydrological processes, and other key indicators from hydrological, ecological, and environmental perspectives, highlighting the effects of climate change and human activities on river ecosystems [24]. Furthermore, scholars have explored ecological restoration effects and water resource governance strategies [25]. The downside is that few scholars have studied river connectivity and the impact of this connectivity on the structure and function of biological communities in depth. In this research, 12 monitoring sites were deployed along the mountainous gorge section of the Yongding river, and field surveys of benthic fauna, phytoplankton, zooplankton, and fungi were conducted in April 2024, June 2024, and September 2024, respectively (Fig. 1).

Field monitoring and sample processing

Benthic fauna was collected at each monitoring site by placing the bottom of the Sobel collection net (area, 0.09 m^2; mesh aperture, 0.25 mm) close to the channel substrate [26]. The material collected in the mesh pockets was cleaned and transferred from the dead branches and leaves. The substrate and benthic fauna from the mesh pockets were transferred into a water basin with an appropriate volume of water to facilitate stirring. Debris such as branches and leaves was carefully removed to ensure no organisms adhered. The remaining substrate was gently agitated, allowing the lighter benthic fauna to float in the water column, which was then immediately poured through a 40-mesh sieve. This process was repeated several times to ensure complete collection. Once the collection was complete, the benthos was immobilized by preservation in 75% alcohol solution. Finally, the density (ind/m^2) and biomass (g/m^2) of benthic fauna within each sampling site were calculated and the measurements were recorded.

A 5-l surface water sample was collected at each monitoring point and then fixed by adding approximately 1% to 1.5% of the water sample volume of Lugol's solution. The water samples collected in the field were shaken well, and then 1 l was measured and put into a dispensing funnel or precipitation bottle and left to stand for 24 to 36 h [26]. A fine siphon tube (latex; inner diameter, 0.3 mm) was used to carefully remove the upper clear liquid, leaving approximately 50 ml of concentrated precipitate at the bottom of the container. The concentrate was then transferred into a 50- to 60-ml plastic bottle (with a 30-ml calibration mark indicated on each bottle). Rinse the inner wall and bottom of the precipitation bottle with a small amount of distilled water for 2 to 3 times, pour the rinsing solution into a small plastic bottle, and then continue the vial for more than 24 h of static

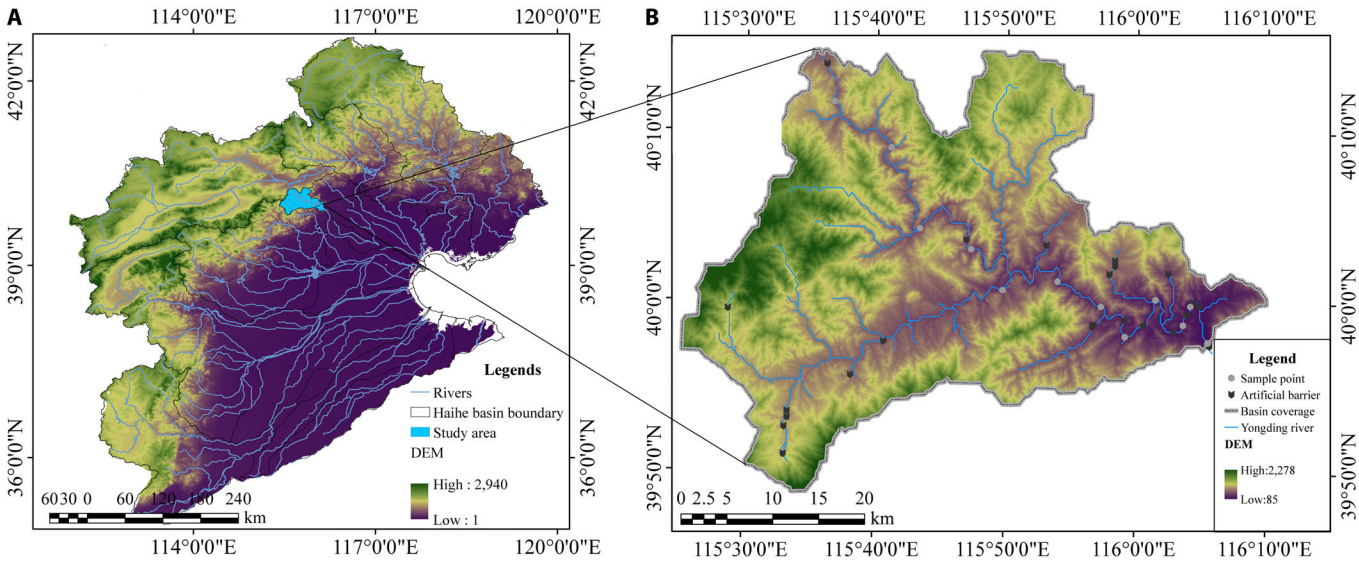

Fig. 1. Location of the research area and illustrations of monitoring points and obstacles. (A) Haihe river basin. (B) Yongding river basin.

precipitation. Finally, it was siphoned and volume-fixed to 30 ml [26]. A 0.1-ml counting frame with a counting area of 20 mm × 20 mm was used, in units of individuals per liter. Identification and enumeration of phytoplankton was carried out under a microscope, and phytoplankton density was calculated (Eq 1). The number of cells of a particular phytoplankton in a water sample derived from quantitative measurements was multiplied by the specific gravity to obtain the biomass (wet weight).

$$N = \frac{C_s}{F_s \times F_n} \times \frac{V}{U} \times P_n \quad (1)$$

In Eq. 1, N is the density of phytoplankton cells (or individuals) in 1 l of water sample in 10^4 cells/l; C_s is the area of counting frame in mm^2; F_s is the area of the field of view in mm^2; calculation of the field of view area: the diameter of the field of view under a certain magnification is determined by micrometer of the objective lens (usually ×400 or ×600), and it is calculated according to the formula of the area of the circle, πr^2. F_n is the number of counted fields of view; V is the volume of 1 l of water sample after sedimentation and concentration, in milliliters; U is the volume of the counting frame, in milliliters; P_n is the number of phytoplankton cells counted per slice, in pieces.

A total of 10 l of water was collected at each monitoring point using a water sampler, filtered and concentrated with a #13 plankton net, and then preserved by adding formaldehyde solution equivalent to approximately 1% of the sample volume. For the counting of branchiopods and copepods, 10 l of filtered concentrated sample was shaken well, 5 ml was quickly aspirated into a 5-ml counting frame, and counted as a whole under a 40× power microscope. Two slices were counted for each sample (with an error of no more than ±15%), and the mean value was obtained. Calculate the density of branchiopods and copepods in water samples according to Eq. 2. Based on the approximate shape of the zooplankton, the data required to calculate the volume of the species were measured under a microscope. The volume is multiplied by the density to get the weight (wet weight) of the species of zooplankton.

$$N_i = \frac{C \times V_1}{V_2 \times V_3} \quad (2)$$

In Eq. 2, N_i is the number of individuals of class i zooplankton per liter of water sample in individuals per liter; C is the number of individuals obtained by counting in individuals; V_1 is the volume of the concentrated sample in milliliters; V_2 is the calculated volume in milliliters; and V_3 is the volume of the sample in liters.

In addition, 3 l of surface water was collected as environmental samples in sterile collection bottles. The collected samples were vacuum-extracted using a polyester fiber filter membrane with a pore size of 0.22 μm. The collected colonies were immediately put back into a −80°C refrigerator for storage. DNA extraction was followed by polymerase chain reaction (PCR) amplification of the fungal ITS region using specific primers, fluorescence quantification, and quality control. High-throughput sequencing of each sample was conducted using a MiSeq sequencer. Raw sequences that passed the initial quality screening were assigned to libraries and samples based on index and barcode information, with barcode and primer sequences subsequently removed. Sequence denoising was performed following the qiime2 analysis pipeline. Following the QIIME2 analysis pipeline for sequence denoising, stringent quality filtering was applied, yielding an average of 126,990 high-quality fungal sequences per sample, which ensured adequate sequencing depth for subsequent community analysis. The distribution of amplicon sequence variants (ASVs) across different samples was used to assess alpha diversity, while sequencing depth adequacy was evaluated using rarefaction curves.

The formulas for the degree of dominance of benthic, zooplankton, phytoplankton, and fungal species and the degree of difference in the composition of dominant species are given below (Eq. 3).

$$Y = \frac{N_i}{N} \times f_i \quad (3)$$

$$D = \left(1 - \frac{S}{N}\right) \times 100\% \quad (4)$$

In Eq. 3, N_i denotes the number of individuals of the ith species; N denotes the total number of species; and f_i denotes the frequency of occurrence of the ith species in all sample sites. Y is the degree of dominance. Species with $Y \geq 0.02$ are taken

as dominant species [27]. In Eq. 4, D denotes the degree of variation in the composition of dominant species; N denotes the total number of dominant species; and S denotes the total number of the same dominant species under different river connectivity.

River connectivity and barrier prioritization

The connectivity index was categorized into catchment connectivity index (CCI) [28] and river connectivity index (RCI) [29]. The RCI was calculated at the reach scale. Both CCI and RCI range from 0 to 1. Higher CCI values were associated with greater longitudinal connectivity at the watershed scale. Higher RCI values were associated with reaches that were more easily accessible from other reaches within the watershed. Both CCI and RCI are close to 0, indicating a more fragmented stream landscape at the catchment and reach scales, respectively.

$$\mathrm{CCI} = \sum_{i=1}^{n}\sum_{j=1}^{n} I_{ij}\frac{w_i w_j}{w^2} \tag{5}$$

$$I_{ij} = c_{ij}B_{ij} \tag{6}$$

$$\mathrm{RCI}_i = \sum_{j=1}^{n} I_{ij}\frac{w_j}{w} \tag{7}$$

CCI was defined as a weighted sum of diffusion probabilities (see Eq. 5), where w_i and w_j are the weights of the ith and jth reaches, respectively. W is the sum of the weights of the n reaches. I_{ij} is the probability of dispersal (see Eq. 6), i.e., the probability that organisms originally located in reach i will disperse to reach j. Decompose I_{ij} into a component of structural connectivity (barriers) and a component of functional connectivity (species dispersal), where c_{ij} depends entirely on spatial structure and the number of barriers, while B_{ij} depends on the spatial arrangement of the watershed and the ability of the species to disperse. Removing the first term of the summation in Eq. 5 defines a reach-level connectivity index, or RCI, for the ith reach in the catchment (see Eq. 7).

Barrier prioritization (BP) is based on the relative impact of CCI on landscape fragmentation [28]. The value of BP lies between 0 (when obstacles have no influence on fragmentation) and infinity (when the landscape is entirely divided). The BP ranking could be utilized to assess the extent of connectivity enhancement when a specific arrangement of obstacles is eliminated.

$$\mathrm{BP} = \frac{\mathrm{RCI}_y - \mathrm{CCI}_x}{\mathrm{CCI}_x}100 \tag{8}$$

In Eq. 8, CCI_x is the index value calculated for the current setting. RCI_y is the metric value determined after the obstacle was removed.

The computation of RCI and BP was realized with the R language "riverconn" package [30]. It could calculate different indices derived from the provided geographic data and its characteristics under various configurations determined by the user. The hydrological data are sourced from the free-flowing rivers (FFRs) [4]. Obstacle distribution data were obtained using Google Earth pro visual interpretation. There were 4 main types of obstacles (dams, weirs, sluices, and culverts). RCI for each reach and BP for each obstacle were calculated. Stream reaches with high RCI rankings (rank 1 being the highest) have high restoration potential. BP interpreted this as prioritizing those obstacles that were cleared. Higher ranked obstacles (rank 1 being the highest) will result in greater improvement in CCI. RCI was assessed separately using 4 different parameter settings including DCI, IIC, population connectivity index of fish (PCIF), and population connectivity index of passive organism (PCIP). BP was assessed using PCIP. DCI and IIC quantify structural connectivity, while PCIF and PCIP assess functional connectivity patterns. See the "riverconn" package documentation for a complete overview [30].

Statistical analysis

Alpha diversity indices and biomass of benthos, zooplankton, phytoplankton, and fungi were calculated from field survey data. Due to differences in aquatic life between seasons, we calculated diversity indices and biomass means. These indices included the Margalef richness index, the Shannon–Wiener diversity index, the Pielou evenness index, and the Ace richness index (for fungi). Secondly, Shapiro–Wilk normality test was conducted to examine the significance of diversity index and biomass [31]. Based on the results of the K-means clustering analysis (using Euclidean distance and a maximum of 10 iterations), we categorized the streams into 2 groups: high connectivity and low connectivity. In this study, t tests and rank sum tests were used to assess differences in aquatic communities across river connectivity conditions. A t test was used for indices that satisfied a positive distribution, and a rank-sum test was used for indices that did not satisfy a positive distribution (benthic, zooplankton, and diatom abundance; zooplankton and phytoplankton biomass). To analyze the trend of biodiversity with RCI (using PCIP), we performed a least-squares linear regression, with biodiversity as the dependent variable and RCI as the independent variable. The significance of the regression model was evaluated using the P value of the F statistic (typically $P < 0.05$ indicating a statistically significant relationship), and the goodness of fit was reported using the coefficient of determination (R^2). NS: $P > 0.05$, $^*P \leq 0.05$, $^{**}P \leq 0.01$, $^{***}P \leq 0.001$.

Results

Spatial variation in the RCI of the Yongding River

The RCIs for different settings were distributed between 0.0003 and 0.3978. A higher RCI ranking indicated better river connectivity. In comparison, DCI had higher values and the ranked results were DCI (0.217 ± 0.152) > IIC (0.167 ± 0.12) > PCIF (0.152 ± 0.102) > PCIP (0.066 ± 0.078). The upper and middle reaches of the DCI had higher values, indicating better connectivity (Fig. 2A). IIC had better midstream connectivity and poorer upstream and downstream (Fig. 2B). PCIF and PCIP were better midstream mainstem connectivity (Fig. 2C and D). For the first 25 reaches, the PCIP was highly differentiated from the DCI, IIC, and PCIF (Fig. 3A). On the whole, DCI and IIC trend changes were more similar. Furthermore, RCIs were clearly categorized into 2 types: high connectivity and low connectivity (Fig. 3B).

Effects of river connectivity on dominant species composition

The benthic fauna was dominated by *Gammarus* sp. (high connectivity) and *Chironomidae* sp. (low connectivity), and the

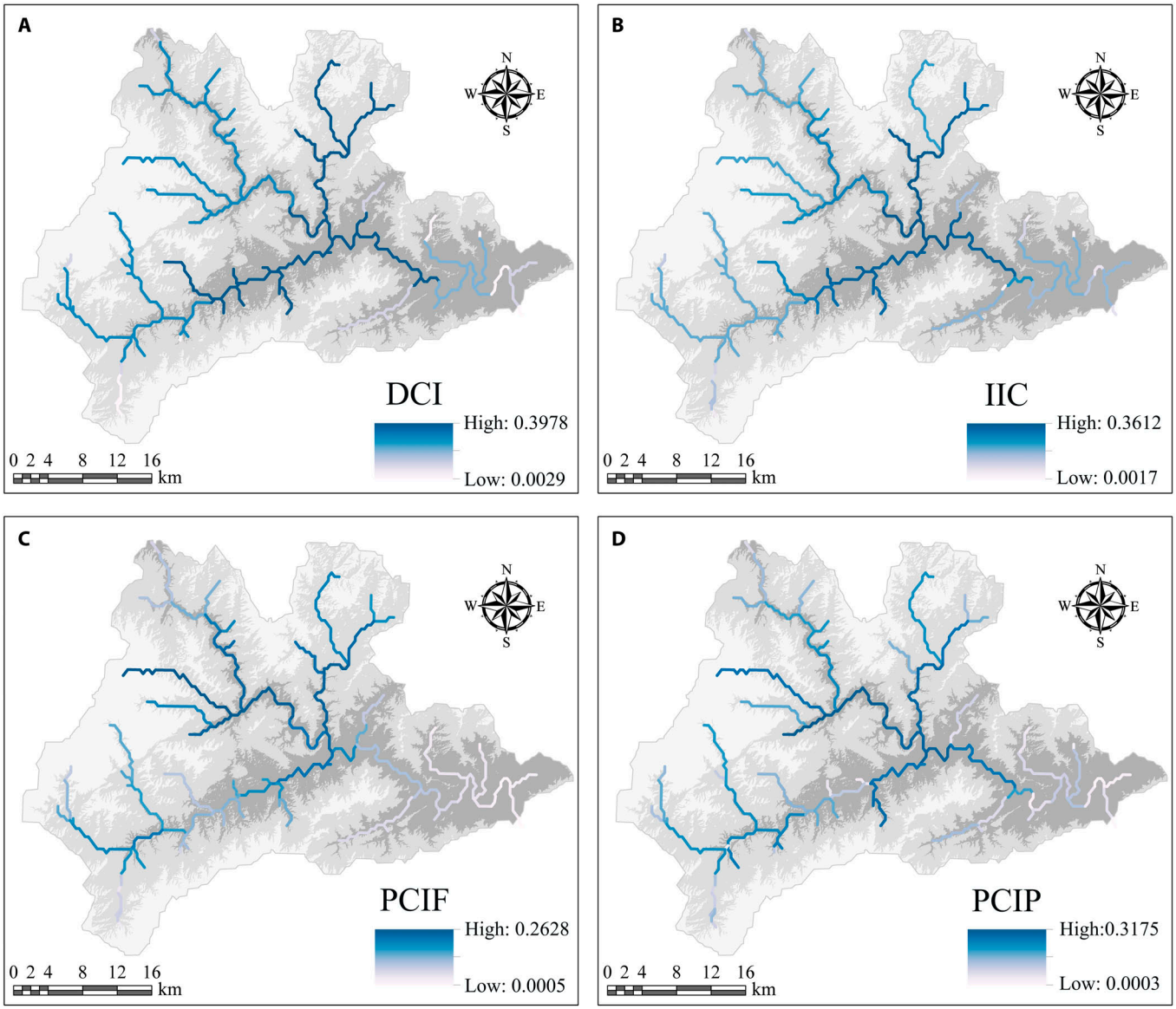

Fig. 2. Spatial variation in the river connectivity index of the Yongding River. (A) DCI, dendritic connectivity index. (B) IIC, integral index of connectivity. (C) PCIF, population connectivity index of fish. (D) PCIP, population connectivity index of passive organism. DCI and IIC for structural connectivity; PCIF and PCIP for functional connectivity.

variability in the composition of dominant species under different river connectivity was 62.5% (Fig. 4A). The dominant species of zooplankton under different river connectivity were mainly *Cyclops* sp., and the composition difference of dominant species was 50% (Fig. 4B). *Microcystis* sp. was the main dominant species of phytoplankton under different river connectivity, and the composition difference of dominant species was 42.9%(Fig. 4C). The dominant species of fungi were *Clydaea vesicula* (high connectivity) and *Amniculicola lignicola* (low connectivity), with a 33.3% difference in dominant species composition across river connectivity (Fig. 4D).

Effects of river connectivity on diatom richness

River connectivity significantly affected phytoplankton richness (Fig. 5A and B). Various biodiversity indices and biomass of benthic fauna, zooplankton, and fungi had no significant response to river connectivity (Figs. S1 and S2). In addition, there were significant differences in diatom richness at different river connectivity levels (Fig. 5C). More importantly, as RCI increased, diatom richness showed a significant downward trend (Fig. 5D). In addition, neither green algae nor the remaining phytoplankton taxa were markedly different (Fig. 5C and Fig. S3).

Discussion

The complexity of organism distribution and movement poses major challenges to establishing a universal connectivity-biome causal framework for river management. This study integrates river network structure into the analysis of biological communities and hydrological processes, focusing on the responses of producers (phytoplankton), primary consumers (zooplankton and benthic fauna), and decomposers (fungi) under different connectivity conditions. Our findings indicate that organisms at different trophic levels exhibit varied sensitivities to river connectivity, with phytoplankton responding most strongly. These

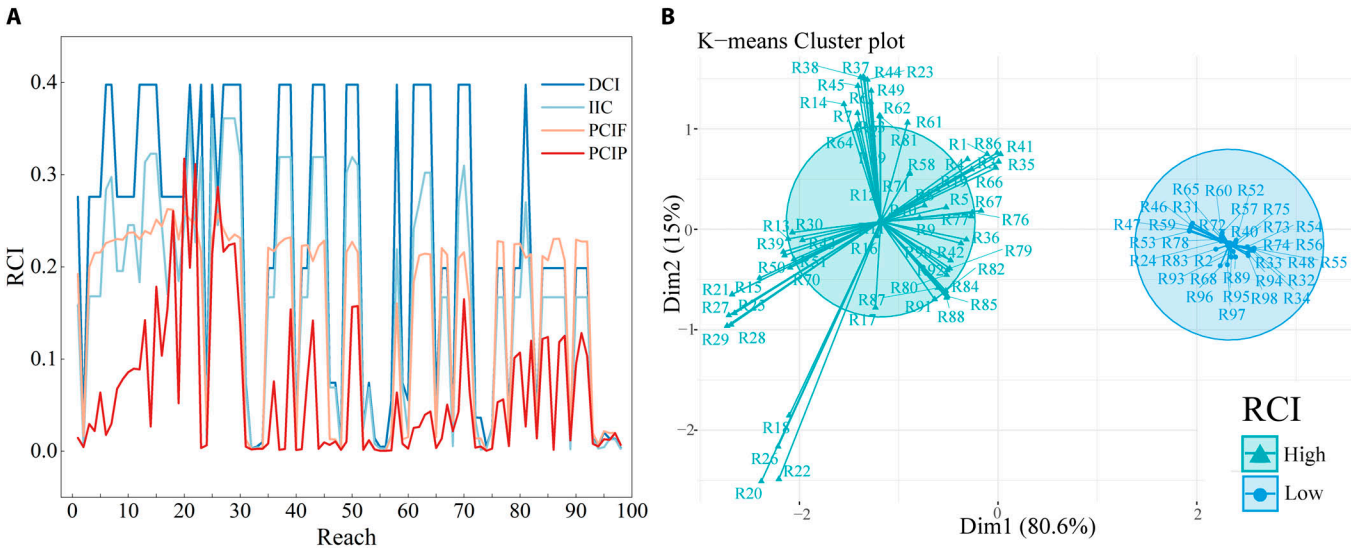

Fig. 3. Comparative analysis of RCI for different settings. (A) Comparison of RCI trend changes in different river reaches. (B) K-means clustering analysis of different RCI. DCI, dendritic connectivity index; IIC, integral index of connectivity; PCIF, population connectivity index of fish; PCIP, population connectivity index of passive organism.

results underscore the importance of employing precise connectivity indices to evaluate river connectivity–biome relationships.

Most current river restoration efforts focus on modifying channel morphology or enhancing habitats; however, these approaches often yield limited success in restoring biodiversity and associated species [32]. Consequently, there is a growing consensus among scientists for a process-based restoration approach that emphasizes reconnecting rivers and restoring essential physical and ecological processes to improve ecosystem function and stability [33]. Our study provides empirical support for this approach by moving beyond single-species or single-trophic-level assessments. By simultaneously evaluating the responses of benthic, planktonic, and microbial communities to connectivity gradients, our work offers a more comprehensive, multitrophic perspective on how restoration of connectivity can influence entire ecosystem structure. The framework and findings from the Yongding River case study, particularly the varied sensitivities observed across trophic levels, can inform more predictive and effective restoration strategies in other regulated river systems.

Assessment differences in river connectivity indices

The results indicate that different connectivity indices exhibit distinct patterns in river connectivity assessment. These differences carry clear ecological implications, reflecting the theoretical foundations and evaluation perspectives underlying each index. As a typical structural connectivity index, DCI yields the highest values, primarily capturing the physical configuration of the river network and the distribution of reach lengths [6]. It represents the system's maximum potential connectivity under idealized conditions. IIC, also a structural metric, incorporates a dispersal distance parameter, resulting in generally lower estimates than the DCI and offering a more realistic reflection of distance-limited connectivity in ecological systems. In contrast, functional connectivity indices (PCIF and PCIP) further integrate species-specific ecological traits, but their differing dispersal simulation methods lead to discrepancies in outcomes [30]. Overall, structural connectivity provides the physical foundation for functional connectivity, and its degradation often constrains the realization of ecological processes and functions [30]. However, the specific relationships between different connectivity indices and ecological processes remain insufficiently understood, representing an important direction for future research.

Given the conceptual and ecological distinctions among connectivity indices, their applicability should be determined by the specific research objectives and focal taxa [10]. In practical studies and conservation planning, it is essential to account for the target species dispersal capacity, habitat requirements, and the geomorphological characteristics of the river system when selecting appropriate indices. A well-chosen index can not only improve the identification of key barriers but also optimize conservation prioritization, thereby ensuring both the scientific robustness of research conclusions and the effectiveness of management actions.

Effects of river connectivity on organisms at different trophic levels

We observed that diatom richness was highly responsive to stream connectivity, decreasing as the RCI increased. Prior research has demonstrated that water flow management and dam construction markedly affect diatom richness, diversity, and community structure [34,35]. Dams alter river habitats, hydrological conditions, and key physical and chemical parameters, leading to notable shifts in diatom life forms and taxa, and consequently, marked differences in biodiversity [36]. Additionally, barriers impact plant communities by modifying flow regimes, thereby reducing dispersal capacity and altering dispersal timing [12]. In slow-moving habitats, trapped drifting propagules can interrupt hydraulic transport, potentially enhancing algal community richness [37]. This dispersal mechanism may influence both the establishment of populations and overall biodiversity. Moreover, increased RCI often correlates with higher flow velocity, which can physically dislodge diatom cells and reduce settlement, while enhanced nutrient dilution under high connectivity may intensify competition among algal species, further lowering diatom richness. Another possible mechanism is that vertical fragmentation reduces herbivore density and biomass, indirectly increasing

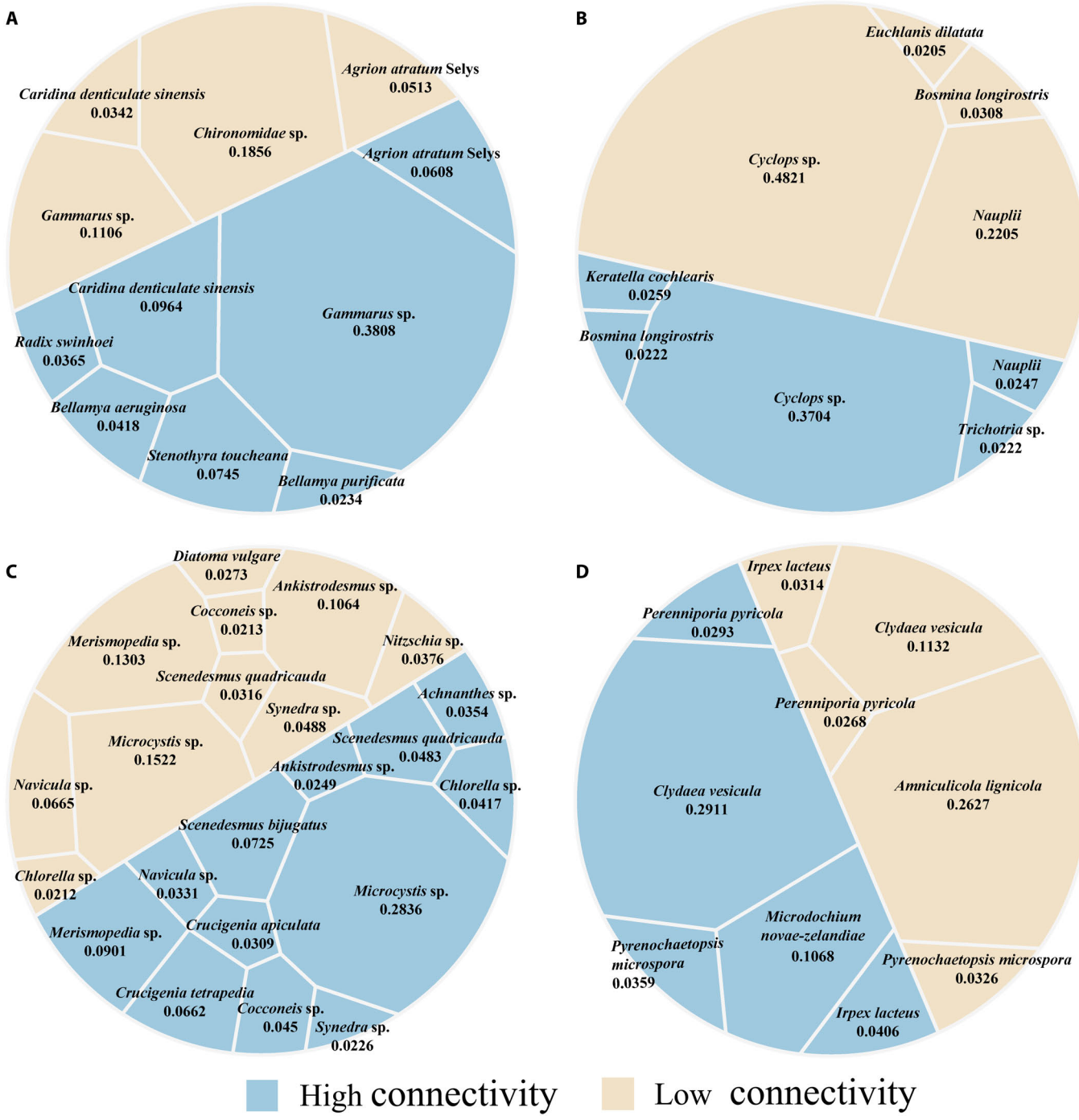

Fig. 4. Effects of river connectivity on aquatic species composition. (A) Benthos species composition. (B) Zooplankton species composition. (C) Phytoplankton species composition. (D) Fungi species composition.

diatom abundance under favorable conditions [38]. Furthermore, spatial heterogeneity maintained by connectivity is instrumental in shaping benthic community structure across various scales [39]. Connectivity has also been identified as a major driver of community change in the spatial structure of diatom assemblages in tropical water storage [40]. The functional characteristics of diatoms reflect longitudinal changes in water flow and ecological conditions, suggesting their potential to document hydrological connections between regions [41]. Diatoms may thus serve as useful indicators for assessing hydrologic connectivity and the success of river restoration efforts [42]. Given their pronounced response to hydrological change, diatom communities are powerful bioindicators of functional connectivity. We therefore recommend their integration into biomonitoring programs. Monitoring diatom community structure provides a clear and measurable way to assess the ecological impacts of fragmentation and to evaluate the effectiveness of connectivity restoration efforts (e.g., dam removal or modification). Such information supports adaptive management by enabling decisions to be refined based on monitoring feedback, ultimately promoting more effective

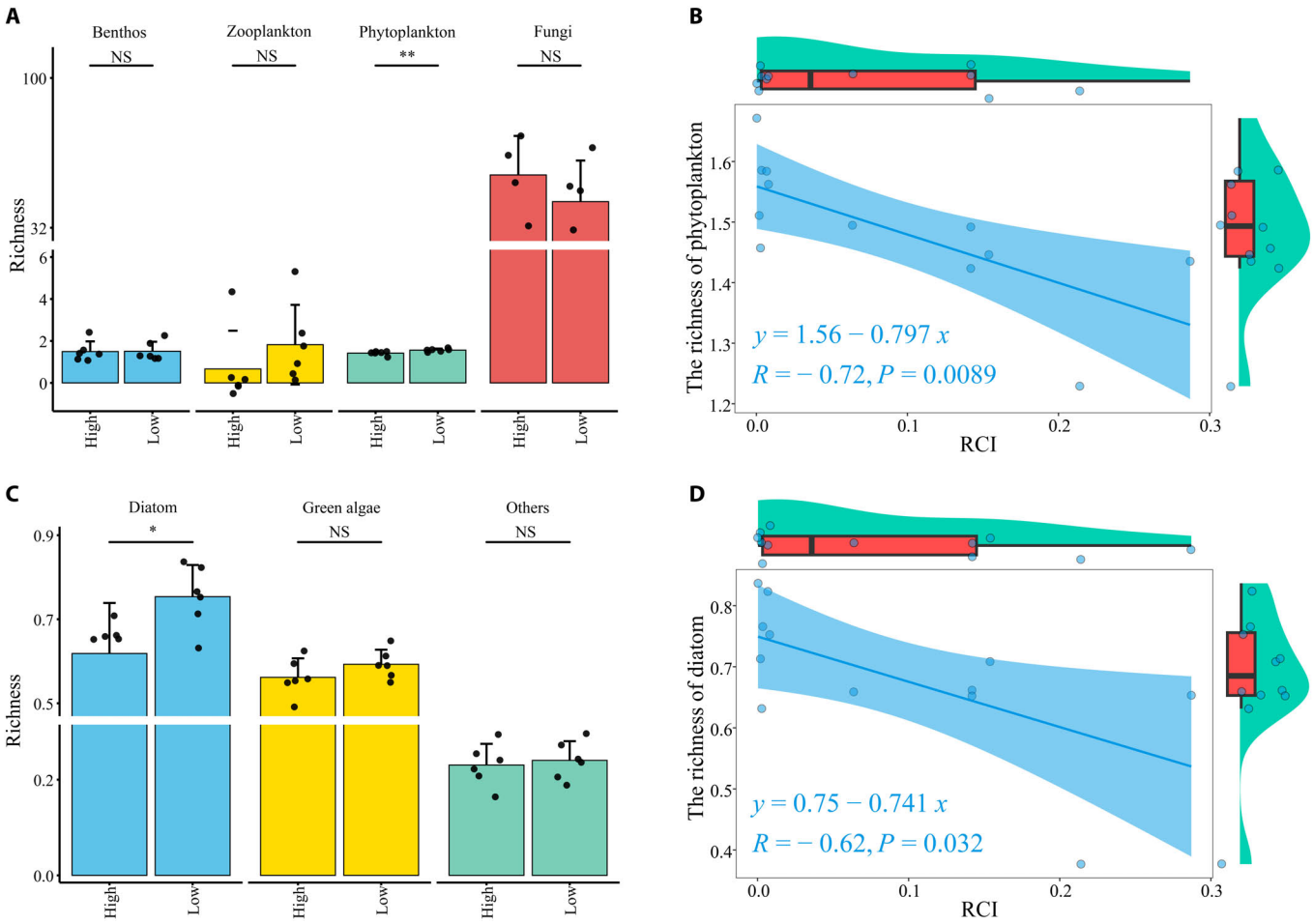

Fig. 5. Effects of river connectivity on aquatic organism richness. (A) Variability in the richness of different aquatic organism taxa under different river connectivity. (B) Changing trend of phytoplankton richness with RCI. (C) Difference in richness of different phytoplankton groups under different river connectivity. (D) Changing trend of diatom richness with RCI.

strategies to mitigate fragmentation impacts and improve river ecosystem health.

Moreover, organisms at different trophic levels exhibited varying responses to river connectivity. The variability in the dominant species composition of benthos, zooplankton, phytoplankton, and fungi under different connectivity conditions was 62.5%, 50%, 42.9%, and 33.3%, respectively. These results suggest that there is no simple, linear correlation between river connectivity and organismal responses. This complexity may be related to factors such as species composition, river geomorphology, topography, hydrology, dam operations, and hysteretic responses. Specifically, diatom responses may be mediated by interactions between flow regimes and nutrient availability, where higher connectivity increases flushing and nutrient mixing, potentially disadvantaging slower-growing or competitively weaker diatom taxa. For groups such as fungi and zooplankton, their relatively weak responses to RCI may be explained by indirect trophic interactions, where changes in phytoplankton communities propagate through the food web but attenuate along the cascade. More research is needed to elucidate the interrelationships among these variables [43]. While earlier research have documented substantial losses in mollusk and zooplankton diversity due to disruptions in lake–river connectivity [44], our investigation did not observe this pattern. This discrepancy may stem from differences in study systems; many previous studies focused on river–floodplain systems that emphasize lateral connectivity, while the responses of freshwater organisms to river connectivity can vary with climatic zone, elevation, and proximity to dams [13]. Riverine ecosystem alterations are often the result of multiple, interacting impact mechanisms. One plausible mechanism is the trophic cascade effect [45]. Drawing from both upward and downward food chain dynamics, we hypothesize that alterations in phytoplankton communities due to river connectivity changes can cascade to affect benthic, zooplankton, and fungal communities. Further research on these dynamics is necessary to better understand the impacts of river fragmentation on freshwater biodiversity, ecosystem functioning, and human well-being.

Implications for river connectivity restoration

Quantifying river connectivity is a critical first step in freshwater biodiversity conservation. Discussions should now focus on how to effectively restore river connectivity. Restoring connectivity has increasingly been recognized as a viable option for improving aquatic ecological health and promoting population recovery [46]. Although barrier removal has proven effective in restoring stream continuity, limited restoration resources necessitate a prioritization strategy for dam removal [6,9].

Here, we discuss the sequencing strategy for connectivity restoration in the Yongding River. Our results show that removing barriers on the mainstem brings the greatest improvement

in connectivity compared with removing barriers on tributaries (Fig. 6). This suggests that the mainstem should be the first priority for ecological restoration. However, management decisions are often limited by economic and social feasibility. The removal of large barriers can be costly, technically difficult, and hard to coordinate among stakeholders. In contrast, removing several small barriers may be more cost-effective and can provide measurable short-term gains, even though each individual contribution is small [47,48]. These 2 approaches are not in conflict but can complement each other. Removing mainstem barriers is the scientific priority for achieving substantial ecological benefits. At the same time, removing smaller barriers provides a practical pathway for phased restoration under real-world constraints. Therefore, effective biodiversity conservation requires that connectivity management follows ecological priorities while also considering costs, social needs, and regional goals.

The Yongding River study revealed both the sensitivity and variability of different freshwater taxa to changes in river connectivity. This variability necessitates consideration of the specific needs of different taxa when designing river restoration strategies. Furthermore, quantifying river connectivity is essential for assessing dam prioritization, as it can help determine which barrier removals will most effectively enhance connectivity and provide a robust scientific basis for ecological restoration. Importantly, regional differences in river connectivity suggest that restoration plans should aim to optimize connectivity across entire river networks. The findings from the Yongding River case study are primarily based on local conditions, and their direct applicability to other regions may be limited. However, the methods and detailed observations presented here could offer a useful example for conducting similar assessments in other regulated river systems. This study adds to the understanding of connectivity–ecology relationships in heavily impacted temperate rivers and may support the development of more context-specific restoration strategies in comparable environments.

Limitations and future directions

It is important to acknowledge several limitations of this study. First, the relatively short monitoring period may not fully capture the long-term dynamics of biological communities in response to changes in connectivity. Second, while a purposive sampling strategy was employed to capture key hydrological and geomorphological gradients, the spatial resolution may be insufficient to represent the fine-grained heterogeneity across the entire river basin. Third, the scarcity of relevant studies conducted under comparable hydro-geomorphological contexts limits robust cross-system comparisons. Fourth, as a case study of the Yongding River, the findings may have limited applicability to river systems with distinctly different climatic, hydrological, or ecological conditions. Fifth, the sampling was confined to spring, summer, and autumn (April, June, and September) of 2024, lacking winter data. The freezing of the Yongding River in winter may alter connectivity conditions and biological communities, and thus, the exclusion of winter sampling may lead to an underestimation of the impact of seasonal dynamics on connectivity–biological relationships. Despite these limitations, this study establishes a valuable foundation for understanding connectivity–biota relationships in regulated temperate rivers. Future research should incorporate multiyear monitoring encompassing diverse hydrological cycles, including seasonal variations such as winter conditions, expand comparative analyses across broader geographical scales, and employ higher-density sampling networks to validate and refine the observed patterns at more localized scales. Furthermore, integrating advanced approaches such as molecular ecology (e.g., eDNA), ecological modeling, and remote sensing will be essential to achieve a mechanistic understanding of how connectivity restoration shapes ecosystems, thereby informing more effective management and restoration strategies across diverse riverine landscapes.

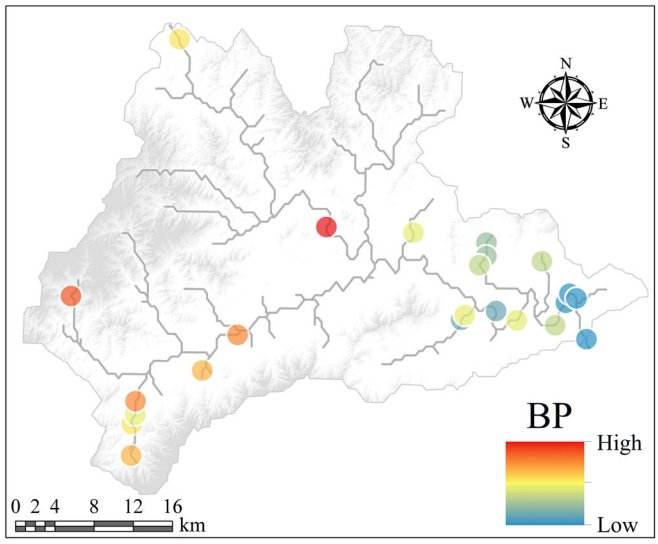

Fig. 6. Prioritization of barrier restorations in the Yongding river.

Conclusion

The Yongding River in China was utilized as the research site in this study. Through a combination of field surveys and model simulations, the effects of river connectivity on passive biological communities were synthesized through field surveys and model simulations. Notably, it was found that there were variations in the response of different biological taxa to river connectivity. Increased river connectivity showed a strong negative correlation with increased diatom richness, suggesting that increased river connectivity may reduce diatom richness, indicating that enhanced connectivity may, somewhat counterintuitively, reduce diatom diversity. These findings highlight the crucial role of river connectivity in shaping, rather than simply supporting, the diversity and integrity of freshwater ecosystems. From a management perspective, we further evaluate the order of priority removal of man-made obstacles for the optimization of river connectivity. Taken together, this research offers new insights into the impact of river connectivity on passive biological communities and offers recommendations for the sustainable management and restoration of river ecosystems.

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and methodology. S.Z.: Investigation. H.G.: Investigation. L.L.: Investigation. Z.Z.: Conceptualization, supervision, funding acquisition, writing—review and editing, and validation.
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Data Availability

Data are available on request from the authors.

Supplementary Materials

Figs. S1 to S3

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Response Mechanisms of Passive Biotic Communities to Changes in River Connectivity

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Rapid urban development has led to the anthropogenic disruption of natural river connectivity, posing unprecedented threats to aquatic biological communities. Understanding how river connectivity influences the structure of these communities is crucial, particularly in urban mountainous regions where this topic remains underexplored. Here, we assessed river connectivity in the Mother River of Beijing, one of the world's largest megacities, and analyzed its effects on the biodiversity, dominant species, and biomass of benthic fauna, zooplankton, phytoplankton, and fungi. Our results showed that the river connectivity index (RCI) ranged from 0.0003 to 0.3978, with higher connectivity observed in the middle reaches of the river. RCI values were distinctly categorized into 2 types: high connectivity and low connectivity. Organisms at different trophic levels exhibited varying responses to river connectivity, with the composition of dominant benthic species differing by 62.5% between connectivity conditions, a higher variation than that observed in other taxa. Notably, diatom richness displayed significant spatial heterogeneity and was strongly negatively correlated with RCI. Our findings demonstrate that river connectivity exerts taxon-specific effects across multiple trophic levels, underscoring the need to consider both faunal diversity gains and potential diatom losses when designing urban river restoration and conservation strategies.
Image

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