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Hydrological variation between dam-induced different backwaters intensifies dispersal limitation among riparian plant communities

Jinxia Huang · Wanyu Wang · Reija Hietala · Shengjun Wu · Maohua Ma

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Abstract Unimpeded river flow is indispensable for species migration, yet dam constructions disrupt this process. Although river discontinuity has been studied across a dam, a comprehension of the ecological fragmentation caused by the reservoir backwaters behind a dam remains constrained. This study assessed the beta diversity, including taxonomy, dispersal traits, and phylogenetics, and analyzed their relationship with environmental and geographical distance in the Three Gorges Reservoir of southern China. The reservoir studied was divided longitudinally into three sections: stable backwater, fluctuating backwater, and an intercross section in between. The distance-decay effect was found most pronounced in the intercross section, illustrating how hydrological fragmentation between the backwaters causes ecological barriers along the reservoir of a dam. Furthermore, beta diversity of the species within a functional group characterized by the hydrochory dispersal trait was found a strong link to the distance-decay effect in the backwater intercross, pointing to the dispersal limitation of hydrochory is intensified. Our research emphasizes the importance of addressing the dispersal limitations of plant propagules arising from the fragmentation of flow patterns caused by the dam-induced different backwaters. This highlights the urgent need to enhance connectivity between the backwaters to mitigate ecological barriers, thereby aiding in the restoration of riverbanks.

Keywords Backwater · Beta diversity · Dispersal limitation · Plant community · Riparian habitat · Three Gorges Reservoir

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J. Huang
Chongqing Jiaotong University, Chongqing 400074, China
e-mail: huangjinxia@cigit.ac.cn

J. Huang · W. Wang · S. Wu · *Present Address:*
M. Ma (✉)
Chongqing Institute of Green and Intelligent Technology, Chinese Academy of Sciences, No.266 Fangzheng Ave., Shuitu Town, Beibei Dist., Chongqing 400714, China
e-mail: mamaohua@cigit.ac.cn

W. Wang
e-mail: wangwanyu21@mails.ucas.ac.cn

S. Wu
e-mail: wsj@cigit.ac.cn

R. Hietala
Pyhäjärvi Institute, Teollisuustie 4, 27510 Eura, Finland
e-mail: reija.hietala@pji.fi

Introduction

A free flow of a river is vital for riverscape connectivity, supporting diverse life forms and maintaining ecological equilibrium in watershed ecosystems. The

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River Continuum Concept (RCC) proposed by Vannote et al. (1980) introduced a framework for comprehending longitudinal variations in river ecosystems, emphasizing the continuum of biological and physical processes from headwaters to downstream reaches. This concept laid the foundation for understanding how factors such as flow regime and riparian vegetation influence ecological continuity along watercourses (Surmacz et al., 2024).

However, anthropogenic interventions in river hydrology, such as dam constructions, disrupt water flow continuity, thus leading to river fragmentation and hindering species dispersal. Thereby, Ward and Stanford (1995) proposed the Serial Discontinuity Concept (SDC) to address these disruptions, highlighting how dams alter river flow patterns, species migration, and habitat connectivity. In particular, the dispersal, distribution and composition of riparian vegetation are mostly affected along the dam-disrupted river (Wang et al., 2022). While studies have extensively explored the ecological impacts of dam constructions on downstream ecosystems of the rivers affected (Knott et al., 2024), there remains a significant gap in understanding whether and how the species migration along the upstream behind a dam could be disrupted.

One significant aspect of dam-induced alterations in the upstream is the creation of backwater effect within a reservoir (Zhang et al., 2023). The backwater effect refers to the dam upstream where the river hydrological patterns are changed due to the regulation of a dam. This effect is usually examined vertically, by identifying ecological impacts triggered by water-level changes (Liro et al., 2020). Yet, the longitudinal difference of reservoir backwaters may hint important ecological meaning but relatively neglected.

Longitudinally, the dam-induced backwaters can be fragmented into stable and fluctuating backwater. Since the stable backwater is close to dam, it is directly influence by dam operations, and often exhibits relatively stable changes of water-level throughout the year. In contrast, the fluctuating backwater extends from the end of the stable backwater section up to the tail end of the reservoir, experiencing the combined effects of reservoir regulation and natural flooding events coming from the upstream outside the reservoir (Li et al., 2023). Thus, the fluctuating backwaters are characterized by varying water-level, influenced not only by the dam but also by seasonal fluctuations in precipitation and flood.

Furthermore, the longitudinal fragmentation in reservoir backwaters, controlled by dam water levels, can intensify ecological dynamics (Poff and Zimmerman, 2010). Periodic water-level changes significantly affect riparian habitat structure, nutrient cycling, and species composition (Sha et al., 2015; Hu et al., 2019). Distinct hydrological characteristics of the backwaters may disrupt ecology and impact species movement and distribution (Burdis et al., 2020). For instance, the stable backwater provides consistent habitats for some species, aiding their establishment (Tan et al., 2019), but limits species adapted to dynamic environments, reducing genetic exchange and biodiversity (Lawson et al., 2015). Conversely, fluctuating backwater creates dynamic habitats; challenging for maladaptive species but advantageous for those adapted to variability, enhancing species diversity and ecosystem resilience (Van Veen and Sasidharan, 2021).

Despite the observable hydrological change within reservoirs, there is currently insufficient evidence to definitively establish the presence of river ecological connectivity behind the dam, particularly in terms of species dispersal limitations across the different backwaters. While the SDC posits that human alterations (Xie et al., 2024), such as dam construction, disrupt the natural species dispersal across a dam, applying this concept to the upstream behind the dam requires further empirical investigation. Therefore, this gap in knowledge prompts a critical research question: How do hydrological fragmentation induced by dams, particularly the formation of reservoirs and the resulting variations in backwaters, affect the turnover of riparian plant communities and species dispersal, thus contributing to ecological connectivity within the reservoir?

Beta diversity serves as a crucial ecological proxy for understanding community turnover and species dispersal along rivers, which can quantify differences in species composition and structure between riparian plant communities (Legendre, 2014; Janauer et al., 2021). Baselga (2010) proposed that partition beta diversity into species turnover and nestedness components. These components are shaped by ecological processes such as competition and migration (Fu et al., 2019). Incorporating dispersal traits and phylogenetic beta diversity (Swenson, 2011; Si et al.,

2016) deepened insights into community structure and genetic relationships. In dam-affected rivers, such multifaceted beta diversity analyses are crucial for evaluating species dispersal and informing conservation strategies that preserve ecosystem integrity.

Habitat loss and fragmentation remain among the gravest threats to biodiversity (Zhao et al., 2021). Human-induced landscape changes, such as construction of dams, have reduced biodiversity and reshaped the composition of communities. This study examined these effects in the Three Gorges Reservoir (TGR) of China's Yangtze River. Before impoundment, the Three Gorges area supported rich flora and fauna, facilitating longitudinal and lateral migrations that sustained dynamic riparian communities (Su et al., 2022). However, the construction of the Three Gorges Dam (TGD) has significantly altered hydrological dynamics, which have significantly increased the fragmentation of riparian habitats, consequently changing the plant community composition and structure. In addition, as fragmentation increased, the dispersal limits of species was strongly affected (Jamoneau et al., 2012). While there is debate about the effectiveness of species passages around the dam, the impact on plant propagule migration within the reservoir has been understudied. Despite recognizing that ecological passages might not fully address the impacts of backwaters on river connectivity (Knott et al., 2024), conclusive evidence is still lacking. Hence, further research is crucial to understand the ecological impacts of dam-induced backwaters, which is vital for restoring dam-affected riverbank habitats.

Motivated by these considerations, the current research seeks to explore if and in what ways ecological barrier is affected by the backwater fragmentation in a reservoir, specifically by examining the beta diversity among riparian plant communities along the TGR. By integrating the Serial Discontinuity Concept (SDC) with the backwater effect across three distinct hydrological sections, we hypothesize that the hydrological difference between backwaters may create ecological barrier, which hinder the longitudinal dispersal of plant propagules, leading to spatial discontinuities in community structure. And these barriers, exacerbated by anthropogenic hydrological regulation, which restrict species dispersal and affect riparian community similarity throughout the reservoir, as depicted in a conceptual figure (Fig. 1). To test this hypothesis, this study aims to answer following three questions: (1) How do different backwaters impact the similarities between riparian communities? (2) How is beta diversity within different backwaters related to environmental and geographical distances between riparian communities? (3) To what extent and in what ways do plant dispersal traits play a role in the impact of different backwaters on beta diversity?

To make our hypothesis testable, we explicitly state three predictions for the three questions: (1) in the intercross section, where hydrological fluctuations are most pronounced, riparian community similarity will decline most steeply with distance, compared to

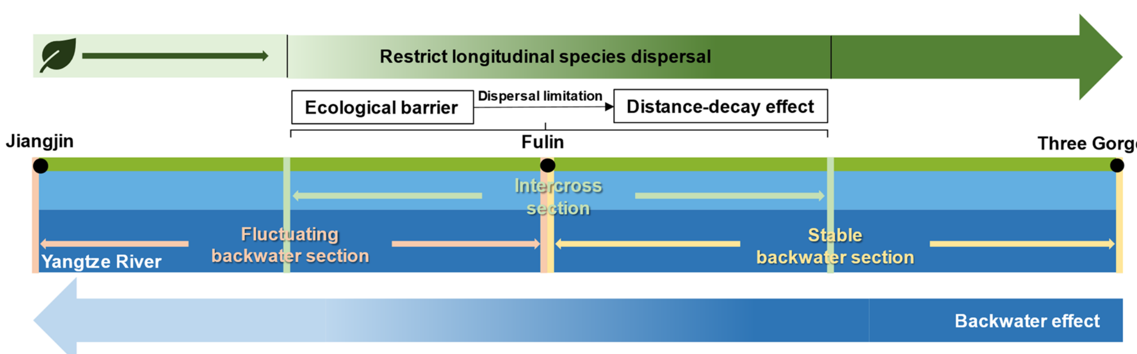

Fig. 1 This conceptual figure illustrates the study's hypothesis by dividing the reservoir into three longitudinal sections at Fuling District: stable backwater, fluctuating backwater, and an intercross section in between. (i) Blue gradient arrow indicates the diminishing backwater capacity from the reservoir head to its tail. (ii) Green gradient arrows depict the hypothesized intensification of restriction on longitudinal species dispersal in the intercross section, driven by dispersal limitation along the river

both the stable and fluctuating backwaters; (2) especially in the intercross section, geographical distance will explain more of the variation in beta diversity than environmental distance, reflecting a dominant dispersal limitation signal imposed by backwater fragmentation; (3) hydrochory functional group will show the strongest distance-decay effect, demonstrating that backwater-induced barriers severely impede plant propagule dispersal. Through empirical investigation and statistical analysis, this study contributes novel insights into the ecological connectivity in the dammed riverine ecosystems and inform strategies for their restoration and management.

Materials and methods

Study area

The study area (Fig. 2) is located in riparian habitats along the TGR. These habitats had been formed as a result of the TGD construction since 2006, positioned in the upstream region of the Yangtze River, within the Chongqing Municipality and Hubei Province in southern China (106°20′-110°30′ E, 29°16′-31°50′ N) (Fig. 2). Approximately two decades following the dam's establishment, there was a rapid degradation of vegetation within the original riparian habitats. Vegetation of the riparian habitats has been re-succeeding alongside the reservoir. This led to the eradication of perennial shrubs and trees, resulting in a simplified community structure and a noticeable prevalence of the species with strong dispersal abilities occurrences (Zhu et al., 2020). From the initiation of the dam

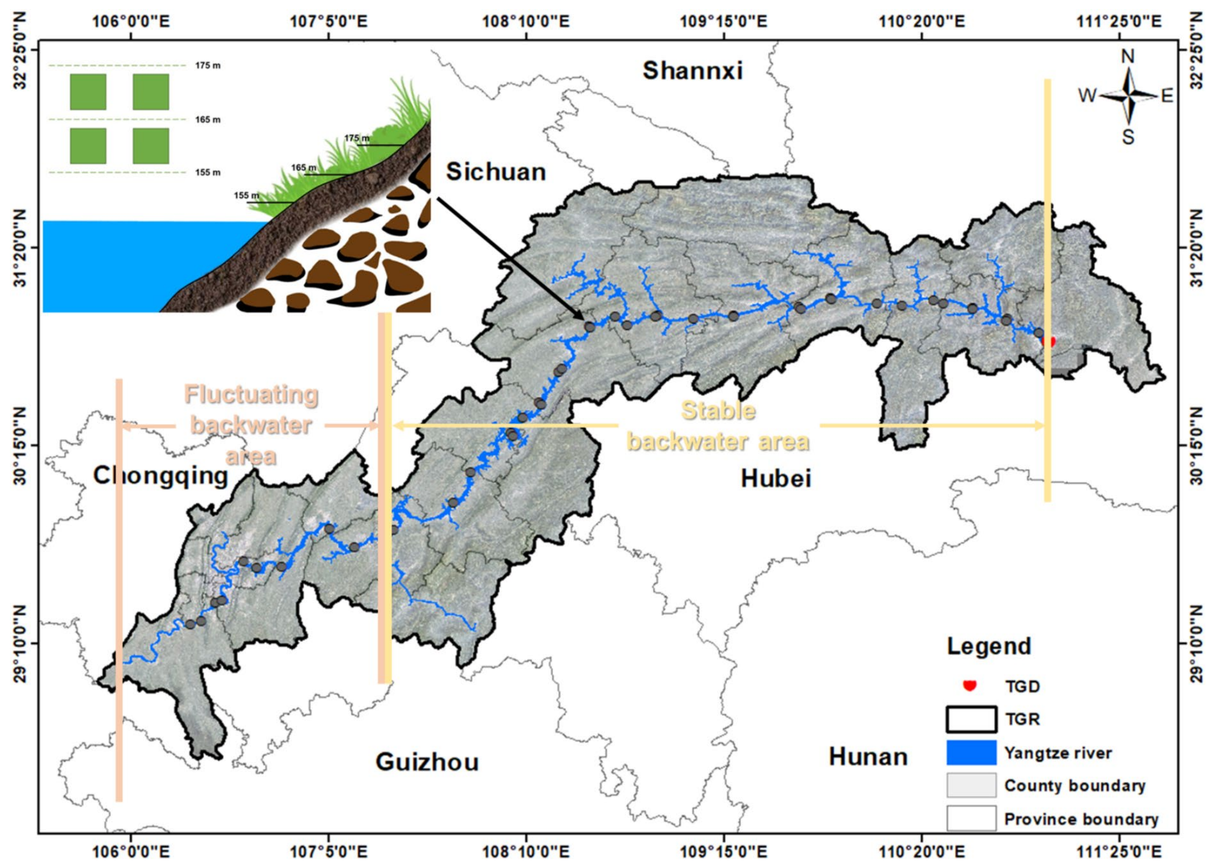

Fig. 2 Study area and sampling sites along the TGR. Each sampling site was situated at two different water-level: 155–165 m and 165–175 m

operation to the present, the community succession has been advancing to the herbaceous stage, primarily comprising annual and perennial herbaceous species (Yang et al., 2014; Zheng et al., 2021; Huang et al., 2024).

The riparian habitats emerge within the water-level fluctuation zones, characterized by a 30 m variance from 145 to 175 m.a.s.l (meters above sea level, hereinafter referred to as meters), extending over a distance of 661 km, and covering a total area of 349 km^2. The water-level varies periodically, rising and falling as controlled by the dam. During the period of low water-level, large area of exposed land in riparian habitats appears, allowing species to disperse into these opened habitats through a source-sink process.

Segments of reservoir backwaters

Due to hydrological changes triggered by the dam's operation, two distinct backwaters are emerging longitudinally. As identified by Su et al. (2012), the Fuling District serves as the boundary between the two backwaters (Fig. 2). The upstream from the Fuling to the dam is identified as the stable backwater, which is directly influenced by the dam and experiences stable periodic water-level changes from 145 to 175 m. The downstream, from the Jiangjin District at the tail end of the TGR to the Fuling district, is identified as the fluctuating backwater, where both natural flooding and dam regulation impact the river flow pattern and its riparian ecosystem.

Sampling design

Field surveys along the riparian habitats were conducted in July and August of 2021. Combined with high-resolution remote sensing images, considering vegetation growth and accessibility, a total of 43 survey sampling sites were set up on both sides of the reservoir of 661 km long behind the TGD (Fig. 2). To make the sampling data more comprehensive and representative, the selection of sites was based on stratified random sampling and taken steps to control for potential extraneous factors that might influence the results of the study by selecting sampling sites with similar soil types. In addition, terrain slope and surrounding land-use also kept similar.

Alongside the stable backwater, riparian habitats emerge within the water-level from 145 to 175 m. However, because of natural flooding events originating from upstream outside the reservoir, the fluctuating backwater typically cannot reach a water-level of 145–155 m. To maintain compatibility between different backwaters, in this study, at each sampling site, vegetation and soil samples were collected from the two water-level along the riparian habitats: 155–165 m (low water-level) and 165–175 m (high water-level), which are commonly observed across the backwaters. In addition, because of the dam regulation, the low water-level zone remains submerged for a longer period compared to the high water-level zone, resulting in a shorter plant growth period for the former and a longer growth period for the latter, as shown in Fig. 2. At each water-level, 2 quadrats of 1 × 1 m in size were established, making a total of 4 quadrats per site. However, at some sites where riparian vegetation remained highly homogeneous at the same water-level, we placed only one quadrat at that water-level to avoid redundant sampling. Across the riparian zones on both sides of the reservoir, 146 quadrats were distributed. These quadrats were positioned to minimize human disturbances. Additionally, a Real-Time Kinematic GPS was utilized to pinpoint the location of each quadrat and to document their altitudes in the field.

Furthermore, sampling sites were re-grouped based on the different backwaters. To further explore how varying hydrological patterns in the backwaters affect the beta diversity of plant communities, an intercross section was established between the two backwaters. Given that the length of the fluctuating backwater section is approximately 160 km in watercourse. To maintain consistency in length and the number of sampling sites for comparison among the different backwaters, in the subsequent analysis of this study, the range of re-grouped sampling sites was set to 160 km long in watercourse for both the stable backwater and the fluctuating backwater, as well as the intercross section (Fig. 3).

Water-level change across different backwaters

The Three Gorges Dam (TGD) has significantly altered the hydrological regimes, especially the water levels. Due to the regulation of the dam, difference in the water-level between the stable backwater and the intercross section is much smaller than it was before the dam's construction, particularly

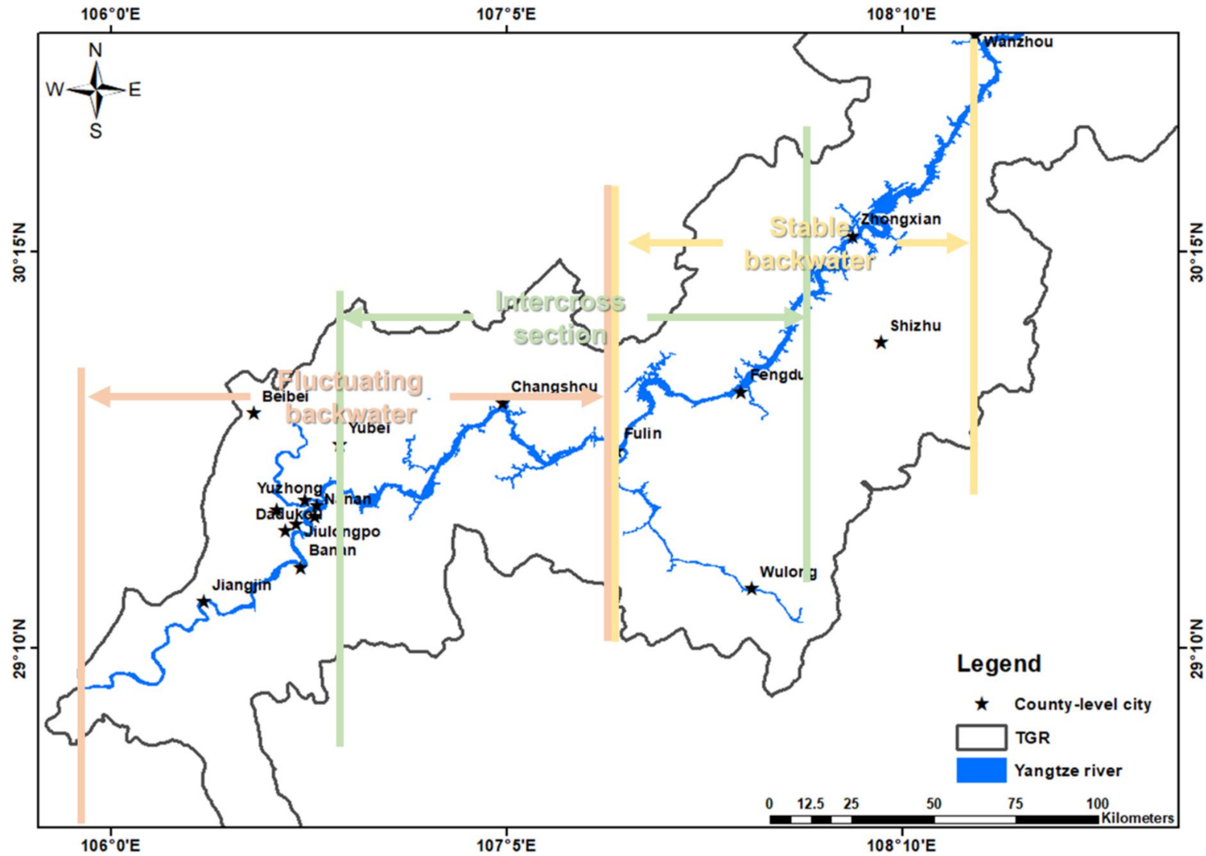

Fig. 3 The three divided backwater sections: fluctuating backwater, stable backwater, and the backwater intercross section along the TGR

during impoundment period (Fig. 4). However, the water-level in the fluctuating backwater consistently remains higher than that of the stable backwater and the intercross section.

Plant species and traits

In each quadrat, all plant species appeared were recorded, and the average height and coverage of each species were measured. The identification of plant species was carried out using the Flora Reipublicae Popularis Sinicae (http://www.iplant.cn/frps). According to a study by Fraaije et al. (2019) on the dispersal mechanisms of riparian plants, dispersal traits of plant propagules in the source-sink dynamic process were identified as key functional characteristics that influence the formation of riparian plant communities. Additionally, beta diversity is closely linked to species dispersal traits (Saito et al., 2015). As a result, this study focused on examining the dispersal traits of plants, as detailed in Table 1. The plant dispersal traits were gathered from various online trait databases: Biolflor (https://www.ufz.de/biolflor/index.jsp), the LEDA trait-base (https://uol.de/en/landeco/research/leda), and the Flora Reipublicae Popularis Sinicae (http://www.iplant.cn/frps). The surveyed species were subsequently categorized into different functional groups based on their dispersal traits.

Soil samples

In each quadrat, soil samples were collected by ring knife method, and soil bulk density, soil moisture, pH, Soil Organic Matter (SOM), Total Nitrogen (TN), Total Carbon (TC), Total Phosphorus (TP) and Total Potassium (TK) were measured in the laboratory. Soil samples were collected at the same time as

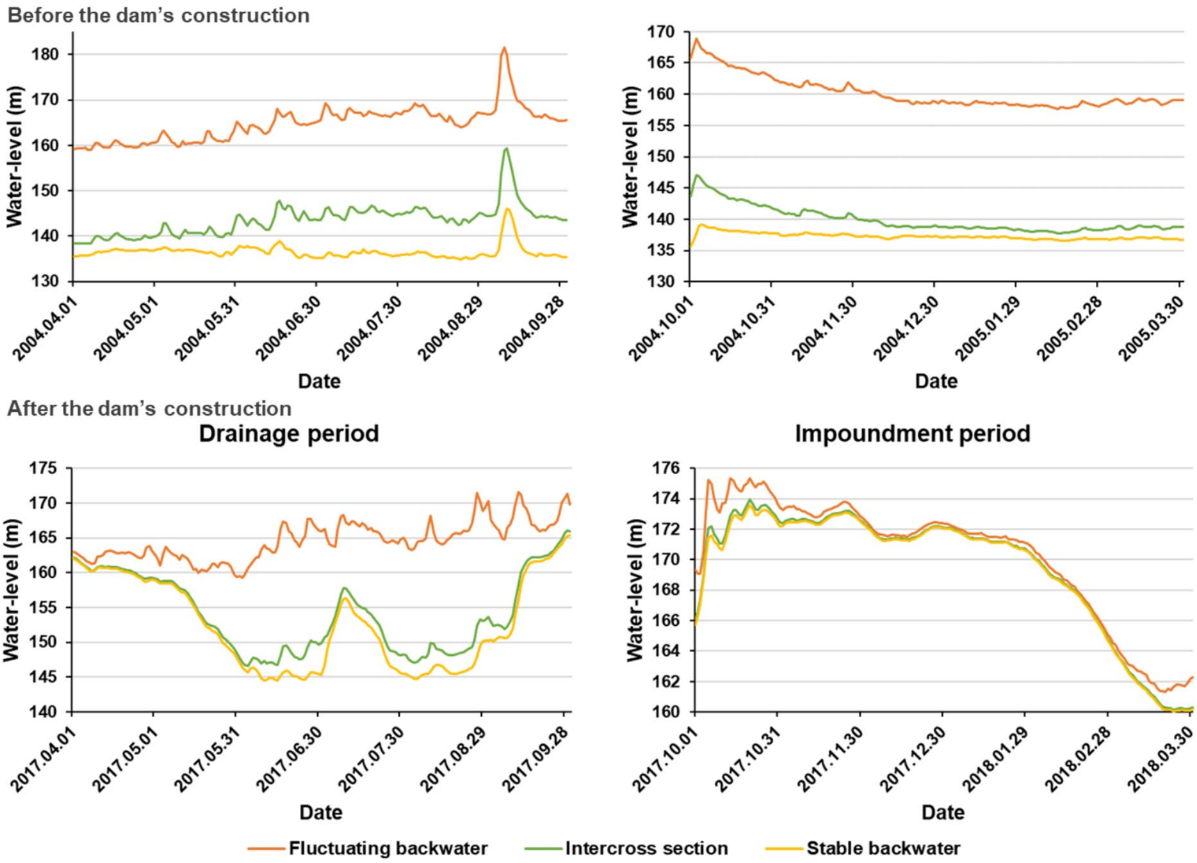

Fig. 4 The daily average water-level changes in stable, fluctuating and intercross backwater before and after TGD constructed. The data of the fluctuating backwater was from the Cuntan hydrological station (106°36′, 29°37′), the data of the stable backwater was from the Wanxian hydrological station (108°24′, 30°47′), and the data of the backwater intercross section between the two in the Fuling District was from the Qingxichang hydrological station (107°27′, 29°48′)

Table 1 Functional traits of the plant dispersal type in this study

Dispersal type	Description
Endozoochory	Diaspores inside the animal
Exozoochory	Diaspores carried on the outside by animal
Myrmecochory	Plants disperse seeds by ants
Anemochory	Plants disperse seeds by wind, which is common in arid and semiarid systems
Hydrochory	Seed dispersal by water, is especially common in species which colonize low-lying areas that are flooded for longer periods
Autochory	Plants are equipped with an autonomous mechanism involved in seed dispersal
Ballochory	Plants eject seeds through internal mechanical energy

the vegetation sample survey. In the 155–165 m and 165–175 m water-level of the riparian zone, the soil samples were taken according to the stratified random sampling method, by the plum blossom setting method in the range of 1 × 1 m. The 0–30 cm surface soil undisturbed soil was taken with a stratified sampler, and each sample was about 2 kg. Three parallels were collected every 10 cm depth of 100 cm^3 ordinary cutting ring sample for the determination of soil bulk density and soil moisture. Soil bulk samples were collected from 0 to 30 cm, and three parallel samples were collected at each 10 cm depth and then mixed to determine other physical and chemical indicators.

The soil bulk density was measured by ring knife weighing method. Soil moisture was measured by drying method, expressed by mass water content. The pH was extracted by 1:2.5 soil–water ratio and determined by composite electrode method. TC and TN were determined by elemental analyzer. TP and TK were determined by alkali fusion-molybdenum antimony anti-spectrophotometric method.

Beta diversity, environmental distance and geographical distance

The Bray–Curtis distance index was employed to quantify beta diversity, reflecting differences in species composition between plots, and this calculated three forms of beta diversity: taxonomic, dispersal trait, and phylogenetic. Beta diversity was further decomposed into turnover (βturn) and nestedness (βnest) components using the 'betapart' toolkit (Si et al., 2017).

Environmental distance among riparian plant communities was examined by standardizing soil data from sampling quadrats and converting them into a Euclidean distance matrix. Geographical distances between different riparian communities were determined using GPS coordinates to calculate watercourse distances in ArcGIS 10.7. The distance between plots at each water-level was calculated using the same method.

Statistical analysis

To analyze species composition differences, the distance-decay curve slope was measured by least squares regression of the log-transformed community similarity (1-Bray–Curtis distance index) against the log-transformed geographical distance, representing a changing rate of the community similarity.

And then, this study employed the Mantel test to investigate the relationship of environmental and geographical distance with beta diversity and its two components. The test compared the two distance matrices to evaluate their influence on compositional dissimilarities among various plant communities.

Finally, multiple regression on distance matrices (MRM) was employed to analyze the contribution effects of environmental and geographical distances on beta diversity. MRM extends the Mantel test by quantifying the explanatory power of multiple independent factors simultaneously. Here, beta diversity served as the dependent variable, and the two distance indices were the independent variables. Furthermore, by the MRM, we could perform variance partitioning analysis to further decompose the effects of the two distance indices on the dependent variable. This approach enabled us to determine their interaction effects and quantify the proportion of explained variance attributed to both the interaction and the unexplained components.

Results

Beta diversity and its relationship with environmental and geographical distance across the entire length of the reservoir

Throughout the entire reservoir, the geographical distance-decay effect on beta diversity was evident, with an especially pronounced effect observed at the high water-level (165–175 m) (Fig. 5; Online Appendix S1). The geographic distance-decay effect was further proved by the Mantel test. The results showed that at the high water-level, environmental and geographic distance showed a significant positive correlation with the taxonomic beta diversity (Table 2). In addition, geographic distance was more correlated with beta diversity than environmental distance. After decomposing beta diversity into turnover and nestedness components, it was found that geographic distance and environmental distance more readily influence species turnover between communities, whereas these distances overall exhibited no significant impact on nestedness component.

Beta diversity and its relationship with environmental and geographic distance across different backwaters

Based on the above analyses along the entire reservoir, beta diversity at the high water-level was more significantly correlated with geographical distance between communities. Therefore, the subsequent

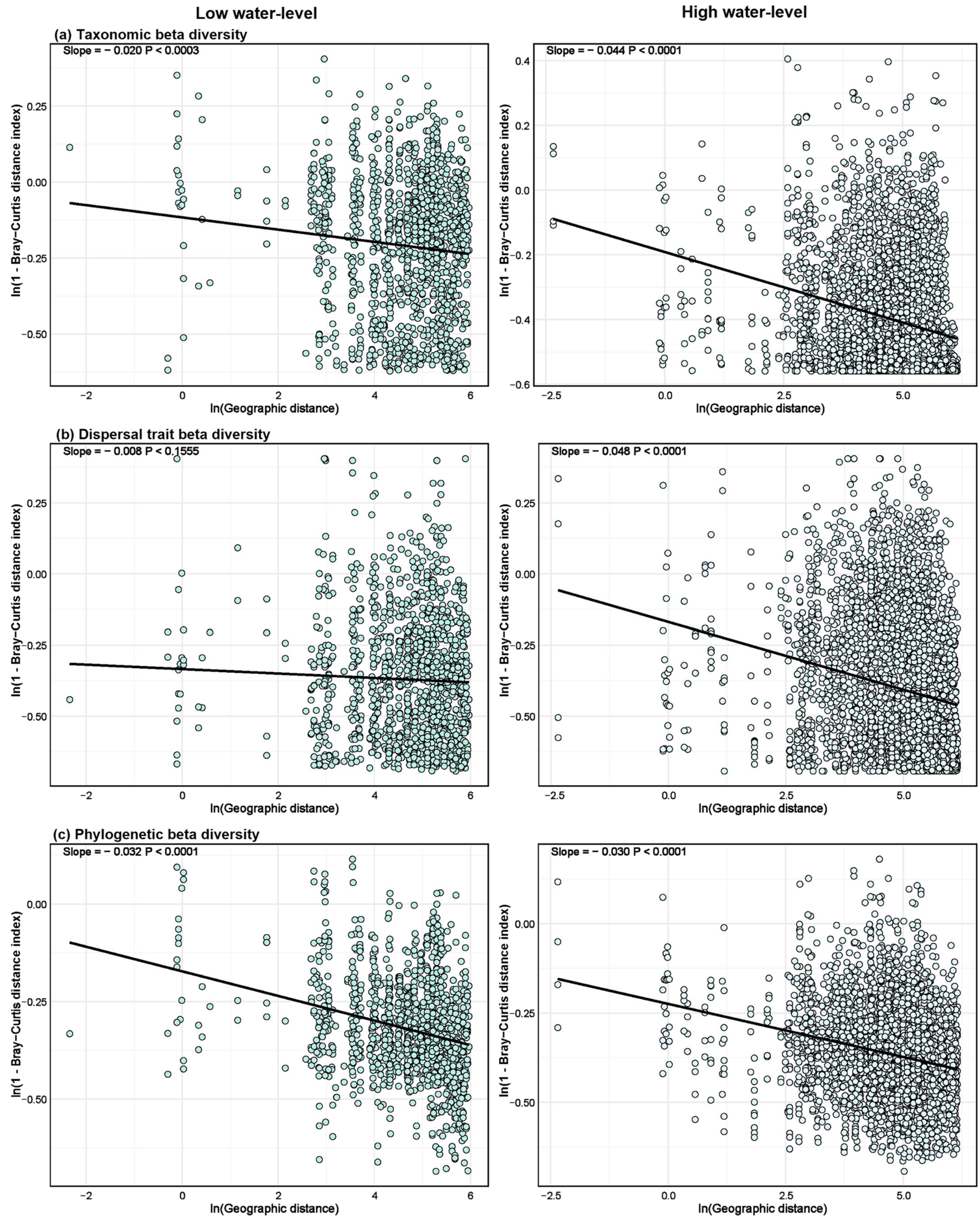

Fig. 5 The distance-decay curves of the beta diversity across the entire length of the reservoir

Table 2 Analysis of correlation of beta diversity with environmental and geographic distance by the Mantel test

Beta diversity	Water-level	Distance	Components of beta diversity		
			Total	Turnover	Nestedness
Taxonomic	Low	Environmental	-0.048^{NS}	-0.137^{NS}	0.171^{**}
		Geographic	0.076^{NS}	0.080^{NS}	-0.026^{NS}
	High	Environmental	0.175^{***}	0.141^{**}	-0.029^{NS}
		Geographic	0.379^{***}	0.372^{***}	-0.302^{NS}
Dispersal trait	Low	Environmental	0.039^{NS}	0.049^{NS}	-0.038^{NS}
		Geographic	0.059^{NS}	0.089^{*}	0.021^{NS}
	High	Environmental	0.088^{*}	0.107^{*}	-0.054^{NS}
		Geographic	0.264^{***}	0.289^{***}	-0.104^{NS}
Phylogenetic	Low	Environmental	0.095^{NS}	0.059^{NS}	0.029^{NS}
		Geographic	0.277^{***}	0.108^{*}	0.181^{***}
	High	Environmental	0.082^{*}	0.109^{*}	-0.045^{NS}
		Geographic	0.268^{***}	0.212^{***}	0.017^{NS}

$^{***}P < 0.001$
$^{**}P < 0.01$
$^{*}P < 0.05$
$^{NS}P > 0.05$

analysis of beta diversity focused on at the high water-level (Online Appendix S2).

Taxonomic similarity significantly declined with increasing geographical distance ($P < 0.0019$, $P < 0.0001$, Fig. 6a) in both the fluctuating backwater and intercross sections, especially in the intercross section, with a slope of 0.062 for the distance-decay curve. The Mantel test showed significant positive correlations between taxonomic beta diversity and both geographical and environmental distance in these sections, with geographical distance having a stronger correlation, particularly in the intercross section (Table 3). In stable backwater, only geographical distance significantly correlated with beta diversity. Analysis of beta diversity components revealed that species turnover alone significantly correlated with both distances, showing a more pronounced decay effect for geographical distance.

Dispersal-based beta diversity exhibited a similar distance-decay effect to the taxonomic beta diversity in both fluctuating backwater and intercross sections ($P < 0.02$, $P < 0.0023$, Fig. 6b), with the intercross section showing a steeper slope of 0.06 and a more pronounced distance-decay effect. Mantel test analysis revealed that within the intercross section, geographical distance had a significant positive correlation with both total beta diversity and turnover of dispersal traits (Table 3). In the other sections, no significant correlations were observed.

Analysis of the relationship between phylogenetic beta diversity and geographical distance revealed that only the backwater intercross section exhibited a distance-decay effect with a slope of 0.047 ($P < 0.0001$, Fig. 6c). Mantel test results further indicated that geographical distance was significantly positively correlated with both total and turnover components of phylogenetic beta diversity, with the strongest effect in the backwater intercross section, followed by the fluctuating backwater, and extended to the stable section as well (Table 3).

Beta diversity of the species within functional groups of dispersal traits across different backwaters

To explain the distance-decay effect, the beta diversity of taxonomic species within functional groups based on dispersal traits was analyzed across the three backwater sections (Fig. 7). A significant link was found between the beta diversity of hydrochory dispersal traits and the distance-decay effect, with the intercross section exhibiting the steepest slope, indicating the strongest distance-decay effect there.

Using MRM (Fig. 8), it was further analyzed how environmental differences, and geographical distances contribute to beta diversity and species turnover in the hydrochory dispersal trait across different backwater sections. Results highlighted that the distance-decay effect was most pronounced in the intercross section, with geographical distance being the most significant factor.

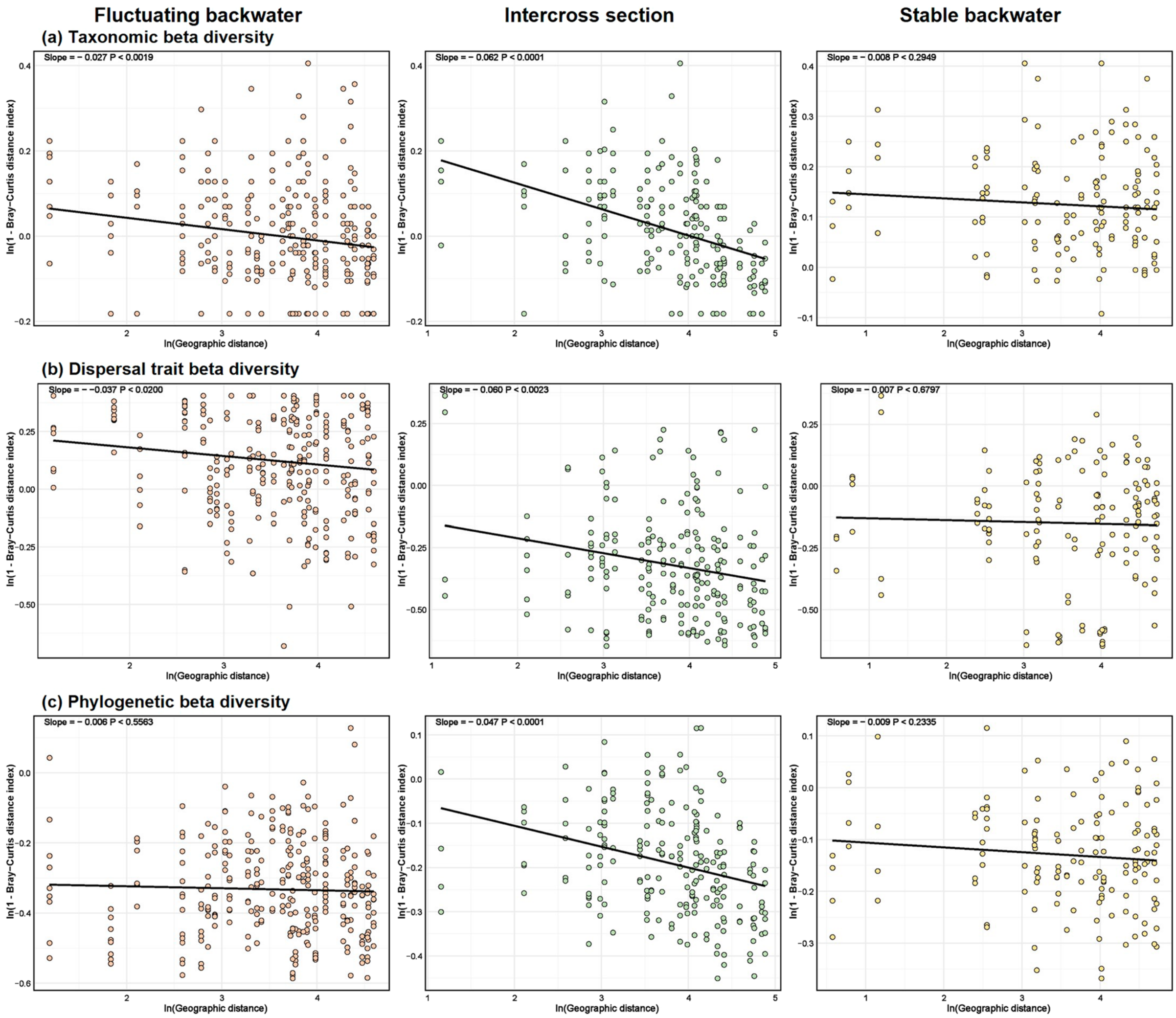

Fig. 6 The distance-decay curves of the beta diversity across different backwaters

Discussions

This study investigated beta diversity among riparian plant communities along the TGR on China's Yangtze River. The results demonstrated that beta diversity distribution is more influenced by spatial distance than environmental distance between the communities. This significant spatial signal was observed at the high impoundment water-level, particularly at the intercross section between stable and fluctuating backwater within the reservoir. Species turnover emerged as the primary component of beta diversity along the TGR. Further, this study revealed the presence of ecological fragmentation within the reservoir, especially across different backwaters, primarily due to limitations in hydrochory dispersal. The findings indicate that the various backwaters created by the dam lead to the fragmentation of riparian habitats, resulting in dispersal limitations within the reservoir.

Distance-decay effect is more pronounced at high impoundment water-level

The rise in water levels due to dam impoundment significantly relates to the geographical distance-decay of species turnover through a complex interaction of hydrological and ecological mechanisms. This phenomenon occurs because the variation in the

Table 3 Analysis of correlation of beta diversity with environmental and geographical distance by the Mantel test

Beta diversity	Backwater	Distance	Beta diversity		
			Total	Turnover	Nestedness
Taxonomic	Fluctuating	Environmental	0.157^{*}	0.179^{*}	-0.066^{NS}
		Geographic	0.325^{**}	0.262^{**}	-0.055^{NS}
	Intercross	Environmental	0.316^{**}	0.289^{**}	-0.149^{NS}
		Geographic	0.533^{***}	0.485^{***}	-0.229^{NS}
	Stable	Environmental	0.095^{NS}	0.161^{NS}	-0.166^{NS}
		Geographic	0.188^{*}	0.152^{*}	-0.050^{NS}
Dispersal trait	Fluctuating	Environmental	0.023^{NS}	0.002^{NS}	0.030^{NS}
		Geographic	-0.052^{NS}	-0.022^{NS}	-0.015^{NS}
	Intercross	Environmental	0.148^{NS}	0.146^{NS}	-0.032^{NS}
		Geographic	0.153^{*}	0.159^{*}	-0.014^{NS}
	Stable	Environmental	-0.175^{NS}	0.019^{NS}	-0.127^{NS}
		Geographic	-0.006^{NS}	0.158^{*}	-0.082^{NS}
Phylogenetic	Fluctuating	Environmental	-0.032^{NS}	0.009^{NS}	-0.017^{NS}
		Geographic	0.185^{*}	0.211^{**}	-0.095^{NS}
	Intercross	Environmental	0.073^{NS}	0.130^{NS}	-0.080^{NS}
		Geographic	0.405^{***}	0.339^{***}	0.037^{NS}
	Stable	Environmental	0.017^{NS}	0.103^{NS}	-0.144^{NS}
		Geographic	0.144^{*}	0.164^{*}	-0.111^{NS}

$^{***}P < 0.001$
$^{**}P < 0.01$
$^{*}P < 0.05$
$^{NS}P > 0.05$

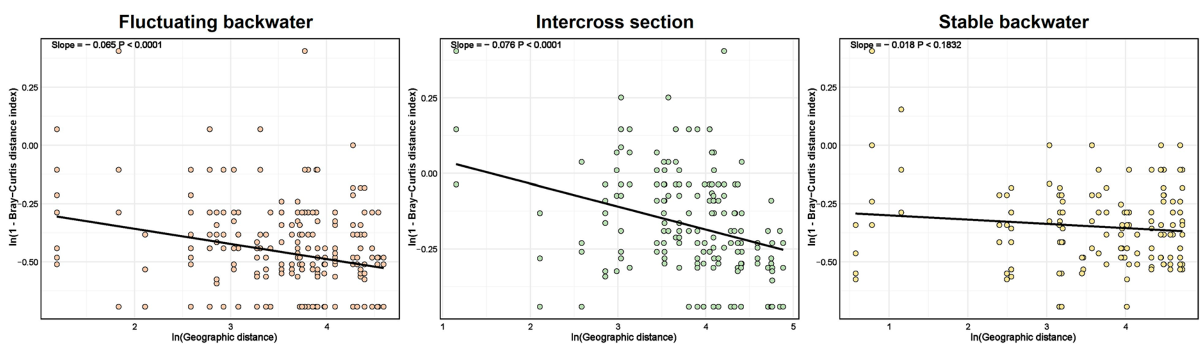

Fig. 7 The distance-decay curves of the beta diversity of the species within a functional group characterized by the hydrochory dispersal trait across different backwaters

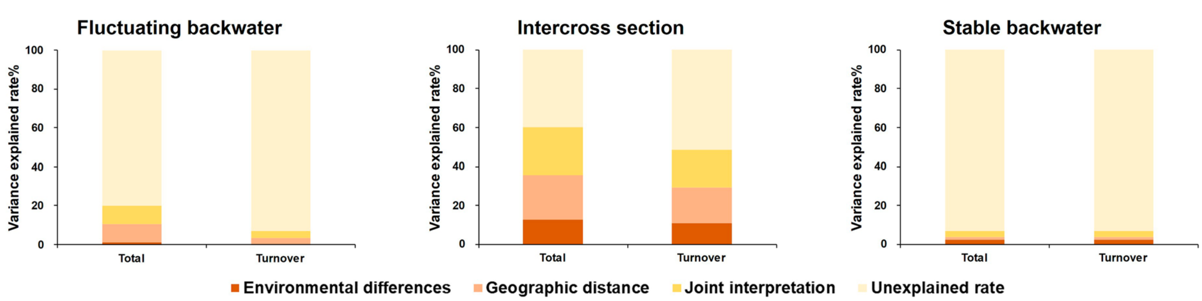

Fig. 8 Variance in beta diversity and its turnover component of the species within a functional group characterized by the hydrochory dispersal trait, as explained by environmental and geographical distance across different backwaters

impoundment water-level between the stable backwater section and intercross section decreases significantly compared to the variation before the dam was built, especially during the impoundment phase (Fig. 4). This altered flow pattern forms a barrier that obstructs dispersal. The impoundment phase takes place in autumn when most riparian species produce propagules, resulting in a concentrated dispersal period that amplifies the spatial effect. Additionally, as the reservoir's water-level rises, it inundates terrestrial and riparian habitats, transforming them into aquatic ecosystems. This inundation causes significant disruptions to existing plant communities, with annual species being particularly affected (Delgado et al., 2018). As a result, species turnover increases, leading to a more pronounced distance-decay effect. The inundation is also likely to create a heterogeneous mosaic of habitats that differ across spatial scales, thereby fostering distinct community compositions (Souza et al., 2021).

Moreover, given that the mean flow velocity significantly decreased from 2004 to 2010 (Liu et al., 2024), the reduced flow speeds during the impoundment phase further exacerbate the distance-decay effect. The fluctuating backwaters are more susceptible to natural flooding events, which introduce additional variability in the water-level and flow dynamics. Such natural disturbances can engender ephemeral habitats and opportunities for a diverse array of species to colonize and establish. The interaction between the stable conditions proximal to the dam and the dynamic condition in the fluctuating backwaters creates a mosaic of habitats with varied species compositions, thereby intensifying the spatial signal.

Furthermore, this phenomenon may be attributed to a combination of elevated water-level, reduced flow velocities, pronounced flux variations, and the influence of natural flooding. These factors collectively foster highly dynamic and heterogeneous environments, which in turn promote elevated rates of species turnover and contribute to substantial spatial variation in beta diversity.

Distance-decay effect is intensified between the different backwaters

This study revealed a strong geographical distance-decay effect on beta diversity between different backwaters, indicating a hydrological fragmentation barrier. During the impoundment phase, similar water-level between stable backwaters and intercross sections act as a barrier to propagule dispersal from fluctuating backwaters downstream to stable backwaters. The observed decline in species similarity with increasing distance reflects dispersal processes across intercross section, with closer communities sharing more species due to spatial autocorrelation (Saade et al., 2022). This spatial effect functions as a spatial filter, influencing species turnover while having no significant impact on nestedness, thereby highlighting dispersal limitation (Wen et al., 2016).

The study aligns with observations in other riverine ecosystems, showing that beta diversity in hydrophyte plant communities were more strongly positive correlated with geographical distances (Bertuzzi et al., 2019). While niche-based theories suggest examining beta diversity responses to distances to understand local and regional processes (Mruzek et al., 2022), the strong spatial signal in this study indicates that dam-induced hydrological changes may override species sorting, thereby reducing the impact of environmental distance on beta diversity.

The spatial signal of distance-decay is particularly evident in dam-induced backwaters, thus alters hydrological regimes disrupts natural processes and isolate plant communities (Soons et al., 2017). Riparian habitats in fluctuating backwaters experience heterogeneous water levels, unlike the stable backwater areas (Li et al., 2023). Hydrological changes in the riverine ecosystem create diverse dispersal pathways for plant propagules (Fraaije et al., 2019), especially where dam-induced backwater converges with the natural longitudinal downstream flow. The resulting in-directional hydrological regime significantly constrains hydrochory dispersal, highlighting dam-induced hydrological discontinuities shape riparian community composition in reservoirs (Souza et al., 2019). These alterations influence biodiversity and community structures by modifying species migration. Consequently, hydrological fragmentation between the different backwaters significantly influences riparian community dynamics, indicating ecological discontinuity upstream of dams.

Dispersal limitation leads to distance-decay effect across the backwaters

This study identified a significant correlation between beta diversity of species within hydrochory functional group and geographical distance in the backwater intercross section. The findings suggest that limitations in hydrochory dispersal significantly shape observed patterns. Specifically, this finding underscores the pivotal role of hydrochory dispersal trait in determining the strong spatial signature across different backwaters.

When species turnover dominates beta diversity, it implies that differences in species composition between communities are primarily driven by species replacement rather than nestedness. Dispersal limitation restricts species movement across space, leading to variations in species composition among distant communities (Dallas et al., 2020). Barriers such as geographical features, habitat fragmentation, or inherent limitations in species' dispersal capabilities can impede effective dispersal over distances (González-Caro et al., 2021). Thus, a significant correlation between beta diversity and geographical distance, with turnover as the primary driver of beta diversity, supports the notion that dispersal limitation is a key factor in determining species composition patterns along the river. Our analysis of phylogenetic beta diversity provided further evidence that hydrological fragmentation affects the evolutionary structure of riparian communities. Specifically, we observed a distance-decay pattern in phylogenetic dissimilarities within the intercross section, indicating that reservoir-induced ecological barriers not only alter species turnover but may also shape how lineages assemble over evolutionary timescales.

Additionally, the concept of source-sink dynamics provides insight into how dispersal limitation contributes to ecological discontinuity in river systems (Jones, 2010). In contrast, source-sink dynamics involve organisms from a source population colonizing and establishing populations in distant areas, often facilitated by the water flow in river ecosystems (Merritt et al., 2010). Therefore, understanding source-sink dynamics and dispersal limitation is crucial for explaining the ecological discontinuities observed in river systems.

Moreover, when physical barriers obstruct dispersal, the colonization of new habitats is impeded, leading to ecological discontinuity (Sun et al., 2022). In a river system fragmented by dam-induced backwaters, species from upstream areas may be unable to disperse downstream, resulting in distinct communities with different species compositions above and below these barriers (Burdis et al., 2020). This lack of gene flow and colonization across barriers can cause genetic isolation and divergence between populations, further reinforcing ecological barriers.

Implications to riverbank restoration of the dam-affected river

There is presently considerable discourse concerning the dismantling of dams to rehabilitate riverscapes. Nevertheless, in developing countries, this strategy has not been extensively adopted due to a range of economic, energy, flood control, technical, and policy factors that underscore the importance of the functionalities afforded by existing dams. Consequently, initiatives along the dammed rivers are predominantly focused on riverbank restoration programs, in which the efficacy of mobile species passages designed to circumvent dams has been a topic of considerable discussion. This study underscores that river discontinuity can also manifest within the reservoir behind a dam, thereby highlighting the necessity for a comprehensive approach to river restoration and management. Such an approach should encompass not only the implementation of eco-friendly dam structures but also strategies aimed at addressing the fundamental causes of backwater variations (Liro et al., 2020). Measures such as modifying dam operations or restoring natural riverine processes can play a pivotal role in mitigating the impacts of river discontinuity on mobile species (Karatayev et al., 2020).

In particular, a national initiative was proposed to restore river ecosystem processes along the Three Gorges Reservoir. By adopting a more inclusive and ecologically sensitive approach, we can enhance the resilience of riverbank ecosystems and promote the long-term conservation of riparian biodiversity. In this context, constructing features like stepping-stones in the intercross sections of backwaters could be an effective strategy to enhance connectivity and facilitate species dispersal. Stepping-stones can serve as intermediate habitats, allowing species to move across fragmented riverscapes (Hannah et al., 2014), thereby mitigating the fragmentation created by fluctuating and stable backwaters.

Conclusions

This study reveals that the spatial signal was strongest in the intercross backwater section due to the dispersal limitation imposed by hydrochory. Our findings highlight an ecological barrier within the reservoir, particularly at the junction between distinct backwaters influenced by dam operations. Future experimental simulations will investigate the effects of various backwaters on propagule movements and trajectories.

This study extends the applicability of the SDC to the upstream of a dam, enhancing our understanding of river ecosystem responses to anthropogenic fragmentation. The results demonstrate the pivotal impact of hydrological fragmentation in altering species dispersal and connectivity along river ecosystems. Therefore, mitigating the barrier effects of river fragmentation induced by the dam backwaters requires ecologically informed dam regulation.

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Data availability Data will be made available on request.

Declarations

Conflict of interest The authors declare no conflict of interest.

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