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Research article

Integrating the flow regime and water quality effects into a niche-based metacommunity dynamics model for river ecosystems

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ABSTRACT

Aquatic community dynamics are closely dominated by flow regime and water quality conditions, which are increasingly threatened by dam regulation, water diversion, and nutrition pollution. However, further understanding of the ecological impacts of flow regime and water quality conditions on aquatic multi-population dynamics has rarely been integrated into existing ecological models. To address this issue, a new niche-based metacommunity dynamics model (MDM) is proposed. The MDM aims to simulate the coevolution processes of multiple populations under changing abiotic environments, pioneeringly applied to the mid-lower Han River, China. The quantile regression method was used for the first time to derive ecological niches and competition coefficients of the MDM, which are demonstrated to be reasonable by comparing them with the empirical evidence. Simulation results show that the Nash efficiency coefficients for fish, zooplankton, zoobenthos, and macrophytes are more than 0.64, while the Pearson correlation coefficients for them are no less than 0.71. Overall, the MDM performs effectively in simulating metacommunity dynamics. For all river stations, the average contributions of biological interaction, flow regime effects, and water quality effects to multi-population dynamics are 64%, 21%, and 15%, respectively, suggesting that the population dynamics are dominated by biological interaction. For upstream stations, the fish population is 8%–22% more responsive to flow regime alteration than other populations, while other populations are 9%–26% more responsive to changes in water quality conditions than fish. For downstream stations, flow regime effects on each population account for less than 1% due to more stable hydrological conditions. The innovative contribution of this study lies in proposing a multi-population model to quantify the effects of flow regime and water quality on aquatic community dynamics by incorporating multiple indicators of water quantity, water quality, and biomass. This work has potential for the ecological restoration of rivers at the ecosystem level. This study also highlights the importance of considering threshold and tipping point issues when analyzing the "water quantity-water quality-aquatic ecology" nexus in future works.

1. Introduction

With the globally increasing socioeconomic development by sacrificing the ecologically environmental benefits, there is an increasing worldwide social and political concern on sustainable freshwater ecosystems (Hillebrand et al., 2020; Kuriqi et al., 2021; Mlynski et al., 2021; Palmer et al., 2005). However, freshwater ecosystems, especially rivers, are increasingly threatened by dam regulation, water diversion, and nutrition pollution (Grill et al., 2019; Lu et al., 2021; Mor et al., 2018; Palmer and Ruhi, 2019). Consequently, hydrological characteristics and water quality are significantly altered, resulting in adverse

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Index of notations and abbreviations

Notations

N_i	density of population i [kg/d, cells/L, mg/L, or kg/m^2]
r_i	intrinsic growth rate of population i [month^{-1}]
K_i	environmental carrying capacity of population i [kg/d, cells/L, mg/L, or kg/m^2]
f	an environmental indicator
α_{ij}	integrated competitive coefficient of population j on population i
α_{ij}^f	competitive coefficient of population j on population i in terms of indicator f
J	total number of populations
M	total number of flow regime indicators
L	total number of water quality indicators
FR^m	value of the m-th flow regime indicator [m^3/s]
WQ^l	value of the l-th water quality indicator [°C, mg/L, or dimensionless]
z_i^m (z_i^l)	environmental optimum of population i to indicator m (l) [m^3/s, °C, mg/L, or dimensionless]
B_i^m (B_i^l)	niche breadth of population i along indicator m (l)
B_i^f	niche breadth of population i along the dimension of f
I_i	immigration of population i from elsewhere [kg/d/month, cells/L/month, mg/L/month, or kg/m^2/month]
E_i	actual emigration of population i to elsewhere [kg/d/month, cells/L/month, mg/L/month, or kg/m^2/month]
E_i^{up} (E_i^{down})	actual upward(downward) emigration of population i [kg/d/month, cells/L/month, mg/L/month, or kg/m^2/month]
$E_i^{'}$	theoretical emigration that is determined by the successful number of N_i draws from a binomial distribution $E_i^{'} \sim B(N_i, P_i)$ [kg/d/month, cells/L/month, mg/L/month, or kg/m^2/month]
O_i	unexplained variation in the density of population i [kg/d/month, cells/L/month, mg/L/month, or kg/m^2/month]
F	a certain environmental condition of f
F_{max} (F_{min})	maximum(minimum) value of f
ε	average discrete step size for the continuous range of [F_{min}, F_{max}]
P_i^F	probability that individuals of population i prefer the environmental condition range of [$F - \varepsilon$, F]
R	discrete number for the continuous variable f
w_i^{up} (w_i^{down})	weight of upward(downward) emigration of population i
L^{up} (L^{down})	geographical distance from the upstream(downstream) adjacent station [km]

Abbreviations

FRE(s)	flow regime effect(s)
WQE(s)	water quality effect(s)
MDM	metacommunity dynamics model
PDF	probability density function
NSE	Nash efficiency coefficient
r	Pearson correlation coefficient
Q	Discharge
AT	Air temperature
WT	Water temperature
pH	Potential of hydrogen
SS	Suspended solids
DO	Dissolved oxygen
COD_{Mn}	Chemical oxygen demand
BOD_5	Biochemical oxygen demand
SO_4	Sulphate
NH_3–N	Ammonia nitrogen
NO_2–N	Nitrite nitrogen
NO_3–N	Nitrate nitrogen
TP	Total phosphorous
F	Fluoride
Cl	Chloride
TH	Total hardness

effects on the aquatic community's function, structure, and dynamics (Benjankar et al., 2018; Sabzi et al., 2019). This has compelled relevant scholars to move from morphological to ecosystem-level "process-based" practices, which focus on dual efforts of restoring flow regimes and controlling water pollution to improve aquatic ecosystems (Geary et al., 2020; Joseph, 2020; Thompson et al., 2020). Thus, further understanding of both flow regime effects (FREs) and water quality effects (WQEs) in river ecosystems has been in high demand. FREs and WQEs refer to the ecological impacts of spatiotemporal changes in flow regime and water quality conditions on multi-population dynamics, respectively.

Existing studies have discussed that the structure and function of a riverine ecosystem, as well as many adaptations of its biota, largely depend on flow regime and water quality (Aspin et al., 2020; Baker et al., 2020; Harper et al., 2020; Nilsson and Renofalt, 2008; Palmer and Ruhi, 2019; Stoffels et al., 2020; Zhao et al., 2018). Variables related to flow regime (such as discharge and velocity) and water quality (such as water temperature and total phosphorous) constitute essential environmental factors affecting aquatic organisms. Annual changes in flow and water quality conditions play an important role in population dynamics by modifying reproductive success, natural flow, and biotic interactions (Dodds, 2007; Poff and Ward, 1989). From the perspective of flow regime, the magnitude, duration, timing, rate of change, and frequency of flow events are usually the key driving factors for maintaining the diversity of fish, phytoplankton, and invertebrates (Fornaroli et al., 2020; Wang et al., 2021b). Eutrophic flows can substantially alter species composition and abundance (Dodds, 2007; Lobera et al., 2017). It is essential to consider mitigation measures to preserve the riverine ecosystem, although the ecological impacts may not be similar in different regions and flow regimes. Among the mitigation measures, environmental flows are the most common way to ensure the good ecological status of the riverine ecosystem downstream of the water facilities (Kuriqi et al., 2019a). The renewed Brisbane declaration (Arthington et al., 2018) defines environmental flows as "the quantity, timing, and quality of freshwater flows and levels necessary to sustain aquatic ecosystems which, in turn, support human cultures, economies, sustainable livelihoods, and well-being." From this perspective, the implementation of environmental flows is an important means of protecting river ecosystems and mitigating the environmental impacts caused by human activities, particularly in fragile and shallow water ecosystems (Kuriqi et al., 2020). Environmental flows usually are set by considering the magnitude, frequency, duration, timing, and rate of change of flows released downstream of the diversion in order to achieve multiple objectives such as hydropower production, biodiversity conservation, surface and groundwater balance, water quality improvement, and a healthy hydrological cycle (Kuriqi et al., 2019b, 2021). Water managers strive to achieve an environmental flow regime that supports human uses and the essential geomorphological and biological processes needed for healthy river ecosystems (Mlynski et al., 2021). The flow-ecology relationships are essential to predict potential ecological consequences caused by the flow regime alteration. From the perspective of water quality, severely nutrient-polluted waters often accelerate the rampant growth of toxic cyanobacteria, which will pose a direct threat to the survival of aquatic organisms when the concentration of pollutants exceeds their tolerance limit (Zhang et al., 2009). Alterations in water quality (such as dissolved oxygen and organic compounds) can directly or indirectly affect the distribution and density of aquatic organisms. For instance, ecological responses of aquatic organisms to seasonal flow and water temperature variability may be confounded by alterations in water quality. Fluxes of organic compounds may swamp natural intra-annual fluctuations in the availability of environmental resources (Cook et al., 2018). Thus, the interaction between biotic and abiotic environments is the basis for understanding and managing aquatic ecosystems.

Historically, interactions, feedback, and dependencies between biotic and abiotic components of ecosystems remain issues. The information available to integrate the interaction between biotic and abiotic environments was so limited that it is challenging to predict nonlinear ecosystem dynamics. This strong demand for big data makes it challenging to build complex models (Geary et al., 2020), but this has gradually improved in the past ten years (Fournier et al., 2017; Gravel et al., 2006; Loreau et al., 2003; Shoemaker and Melbourne, 2016). For example, Thompson et al. (2020) proposed a general process-based metacommunity framework that unites local and regional scale theories of ecological community dynamics. Besides, the disciplines of hydrology, environment, and ecology have made significant progress in forecasting river runoff, water environmental capacity, and population dynamics. These relevant studies have laid the foundation for identifying the FREs and the WQE in river ecosystems. However, river regulation (flow regime related) and eutrophication (water quality related), two of the most pressing threats to global freshwater biodiversity, are often separately considered by researchers (Aspin et al., 2020; Palmer and Ruhi, 2019). Applied ecology has historically approached management using a simplified single-species or single-threat frame for decision problems (Geary et al., 2020), and the FREs and WQEs have less commonly been simultaneously included in existing ecological models, although each of these drivers is the subject of substantive bodies of literature. The experience of multiple failures considering only a single threat or a single species has prompted management at the ecosystem level. Therefore, it is not only necessary but also healthier to manage from a system level of "water quantity-water quality-aquatic ecology" nexus than from a single point of view which has been exposed as inadequate in ecological restoration, biodiversity conservation, and riverine management.

This study proposes a new niche-based metacommunity dynamics model (MDM) to identify the FREs and the WQEs in aquatic communities. A metacommunity is formalized as a set of local communities where multiple populations compete and can disperse among local communities distributed in space (Leibold et al., 2004). The novelty of the work is an attempt to quantify the effects of hydrological conditions and water quality changes on aquatic population dynamics, which provides the potential for ecological restoration of rivers at the ecosystem level. Such analyses that attempt to relate abiotic environment to ecological niche considering multiple indicators of water quantity, water quality, and biomass have not been conducted yet. Furthermore, this is a pioneering study under the current conditions of river ecosystems in China. This study focuses on achieving three main objectives: (1) to establish a new niche-based MDM to quantitatively describe the magnitude of the impacts of flow regime and water quality on aquatic community dynamics by incorporating multiple water quantity, water quality, and biomass indicators; (2) to evaluate the performance of the MDM in terms of both quantitative and qualitative levels, where the quantitative evaluation shows the fitness degree between simulated and observed values by using several commonly used effectiveness evaluation metrics, and the qualitative evaluation analyzes the reasonableness of multiple model parameters by comparing to empirical evidence; (3) to explain the differences in ecological responses of various aquatic organisms to flow regime and water quality from the perspective of different stations from upstream to downstream of a river.

2. Methodology

The schematic diagram of the methodology is presented in Fig. 1.

(1) In Section 2.1, a general metacommunity framework is introduced, and a detailed description of metacommunity dynamics is conducted. The metacommunity dynamics are driven by the joint contribution of biological interactions, influences of flow regime and water quality, and dispersal. This section provides a general understanding of metacommunity dynamics and lays the foundation for establishing the MDM.

(2) In Section 2.2, the time series of flow regime indicators, water quality indicators, and biomass are used as input data. The quantile regression method is used to estimate functional relationships among abiotic and biotic variables. Four function types (i.e., linear, quadratic, logarithmic, and exponential) are set for quantile regression because the statistical relationships between biotic and abiotic environmental indicators are complex. The model parameters will vary under different function types. The suitable function type for each pair of populations and environmental indicators is determined by evaluating the robustness of critical parameters of the quantile regression curves, such as coefficient and intercept. The environmental optimums, the niche breadths, and the competition coefficients under suitable function types are regarded as the final results. The FREs and WQEs are then calculated based on the above parameters and time series data. The MDM is finally established by incorporating a traditional multi-population model, FREs and WQEs, emigration, and immigration.

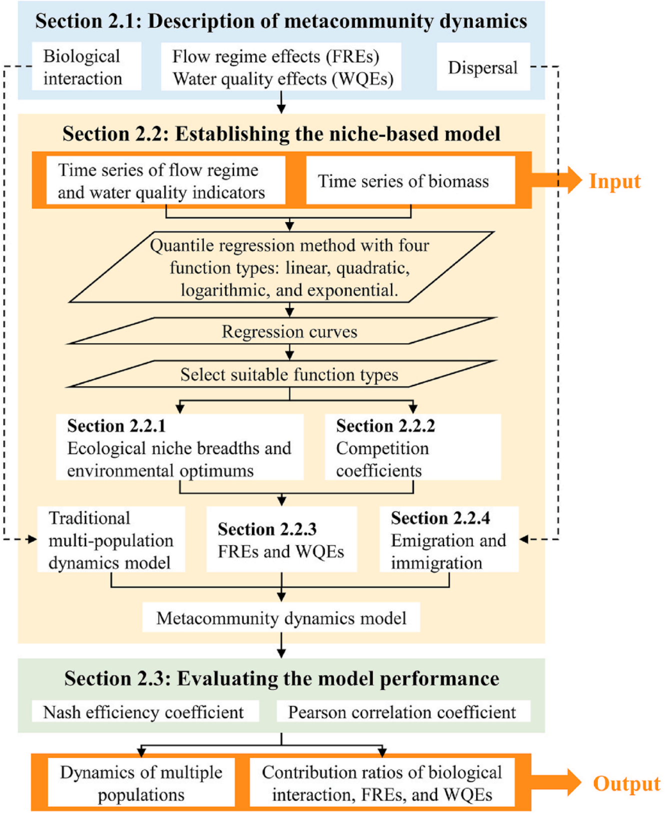

Fig. 1. Schematic diagram of the methodology.

(3) In Section 2.3, the evaluation method of the model performance is introduced. The model parameters are validated and calibrated according to the model performance. Finally, the MDM outputs the dynamics of multiple populations and the contribution ratios of biological interaction, FREs, and WQEs.

(4) In Section 2.4, the methodology limitations are clarified.

2.1. *Description of metacommunity dynamics*

Fig. 2 generally describes the metacommunity dynamics in a river ecosystem. For the river ecosystem, the abiotic and biotic environments closely interact via energy flow, nutrient cycle, and information transmission. Multiple water quality indicators (e.g., water temperature, chemical oxygen demand, and total phosphorous) and flow regime indicators (e.g., discharge and velocity) mainly constitute the abiotic environment. The flow regime and water quality conditions vary across time and space, so the population dynamics are consequently influenced. The multi-population dynamics with abiotic impacts differ from those occurring under biotic interactions. Biotic interactions denote the effect that various populations have on each other in a community. They include intraspecific relationships and interspecific relationships. Intraspecific refers to the relationship between individuals within the same population. Interspecific refers to the relationship among different populations (Dodds and Whiles, 2020). Local-scale community dynamics are strongly driven by biotic interactions influenced by intrinsic growth rate and competition. Density-independent abiotic environmental factors can alter the niche breadth of interacting populations, which modifies density-dependent biotic interactions by changing the competition coefficient (Ives and Cardinale, 2004).

Various upstream and downstream habitats are regarded as multiple local communities with functional connections. Dispersal connects these communities via immigration and emigration, with more individuals moving between close-by habitats.

2.2. *Establishing the niche-based model*

In the past decades, most niche-based metacommunity theories assume that intraspecific and interspecific competitions are equal (Fournier et al., 2017; Gravel et al., 2006; Liautaud et al., 2019; Loreau et al., 2003; Shoemaker and Melbourne, 2016). However, the local coexistence theory and empirical evidence showed that this is rarely the case (Adler et al., 2018; Chesson, 2000) because different species have different resource availability, resulting in density-dependent competition. The intensity of biotic interactions between populations and competitors largely depends on the overlap degree of resource use (i.e., niche overlap). Therefore, it is necessary to establish niche-based MDM, which closely links abiotic environment, niche, and competition. These three common core processes drive the metacommunity dynamics and are rooted in classic theory. The MDM can reveal how the flow regime and water quality affect the community dynamics by governing the niche breadth and competition coefficient. The MDM can be widely used in river ecosystems with multiple habitats from upstream to downstream.

The niche-based MDM is presented as follows for a population *i* of a local community (Thompson et al., 2020; Wang et al., 2021b):

$$\frac{dN_i}{dt} = r_i N_i \times \left[1 - \frac{N_i}{K_i} - \sum_{j=1, j\neq i}^{J} \alpha_{ij}\frac{N_j}{K_j} - \sum_{m=1}^{M}\left(1 - \exp\left(-\frac{\left(FR^m/z_i^m - 1\right)^2}{4\left(B_i^m\right)^2}\right)\right) - \sum_{l=1}^{L}\left(1 - \exp\left(-\frac{\left(WQ^l/z_i^l - 1\right)^2}{4\left(B_i^l\right)^2}\right)\right)\right] + I_i - E_i + O_i \tag{1}$$

where N_i denotes the density of population *i*, r_i denotes the intrinsic growth rate of population *i*, K_i denotes the environmental carrying capacity of population *i*, α_{ij} denotes the competitive coefficient of population *j* on population *i*, *J* is the total number of populations, *M* is the total number of flow regime indicators, FR^m denotes the value of the *m*-th flow regime indicator, z_i^m denotes the environmental optimum of population *i* to indicator *m*, B_i^m denotes the niche breadth of population *i* along indicator *m* that determines the rate at which growth is reduced by a mismatch between z_i^m and FR^m, *L* is the total number of water quality indicators, WQ^l denotes the value of the *l*-th water quality indicator, z_i^l denotes the environmental optimum of population *i* to indicator *l*, B_i^l denotes the niche breadth of population *i* along indicator *l* that determines the rate at which growth is reduced by a mismatch between z_i^l and WQ^l, I_i denotes the immigration of population *i* from elsewhere in the metacommunity, E_i denotes the emigration of population *i* to else-

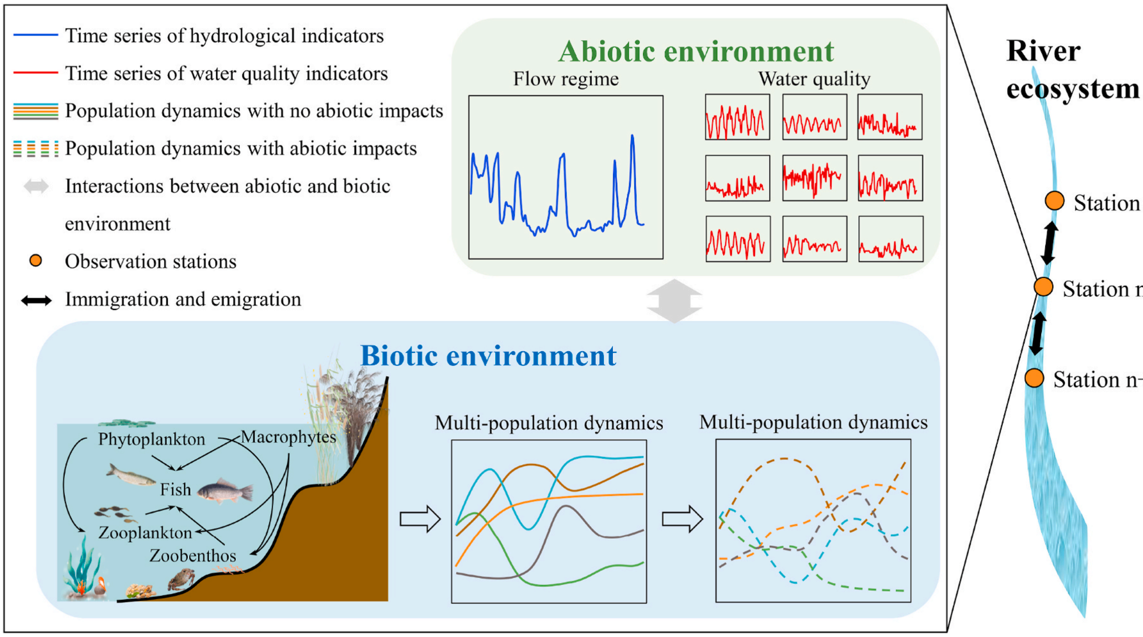

Fig. 2. A schematic representation of the metacommunity dynamics in the river ecosystem.

where in the metacommunity, and O_i accounts for unexplained variation in the density of population i (e.g., influence of human activities). Note that r_i, K_i, α_{ij}, z_i^m, B_i^m, z_i^l, B_i^l are constant values for population i to a specific environmental indicator, where B_i^m and B_i^l are both no less than 0 while no greater than 1. Also, note that FR^m and WQ^l are both no less than 0. In addition, the model involves three assumptions: (1) All individuals in the same population can survive independently and without differences. (2) The intrinsic growth rates and the environmental carrying capacities are constants. (3) There is no time lag in the response of individuals' actual growth rates to population dynamics.

2.2.1. *Ecological niches*

The concept of the ecological niche was introduced by Grinnell (1917) to describe the habitat requirements of a species to survive and reproduce. Afterward, the definition has been expanded in terms of multiple resources, biotic and abiotic interactions, and so on. Herein, the ecological niche of a population indicates its position within an ecosystem, describing both the range of abiotic environmental conditions it requires and its ecological role in the environment (Moore, 2013), which is not at odds with the previous definitions. The hydrological conditions, the trophic states, and the physical and chemical properties are considered in the river ecosystems.

The ecological niche can be viewed as an n-dimensional hypervolume, with each dimension corresponding to the suitable range of an environmental indicator. When the abiotic niche (i.e., B_i^m or B_i^l) is narrow, the population growth drops quickly if it is in suboptimal environmental conditions. Environmental heterogeneity will affect population growth less when the abiotic niche is broad.

The measurements of niche breadth have been developed for decades (Colwell and Futuyma, 1971; Feinsinger et al., 1981; Hurlbert, 1978; Levins, 2020; Petraitis, 1979; Schoener, 1974; Smith, 1982). Yet, the previous methods are not applicable to this study due to the non-discrete environmental resources (e.g., temperature) and the limitations of the observed data. A novel method of calculating the niche breadth is proposed to address this issue based on quantile regression. The rationalities of using the quantile regression method are clarified as follows: Firstly, it expands the sample information by estimating the statistical characteristics of the observed data. Secondly, quantile regression is widely used in the field of ecology due to its efficient performance in describing the distribution function between explained variables (e.g., biomass) and explanatory variables (e.g., abiotic environmental factors) in different quantiles (Fornaroli et al., 2020; George et al., 2021; White et al., 2021), especially for the case of multiple explanatory variables. Thirdly, it is a method for estimating functional relationships among variables for all the portions of a probability distribution (Fornaroli et al., 2020). For example, ecological responses of aquatic communities to seasonal flow variability may be confounded by coincident shifts in water quality (Cade and Noon, 2003). Then, the quantile regression is more robust than the ordinary least squares. Finally, quantile regression results are used to derive multiple parameters including ecological niches, environmental optimums, and competition coefficients for various populations.

As shown in the left panel of Fig. 3, the regression curves of different quantiles are obtained under a specific function type. The quantiles begin with 0.01 and end at 0.99 with a 0.01 increment, but the regression estimates are merely shown with 0.1, 0.3, 0.5, 0.7, and 0.9 quantiles for convenience of observation. For instance, The number of samples below the 0.9 quantile regression curve accounts for 90% of the total samples. The probability density function (PDF) of biomass along all quantiles at each environmental condition can be drawn based on the regression curves. The PDF is a function whose value at any given point in the sample space can be interpreted as providing a relative likelihood that the value of the random variable would be close to that sample (contributors, 2022). Each PDF peak refers to the maximum value where the biomass has the highest probability of occurrence. The PDF peaks of different environmental conditions are connected to obtain the integrated fitting curve (i.e., the solid red line in the middle panel of Fig. 3). The integrated fitting curve shows the variation of biomass occupying different environmental resource conditions. The maximum value of the integrated fitting curve denotes the environmental optimum where biomass reached its highest value. The probability that individuals of a population prefer a specific environmental condition can be illustrated by the area presented in the right panel of Fig. 3, which is calculated by:

$$P_i^F = \frac{\int_{F-\varepsilon}^{F} N_i df}{\int_{F_{min}}^{F_{max}} N_i df} \tag{2}$$

where N_i denotes the density of population i, f denotes an environmental indicator, F denotes a certain environmental condition of f, F_{max} denotes the maximum value of f, F_{min} denotes the minimum value of f, ε denotes the average discrete step size for the continuous range of $[F_{min}, F_{max}]$, and P_i^F denotes the probability that individuals of population i prefer the environmental condition range of $[F - \varepsilon, F]$. Note that ε is a minimal amount compared to the range of $[F_{min}, F_{max}]$.

The niche breadth of population i along the dimension of f is then calculated by:

$$B_i^f = \frac{1}{R \times \int \left(P_i^F\right)^2 df} \tag{3}$$

where R denotes the discrete number for the continuous variable f, and B_i^f indicates the niche breadth of population i along the dimension of f. The meanings of other variables are the same as that in Eq. (2).

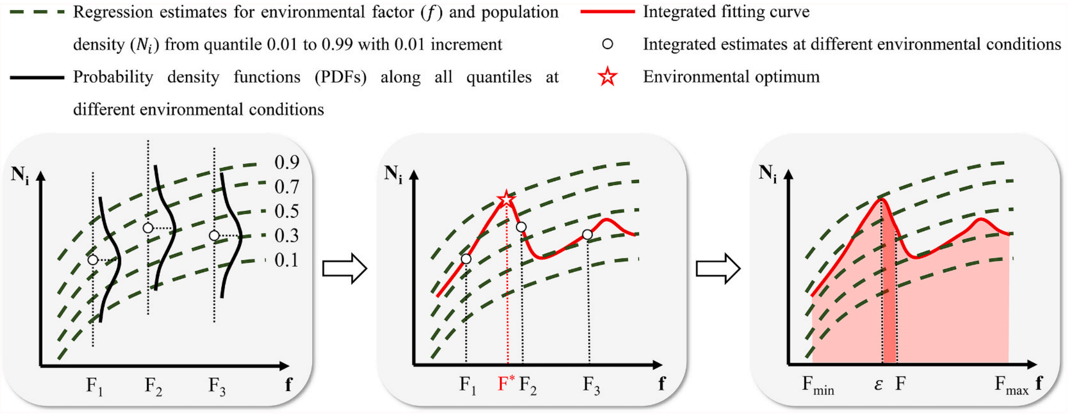

Fig. 3. Derivation of the ecological niche breadth. F_1, F_2, and F_3 are several environmental conditions of indicator f. $F^{'}$ indicates the environmental optimum. The ratio of dark red area to light red area indicates the probability that individuals prefer the environmental condition range of $[F - \varepsilon, F]$.

2.2.2. Competition coefficients

Various competitive scenarios are generated by different strengths of interspecific competition, which can vary with abiotic environmental conditions (Germain et al., 2018). Existing studies generally assume that the competition coefficients are fixed across time and space because different interspecific competition strengths with varying environmental conditions would dramatically complicate the population dynamics model. Despite this, the time-varying flow regime and water quality conditions are considered to derive a more specific competition coefficient between each pair of populations.

As shown in Fig. 4, each niche axis represents an independent environmental factor. Niche partitioning has been shown in many aquatic organisms. Theoretically, one population will exclude the other if they have the same niche, so the niches of coexisting populations can be similar but not identical. No competition will happen if the niches do not overlap each other. In contrast, competition may occur if one population's niche overlaps another. For instance, sunfish preferentially feed in open water, where they can gain the most energy, but the feeding area may shrink in the presence of a competitor (Vanni et al., 2009).

The niche overlap is usually used to evaluate competition coefficients in the famous Lotka-Volterra equation (May, 1975). However, competition may only necessarily be caused by overlap if the environmental resources are limited. This paper assumes that all environmental resources are limited and independent of each other. Other interspecific interactions except competition are not considered. The competition coefficient between each pair of populations can be obtained based on the niche overlap theory and quantile regression as follows (Li et al., 2006):

$$\alpha_{ij}^{f} = \frac{\int P_i^F P_j^F df}{\int \left(P_i^F\right)^2 df} \tag{4}$$

$$\alpha_{ij} = \sqrt{\sum_{f=1}^{M+L} \left(\alpha_{ij}^{f}\right)^2 \Big/ (M+L)} \tag{5}$$

where α_{ij}^{f} denotes the competitive coefficient of population j on population i in terms of indicator f, and α_{ij} denotes the integrated competitive coefficient of population j on population i by considering M flow regime indicators and L water quality indicators. Note that $\alpha_{ij}^{f} \neq \alpha_{ji}^{f}$, and $\alpha_{ij} \neq \alpha_{ji}$. The meanings of other variables are detailed in Eq. (1) and Eq. (2).

2.2.3. Flow regime and water quality effects

The abiotic environmental conditions (i.e., flow regime and water quality) vary in space and time, giving rise to influences on density-independent growth. The density-independent growth depends on the shape of abiotic niches, which are often thought to have a Gaussian shape, especially in population dynamics models (Thompson et al., 2020). Likewise, the FRE and the WQE are assumed to follow a Gaussian response curve over the abiotic environmental gradient in the metacommunity. FRE and WQE refer to the ecological impacts of each flow regime indicator and each water quality indicator on multi-population dynamics, respectively. FREs and WQEs are the accumulation of FRE and WQE, respectively. Finally, after repeated tests, the FRE and the WQE are determined by $1 - \exp\left(-\frac{(FR^m/z_i^m - 1)^2}{4(B_i^m)^2}\right)$ and $1 - \exp\left(-\frac{(WQ^l/z_i^l - 1)^2}{4(B_i^l)^2}\right)$, respectively. They are integrated into the MDM (i.e., Eq. (1)) to describe the cumulative effects of multiple abiotic environmental factors on population dynamics. Note that the form of $1 - \exp\left(-\frac{(FR^m/z_i^m - 1)^2}{4(B_i^m)^2}\right)$ is taken as the FRE but not the form of $\exp\left(-\frac{(FR^m/z_i^m - 1)^2}{4(B_i^m)^2}\right)$. The rationality of FRE is elaborated as follows for population i in terms of flow regime indicator m, while the rationality of WQE can be explained likewise:

FRE $= 0$ when the flow regime condition FR^m equals to the environmental optimum z_i^m. In this case, FR^m has no negative effect on population density growth. The FRE will be enhanced with increasing or decreasing FR^m.

$0 < \text{FRE} \leq 1 - \exp\left(-\frac{1}{4(B_i^m)^2}\right)$ when the flow regime condition FR^m is lower than the environmental optimum z_i^m. In this case, FRE decreases from $1 - \exp\left(-\frac{1}{4(B_i^m)^2}\right)$ to 0, with FR^m increasing from 0 to z_i^m. The negative effect on the population growth increases as FR^m decreases from z_i^m because the environmental condition gradually deviates from the environmental optimum. The broader niche (i.e., the larger B_i^m) represents the smaller FRE when FR^m equals 0 for different environmental indicators because the population is less sensitive to the environmental factors with broader niche compared to the narrower one.

$0 < \text{FRE} < 1$ when the flow regime condition FR^m is greater than the environmental optimum z_i^m. In this case, FRE increase from 0 to infinitely close to 1 as FR^m increases from z_i^m. The negative effect on the population growth increases to the maximum as FR^m increases from z_i^m to infinity, which can be interpreted as the environmental condition of infinite FR^m is no longer suitable for species to survive.

Each environmental factor plays an essential role in governing population dynamics. The population dynamics may not be able to withstand the harmful disturbance caused by one or two critical factors absurdly deviating from their environmental optimums. However, the environmental conditions of other factors are suitable for the population. Thus, the FREs of multiple environmental factors are accumulated rather than averaged, where the average cannot reflect the cumulative complexity of abiotic environmental conditions.

2.2.4. Emigration and immigration

Dispersal is incorporated via the emigration term E_i and the immigration term I_i. I_i can be derived by E_i of adjacent sites, and E_i is defined as follows for the concatenated metacommunity in the river ecosystem (Thompson et al., 2020):

$$E_i = E_i^{up} + E_i^{down} \tag{6}$$

$$E_i^{up} = E_i^{'} \exp\left(-w_i^{up} L^{up}\right) \tag{7}$$

$$E_i^{down} = E_i^{'} \exp\left(-w_i^{down} L^{down}\right) \tag{8}$$

where E_i denotes the actual emigration, E_i^{up} denotes the upward emigration, E_i^{down} denotes the downward emigration, $E_i^{'}$ denotes the

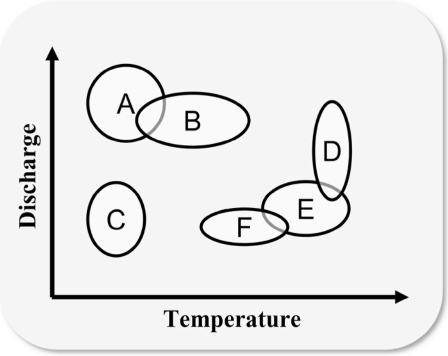

Fig. 4. Projection of six populations (A–F) onto two of the principal niches axes (discharge and temperature). The oval surrounding each population represents the region of the discharge and temperature space the population occupies. Ovals that overlap one another represent regions in which multiple populations compete for resources.

theoretical emigration that is determined by the successful number of N_i draws from a binomial distribution $E_i' \sim B(N_i, P_i)$, w_i^{up} is the weight of upward emigration, w_i^{down} is the weight of downward emigration, L^{up} is the geographical distance from the adjacent upstream station, and L^{down} is the geographical distance from the adjacent downstream station.

Please see **Sections S1, S2,** and **S3** for detailed descriptions of the emigration and immigration, the growth rate, and the environmental carrying capacity, respectively.

2.3. *Evaluating the model performance*

The evaluation of the MDM is conducted in terms of two aspects. One is the quantitative evaluation by calculating the Nash efficiency coefficient (NSE) and the Pearson correlation coefficient (r). The simulation performance can be preliminarily evaluated by comparing simulated and observed values. The other is the qualitative assessment by analyzing various variables, including niche breadth, environmental optimums, and competition coefficients. Then, the contribution ratio of the flow regime and water quality effects on metacommunity dynamics can be determined to further evaluate the model performance by comparing it with the empirical evidence.

2.4. *Limitations*

The study inevitably has limitations due to the complexity of aquatic ecosystems, model assumptions, and simplifications. First, this study ignores trait variation among individuals concerning their morphology, physiology, and behavior. All individuals in the same population are assumed to be equal. The methodology is consequently not applicable to long-term simulations (e.g., hundreds of years) because the heritable characteristics of biological populations change significantly during long-term evolutionary processes (Gregory, 2009). Then, the model simplications about niche distribution, competition, and dispersal will lead to relatively imprecise simulation results, but these simplications are commonly used in studies within the relevant field. More precise derivations for niche breadth, competition coefficients, and migration would be better in future works. In addition, the great demand for data complicates the pre-study work, and cumbersome data processing is needed to meet the model's requirements for data format.

Although these limitations may be significant for specific cases, they have a limited effect on the main findings and conclusions by considering the objectives of this study.

3. Materials and data

3.1. *Study area*

The Han River is the largest tributary of the Yangtze River, China. The middle and lower reaches of the Han River (Fig. 5), which is in a subtropical monsoon climatic zone, are selected as the study area due to its abundant water and aquatic biological resources. Six gage stations are set to observe the river's biomass, hydrological, and water quality data. The six stations from upstream to downstream are Huangjiagang, Xiangyang, Huangzhuang, Shayang, Xiantao, and Hanchuan, which can be regarded as multiple local communities linked by emigration and immigration. Please see **Section S4** for a more detailed description of the study area.

3.2. *Data*

Three categories of data are used in the MDM (please see Table S1). The data include five biomass indicators, one flow regime indicator, and fifteen water quality indicators. All the data are observed at the six stations along the mid-lower Han River. The time scale of the data is a month, where the biomass data are measured once a month, and the flow regime and water quality data are the monthly averages. The length of the data series varies by data category and station. The longest spans seven and a half years, and the shortest is one and a half years. The monitoring station placement, sampling programs, and analytical methods for each type of data are detailed in "Regulation for Water Environmental Monitoring (SL 219–2013)" and will not be repeated in this paper due to space limitations and data complexity. Inevitable errors may exist in the data due to different measuring instruments, varying weather, and human activities. Still, the errors are within the acceptable range by reviewing the data's consistency, representativeness, and accuracy.

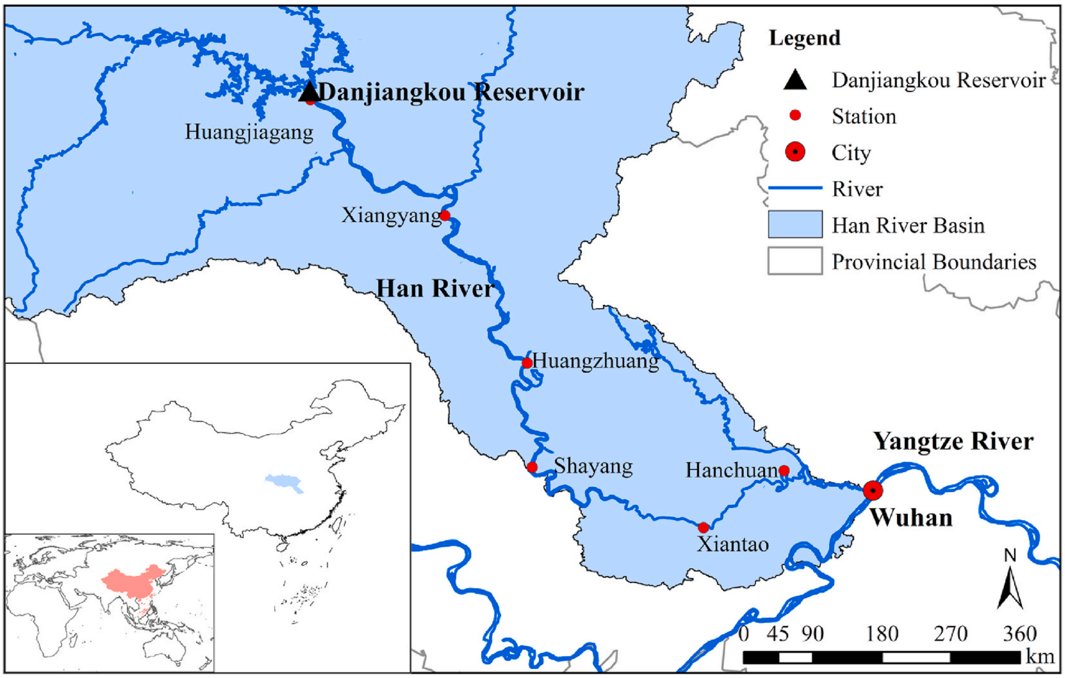

Fig. 5. Middle and lower reaches of the Han River, China.

Specifically, five biomass indicators are fish, phytoplankton, zooplankton, zoobenthos, and macrophytes. They represent the primary aquatic biological resources in the middle and lower reaches of the Han River. Each indicator refers to the synthesis biomass of multiple species at the same station. For example, the population density of zooplankton indicates the biomass of entire groups of *Cladocera*, *Copepod*, *Nauplius*, *Protozoa*, and *Rotifer*. The concept of synthesis biomass facilitates simulation at the ecosystem level and has significant implications for aquatic ecological restoration and management. For instance, fish and phytoplankton may compete for flow, water temperature, and total phosphorus resources. The abiotic environment conditions can be regulated to bring the ecosystem to a better state when competition is identified. The biomass data are normalized to 0.01–0.99 because the magnitude of different biomass indicators varies greatly. Note that the normalization range does not start from 0 to avoid the calculation bug with 0 as the denominator.

One flow regime indicator is discharge. Discharge has been widely used as a critical index that can directly reflect the flow regime of a river in many studies on hydrological alteration (Aspin et al., 2020; Palmer and Ruhi, 2019; Tonkin et al., 2018). Although the simple monthly average discharge may not capture the effects of a river's diverse flow regime components (i.e., magnitude, duration, frequency, timing, and rate of change), it is selected as an indicator for the following reasons. On the one hand, the monthly-scale discharge is matched to the scale of biomass data. On the other hand, the flow regime components are used to describe the overall performance of hydrological alteration over some time. Still, they are not applicable for describing the real-time response of a dynamic population system to flow regime compared to time-varying discharge. The discharge time series implicitly includes the magnitude, duration, frequency, timing, and rate of change of a flow event. In addition, the water level and flow velocity are not included because they strongly correlate with discharge from the knowledge of hydraulics. Overall, it is practical to select discharge as the flow regime indicator.

Fifteen water quality indicators are air temperature (AT), water temperature (WT), potential of hydrogen (pH), suspended solids (SS), dissolved oxygen (DO), chemical oxygen demand (COD_{Mn}), biochemical oxygen demand (BOD_5), sulphate (SO_4), ammonia nitrogen (NH_3–N), nitrite nitrogen (NO_2–N), nitrate nitrogen (NO_3–N), total phosphorous (TP), fluoride (F), chloride (Cl), and total hardness (TH). These indicators include physicochemical metrics, inorganic compounds, and organic compounds, which are the key factors affecting metacommunity dynamics in the middle and lower reaches of the Han River.

3.3. Simulation details

The overlap period of all data is determined as the simulation period. The time step is a month. Please see **Section S5** for more information about simulation details, especially the parameters setting.

4. Results and discussion

4.1. Environmental optimums for multiple populations

The environmental optimums (Table 1) are determined under the suitable function types for multiple populations to different abiotic environmental factors. Please see **Section S6** for more details about the suitable function types and the environmental optimums.

4.2. Ecological niches for multiple populations

Fig. 6 shows the quantile regression results for fish biomass and abiotic environmental indicators under suitable function types. It can be found from the integrated fitting curves that the fish population shows a significant ecological response to discharge and WT. In contrast, AT, SS, NO_2–N and Cl show no apparent relations with fish biomass. Nevertheless, the not strongly related environmental indicators may be essential to fish growth. The fish population may not show a significant response to these essential indicators because the fluctuation magnitudes of the indicators are small and within the appropriate range for fish survival. For instance, the fish biomass changes slightly with increasing pH and DO values because most pH and DO values in the studied reaches fall in the appropriate range (i.e., 7–8.5 of pH, and 6–10 mg/L of DO). Despite this, pH and DO are critical environmental factors to fish.

Judging from the regression results with different quantiles, the estimation curves with high quantiles deviate significantly from the integrated fitting curve for several indicators (e.g., AT, SS, DO, F, Cl, and TH). This can be interpreted as the fish population being less affected by these indicators, resulting in high quantile samples under the dominance of other critical indicators. In addition, the estimation curves with different quantiles may show divergence as the value of the environmental indicator increases (or decreases), which indicates that the population dynamics are less dominated by the current indicator when it exceeds the appropriate threshold.

Similar analysis can be conducted on phytoplankton, zooplankton, zoobenthos, and macrophytes (Figs. S1–S4). The analysis of quantile regression results is simplified since this paper does not aim to explore the ecological responses of multiple populations to different abiotic environmental indicators.

Table 1
Environmental optimums for multiple populations.

Abiotic environmental indicators	Populations				
	Fish	Phytoplankton	Zooplankton	Zoobenthos	Macrophytes
Q (m^3/s)	2208.39	353.00	1904.49	332.45	332.45
AT (°C)	23.06	1.00	37.13	0.00	33.47
WT (°C)	24.00	5.53	30.73	16.62	15.48
pH	6.83	8.56	6.65	6.65	6.65
SS (mg/L)	3.42	78.33	61.99	1.27	1.27
DO (mg/L)	6.16	12.98	5.55	5.55	12.14
COD_{Mn} (mg/L)	3.90	3.82	3.87	1.40	1.47
BOD_5 (mg/L)	3.11	3.04	2.85	0.25	0.25
SO_4 (mg/L)	23.81	51.30	50.37	38.90	20.71
NH_3–N (mg/L)	0.85	0.93	0.93	0.01	0.01
NO_2–N (mg/L)	0.01	0.05	0.06	0.00	0.00
NO_3–N (mg/L)	1.08	0.58	0.58	0.23	0.23
TP (mg/L)	0.16	0.18	0.08	0.15	0.01
F (mg/L)	0.09	0.41	0.42	0.33	0.09
Cl (mg/L)	4.39	18.17	20.13	17.55	3.09
TH (mg/L)	122.90	180.83	185.74	155.73	116.10

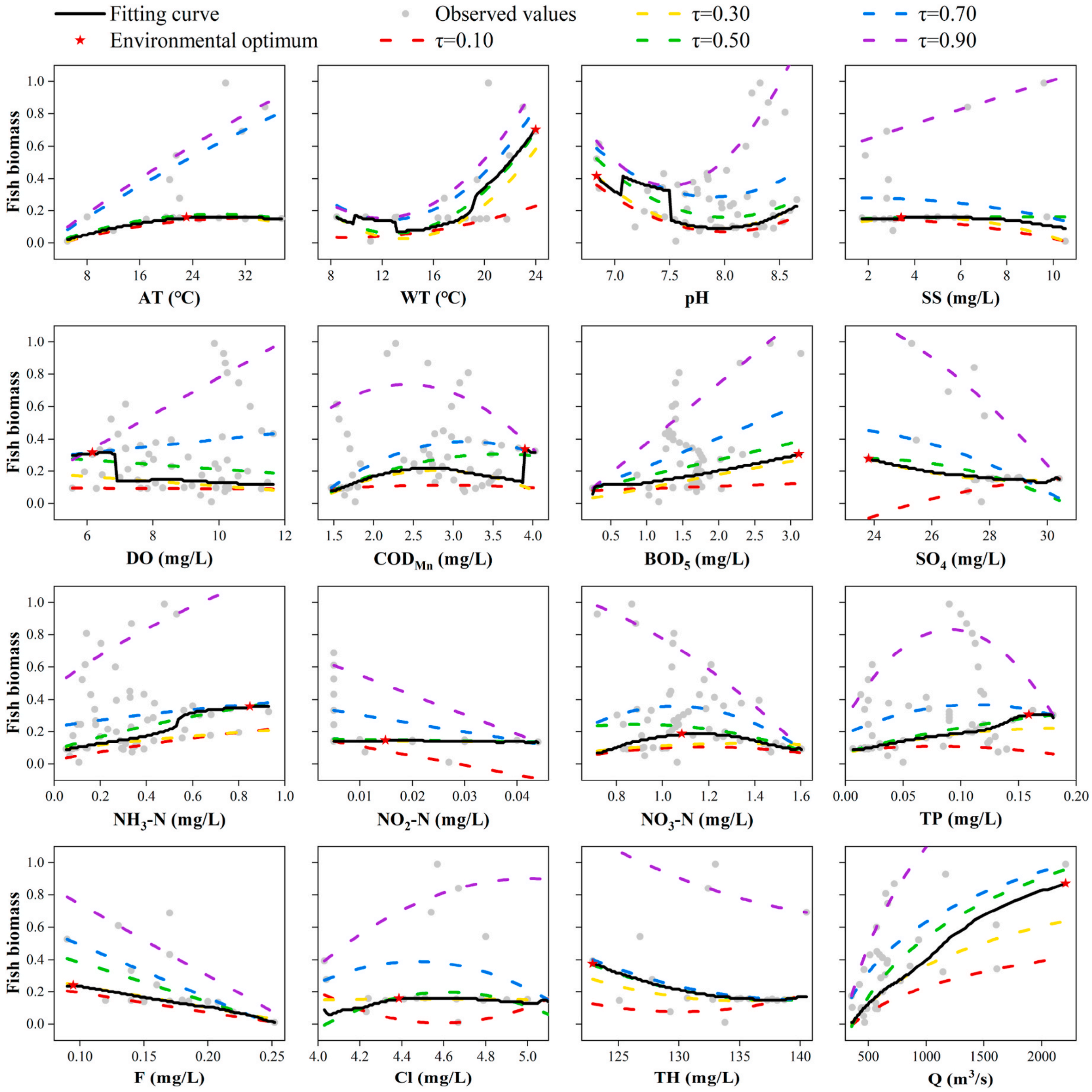

Fig. 6. Quantile regression results for fish biomass and abiotic environmental indicators. The red, yellow, green, blue, and purple dotted lines denote the estimation curves under 0.1, 0.3, 0.5, 0.7, and 0.9 quantiles, respectively. The dark solid line denotes the integrated fitting curve. The red star denotes the environment optimum. The vertical axis indicates the normalized biomass data.

The niche breadths of multiple populations along different environmental factors are presented in Fig. 7 based on the quantile regression results. A broader niche indicates less specialization for a population. From the point of view of populations, the niche breadths of fish are the narrowest among all populations in terms of the three dimensions of Q, WT, and NH_3–N, which indicates that the requirements of the fish population for these three indicators are demanding. The niche breadths of zoobenthos are the broadest among all populations in terms of the six dimensions of AT, SS, DO, BOD_5, NH_3–N, and NO_2–N, which indicates that zoobenthos is unlikely to compete with other populations in the use of these environmental resources. For example, zoobenthos has an advantage in competing for DO because they can survive in a broad range of DO. The niche breadths of macrophytes are the narrowest among all populations in terms of the six dimensions of AT, SS, COD_{Mn}, BOD_5, NO_3–N, and TP, which indicates that macrophytes are sensitive to these indicators. The realized niche of macrophytes may be easily altered by changing conditions of these indicators to put macrophytes in an inferior position in the competition. From the point of view of abiotic environmental indicators, the influence of flow regime on fish population is more significant than that on other populations, leading to the narrowest niche breadth of fish along the dimension of discharge. DO is necessary for the photosynthesis of phytoplankton. As a result, the niche breadth of phytoplankton is narrower than other populations (especially for zoobenthos) in terms of the DO dimension. Thermal thresholds are weak for phytoplankton and zooplankton, as shown by the population distribution across wide ranges of latitude and elevation, but they are more critical for large invertebrates and especially for fishes (Lewis, 2021). Likewise, the ecological niche of all pairs of populations and abiotic environmental indicators can be illustrated in the same way.

4.3. Niche-based competition among populations

The competition coefficients among multiple populations are calculated according to the niche overlap theory (Fig. 8). The competition coefficients (i.e., $\alpha(4,1)$, $\alpha(4,2)$ $\alpha(4,3)$, and $\alpha(4,5)$) resulting from other populations occupying the resources of zoobenthos are generally significant because zoobenthos occupies broad niches along multiple dimensions of abiotic environmental indicators. In contrast, the

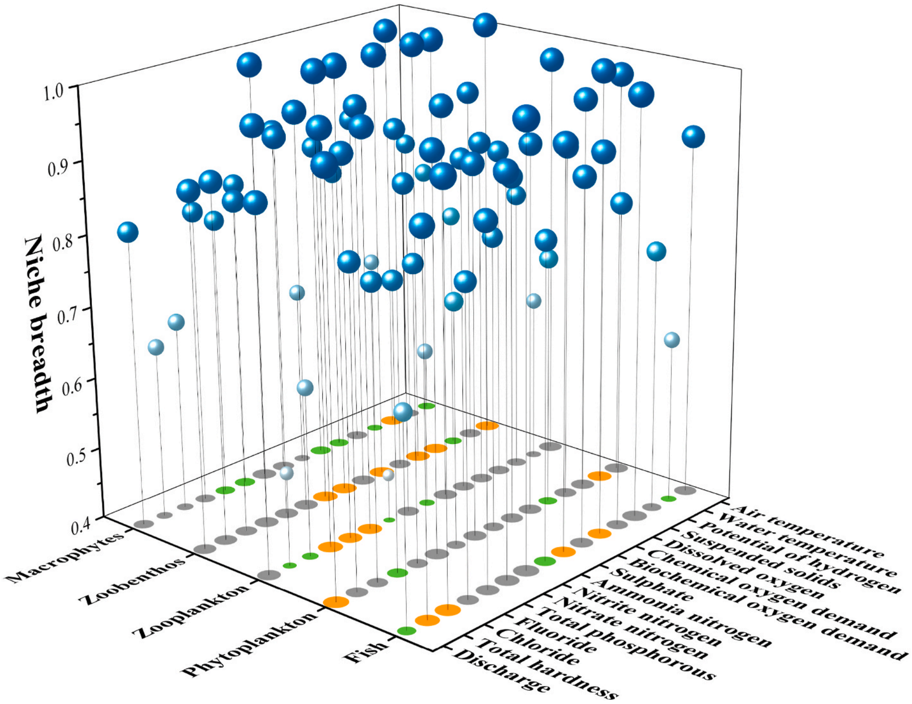

Fig. 7. Niche breadths of multiple populations along different abiotic environmental factors. All spheres are projected as circles on the horizontal plane. The size of spheres indicates the niche breadth. The broadest niche breadth along each dimension of environmental indicator is denoted by an orange circle, while the narrowest niche breadth is denoted by a green circle.

competition coefficients (i.e., $\alpha(5,1)$, $\alpha(5,2)$, $\alpha(5,3)$, and $\alpha(5,4)$) resulting from other populations occupying the resources of macrophytes are generally small. For another example, the competition coefficients (i.e., $\alpha(1,2)$, $\alpha(1,3)$, $\alpha(1,4)$, and $\alpha(1,5)$) of other populations on fish population are relatively small in terms of Q and WT. This can be interpreted as the fish population is unlikely to have niche overlap with other populations due to its narrower niche breadth along the dimensions of Q and WT than others. It can be found that the integrated competition coefficients for all pairs of populations are retained at high levels (>0.7), which accords with the characteristics of a complex river ecosystem. The above mutual demonstration analysis of ecological niche and competition coefficient shows that the results are reasonable.

4.4. *Simulation results of metacommunity dynamics*

Fig. S5 shows the simulated coevolution of metacommunity dynamics at different stations. As shown in Fig. 9, the simulation results show that the NSEs for fish, zoobenthos, and macrophytes are more than 0.66, while the rs for them are no less than 0.71. Both the NSE and r for the fish population are 0.94. The NSE and r for the zoobenthos population are 0.76 and 0.78, respectively. Thus, the simulation results of fish and zoobenthos are the best. The worst simulation is for phytoplankton, whose NSE and r are 0.30 and 0.41, respectively. This is acceptable because phytoplankton (especially for diatoms) grow rapidly in winter due to the low water temperature, the abundant light caused by low water level, the slow flow velocity, and the nutrients released by the natural withering of aquatic vegetation (Wang et al., 2016). In addition, fish, phytoplankton, and zooplankton are simulated better at upstream stations (i.e., Huangjiagang and Xiangyang), while zoobenthos and macrophytes are simulated better at the downstream stations (i.e., Xiantao and Hanchuan). Zoobenthos and macrophytes tend to live at the bottom or bank of the river, where the flow velocity is slower than the central river and upstream stations. Consequently, the dynamics of zoobenthos and macrophytes are less influenced by flow regime alteration. The simulation results of animal populations are better than those of plant populations, which may be due to their stronger stability and resistance to external environmental disturbances. Therefore, the simulation results are acceptable in magnitude and trend based on the above analysis.

To further illustrate the robustness of the model, the sensitivity analysis of model parameters was conducted in **Section S7**.

4.5. *Effects of flow regime and water quality on metacommunity dynamics*

The contribution ratios of the effects of biotic interactions, flow regime, and water quality on metacommunity dynamics are compared among different populations and stations (Fig. 10).

For the upstream Huangjiagang and Xiangyang stations, the FREs on fish are more significant than that on other populations by 8%–22%. The WQEs on phytoplankton, zooplankton, zoobenthos, and macrophytes are more significant than that on fish by 9%–26%. The contribution ratios of FREs are 30% and 25% on fish at Huangjiagang and Xiangyang stations, respectively, which are larger than WQEs (16% and 14%, respectively). The contribution ratios of WQEs are more than 25% on phytoplankton and macrophytes at upstream stations, which are larger than FREs (lower than 17%). This can be interpreted as the flow regime of the upstream reach below the Danjiangkou Reservoir varies significantly because of dam regulation (Wang et al., 2021a). Consequently, fish shows a more significant ecological response to hydrological alteration than other species at upstream stations. For instance, streamflow alteration can affect the body size, the periodic life-history strategies, and the community structure of the fish population (Zhao et al., 2018). The metabolic rate of specific fish and benthos can be improved within a certain range of velocity or discharge, thus providing necessary flow conditions for spawning (Palmer and Ruhi, 2019). The water quality conditions may be primarily influenced by hydrological alteration at upstream reaches, so the dynamics of phytoplankton and macrophytes are represented to have a stronger response to WQEs than fish at upstream stations (Alahuhta et al., 2018; Wang et al., 2016).

For the downstream Hanchuan station, the contribution ratios of FREs reach the lowest (lower than 1%) due to the most stable flow

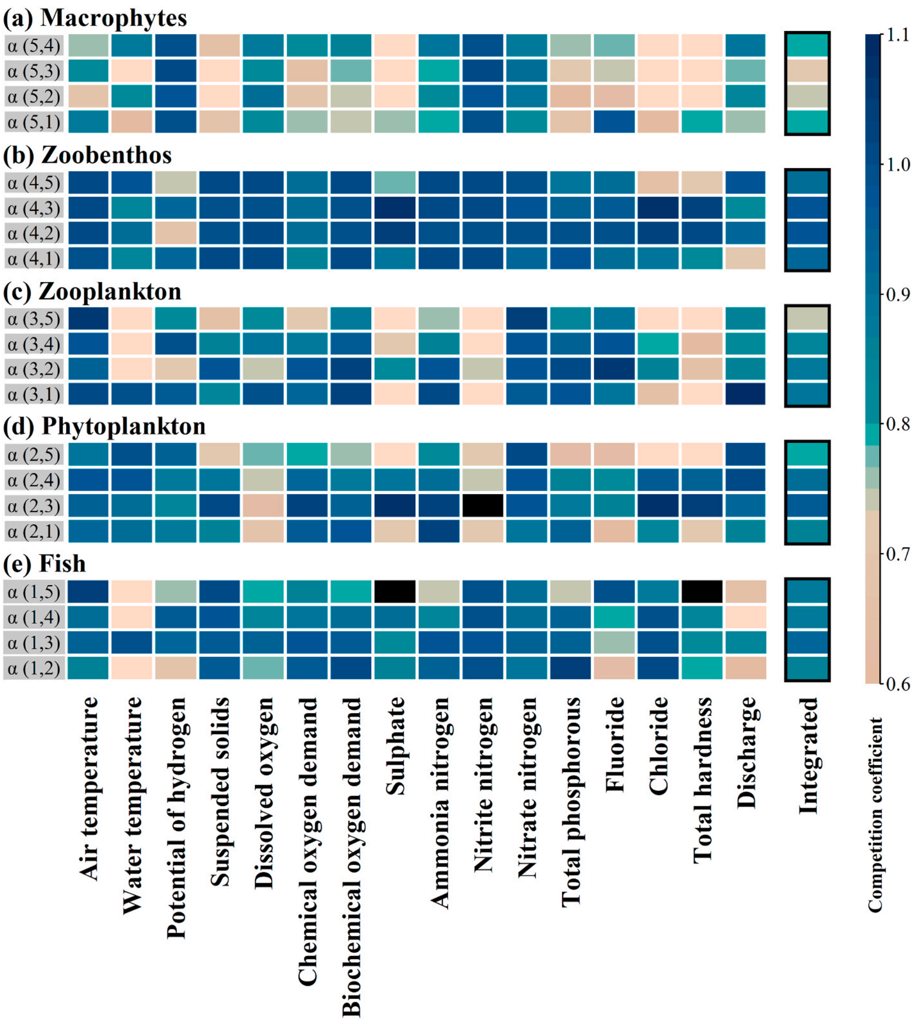

Fig. 8. Competition coefficients among multiple populations. The numbers 1 to 5 denote fish, phytoplankton, zooplankton, zoobenthos, and macrophytes. For example, $\alpha(5,4)$ indicates the competition coefficients between macrophytes and zoobenthos. Note that $\alpha(5,4)$ is not the same as $\alpha(4,5)$.

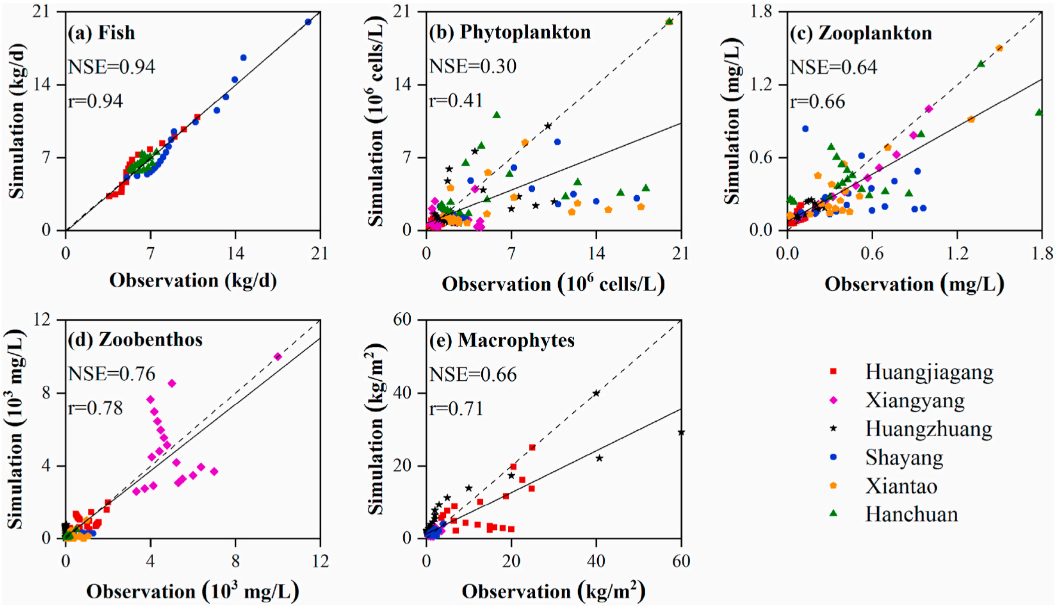

Fig. 9. Simulation performance of the metacommunity dynamics illustrated by the Nash efficiency coefficient (NSE) and the Pearson correlation coefficient (r).

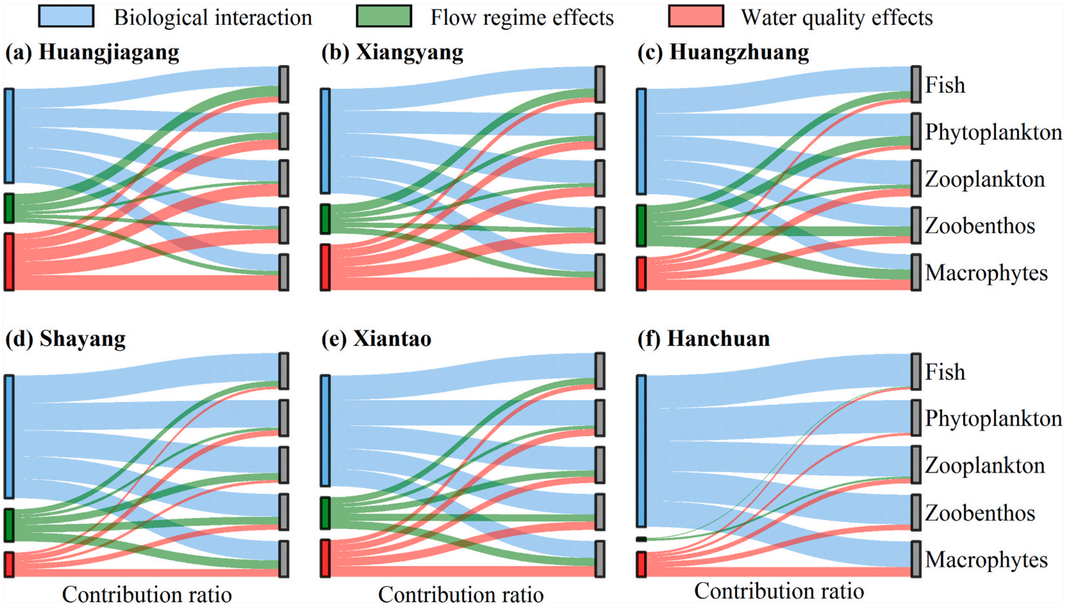

Fig. 10. Comparison of the effects of biological interactions, flow regime, and water quality on metacommunity dynamics for the river ecosystem.

regime condition of all stations. In contrast, studies have shown that in the lower reaches of rivers with stable hydrological conditions, phytoplankton and zooplankton are strongly influenced by flow regime alteration (Xie et al., 2006). For example, the velocity exceeding a certain threshold can effectively avoid phytoplankton-related bloom events (Li et al., 2013). Slower velocity reduces the degradation efficiency of pollutants, resulting in the rapid growth of phytoplankton (e.g., diatom). From this point of view, the direct cause of bloom events is water quality rather than flow regime, so the findings of this study do not contradict previous research. In addition, from upstream to downstream, the FREs on different populations tend to be balanced, and the WQEs on phytoplankton, zooplankton, zoobenthos, and macrophytes are gradually decreased.

For all stations, water quality shows 9%–14% greater effects than flow regime on phytoplankton, zooplankton, zoobenthos, and macrophytes, while flow regime shows 7% greater effects than water quality on fish. In addition, the average contribution ratios are 64%, 21%, and 15% of biological interaction, WQEs, and FREs, respectively, for all stations and populations. The population dynamics are dominated by biological interaction, although existing studies have discussed the hypothesis that aquatic community dynamics depend largely on flow regime (Horne et al., 2019; Robson et al., 2017). Nevertheless, the dominance of biotic interactions on population dynamics may be weaker than flow regime or water quality when abiotic environmental conditions exceed the acceptable threshold for the aquatic community systems (Wang et al., 2021b).

It should be noted that the abiotic environmental indicators are used in deriving FREs, WQEs, and interspecies interaction, but they do not conflict. The abiotic environment is described as a static space when calculating the competition coefficient based on the niche overlap theory. In fact, the abiotic environment is spatiotemporally changeable. Therefore, the FREs and WQEs reflect dynamic progress, while the biotic interactions illustrate the static influence of the abiotic environment on the metacommunity.

5. Conclusions

A new model (i.e., the MDM) is established to integrate the effects of flow regime and water quality on metacommunity dynamics. This is accomplished by coupling ecological niches and competition coefficients based on the quantile regression method. The following conclusions are drawn by applying the MDM to the mid-lower Han River, China.

(1) The FREs and the WQEs are modeled using multiple parameters, including ecological niches, environmental optimums, and competition coefficients. These parameters are calculated based on the quantile regression via four statistical functions (i.e., linear, quadratic, exponential, and logarithmic) to account for aquatic organisms' linear and non-linear ecological responses. The quantile regression method shows advantages in describing the distribution function between explained and explanatory variables in different quantiles, especially in the case of multiple explanatory variables (e.g., multiple abiotic environmental indicators). The ecological niches and competition coefficients are demonstrated to be reasonable by comparing them with empirical evidence.

(2) The simulation results show that the MDM performs effectively in simulating metacommunity dynamics. The MDM performs the best regarding the fish population, for whom both the Nash efficiency coefficient and Pearson correlation coefficient are 0.94. The Nash efficiency coefficients for fish, zooplankton, zoobenthos, and macrophytes are more than 0.64, while the Pearson correlation coefficients for them are no less than 0.66. The performance for phytoplankton was relatively poor because it grew rapidly in winter due to the low water temperature and the slow flow velocity, resulting in inevitable outlier values.

(3) The FREs and the WQEs on the metacommunity are elaborately quantified using the MDM. The FREs are greater than WQEs on fish, whereas the WQEs are greater than FREs on phytoplankton and macrophytes in upstream reaches where the flow regime is generally changeable. The FREs on multiple populations reach the lowest (lower than 1%) at the downstream station due to the most stable flow regime condition of all stations. Water quality shows more significant effects than flow regime on phytoplankton, zooplankton, and macrophytes from upstream to downstream. For all river stations, the average contributions of biological interaction, flow regime effects, and water quality effects to multi-population dynamics are 64%, 21%, and 15%, respectively, suggesting that the population dynamics are dominated by biological interaction.

This study provides a new approach to identifying how the freshwater environment influences community dynamics, and it links multi-population structures at different trophic levels in aquatic ecosystems to metacommunity processes. The following recommendations are considered the focus for future works based on the current research. (1) The proposed MDM can be easily modified to incorporate the stochasticity of environmental variables to explore the stability and threshold issues of the "water quantity-water quality-aquatic ecology" system. (2) The MDM has potential to be widely used in other aquatic ecosystems where ecological restoration is urgently needed due to dam regulation and water pollution. It is imperative to expand the research geographically to obtain more comprehensive information about the ecological impacts of flow regime and water quality, especially in those countries or areas with very few or no studies. (3) There is an urgent need for sufficient data to demonstrate specific ecological impacts. Techniques related to ecological monitoring need to be urgently optimized to obtain observations of flow, pollutants, and biomass at daily or even hourly scales. Big data are essential in validating and further improving mathematical models or existing mitigation measures. Research related to big data can extend this model to a broader range of biological communities and provide more instructive strategies for biodiversity conservation, reservoir ecological operation, and environmental flows. (4) Building on this work would help researchers better understand aquatic ecosystems in a changing environment, especially if they utilize it to connect other bodies of ecological theory and empirically test its effectiveness in various natural ecosystems.

Credit author statement

Yibo Wang: Conceptualization, Methodology, Writing - Original Draft, Writing - Review & Editing, Software, Validation and Formal Analysis. **Pan Liu**: Writing - Review & Editing, Conceptualization and Supervision. **Dimitri Solomatine**: Writing - Review & Editing and Supervision. **Liping Li**: Data Curation. **Chen Wu**: Resources. **Dongyang Han**: Resources. **Xiaojing Zhang**: Resources. **Zhikai Yang**: Resources. **Sheng Yang**: Resources.

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.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2023.117562.

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