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Review

River network connectivity and fish diversity

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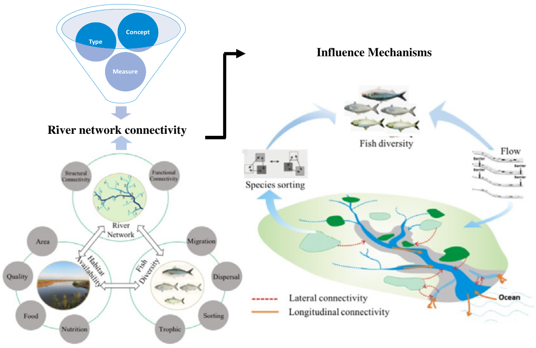
HIGHLIGHTS

- River network connectivity (RNC) includes structural and functional connectivity.
- RNC has a significant impact on fish diversity.
- Sustaining RNC promotes fish diversity in longitudinal and lateral axes.
- Sorting, dispersal, and habitat are the main factors driving the distribution of fish diversity.

GRAPHICAL ABSTRACT



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ABSTRACT

Frequent and severe disruptions of natural river flows associated with human activities significantly alter hydrological connectivity in large river networks, with deleterious effects on fish diversity. Understanding the relationship between fish diversity and river network connectivity is fundamental to ensuring species persistence, ecosystem integrity, and human well-being. Here, we provide a review of the mechanisms by which river network connectivity (RNC) affects fish diversity. We review the relationships between forms, systems and types of RNC and fish diversity, based on more than 100 previous studies. In summary, sustaining RNC promotes fish diversity in longitudinal and lateral axes, and species sorting, dispersal dynamics, and habitat availability are the main factors driving the distribution of fish diversity, followed by nutrition and trophic dynamics. Our work highlights the effects of RNC on fish diversity, and provides a mechanistic understanding of how RNC affects fish diversity across river basins, thus providing scientific guidance for protecting fish biodiversity and improving the health of river network ecosystems.

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1. Introduction

Rivers are spatially organised into hierarchic dendritic networks (Tonkin et al., 2018), with water flow driving the connectivity among river network pathways (Wiens, 2002). River network connectivity (RNC) is defined as water-mediated transfer of matter, energy, and organisms along longitudinal (upstream-downstream), lateral, and vertical dimensions (Pringle, 2003; Allan and Castillo, 2007). RNC is an important factor for supporting the functional integrity of river ecosystem (Xia et al., 2012). The connection between the river and its nearby floodplains can promote the exchange of organisms and nutrients, facilitating geomorphic development of and access to additional habitats (Klein and Vanderpoorten, 1997; Reid et al., 2016). A well-connected river network can support a relatively stable nutrient status in a varying environment and have a significant effect on the maintenance of biological diversity (Obolewski, 2011; Kaus et al., 2019). Alterations to RNC are associated with changes in ecological processes, such as the abnormal migration and reproduction of aquatic organisms when the physical habitat significantly varies (Florsheim and Mount, 2003), which affect the distribution of biological communities and biodiversity in river networks (Girvetz et al., 2008; Huang et al., 2012; Shrestha et al., 2012; Kaus et al., 2018). Thus, RNC is a key factor influencing the health of river ecosystems and is an important criterion for evaluating the health of river networks (Rogers and Biggs, 1999).

Strong hydrological connectivity in a network promotes energy and nutrient cycling, and provides important habitats for a variety of birds, fish and benthic organisms. Connectivity within river networks is a major factor for promoting community assembly and dynamics (Lowe, 2006; Carrara et al., 2012; Altermatt et al., 2013; Phillipsen et al., 2015; Seymour et al., 2015). The structure of river network branches constrains biological organisms in different ways depending on their modes of connectivity (Rodriguez-Iturbe and Rinaldo, 2001), which can exert strong controls on metapopulation and metacommunity dynamics, to shape the patterns of biodiversity (Fausch et al., 2002; Campbell et al., 2007; Altermatt and Fronhofer, 2018), especially through regulating the extent and rates of dispersal within the river network (Rodriguez-Iturbe et al., 2009). Many organisms in streams, such as benthic invertebrates (Petersen et al., 2004), fishes (Olden et al., 2001; Dias et al., 2013), and plants (Schmiedel and Tackenberg, 2013), are confined to these aquatic dispersal corridors. In this sense, while some plants, amphibians and adult insects are able to disperse overland (Bunn and Hughes, 1997; Lancaster and Downes, 2013), fishes have to follow the watercourses to arrive at habitats in the stream network (Olden et al., 2001; Fagan et al., 2002; Landeiro et al., 2011; Dias et al., 2013). Thus, fish assemblages are more directly influenced by the structure of the river network compared to those that disperse overland. The dendritic connectivity structure of river networks plays a dominant role in the fish diversity (Brown and Swan, 2010). Therefore, effective conservation of fish diversity depends heavily on protection of connectivity in river networks.

Longitudinal and lateral hydrological connectivity gradients are significant for promoting fish assemblage structure and diversity. Supporting research on this topic includes dispersal processes (Lemke et al., 2017; Leitão et al., 2018; Warry et al., 2018), habitat connectivity (Smith et al., 2017; Galib et al., 2017), trophic dynamics (Sullivan et al., 2015; Altermatt and Fronhofer, 2018; Anderson and Hayes, 2018), nutrient transport (Helton et al., 2018) and disease spread (Carraro et al., 2018; Ciddio et al., 2017). A broad range of approaches are adopted, including field investigation (Lemke et al., 2017; Smith et al., 2017; Leitão et al., 2018), experimental studies (Altermatt and Fronhofer, 2018), model simulation (Muneepeerakul et al., 2008; Auerbach and Poff, 2011; Peterson et al., 2013; Carrara et al., 2013; Seymour et al., 2015; Altermatt and Fronhofer, 2018), and conceptual synthesis (Fagan, 2002; Campbell et al., 2007; Tonkin et al., 2018). Explicit consideration of dendritic patterns of the river network is important for studying fish diversity patterns (Fagan, 2002; Campbell et al., 2007). Small-scale field investigations and simulation experiments have found that the diversity of fish under different connected conditions differs significantly (Aarts et al., 2004; Cetra et al., 2017; Nicol et al., 2017; Smith et al., 2017). Numerical modeling approaches have been used to study the response of fish diversity to changes of RNC at a large scale (Campbell et al., 2012). Overall, the structure of the network and spatial dynamics along the river network clearly influence the dynamics of fish populations and communities. However, there is a need for a systematic review of how RNC affects fish diversity and what kind of influences are introduced.

The aim of this issue is to highlight the significance of river network connectivity on structuring fish diversity, particularly through metacommunity dynamics and associated dispersal processes. This topic has received great attention and has been under rapid growth in recent years. To evaluate the influence of RNC on fish diversity and the corresponding approach and processes of this influence, we searched the following combination of title/keywords/abstract in the Web of Science Core Collection database (timespan = 1 January 1991–31 December 2018; field = topic: fish* and diversity* and (connect* or connection* or connectivity* or connectivities* or fragmentation* or fragmented*)) (Fig. 1). The proportion of articles on fish diversity that explicitly consider connectivity has grown steadily over the observation period. In this review, we address the following topics: (1) epitomize the concept, types and measurement approaches of RNC; (2) summarize previous research of RNC impact on fish diversity; and (3) take the first step toward synthesizing the knowledge of mechanisms by which RNC affects fish diversity. We explicitly consider both dispersal and habitat availability. Understanding how connectivity of river networks affects fish diversity is vital for the development of basic riverine metacommunity ecology, as well as monitoring, intervention, management, conservation, and restoration in river networks (Siqueira et al., 2012; Heino, 2013; Tonkin et al., 2014; Carraro et al., 2018). To promote the investigation of this rapidly growing area, we provide a conceptual synthesis to analyze and understand the significance of RNC on fish

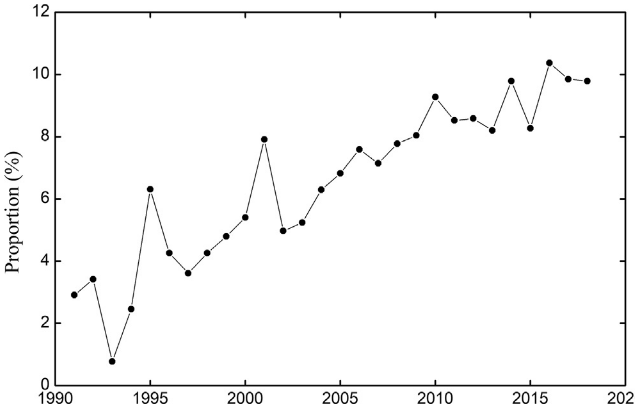

Fig. 1. The proportion of articles investigated in the Web of Science Core Collection database from 1 January 1991 to 31 December 2018. The y-axis is the proportion of articles number investigated by term (field = topic: fish* and diversity* and (connect* or connection* or connectivity* or connectivities* or fragmentation* or fragmented*)) in that same year for fish diversity investigated by term (field = topic: fish* and diversity*).

diversity in riverine ecosystems, and to identify the potential approaches for promoting knowledge in this arena.

2. Definitions: concept, types and degree of connectivity in river networks

2.1. Concept and characteristics of river network connectivity

The concept of river connectivity originated from the “river continuum” (Vannote et al., 1980; Fausch et al., 2002), later extended to consider river systems as a unique landscape type (Amoros and Roux, 1988). The latter authors defined “river connectivity” as the relationship between the spatial structure and function of the river landscape, which is used to measure the degree of correlation between landscape units and represents a parameter of landscape function (Amoros and Roux, 1988; Fausch et al., 2002). By the end of the 1990s, the concept had been widely accepted (Xia et al., 2017). Other concepts of connectivity include landscape connectivity (Wiens, 2002; Van Looy et al., 2014), hydrologic connectivity (Pringle, 2003; Allan, 2004; Freeman et al., 2007; Turnbull et al., 2008), and ecological connectivity (Turnbull et al., 2008; McKay et al., 2013; Stoffels et al., 2016). Tischendorf and Fahrig (2000), Malard et al. (2002), Wiens (2002) defined connectivity as a corridor landscape that facilitates or impedes the flow of organisms between resource patches from the perspective of landscape ecology. Western et al. (2001) and Freeman et al. (2007) indicated that hydrological connectivity is the migration efficiency of runoff and the material or energy carried from the source region to the drainage area based on hydrology. Pringle (2003) defined hydrological connectivity as the ability to migrate and transmit substances, energy and organisms within and between hydrologic cycle elements. Hydrological connectivity is a dynamic property of interconnected flows of substances, energy and information in the river system (May, 2006; Turnbull et al., 2008; McKay et al., 2013; Stammel et al., 2016).

River networks are hierarchical branched systems, and are critical for water dispersion (Benda et al., 2004; Campbell et al., 2007). River networks maintain, reconstruct and build hydrological connectivity, while also maintaining relatively stable water flow and corresponding substance circulation (Xia et al., 2012). RNC results from the interaction of water flow and transfer rate in river basin. The water flow including surface water and groundwater depends on rainfall, runoff, infiltration, evaporation and transpiration (Park et al., 2014). The transfer rate is mainly determined by the slope length, flow path and flow resistance. These processes interact with water resistance, and vary over the depth of water, setting up a nonlinear feedback mechanism among rainfall, permeability, runoff, river water level and runoff coefficient (Wainwright et al., 2011).

2.2. Types of river network connectivity

River networks are four-dimensional natural ecosystems, with connectivity in longitudinal, lateral and vertical axes, and the temporal dimension (Ward, 1989; Merenlender and Matella, 2013; Zhang et al., 2015). In addition, there is connectivity across spatial scales, for example when climate (e.g., precipitation) is combined with these dimensions, the concept is expanded to hydrologic connectivity on landscape, regional, and even global scales (Pringle, 2001). Fish research focuses mainly on longitudinal (He et al., 2017; Smith et al., 2017; Hermoso et al., 2018) and lateral (Czeglédi et al., 2016; Lemke et al., 2017) dimensions of river networks. Longitudinal connectivity indicates the unobstructed migration of organisms, material and energy in the river (Kondolf et al., 2006). Hydrological connectivity, from the source to the estuary, provides the prerequisite for nutrient exchange and migration, allows the unobstructed flow of material and energy in the longitudinal axis, and ensures the survival and migration of fish (Stammel et al., 2016). Lateral connectivity of river networks is the interconnection between the main channel, the riverbanks and the floodplain (Kondolf et al., 2006). When the water rises over the banks, the fish enters the beach to spawn or take refuge. When the water level drops, fish return to the channel following the water flow and completes the life cycle (Pascual-Hortal and Saura, 2006).

RNC can be summarized into two categories: structural connectivity and functional connectivity (Bracken and Croke, 2007). Functional connectivity is identified as the interaction between the spatial patterns of river networks and watershed and ecological processes, which refers to the transfer or migration processes of the water flow, nutrients, sediment, and organisms over the basin (Turnbull et al., 2008; Bice et al., 2018; Liu and Wang, 2018; Deng et al., 2018). One key difference that exists between functional connectivity and structural connectivity is the directional element of the connectivity (Turnbull et al., 2008). The criteria for the functional connectivity of river networks, such as water level, flow rate and water quality, etc., have significant seasonal variation. The longitudinal, lateral and vertical functional connectivity of river networks change dynamically in different seasons. The diversity of fish species depends on the structural connectivity and functional connectivity in river networks.

2.3. Measurements of connectivity

Many approaches have been adopted to measure the hydrological connectivity of river networks, including hydrological models, connectivity indices and graph theory. Many models have been developed based on the concept of hydrological connectivity, such as the runoff curve number (SCS-CN model) (Beasley et al., 1980), LAPSUS model (Lesschen et al., 2009) and watershed scale rainfall-runoff models (Birkel et al., 2011). The indices used to measure the connectivity of river networks generally include continuity index, the length of runoff index, the relative surface connection function, dendritic river network connectivity index, longitudinal continuity index, and topographically driven surface flow index (Mayor et al., 2008; Antoine et al., 2009; David et al., 2008; Lane et al., 2009; Deng et al., 2018). There are also biological indices, such as migratory continuity index, fish metrics, and index of biological integrity that measure the river network connectivity, which consider the behavioral responses of organisms to landscape pattern (Kindlmann and Burel, 2008; Li et al., 2013; Zhang et al., 2014; Deng et al., 2018; Lee and An, 2019). Based on graph theory, the flow smoothness is demonstrated through the river network graph model, flow resistance and river weight value, which also gives the weighted connectivity of the river network (Meng et al., 2014).

Studies analyzing the effects of hydrological connectivity on fish are usually based on fish sampling in river segments or sites with different connectivity conditions. For example, river connectivity can be characterized by the gradients of lateral hydrological connectivity in riverine areas and the seasonal connectivity among the main channels of large rivers. Researchers have collected fish samples from main channels, secondary channels, tertiary channels and backwaters to examine the significance of lateral connectivity gradients on fish diversity (Roach et al., 2009). The level of connectivity between rivers and adjacent open water bodies have been described by three levels of temporal connectivity (rarely, occasionally, and frequently) (Bouvier et al., 2009; Lemke et al., 2017) and two levels of spatial connectivity (small and large) (Bouvier et al., 2009; Neiff et al., 2009). Relatively few studies have applied connectivity metrics to assess the effects on fish diversity (Samia et al., 2015).

3. The influence of river network connectivity on fish diversity

Structural connectivity and functional connectivity are repeatedly created and broken in river networks (Branco et al., 2016; Deng et al., 2018; Ward et al., 2018). Short-term changes in hydrological and geomorphic conditions can alter connectivity among surface water habitats, thus RNC's frequent and local fluctuations in time and space can affect biotic processes, such as dispersal, adaptation and speciation, and the distribution patterns of the fish diversity throughout the river network. Based on the abstract, we selected the relevant articles according to the following principles: ① articles that did not involve studies of river ecosystems were excluded; ② articles that did not fit the theme that the impact or mechanism of connectivity on fish diversity were removed; and ③ those about genetic diversity were also removed. Finally, 135 articles were retained for demonstration the effects of different connected forms and types on fish diversity in detail (Figs. 2 and 3).

A large number of studies have been conducted to analyze the effects that connectivity between different ecosystems and elements can bring to fish diversity. Recent research indicated that tributaries connected to headwaters in experimental networks supported the greatest diversity compared to other locations in the network (Altermatt and Fronhofer, 2018). Small tributaries differ from each other in physical, chemical, and biotic attributes, thus providing habitats for a wide range of unique species (Meyer et al., 2007). Therefore, tributaries contribute to maintaining the abundance and diversity of organisms throughout the river network (Clarke et al., 2008; Okano et al., 2018). The connectivity between the main stream of a river and its tributaries creates refuge habitats and species pools, which promotes the maintenance of fish viability and diversity. Whiteside and McNatt (1972) and Meyer et al. (2007) revealed that second-order streams flowing into third- and fourth-order streams have higher Shannon diversity indices of fish assemblages than those flowing into other second-order streams. The higher diversity of the streams flowing into larger streams is a consequence of species in the larger stream moving into the tributaries (Whiteside and McNatt, 1972; Meyer et al., 2007). Fish diversity generally enriches with larger stream size along a gradient of increasing habitat heterogeneity, pool development, and habitat volume (Schlosser, 1987; Meyer et al., 2007). Miyazono and Taylor (2013) found that decreased connectivity from the mainstem can decrease fish species diversity in the tributaries of a desert river system. In intermittent streams, the connectivity of habitats during high-flow periods provides colonized habitats for both the upstream and downstream assemblages (Kadye and Chakona, 2012). River-lake connectivity at the upstream portion also significantly promotes fish diversity (Coops et al., 2008). Penha et al. (2017) found that permanently connected lakes had greater fish diversity than isolated lakes. Historical and current connectivity with riverine and marine environments also supports fish diversity (Whitfield et al., 2017). Vasconcelos et al. (2015) found that fish species diversity increases with larger estuary area and higher connectivity level to the adjacent marine ecosystems.

Fish diversity is closely related to the longitudinal and lateral connectivity of river networks. The loss and degradation of longitudinal connectivity from upstream reaches and their tributaries to downstream sections can threaten the biological integrity of the entire river networks (Meyer et al., 2007). Galib et al. (2017) revealed that fish diversity was different in upstream and downstream locations separated by sluice gates that were in operation over the wet season, but showed little difference when the gates were open. Gehrke et al. (2002) and Walsh et al. (2014) shown that fish diversity was lower above the dam compared to downstream. Thus the maintenance of connectivity to downstream and main stream is critical for fish diversity (Hermoso et al., 2012; Crook et al., 2015). Downstream-related regional variables have been found to have the most significant influence on the structure of fish assemblages, with distance to the downstream confluence an important factor (He et al., 2017). Fish diversity decreases as the distance upstream from the main stream confluence increases Lake et al. (2000), which highlights the significance of connectivity to fish diversity.

Along lateral connectivity, spatiotemporal differences of water currents produce dynamic habitat conditions that influence fish diversity.

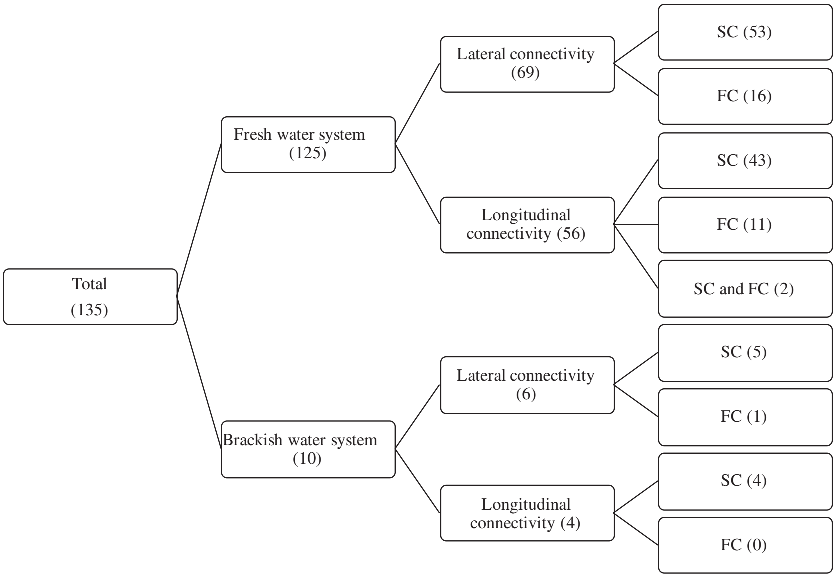

Fig. 2. The number of publications for different connectivity type. SC is structural connectivity and FC is functional connectivity.

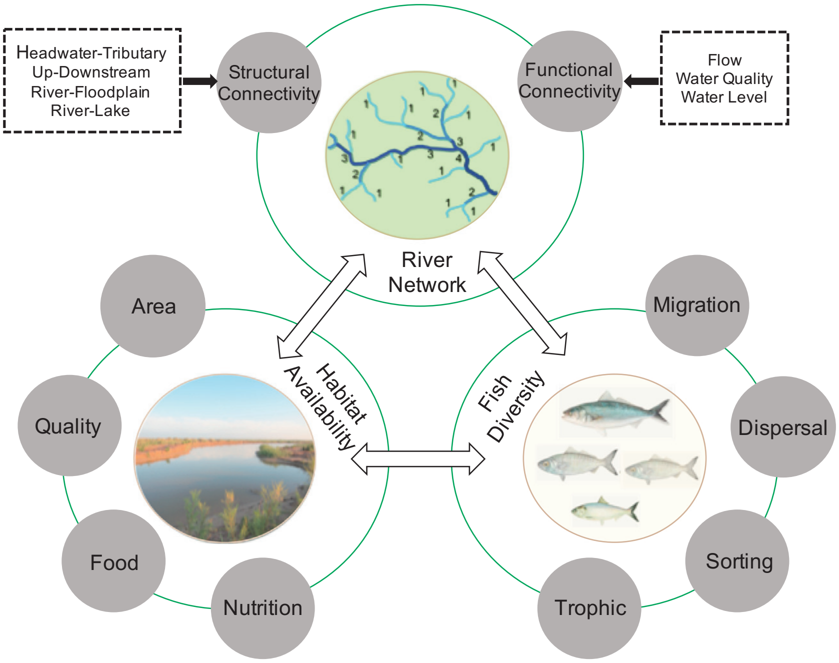

Fig. 3. The core research content for the influence of river network connectivity on fish diversity.

High flows lead to hydrological connection between the main channel and inundated off-channel lakes, wetlands and floodplains, which provide essential habitats for riverine biota (Górski et al., 2013). Seasonal flow and flood pulses determine the degree of connectivity of the main channel to the floodplain and off-channel habitats, and govern riverine fish diversity (Górski et al., 2013). In floodplain ecosystems, lateral connectivity between the river main channel and secondary channels plays a dominant role in shaping fish diversity (Besacier-Monbertrand et al., 2014). Interconnectedness among island floodplain lakes and the adjacent river maintains a higher fish diversity during the flood stage (Lubinski et al., 2008; Roach et al., 2009; Dembkowski and Miranda, 2011; Akasaka and Takamura, 2012; Besacier-Monbertrand et al., 2014), with decreasing diversity of fish species with decreasing hydrological connectivity of floodplain waterbodies (Aarts et al., 2004; Tedesco et al., 2005). Phelps et al. (2015) demonstrated that lateral connectivity increased habitat availability accessible to fishes and then increased fish species diversity. Periodic connection and the associated habitat heterogeneity are thus important for maintaining fish species diversity in large-river floodplain lakes (Dembkowski and Miranda, 2011).

Most studies of longitudinal and lateral connectivity focus on the effects of structural connectivity. Other studies consider the effects of functional connectivity on fish diversity, such as hydrologic regime (Junk et al., 1989), river flows (Teichert et al., 2018), patterns of connectivity (Gido et al., 2013), duration of flooding (Takata et al., 2017), and duration of connectivity (Takata et al., 2017). Few studies take into consideration the effects of structural and functional connectivity on fish diversity in longitudinal and lateral dimensions.

4. Mechanisms by which fish diversity is modified by river network connectivity

The dynamics of RNC have been emphasized when analyzing the patterns and subsequent processes that drive fish assemblage structure. Changes to RNC significantly affect hydrological and material flow processes, and biological migration of rivers (Pringle, 2003; Reid et al., 2016). The destruction of RNC seriously threatens the dispersal and migration of fish, and thus the survival and reproduction of fish (Dong et al., 2016). There are two main obstacles that river networks can bring to fish diversity: the obstacle from its physical structure, and the functional obstacles such as deterioration in water quality. To better understand the factors influencing the fish diversity distribution in riverine ecosystems, we categorize the mechanisms by which RNC affects fish diversity as: (1) species sorting; (2) dispersal dynamics; (3) habitat availability; (4) nutrition and trophic dynamics (Fig. 4).

4.1. Species sorting

The location in a river network plays an important role in fish diversity. Central and peripheral locations within a river network can exhibit divergent dynamics, and structural and functional connectivity vary with river network location. Many experiments and theories support that the spatial configuration of a dispersal river network can influence the community assembly in habitats (Muneepeerakul et al., 2008; Brown and Swan, 2010; Carrara et al., 2012; Peterson et al., 2013; Swan and Brown, 2014; Seymour et al., 2015). When habitats are not well connected via the river network, isolation can occur at much finer spatial scales (Hughes et al., 2009). Headwaters are more easily isolated than downstream locations, due to the limited openness to new arrivals of individuals that disperses within the river network (Brown and Swan, 2010; Clarke et al., 2008; Schmera et al., 2018). Headwater streams differ widely in physical, chemical, and biotic attributes, thus providing habitats for a range of unique species. Therefore, headwater streams collectively contribute more to the biodiversity of river networks (Meyer et al., 2007; Heino et al., 2015). Species sorting is defined as species filtered by environmental factors to occur at environmentally suitable sites, with adequate dispersal rates necessary so that species can track variation in environmental conditions among localities (Heino et al., 2015). In species sorting, species interactions and abiotic environmental conditions filter the suite of species co-occurring at each locality (Leibold et al., 2004; Soininen, 2014). Isolated communicates have lower dispersal rates, and thus longer times are needed for these communicates to be affected through interactions among species and environmental conditions. When dispersal is limited, species are prone to habitats with better environmental conditions, increasing the sorting of species (Heino et al., 2015).

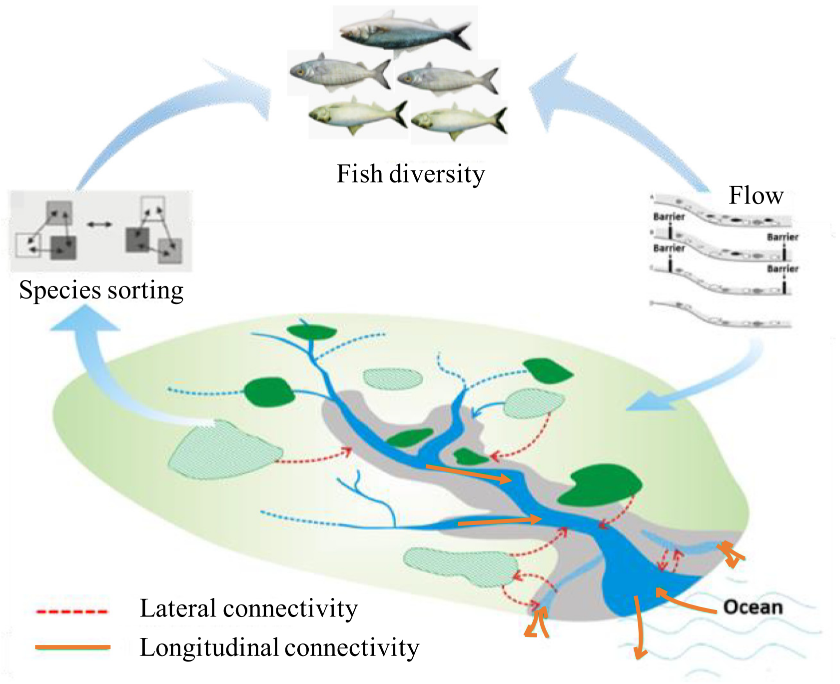

Fig. 4. Conceptual model of the mechanisms of RNC influences on fish diversity.

4.2. Dispersal dynamics

The river network is an important dispersal pathway for aquatic dispersers, especially for fish species (Finn et al., 2006; Finn et al., 2016). The branches of river systems can strongly control metapopulation and metacommunity dynamics (Rodriguez-Iturbe and Rinaldo, 2001), and promote the patterns of biodiversity (Fausch et al., 2002; Campbell et al., 2007; Rodriguez-Iturbe et al., 2009; Altermatt and Fronhofer, 2018), through regulating the extent and rates of dispersal within the river network (Brown et al., 2018; Tonkin et al., 2018). Fish dispersal ability is vital for fish survival and reproduction, as the dispersal behavior helps to escape from predators, capture food, migrate, avoid natural disasters and reproduce. Fishes are under different restrictions from the branching structure of river networks, depending on the mode of branch connectivity. River network ecosystems affect the capability of dispersal for fish communities through its distinctive physical structure and directional physical flow, thus regulating the fish diversity (Tonkin et al., 2018).

The factors of RNC that can affect fish dispersal and migration are not limited to physical structure impediments, but also include runoff, ecological flow and water quality. Even without physical blockages, fishes are not guaranteed to reach the destination of migration, due to the possibility of hydrodynamic conditions impeding movement (Pelicice et al., 2015). The diversity of fish species will exhibit changes when new bridges or barriers are introduced (Watson et al., 2018; Liu et al., 2019). Fishes are well-known victims of dams (Buddendorf et al., 2019; Marques et al., 2018; Liu et al., 2019). The changes of water depths and the patterns of discharge and sediment deposition in the reservoirs and dam tailwaters simplify or remove the niches of many species (McAllister et al., 2001). Additionally, dams block the migration to spawning or feeding grounds and fragment populations along the fluvial continuum (Agostinho et al., 2008; Sá-Oliveira et al., 2015). Since fishes are sensitive to hydrodynamic conditions, they are greatly affected. The hydrodynamic conditions of the river section on the migration path largely determine the success of fish to cross different habitats and reach the end point of migration or the upstream spawning field. Poor water quality and interrupted longitudinal connectivity due to water retention structures, can restrict recolonization from downstream sources and isolate river sections (Cowx and Broughton, 1986; Champkin et al., 2018). River network flow is another important hydrodynamic factor that affects fish dispersal and migration (Crook et al., 2015). Fish migration usually occurs in the season of high flow and fishes may not be able to complete dispersal and migration if the river flow is too small (Ngor et al., 2018; Jaeger et al., 2014; Bower et al., 2019). This will result in the incompletion of important life cycle processes such as feeding, wintering and reproduction, leading to a significant decrease of fish diversity (Jaeger et al., 2014; Zhang et al., 2019).

4.3. Habitat availability

RNC links habitats of fish species in space and time and is a key process that facilitates many life-history functions of fish species under a variety of contexts and scales (Sheaves, 2009). Connectivity with other habitats within the river network plays a vital role in constructing the fish community, as it is crucial for daily feeding excursions, spawning and reproduction (Henderson et al., 2017). The disruption of functional connectivity may negatively affect daily feeding, mate searching and dispersal, which adversely impacts habitats, thus the function of species and communities (Fuller et al., 2015). The loss of RNC is an important human-induced alteration in natural environments and frequently perceived as one of the major threats to global fish diversity (Liermann et al., 2012; Pelicice et al., 2015). The construction of dams results in physical, chemical and biological changes to natural ecosystems, changes natural flow regimes, and has a lasting threat to the connectivity of habitats and the migratory patterns of fish species (McCartney et al., 2001; Grill et al., 2015; Sá-Oliveira et al., 2015). The changes caused by dams directly and indirectly influence a myriad of dynamic factors that affect habitat heterogeneity and ultimately the connectivity of river network (Ward and Stanford, 1995). Through altering physical habitat characteristics and shaping fish assemblages, the loss of connectivity plays a role in shaping river ecosystems (Smith et al., 2017). The number and area of habitat patches, resource distribution and connectivity of populations are also changed by the loss of RNC (Hagen et al., 2012). Thus, RNC influences a very wide range of biological patterns and processes and its loss may lead to the reduction of adaptive potential and biodiversity (Hagen et al., 2012;

Waters and Burridge, 2016). Conversely, the reconnection of habitats can facilitate fish diversity by expanding geographic and temporal ranges, expanding variation of migration timing, and enlarging the body size of juveniles (Diefenderfer et al., 2011).

4.4. Nutrition and trophic dynamics

Connectivity is vital for dynamics, transport and recycling of nutrients. Partial connection to other habitats can increase nutrient inputs (Lemke et al., 2017). Connectivity also provides the opportunity for fishes to utilize multiple nutrient resource patches over space and time, which is necessary during their life-history migrations. This widespread and even obligatory utilization of multiple resource patches demonstrates that connectivity promotes assemblage metastability through multiple patches and carbon sources (Thorp et al., 2006). Additionally, connectivity enhances the survival, growth, productivity and fitness by providing access to a diversity of resources that are not available in only one patch or habitat (Sheaves, 2009).

Even within a single habitat or ecosystem unit, food webs imply connectivity. In marine systems, food webs are complex due to ontogenetic omnivory (Polis and Strong, 1996), where nursery ground function is widespread. When the complexity necessitated by ontogenetic omnivory is added to that engendered by extensive connections between habitat units, it is clear that food webs must be diversified and anastomosed into complex multifaceted networks with a range of trophic consequences (Sheaves, 2009).

5. Conclusions and future outlook

Hydrological connectivity affects fish diversity, species richness and abundance, species evenness, mean fish density, fish assemblage structure, and rates of immigration and emigration (Davis et al., 2014; Landress, 2016; Tétard et al., 2016). Alterations to the spatial configuration of habitats and the characteristics of areas among patches may reduce the connectivity between temporary and permanent aquatic habitats and may prevent their use by aquatic organisms (Mossop et al., 2015; Selleslagh et al., 2015). Many studies have found that fish species diversity is directly related to relatively stable hydrological connections (Bouvier et al., 2009; Samia et al., 2015). Both indirect and direct gradient analyses indicate a significant correlation between fish diversity and site connectivity (Landress, 2016). During floods, hydrological connectivity among waterbodies facilitates dispersal of fishes, such that after a flood, the fish assemblages structure changes with the condition of the hydrological connectivity (Stoffels et al., 2016). These studies illustrate that the hydrological connectivity plays an important role in shaping the fish diversity.

Although many studies have demonstrated impacts of RNC on fish diversity, there are still many aspects to be strengthened in future research. For example, there is a need for more studies at larger spatial scales, longer-time monitoring, with deep_understanding of connectivity and comprehensive connectivity indicators, and greater in-depth assessment of mechanisms. Studies that have assessed the effects of connectivity on fish assemblage structure have been largely limited in spatial and temporal scales of analysis. Spatially, most studies are confined within the scale of the sampling unit, such as, salt-marsh system, small wetlands, lakes, river segment, confluence of creek, and individual monitoring station, with few studies focused on large scale, such as, the entire coast, and the river basin (Bouvier et al., 2009; Hurd et al., 2016; Landress, 2016; Stoffels et al., 2016). Temporally, field sampling experiments are completed within a limited period of time, for example, a season, or one or two years (Roach et al., 2009; Selleslagh et al., 2015; Stoffels et al., 2016). Studies with longer time scales are usually based on models or data synthesis (Mossop et al., 2015). The lack of long-sequence field monitoring data limits the research on the effects of RNC on fish diversity.

Although connectivity is an obvious feature of river networks, investigation of its implications has largely been restricted to the migration of fish. However, connectivity has much broader conceptual relevance (Sheaves, 2009). For example, even when there is no physical barrier among habitats, fishes are not able to complete life-history migration among these habitats due to the loss of some functional features, such as the flow of water, water quality changes due to decreased water purification function, thus habitats cannot be considered as connected (Olden and Naiman, 2010; Jaeger et al., 2014). There are also few studies investigating fish diversity under different hydrological connectivity status. Different connectivity indices are used to evaluate the effects of RNC on fish diversity, but these connectivity indices are usually single indicators, which can neither fully reflect the connectivity of river networks nor combine structural and functional connectivity. The relation of these connectivity indices to fish diversity is usually not clear. Consequently, it is extremely urgent to develop novel connectivity indices to measure the influence of RNC intensity on fish diversity.

Few studies consider the mechanisms of RNC influences on fish diversity. The main approaches and key processes of RNC influence on fish diversity include species sorting, dispersal dynamics, habitat availability, trophic dynamics and disease transmission. However, there is no systematic research on RNC and fish diversity influence mechanisms. RNC often affects fish diversity through multiple mechanisms. Changes in fish diversity are usually the result of a combination of different influencing mechanisms which might have complex linkages. In addition, only a few mechanisms of habitat connectivity and dispersal dynamics have been proposed in previous studies. The mechanisms that apply to other species may also explain how fish diversity responds to RNC. For instance, social communities, described for birds, also exist in fish species (Shizuka et al., 2014). Groups of fish individuals are tightly connected with each other through habitat co-membership. The effect of RNC on fish diversity by regulating fish social communities remains to be further studied.

Considering the present research progress for the influence of the RNC on fish diversity, we can do more work to: (1) extend the study area to the whole basin to research the influence of complex connectivity to fish diversity from the perspective of river networks; (2) conduct long-term monitoring experiments and combine monitoring data with model simulations; (3) incorporate network structure, river discharge and other properties into analyses for the development of indices to assess the intensity of RNC; and (4) deeply explore the mechanisms by which RNC influences fish diversity, especially the correlation among various mechanisms.

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Appendix A. Supplementary data

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