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Metacommunity structure of zooplankton in river networks: Roles of environmental and spatial factors

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ABSTRACT

Zooplankton in river systems have seldom been studied in the context of metacommunity ecology. Spatial factors (e.g., river connectivity, directionality, and man-made dams) may play a key role in influencing the metacommunity structure of rotifers because of their small body size and weak mobility. In contrast, local environmental factors (e.g., physicochemical habitat) may be more important to crustaceans due to their larger body size and stronger mobility. We sampled zooplankton and environmental factors during wet and dry seasons from 47 sites along the Ying River in China to assess the roles of the spatial and environmental factors in structuring zooplankton metacommunities. We used Moran's eigenvector map and asymmetric eigenvector map to model the influences of river connectivity, directionality, and man-made dams on zooplankton metacommunity structure. We then used partial redundancy analysis to identify individual and interactive effects of spatial and environmental factors on both the entire zooplankton assemblages and two zooplankton groups of different body sizes and mobility. A total of 101 taxa were identified and taxa richness was higher in the wet season (72) than in the dry season (58). Zooplankton assemblages were primarily dominated by rotifers. For the dry season, environmental factors such as total nitrogen, water temperature, and pH explained a significant portion of variation in zooplankton community; river connectivity was more important than river directionality to zooplankton metacommunity structure. For the wet season, spatial factors were more influential than environmental factors such as dissolved oxygen and water transparency; river directionality played an important role in influencing the spatial structures of both environmental condition and zooplankton metacommunity. We also found significant effects of man-made dams on zooplankton metacommunity structure. Spatial factors are more influential in structuring small body size and weak mobility rotifer communities, while environmental factors are more important in determining the variation of crustaceans due to their larger body size and stronger mobility. We concluded that river connectivity and directionality should be considered as key factors for better understanding the spatial processes of planktonic passive dispersers in river networks. Our study provides new insight on understanding riverine zooplankton metacommunity ecology and contributes to the knowledge of river ecosystem health monitoring and management.

1. Introduction

Metacommunity can be conceptualized as a set of local communities in different locations that are connected by dispersal of multiple potentially interacting individuals (Cottenie et al., 2003; Gilpin and Hanski, 1991). Two contrasting views on metacommunity assembly have emerged (Cottenie, 2005; Dray et al., 2012; Gravel et al., 2006; Leibold et al., 2004). The niche theory emphasizes the importance of species sorting and filtering by local environmental factors and biotic interactions (Leibold et al., 2004; Logue et al., 2011; Urban, 2004), while the neutral perspective underlines the role of spatial factors such as dispersal in structuring a metacommunity (Hubbell, 2001). Recent studies on metacommunity ecology suggested that some metacommunities

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were strongly related to spatial factors while others were associated with environmental factors (Gascón et al., 2016; Heino et al., 2015a,b). However, the co-occurrence of significant environmental control and spatial structuring of metacommunity has been considered as a sign of the mass effects (Ng et al., 2009), which have been suggested to be special cases of the niche theory (Winegardner et al., 2012). A better understanding of the relative roles of local environmental factors and spatial factors such as dispersal in structuring metacommunity is essential for ecology and biodiversity conservation.

One of the main challenges to understand the role of spatial dispersal in structuring metacommunity in a regional process is how to characterize species dispersal abilities at a large spatial scale (Heino et al., 2015a,b). Rivers as a dendritic ecological network (Grant et al., 2007) may provide a unique opportunity in studying the role of species dispersal in affecting metacommunity structure. River networks are spatially asymmetrical and characterized largely by unidirectional flows; hence upstream sites have stronger influence on downstream sites than vice versa (Brown et al., 2011). Branches of rivers can not only act as mediums of connections among interacting local communities, but also form the prime habitats themselves (Grant et al., 2007). The connectivity and directionality of rivers have important influences on the dispersal of organisms (Brown and Swan, 2010; Grant et al., 2007; Liu et al., 2013). For example, the spatial dispersal processes of fish are entirely restricted to the hydrological connections in river networks (Landeiro et al., 2011). The dispersal of passive dispersers, such as drifting macroinvertebrates, proceeds with the direction of the flow (Brown et al., 2011). Different species may differ in their sensitivity to the dendritic structure (Grönroos et al., 2013) and different taxonomic or functional groups may have different responses to the connectivity and flow directionality of the river (Liu et al., 2013). The connectivity and directionality of rivers may vary spatially and seasonally and can be disrupted by man-made river impoundments, which may serve as a proxy for aquatic species dispersal abilities.

The understanding of environmental and spatial factors in structuring the metacommunities of dendritic river network is still limited (but see Brown et al., 2011; Brown and Swan, 2010; Cottenie et al., 2003). This could be largely due to the limitation of analytical methods. Spatial models used in river metacommunity studies have been mostly based on overland distances without taking the real connection network of rivers and directionality of water flow into account. The recent improvement of spatial eigenfunction analysis has made it possible to integrate spatial complexity and to test the competing theories of structuring metacommunities in dendritic networks (Bertolo et al., 2012; Blanchet et al., 2011, 2008a). Several studies on passive dispersal river metacommunities have focused on benthic organisms (Liu et al., 2016 on diatoms and macroinvertebrates; Liu et al., 2013 on diatoms) because these organisms are important functional groups, play key roles in trophic interaction, and are indicators of environmental degradation of aquatic ecosystems. There is little suitable habitat for planktonic organisms such as zooplankton in natural rivers especially in the shallow upstream rivers with rapids; river flow-through lakes, reservoirs, and large rivers with slow flows are exceptions.

The Huaihe River has the highest abundance of dams in China (>11,000 dams) and the Ying River is the most dam-intensive tributary of the Huaihe River. Because of the effect of high-density of dams on water flow, the Ying River has lost many characteristics of natural rivers and is now determined by numerous narrow and interconnected "ponds", especially during the dry season, which provides suitable habitats for planktonic organisms (zooplankton) in the river. Consequently, the Ying River is an ideal system for testing how the composition of metacommunities is regulated in a fluvial environment by providing a typical high flow river condition during the wet season and atypical low flow condition that creates these narrow interconnected pools during the dry season. This flow-regime-driven setup allows the test of mechanisms of the environmental filtering emphasized niche theory (Leibold et al., 2004; Logue et al., 2011; Urban, 2004) and the spatial focused neutral theory (Hubbell, 2001) or the combination of the two in structuring metacommunities.

In this study, we examined the relative importance of environmental and spatial factors in structuring zooplankton (passive dispersers) metacommunities in the Ying River during the wet and dry seasons using a combination of spatial eigenfunction analysis and variation partitioning. We first developed environmental and directional spatial models based on the distance of hydrological connections and the number of man-made dams among sites to compare the effects of environmental factors, directionality, and dams on passively dispersing zooplankton communities in each season. We then compared the community variation of two taxonomic groups of zooplankton that differ in body size and mobility. We expected that river directionality and dams play a vital role in structuring zooplankton metacommunity, and their effects vary between seasons. We also hypothesized that spatial factors are more influential in structuring the small body sized and weak mobility zooplankton group, while environmental factors are more important in determining the community variation of larger body size and stronger mobility crustaceans. To our knowledge, our study is the first to simultaneously study metacommunity structure of two passively dispersing zooplankton groups in a riverine ecosystem by taking spatial factors (river connectivity, directionality and man-made dams) into account simultaneously or individually. This study enhances our understanding of the zooplankton metacommunity structuring process in river systems and helps the interpretation of variation in different taxonomic groups of passively dispersing organisms in future studies on metacommunity ecology.

2. Methods

2.1. Study region and sampling sites

The Ying River is the largest tributary of the Huaihe River in eastern China. The basin area of the Ying River is about 36,651 km^2 with a total river length of 561 km. Plains account for 51.7% of the total drainage area with 29.6% and 18.5% as mountains and hilly areas, respectively. The major land use in the watershed is agriculture (54%). The study area is in the warm temperate zone of semi-humid continental climate with a mean annual temperature from 14 to 16 °C and mean annual precipitation of 770 mm. The wet season generally occurs between June and September, accounting for more than 60% of the annual precipitation. More than 80 man-made dams have been built on the river.

A total of 47 sites were sampled in August 2013 (wet season) and January 2014 (dry season). The selected sites cover the major tributaries of the river network and the main-stem river (Fig. 1).

2.2. Sampling and measurement procedures

Zooplankton were collected in calm days during each season. At each site, 50 l of water were taken from three locations of a river transect: center and each side of the channel. The collected water was filtered through 25 μm mesh size net and then preserved with 4% formaldehyde solution immediately. Approximately 3–5 ml of each sample was counted in the laboratory. After mixing completely, 1 ml of the sample was filled in a 1-ml counting chamber for zooplankton identification. This process was repeated 3–5 times. Zooplankton were counted under a light microscope