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Metacommunities in river networks: The importance of network structure and connectivity on patterns and processes

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Abstract: 1. Rivers are spatially organised into hierarchic dendritic networks. This unique physical structure and the associated directionality of physical flows set them apart from most other environments by regulating the dispersal of resident biota and therefore the distribution of biodiversity. 2. The aim of this special issue is to highlight the importance of the river network on structuring biodiversity, particularly through metacommunity dynamics and associated dispersal processes. 3. The issue covers a wide range of topics, including disease spread, nutrient uptake, trophic dynamics, effects of anthropogenic stressors and the joint roles of dispersal and environmental filtering. Contributions employ a broad range of approaches, including field and laboratory experiments, modelling, population genetics and conceptual synthesis. 4. Although these studies represent just a sample of the research that is being performed on biodiversity and metacommunity dynamics in river networks, several important findings have emerged; a common theme being that the structure of the network and spatial dynamics clearly influence the dynamics of populations and communities, and their functions. By taking a broad taxonomic focus (from diatoms and protists to fish), and spanning a large geographic gradient (from the tropics to the subarctic), this special issue provides a broad look at the dynamics that occur in river networks relating to their unique makeup. We hope that this selection of studies spurs additional research on these interesting, globally important, yet severely threatened ecological systems.

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Metacommunities in river networks: The importance of network structure and connectivity on patterns and processes

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Abstract

1. Rivers are spatially organised into hierarchic dendritic networks. This unique physical structure and the associated directionality of physical flows set them apart from most other environments by regulating the dispersal of resident biota and therefore the distribution of biodiversity.
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KEYWORDS

dendritic network, dispersal, metacommunity, spatial dynamics, stream networks

The metacommunity concept has advanced our understanding of the processes shaping community assembly by emphasising the interdependence of local communities and the regional species pool (Holyoak, Leibold, & Holt, 2005; Leibold et al., 2004). Central to this concept is that communities are shaped by an interplay between local (environmental filtering and biotic interactions; species sorting) and regional (dispersal) processes. It follows that the physical makeup of the environment in which species disperse can regulate

the contribution of regional effects (e.g. rates and directions of dispersal). The unique physical structure and longitudinal continuity of running water systems (Altermatt, 2013) sets them apart from many other systems for the specific dynamics that regulate metacommunity structure and biodiversity in general.

From an ecological standpoint, rivers have historically been viewed in terms of longitudinal zonation along the river continuum (Vannote, Minshall, Cummins, Sedell, & Cushing, 1980). Based on

extensive work on the ecohydrology of river networks and the physical and hydrological laws governing dendritic networks (Rodríguez-Iturbe & Rinaldo, 2001), however, our understanding of biodiversity in these systems has progressed significantly from this historic viewpoint. Although past work on riverine communities had either a localised or linear perspective, the hierarchical dendritic structure of river networks is more readily incorporated in studies seeking to understand biodiversity patterns (Altermatt, 2013; Campbell Grant, Lowe, & Fagan, 2007). This dendritic network organisation, and the physical unidirectional flows associated with this structure (e.g. water, matter, biased dispersal for many organisms), can exert strong controls on metacommunity dynamics and the consequent distribution of biodiversity (Altermatt, 2013; Brown & Swan, 2010; Campbell Grant et al., 2007), depending on dispersal traits (Canedo-Arguelles et al., 2015; Kärnä et al., 2015; Tonkin et al., 2018). In some cases, network structure alone may be sufficient to explain biodiversity at large scales or override other typically strong drivers of freshwater biodiversity such as climate, flow and biogeography (Carrara, Altermatt, Rodríguez-Iturbe, & Rinaldo, 2012; Finn, Bonada, Múrria, & Hughes, 2011; Muneeppeerakul et al., 2008).

The aim of this special issue is to highlight the importance of the river network for structuring biodiversity, particularly through metacommunity dynamics and dispersal processes. We selected a broad range of research themes centred around metacommunity dynamics in dendritic networks, but also including related fields, in order to examine and synthesise the importance of river network properties for the structuring of biodiversity in these unique systems. By taking a broad taxonomic focus, and spanning a large geographic gradient, we aim to provide a broad look at the dynamics that occur in river networks relating to their unique makeup.

The eleven papers in this issue span a variety of approaches, including field (Brown, Wahl, & Swan, 2018) and laboratory experiments (Altermatt & Fronhofer, 2018), modelling (Anderson, Hayes, & Sarhad, 2018; Carraro, Mari, Gatto, Rinaldo, & Bertuzzo, 2018; Helton, Hall, & Bertuzzo, 2018; Valente-Neto, Duraes, Siqueira, & Roque, 2018), species distribution models (de Mendoza et al., 2018), population genetics (Prunier, Dubut, Loot, Tudesque, & Blanchet, 2018) and conceptual synthesis (Tonkin et al., 2018). These studies cover a wide range of topics and focal organisms, including disease spread (Carraro et al., 2018), nutrient uptake (Helton et al., 2018), trophic dynamics (Anderson et al., 2018), effects of anthropogenic stressors (Prunier et al., 2018), and the joint roles of dispersal and environmental filtering in structuring taxonomic groups ranging from diatoms to fishes (Brown et al., 2018; de Mendoza et al., 2018; Jamoneau, Passy, Soininen, Leboucher, & Tison-Roseberry, 2018; Schmera et al., 2018). Finally, the papers cover a broad geographic gradient from the Neotropics of Brazil (Valente-Neto et al., 2018) to subarctic Finland (de Mendoza et al., 2018), thereby avoiding the typical bias to temperate riverine systems only. A common theme among these studies is that the structure of the network and spatial dynamics do indeed regulate dynamics of populations and communities, and their associated functions. Although these represent just a sample of the research that is being performed on biodiversity and

metacommunity dynamics in river networks, several important findings have emerged, which we summarise below.

Studies in this special issue revealed the strength of the river network in regulating dynamics of various ecological phenomena. For instance, Helton et al. (2018) demonstrated that the shape and density of idealised networks can regulate the amount of nitrogen uptake that a river catchment can perform. Specifically, stream networks in narrow catchments removed a higher fraction of nitrate from the catchment, and decreasing drainage density reduced the fraction of nitrate removed from the catchment. The shape of the network was able to explain a considerable amount of variation in how much nitrate was removed, but depended on how much nitrate was added and where in the network. Also using model networks, Carraro et al. (2018) showed, using a spatially explicit metacommunity model, that network structure can regulate the spatial distribution of proliferative kidney disease, which affects salmonid populations. They found that the extent of mixing between low and high order streams can be influenced by the extent of fish mobility within catchments. Their model exhibits clear potential as a tool for tracking and predicting proliferative kidney disease presence and outbreak in river networks. Finally, Prunier et al. (2018) showed that the effects of network structure on genetic diversity of fish can be much higher than those of anthropogenic stressors. They highlight the importance of considering natural network structure and stocking activities for genetic diversity, which are more general and less system specific than the influences of anthropogenic stressors.

Different trophic levels, such as predatory fishes and their macroinvertebrate prey, are commonly studied individually in river network metacommunity models (e.g. Altermatt, Seymour, & Martinez, 2013; Muneeppeerakul et al., 2008), despite strong trophic interactions among them. An inclusion of trophic dynamics into models, however, is critical for a deeper and more realistic understanding of community structure and diversity in real river networks. Anderson et al. (2018) developed and analysed the first metacommunity model in dendritic networks to include direct trophic dynamics. Using a spatially explicit consumer-resource model, they found that trophic dynamics are influenced by the structure of dendritic networks, especially by the nature of the branching in the network. This influence emerges from asynchrony among dynamics of local communities, such that communities at highly connected sites show less variability in the consumer-resource dynamics compared to communities that are more isolated. Importantly, this may not only help in explaining patterns observed in natural metacommunities, but also in guiding management decisions.

Depending on where a community is located in the river network, it can be more or less connected to other potential sources of colonists. The connectivity imbalance between headwaters and mainstems can alter the relative importance of local and regional dynamics (Brown & Swan, 2010). Previous research suggested that central sites within a river network may harbour higher species richness than those in the periphery, a finding supported by both field (Altermatt et al., 2013) and laboratory studies (Carrara et al., 2012; Seymour, Fronhofer, & Altermatt, 2015). Using an experimental

microcosm approach, Altermatt and Fronhofer (2018) demonstrated how differences in network structure can result in differences in the spatial variation of population densities. This finding is predicted by theory, but the study may be the first to demonstrate this experimentally. They found that population densities were highest at nodes connected to headwaters, rather than those in the headwaters themselves or in more central network nodes. Although this study focused on population-level effects, it provides an important hypothesis to be tested by river network ecologists that can scale up to the community level.

In a past analysis examining stream macroinvertebrate community structure, Brown and Swan (2010) demonstrated that more isolated upstream parts of the network (headwater streams) were primarily structured by species sorting, while more central mainstem rivers were increasingly influenced by dispersal (i.e. mass effects). Here, using a manipulative field-based flume experiment, Brown et al. (2018) showed evidence that invertebrate communities in more connected locations in the network (mainstems) were under more dispersal control (reflecting mass effects) than those in isolated (headwater) positions in the network (reflecting species sorting); a finding supported by previous theoretical work (Campbell Grant et al., 2007). They found that headwater-sourced communities were more responsive to dispersal manipulation than mainstem-sourced communities. Brown et al. (2018) interpreted this finding such that mainstem communities may have already been under strong dispersal control via mass effects. Schmera et al. (2018) also tested this hypothesis, which they termed the network position hypothesis (NPH), for multiple taxonomic groups (benthic diatoms, macrophytes, macroinvertebrates and fish) in a Hungarian river network. In general, they found no clear evidence in support of the NPH, with the exception of macroinvertebrate communities; that is, the taxonomic group for which this hypothesis was initially intended. Jamoneau et al. (2018) found that, although environmental filtering was prevalent for benthic diatom communities regardless of watercourse position across a broad geographical gradient, there was an increasing role of mass effects moving from small headwaters to large mainstem rivers (greater beta diversity in headwaters compared to mainstems). This finding thus supported the NPH. They also found that mass effects were more prevalent for motile diatoms (high mobility) compared to low-profile (low mobility) species, which were more environmentally determined.

Metacommunity simulations can help to further tease apart the relative roles of niche, dispersal and stochastic processes (Sokol et al., 2015). These approaches have the advantage that the process begins with a mechanistic understanding of the factors governing metacommunity dynamics, enabling a direct comparison with empirical datasets to test model assumptions. Valente-Neto et al. (2018) used a metacommunity simulation model developed for river networks to predict empirical stream insect diversity in a Brazilian stream network. Their model was parameterised by an aquatic insect species pool, based on empirical data, as well as an environmental gradient and river network structure. Comparing models incorporating different rates of dispersal, oviposition, colonisation, and

mortality, they showed that both deterministic and stochastic processes contribute to observed diversity patterns. However, this was only apparent for medium and low-ability dispersers, with no models able to explain observed patterns for strong dispersers.

The previous studies highlight that the structure of the network matters for the organisation of biodiversity, largely by regulating dispersal. In a review of the literature, Tonkin et al. (2018) provide a conceptual synthesis of the role that the river networks plays in structuring metacommunities in relation to dispersal processes. They developed a conceptual model predicting that the explanatory power of the river network is greatest for aquatic dispersers in mesic systems. By contrast, aerial dispersers in arid systems tend to rely less on the network, utilising other overland pathways of dispersal. Their synthesis found that several factors, including dispersal mode, landscape type, network connectivity, land use, topographic complexity, and biotic interactions were able to regulate the importance of the river network in structuring metacommunities. Moreover, results from the study of de Mendoza et al. (2018) indicated a greater importance of habitat heterogeneity over dispersal in determining insect metacommunity structure in a subarctic network of tributaries, which were directly connected to two mainstem rivers. Nevertheless, the spatial arrangement of their sampling sites did not allow for a strong test of dispersal dynamics in relation to network structure. Their results on the joint importance of environmental filtering and spatial effects on single species distributions were, however, similar to those of a related study that focused on dendritic networks in three separate drainage basins (Heino & de Mendoza, 2016).

Despite their high biodiversity value, river networks are under ever-present threat from global change (Dudgeon et al., 2006; Vörösmarty et al., 2010). To enable better management and conservation of these systems requires looking beyond environmental filtering alone and considering spatial effects from a metacommunity perspective (Altermatt et al., 2013; Heino, 2013; Stoll, Breyer, Tonkin, Früh, & Haase, 2016; Tonkin, Stoll, Sundermann, & Haase, 2014). The research in this special issue has demonstrated some of the important ways that the unique physical structuring of river networks can influence the way in which communities assemble, organisms disperse, diseases spread, and ecosystem processes are performed. However, there are multiple avenues of research that could be expanded on to advance our understanding of the role that the river network plays in regulating metacommunity dynamics and other aspects of biodiversity (Tonkin et al., 2018). We hope that the broad range of novel research in this special issue sparks interest and further research in this important field of freshwater ecology.

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