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Diversity in riverine metacommunities: a network perspective

Florian Altermatt

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Abstract The influence of spatial processes on diversity and community dynamics is generally recognized in ecology and also applied to conservation projects involving forest and grassland ecosystems. Riverine ecosystems, however, have been for a long time viewed from a local or linear perspective, even though the treelike branching of river networks is universal. River networks (so-called dendritic networks) are not only structured in a hierarchic way, but the dendritic landscape structure and physical flows often dictate distance and directionality of dispersal. Theoretical models suggest that the specific riverine network structure directly affects diversity patterns. Recent experimental and comparative data are supporting this idea. Here, I provide an introduction on theoretical findings suggesting that genetic diversity, heterozygosity and species richness are higher in dendritic systems compared to linear or two-dimensional lattice landscapes. The characteristic diversity patterns can be explained in a network perspective, which also offers universal metrics to better understand and protect riverine diversity. I show how appropriate metrics describing network centrality and

dispersal distances are superior to classic measures still applied in aquatic ecology, such as Strahler order or Euclidian distance. Finally, knowledge gaps and future directions of research are identified. The network perspective employed here may help to generalize findings on riverine biodiversity research and can be applied to conservation and river restoration projects.

Keywords Dispersal · Dendritic river network · Connectivity · Centrality · Aquatic invertebrates · River continuum concept · Strahler order

Main text

Over the last few decades, interest in spatial processes has grown tremendously in ecology (Hanski and Gaggiotti 2004; Leibold et al. 2004; Holyoak et al. 2005). Ecologists are aware that most species live in spatially heterogeneous landscapes and that patch size and connectivity shape the composition of local communities. Metacommunity theory provides a conceptual framework to describe spatially heterogeneous landscapes and processes that affect species diversity and distribution. A metacommunity is defined as a set of local communities that are linked by dispersal (Leibold et al. 2004; Holyoak et al. 2005; Altermatt 2012). Metacommunity theory explicitly addresses interactions between species at different spatial scales

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F. Altermatt (✉)
Department of Aquatic Ecology, Eawag: Swiss Federal
Institute of Aquatic Science and Technology,
Überlandstrasse 133, 8600 Dübendorf, Switzerland
e-mail: florian.altermatt@eawag.ch

and addresses how species interactions can influence or be influenced by spatial dynamics. Thereby, the metacommunity concept combines two common features of many biological systems, namely that species are interacting in complex ways and that spatial heterogeneity and fragmentation lead to fragments of suitable habitat patches in a matrix of non-habitat (Altermatt 2012). Human activities such as habitat fragmentation, introduction of invasive species or climate change makes a mechanistic understanding of patterns and processes in heterogeneous landscapes critical (Hanski and Gaggiotti 2004; Holyoak et al. 2005). Ultimately, we want to understand how genetic and species diversity of ecological communities is created and maintained, which requires understanding of ecological and spatial processes.

While the influence of spatial processes on diversity and community dynamics is generally recognized, empiricists have not yet adequately applied the spatial perspective to all habitat types. The majority of studies on metacommunity dynamics focused on habitats characterized as two-dimensional landscapes, including forests, grasslands and pond systems (Fig. 1a). Examples include studies of butterflies (Hanski and Gaggiotti 2004), small mammals (Moilanen et al. 1998), aquatic (Altermatt and Ebert 2008, 2010) and terrestrial arthropods (Gonzalez et al. 1998). Theoretical models (e.g., Hubbell 2001) of these systems

generally use lattice-like grids as landscape approximations (Fig. 1a), where each node represents an individual (e.g., a plant) or a community of interacting species. Local dispersal can occur to any of the eight adjacent nodes. Generally, dispersal is random in direction, and distance varies among species. Consequently, there are different possible dispersal routes between patches. Such an approach, however, is not appropriate for many other natural systems, and processes and patterns may be very different especially in habitat systems that have a dendritic, river-like network structure (Fig. 1b, Fagan 2002; Grant et al. 2007; Fagan et al. 2009). Many natural systems, such as stream and river systems, mountain ranges or cave networks, have a dendritic structure (Rodríguez-Iturbe and Rinaldo 1997; Fagan 2002; Benda et al. 2004). These habitats are not only structured in a hierarchic way (Fig. 2), but landscape structure and physical flows often dictate distance and directionality of dispersal. A dendritic environment can be represented by a geometric pattern of arborescent bifurcation originating from one node and extending out in one direction, forming a hierarchical network of nodes and branches (Fig. 1, Grant et al. 2007; Fagan et al. 2009; Rodríguez-Iturbe et al. 2009; Newman 2010; Peterson et al. 2013). Dendritic networks have two fundamental characteristics (Grant et al. 2007; Rodríguez-Iturbe et al. 2009): (1) Both the branches (edges)

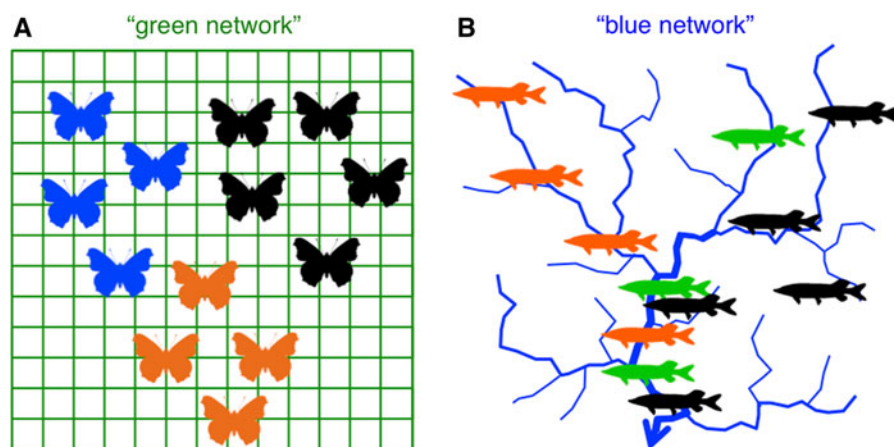


Fig. 1 **a** Two-dimensional lattice landscape and **b** river-like, dendritic landscape. Lattice grids describe connectivity in grassland or forest ecosystems (also called “green networks”), while dendritic landscapes describe connectivity in river systems (also called “blue networks”). When dispersal is restricted to the network branches, the different dispersal paths cause different diversity patterns: In green networks, community similarity is

driven by Euclidian distance, such that species or genotypes of the same type are clustered. In blue networks, diversity patterns are driven by topological distance: Characteristically, diversity is higher at confluences and lower reaches, and there is a high differentiation between headwater communities. Different colored butterflies and fish stand schematically for different species or different genotypes living in these landscapes

and the nodes serve as habitat and (2) the specific spatial connectivity and hierarchical organization of these elements interact with a species' movement behavior, and directional dispersal is common.

Recently, the study of dispersal and diversity pattern in dendritic systems has been spurred by a revival and more general application of graph theory in ecology (Urban et al. 2009; Newman 2010; Peterson et al. 2013). This application resulted in a series of theoretical, comparative and experimental studies (e.g., Grant et al. 2007; Muneeppeerakul et al. 2008; Morrissey and de Kerckhove 2009; Rodriguez-Iturbe et al. 2009; Fagan et al. 2009; Brown and Swan 2010; Carrara et al. 2012, 2013; Peterson et al. 2013), but is only starting to be used by empirical ecologists and conservation practitioners (e.g., Barták et al. 2013;

Göthe et al. 2013). A few reviews have been covering the topic, focusing on theoretical aspects of graph theory (Rodriguez-Iturbe et al. 2009; Peterson et al. 2013) or on more empirical aspects (Grant et al. 2007; Brown et al. 2011). These reviews were generally addressing a readership already familiar with meta-community or network concepts and only marginally focus on conservation aspects. Here, I give an overview of the most recent developments with respect to river network studies and make suggestions for a common approach and terminology in describing and understanding dispersal and diversity patterns in riverine ecosystems. The network perspective employed here helps to generalize findings and can then be applied to environmental and conservation projects.



Fig. 2 Examples to illustrate the variety of riverine habitats, covering headwaters (a–d), midreaches (e–g) and lower reaches (h, i). Headwaters include small tributaries in central European forests (a), glacial streams (b, Swiss Alps) and streams in grassland systems (c, d, both central Europe). Midreaches examples are from alpine areas (e, Sierra Nevada Mountains,

California), central valleys (f, Switzerland) or forests (g, Switzerland). Large rivers of lower reaches are mostly found in lowlands outside mountain ranges (h, River Vakhsh, Tajikistan and i, Oulanka River, Finland; all photographs by F. Altermatt)

High diversity in riverine ecosystems

Understanding community composition and biodiversity patterns across all types of riverine habitats is highly important (Fig. 2). First, while natural riverine ecosystems and adjacent riparian vegetation cover only a small area on earth, they not only comprise a high variety of habitat types (Fig. 2), but also contain a disproportionately large number of species (Fig. 3, Vinson and Hawkins 1998; Dudgeon et al. 2006; Clarke et al. 2008; Vorosmarty et al. 2010). Communities in headwater streams or dendritically organized caves are characterized by high levels of endemism

(Clarke et al. 2008). To protect this diversity, we need a general understanding of ecological processes in dendritic systems. Second, humans depend on the ecosystem functioning of rivers as the most important freshwater source, for fisheries or irrigation (Lowe et al. 2006; Vorosmarty et al. 2010). Ecosystem functioning in riverine systems may not only depend on the local environmental conditions (Woodward et al. 2012), but also on the influx of species and medium from upstream localities (e.g., Singer et al. 2012). The specific river network structure, its branches (edges) and confluence points (nodes), may affect ecosystem processes. For example, biomass



Fig. 3 Examples of typical organisms contributing to the high diversity in riverine ecosystems. Invertebrates (a–c) and amphibians and reptiles (d–f) are not only highly diverse groups, but also commonly used in biodiversity studies, either as indicator species or because of their high iconic value. Understanding the factors driving their distribution and diversity patterns is of high priority in ecology and river management

in particular. **a** amphipod (*Gammarus fossarum*, central Europe), **b** mayfly (*Ecdyonurus helveticus*, central Europe), **c** stonefly (*Perla grandis*, European Alps), **d** California newt (*Taricha torosa*, California), **e** western pond turtle (*Actinemys marmorata* sp. *pallida*, California) and **f** fire salamander (*Salamandra salamandra*, central Europe; all photographs by F. Altermatt)

input in individual reaches is driven by the locally common riparian vegetation or geological ground (e.g., coniferous forests vs. deciduous forests or limestone vs. bedrock catchments) and low dilution of potential nutrient pollution. This may limit or bias nutrient cycling and ecosystem processes (Woodward et al. 2012). At confluences and further downstream sites, however, inflows of different reaches are inter-mixing, either facilitating or interfering with ecosystem processes. Again, this calls for a spatially explicit study, using a river network perspective. Finally, riverine systems are ecological corridors not only for native species (e.g., beavers recolonizing European river systems, Barták et al. 2013), but also for many non-native species and pathogens (Leuven et al. 2009; Rodriguez-Iturbe et al. 2009; Mari et al. 2011), and the proportion of non-native species is exceptionally high in riverine systems (Leprieur et al. 2008; Leuven et al. 2009). Ecologists and conservation practitioners thus depend on a better understanding of dispersal processes in dendritic systems. The predictability of invasion patterns may be affected by the place of introduction and specific dispersal paths. Both aspects may depend on the river network structure. Recent models applying such a network perspective are highly successful in, for example, predicting the spread of the invasive Zebra mussel (*Dreissena polymorpha*) in North America (Mari et al. 2011).

From points to lines...

Ecologists have neglected the dendritic network structure of rivers for a long time (Benda et al. 2004). Biodiversity in rivers was often studied in a non-spatial perspective (Fig. 4b), and local environmental factors of the river habitat (Fig. 2) were postulated as major drivers of community composition (e.g., Death and Winterbourn 1995). The river continuum concept (RCC, Vannote et al. 1980) and more recently the metacommunity concept (Winemiller et al. 2010) added a new perspective from headwaters to mid- and lower reaches (Fig. 4c). The RCC describes the occurrence of organisms and biological properties in rivers in a linear, longitudinal sequence and spurred a large number of studies (e.g., Grubaugh et al. 1996; Vinson and Hawkins 1998). An important postulation of the RCC is a systematic and gradual change between the production and

consumption of organic material from headwaters to mid- and lower reaches, and a change in the associated fauna of grazers, shredders and predators. While highly influential and important, the RCC disproportionately focuses on lower reaches with most headwater communities being neglected.

...to dendritic networks

All rivers form dendritic networks (Fig. 4d). This seemingly obvious fact was already noted by Leonardo da Vinci (Shepherd and Ellis 1997), who recognized universal characteristics in the shape and size of natural drainage systems. In a dendritic river system, the number of headwaters is much larger than the number of mid- or lower reaches (Leopold et al. 1964; Rodriguez-Iturbe and Rinaldo 1997). This creates a characteristic distribution of patch sizes (Fig. 4d).

Only recently, the high variability in diversity of headwater habitats (Fig. 2) and communities therein (Fig. 3) reached more empirical attention (Heino et al. 2003; Clarke et al. 2008; Grant et al. 2010; Finn et al. 2011; Heino et al. 2012). In parallel, comparative studies on biodiversity patterns and community composition started to acknowledge the inherent dendritic organization of river networks (Fagan et al. 2009; Brown and Swan 2010; Grant et al. 2010; Lynch et al. 2011). They found that species richness in dendritic systems is highest at intermediate levels of the branching structure and that species diversity and allelic richness increase at confluences of branches (Fernandes et al. 2004; Grant et al. 2007). A series of mechanistic explanations (reviewed in Grant et al. 2007) and concepts were proposed to explain these diversity patterns, using metacommunity models (Leibold et al. 2004; Muneeppeerakul et al. 2008; Brown and Swan 2010). For example, Muneeppeerakul et al. (2008) used a neutral metacommunity model, which considered distances and dispersal capacities throughout the Mississippi–Missouri river system. The model yielded predictions of spatial biodiversity patterns that are highly comparable to empirical data on the distribution of fish species (Muneeppeerakul et al. 2008). Recent experiments demonstrated that dispersal in dendritic networks *per se* can lead to characteristic diversity patterns (Carrara et al. 2012), characteristic species distributions and productivity

(Carrara et al. 2013), justifying the network perspective.

Dendritic metacommunity models

In river networks, branches and nodes (i.e., river sections and confluences) are habitat for a variety of aquatic organisms, which can disperse along the river network. The metacommunity concept is ideal to address how local community dynamics in individual river sites are linked by dispersal (Leibold et al. 2004; Holyoak et al. 2005). The metacommunity concept offers four different perspectives (patch dynamics, species sorting, mass effects and neutral dynamics, Leibold et al. 2004), which put different strength on

local and regional processes to explain patterns and variation in community composition (definitions after Altermatt 2012): The patch dynamic perspective assumes that all patches are identical. Communities in patches experience stochastic or deterministic extinction, counteracted by dispersal. The species sorting perspective states that communities are mostly driven by different environmental conditions, such that each species prefers specific types of habitat. Differences in habitats among patches create spatial heterogeneity in community composition. The mass effect perspective assumes that the separation of timescales between local and colonization-extinction dynamics is not a prerequisite of metacommunity dynamics. In the mass effect perspective, local population dynamics are quantitatively affected by

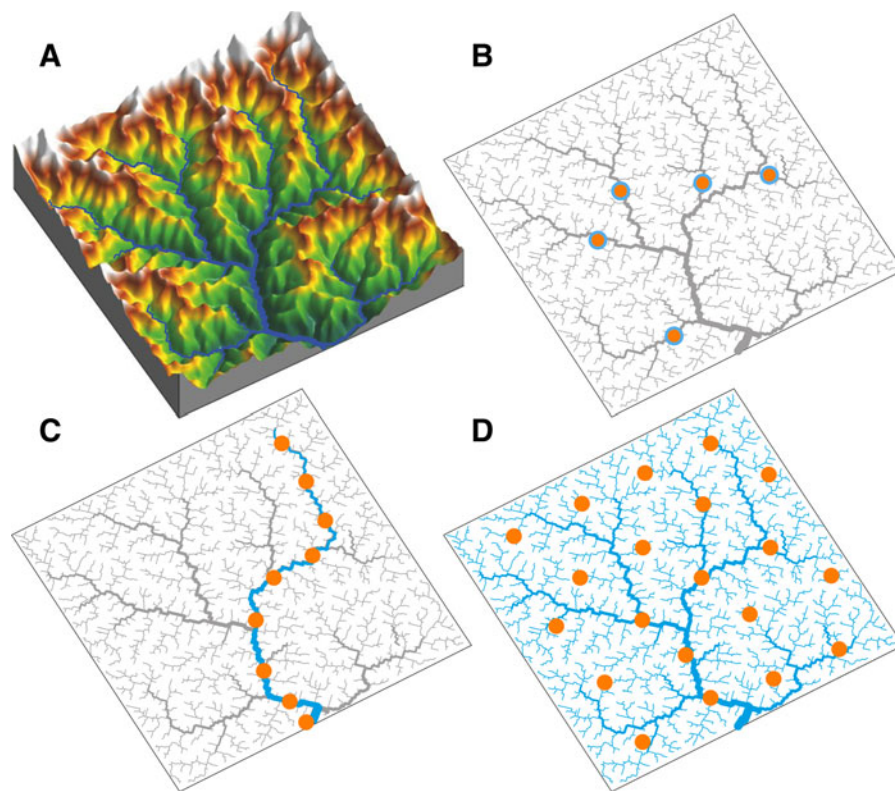


Fig. 4 **a** Geomorphological processes, especially erosion, are forming the characteristic interplay of mountains and valleys in natural landscapes, from which river network structure can be extracted (schematic landscape and river network redrawn after Carrara et al. 2012). **b** Historically, the study of diversity patterns of local communities (orange dots) in rivers focused on a small subset of reaches. Local diversity was mostly explained by local abiotic factors in the immediately surrounding water (blue lines). **c** The river continuum concept extended this

perspective and looked at changes in community composition along a longitudinal river line. Dispersal was acknowledged, but gradual changes in abiotic factors and processes along the river line were still seen as main factors driving diversity patterns. **d** Recently, an all-embracing network perspective started to better integrate dispersal along the characteristic hierarchic river network structure, with its inherent distribution of catchment sizes. Such an approach requires a representative sampling of local communities across the whole network

dispersal dynamics, such that emigration and immigration cause a relevant change in the population- and community dynamics of the respective local patches. Subsequent source–sink effects can influence the relation between local communities and the regional structure. The neutral scenario assumes that species do not differ from each other in their niches and that all have equal fitness in each patch. The composition of local communities is then driven by stochastic processes in a colonization-extinction framework. These four perspectives can be and have been directly applied to riverine systems, where the roles of local and regional processes in shaping community composition have been brought forward. Specifically, this includes dispersal limitation (e.g., Muneepeerakul et al. 2008), mass effect and drift dynamics (e.g., Brown and Swan 2010; Göthe et al. 2013) and species sorting due to differences in patch quality and species-specific ecological requirements (e.g., Thompson and Townsend 2006; Astorga et al. 2012).

Theoretical metacommunity models suggest that diversity in dendritic systems is directly and characteristically affected by dispersal (Fagan 2002; Labonne et al. 2008; Muneepeerakul et al. 2008; Morrissey and de Kerckhove 2009; Rodriguez-Iturbe et al. 2009). These studies explicitly consider the inherent hierarchical structure of dendritic networks and sometimes also directionally biased dispersal (Fagan 2002; Muneepeerakul et al. 2008; Morrissey and de Kerckhove 2009; Rodriguez-Iturbe et al. 2009). Neutral metacommunity models, assuming no demographic differences in species, were able to reproduce biodiversity patterns at large, continental scales (Muneepeerakul et al. 2008). This is suggesting that dispersal limitation alone can be a driving factor of community composition in river systems. However, many further empirical studies indicate that (at least at smaller-than-continental scales) both niche and neutral processes are structuring riverine communities (Thompson and Townsend 2006; Astorga et al. 2012; Altermatt et al. 2013).

A general feature of most metacommunity models is the assumption of restricted dispersal along waterways. In such a framework, Fagan (2002) used simulation models to demonstrate that demographic patterns of a species in dendritic networks differ from expectations based on classical, one-dimensional, stepping-stone models. Specifically, time to extinction is longer in dendritic compared to linear networks, but

only when dispersal is directionally unbiased. Directionally biased dispersal, however, may be common for riverine organisms (Grant et al. 2007). Labonne et al. (2008) used individual-based simulations of an organism with a simple life cycle living in dendritic networks. They found that population demographics are significantly influenced by connectivity (defined as the number of neighbor patches within a given radius) in a surprising way: At high dispersal, connectivity strongly and negatively influences metapopulation size, while variance in occupied patches increases. At low dispersal, local extinction and genetic isolation by distance are promoted by connectivity. However, the model does not consider directionally biased dispersal.

Appropriate metrics and lessons for conservation science

The conventional focus on understanding diversity has been on the individual catchment or local patch scale (Fig. 2). For example, diversity in riverine systems was often linked to local abiotic factors (Fig. 4b) describing patch quality (e.g., pH, temperature, substrate type of riverbed, Power et al. 1988). In response, many river restoration projects have focused on improving these local abiotic factors to increase local biodiversity, but ignoring dispersal processes. While the local conditions in a patch/catchment have been demonstrated to be important for community composition, restoration activities focusing on that scale alone may show weaker responses than might be expected. A key reason for this may be that connectivity is a limiting factor. Dispersal links local communities to the regional species pool (Heino et al. 2003). Recently, Sundermann et al. (2011) found river restoration success to depend strongly on the connectivity of the restored site to the regional species pool. Newly restored sites were not recolonized beyond a distance of about 5 km to the next source population. The distance to potential source populations is thus critical for successful conservation and restoration projects, and dispersal and network positioning need to be considered too, and an incomplete perspective may lead to false conclusions. Consequently, ecologists and conservation scientists depend on appropriate metrics regarding habitat size, species-specific dispersal ability and position of patches within river networks when studying diversity patterns in

river networks. In the following, I outline suitable metrics to describe patch size, dispersal potential and connectivity in riverine networks. A common use of these metrics may not only improve the understanding of diversity patterns, but also help to generalize across river systems.

Dispersal paths, dispersal distance and dispersal directionality

Most dispersal in rivers is along the waterways. Purely aquatic organisms, such as fish, do not traverse land. Even other organisms that have terrestrial life stages, such as riparian plants and aquatic macroinvertebrates with winged adults, mostly disperse along the river network (Elliott 2003). Consequently, distance between patches in a river network should be expressed “as the fish swims,” which is the topological distance (=along-stream distance). Distance “as the crow flies” (i.e., Euclidian distance) often does not reflect actual dispersal pathways (see also Fig. 1). Empirical data on genetic and species richness across space (e.g., Alp et al. 2012; Altermatt et al. 2013) are generally supporting a better explanatory power of topological versus Euclidian or environmental distance (but see Astorga et al. 2012). Topological distance between two randomly selected sites in a river network can be orders of magnitude larger than Euclidian distance (Fig. 5). A short Euclidian distance can thus be deceptive and overestimate connectivity. Using geographic information systems (GIS), topological distance can be easily extracted, making it an appropriate universal distance measure in riverine systems.

Topography defines a unidirectional mass flow in all river systems: The water flows downstream, dictating the flow of nutrients or pollutants. For example, bioavailable dissolved organic matter is shed into headwaters by glacial melt-off. This organic matter is not only highly diverse, but then becomes integrated at different rates into the carbon cycle at further downstream sites (Singer et al. 2012). This directionality of flow is also commonly assumed for passively dispersed organisms, such as plant seeds and planktonic larvae (Bilton et al. 2001; Levine 2003). Even for macroinvertebrates with actively moving life stages, directional downstream dispersal has been commonly assumed (Elliott 1971). Such directional

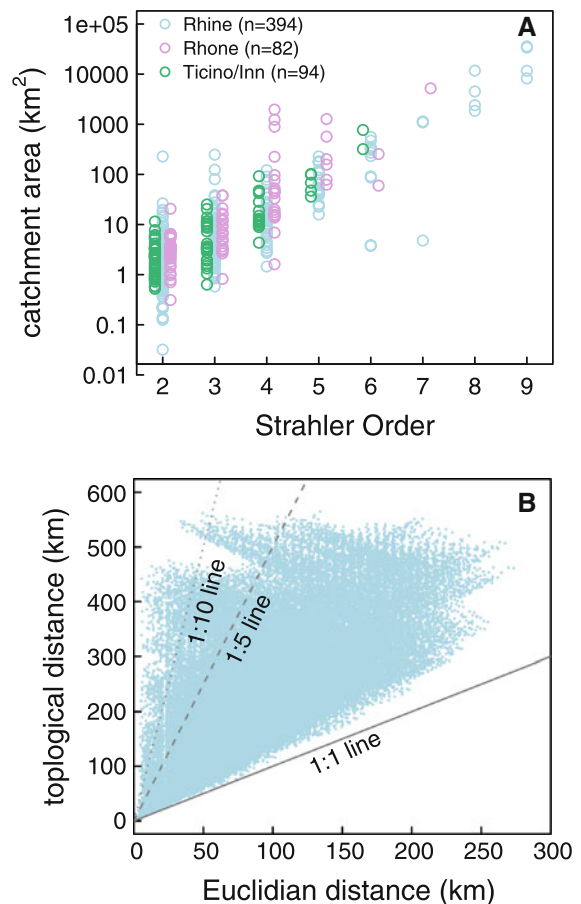


Fig. 5 **a** Strahler order at a river site versus total catchment area (log₁₀-scale) draining into that site for three drainage basins in the Swiss Alps (River Rhine, Rhone, Ticino/Inn; n gives number of sites). Strahler order has been traditionally used to classify river and stream size. However, one Strahler order can cover rivers and streams with catchment area sizes over more than three orders of magnitude, and sites with the same catchment area can fall in three to four different Strahler orders. In a network perspective, catchment area and absolute along-stream distances are thus better descriptors of sites within the river network than Strahler order. **b** Euclidian versus topological distance between 394 randomly chosen sites in the River Rhine drainage basin. Topological (i.e., along-stream) distances can vary over one order of magnitude at a given Euclidian distance

“drift” increases the likelihood that individuals of different species come together at confluences, resulting in higher biodiversity at confluences and downstream sites. Drift may also partly affect the distribution of actively dispersing organisms, such as fish (Fernandes et al. 2004). On the other hand, directional dispersal has strong, and often negative, effects on population dynamics and diversity (Altermatt et al. 2011), especially for headwater sites.

Many species compensate directional downstream drift of larvae by upstream dispersal of adults (Elliott 2003). However, for most groups of organisms, good data on dispersal distance and directionality along riverine networks are lacking. Rare but biologically highly important long-distance dispersers are rarely documented. In this case, highly polymorphic genetic markers can give estimates of gene flow and dispersal distances (e.g., Alp et al. 2012). River restoration projects provide excellent “natural experiments” not only to measure time to recolonization, but also to identify the location of source populations. Eventually, this will lead to an understanding on the commonness of directional dispersal in river systems.

Appropriate metrics

Historically, Strahler order classes (Strahler 1957) were used to describe the hierarchical position within a river network and are still widely applied today. Strahler orders classify streams and rivers in increasing size classes, separating headwaters from mid- and lower reaches. While easily applicable, Strahler order depends on the scale of the map used. Furthermore, streams of very different sizes (i.e., average discharge, river width or depth) may fall into the same Strahler order (Fig. 5). Thus, Strahler order can often not be directly compared between studies and—regarding river sizes—is even inconsistent within a river network. A better, continuous measure of river size is the upstream catchment area draining into a site. Catchment area is a universal descriptor of mean discharge volume (Leopold et al. 1964; Rodriguez-Iturbe and Rinaldo 1997) and directly translates into proportionate river width and depth. Furthermore, land-use analyses in catchment basins can be done in a continuous, scalable manner. Using GIS, one can extract the catchment area draining into a patch for all river networks worldwide. Recent experiments are showing a complex interaction between dendritic connectivity and hierarchical patch size (based on catchment area) on diversity patterns (Carrara et al. 2013). Disentangling the effects of network connectivity and patch size distribution on community composition will be a major field for future comparative studies.

Because dispersal in river networks is often confined to the waterways, some patches within a

river network have a more important role for dispersal compared to other patches. For example, the position of impassable patches (e.g., waterfalls, hydroelectric dams) within a river network may have more or less severe consequences for metacommunity dynamics and should be captured by metrics describing position within the river network. Measures of network centrality measure how important a node in a riverine network is from the viewpoint of connectivity (Urban et al. 2009; Newman 2010; Erös et al. 2011). The most basic centrality measure in a river network is the sum of the distances of a node to all other nodes (along the shortest paths possible), defined as *fareness* (Newman 2010). The inverse of fareness is *closeness*, sometimes also referred to as “*closeness centrality*” or “*ecological diameter*” (Newman 2010; Carrara et al. 2012). The more central a node, the lower is the total distance to all other nodes. Closeness can be regarded as a potential measure of how long it takes an organism to spread from one node to all other nodes in a sequential way. Finally, *betweenness centrality* sums up the number of times a node functions as a bridge along the shortest path between two other nodes, in other words how often a habitat patch functions as a stepping-stone.

A set of new technologies and approaches to merge connectivity and environmental conditions in rivers have been recently developed to improve conservation planning in rivers (e.g., Linke et al. 2012). These approaches are using GIS-based information on habitat type and disturbance and a river connectivity framework to predict the conservation adequacy in rivers. Importantly, connectivity can have a positive effect (e.g., by promoting dispersal of endangered species), but also result in a penalty in the identification of priority areas due to high risk of being affected by pollution or non-native species. The finding that hierarchically organized communities in river networks need new and different conservation strategies starts to be acknowledged (Göthe et al. 2013), but is still lacking practical realization.

The identification of patches and communities that are figuratively and literally “central” to riverine networks is important in directing conservation measures: Central patches may be managed to act as stepping-stones, and colonization is relatively fast after patch restoration or reintroduction or recolonization of rivers by aquatic species (e.g., Barták et al. 2013). If the choice of sites for river restoration projects is based on

political or economic reasons only, patches that are marginal from a network perspective might be restored. Subsequently, these patches will not (or much slower) be colonized by the targeted species, nor will they act as stepping-stones. Such a failure of restoration projects is not too uncommon (Bernhardt and Palmer 2011; Sundermann et al. 2011) and is putting the public acceptance and financial support for restoration projects at risk. Ideally, the choice of sites for river restoration, conservation projects or the removal of dispersal barriers (e.g., building fish ladders at hydroelectric dams) should be guided by the patch's significance from a network perspective. Patches with a high centrality value should be chosen to maximize the spread of reintroduced species or the functioning of restored sites as source populations. Also, measures against non-native species should focus on central patches that act as stepping-stones. Once such central patches are passed through by species, whole new drainage sub-basins can be invaded relatively rapidly (Grant et al. 2012). Thus, to effectively protect sub-basins in river systems against invasions of non-native species, the measures should aim at preventing species colonizing nodes, that is, prevent them getting close to nodes.

Knowledge gaps

Even after decades of study, the drivers of community composition and diversity patterns in natural river systems are still disputed (reviewed in Vinson and Hawkins 1998; Clarke et al. 2008). A network perspective may give a more unifying explanation than the study of specific local environmental factors of a subset of sites. There are still too few empirical studies that comprehensively sampled headwaters, intermediate branches and main river stems (Morrissey and de Kerckhove 2009; Altermatt et al. 2013). It is an open question whether low local (α -)diversity values are always complemented with high among-community (β -)diversity between headwaters (Clarke et al. 2008; Finn et al. 2011). Also, it is unclear whether asymmetric dispersal from the headwaters increases diversity at the confluences, and whether headwater branches are refuges for competitively inferior species (mass effects vs. species sorting, see Fernandes et al. 2004; Brown and Swan 2010). Furthermore, diversity patterns of actively dispersing

freshwater organisms, such as fish, are explained differently (Muneepeerakul et al. 2008; Grant et al. 2010) than diversity patterns of more passively dispersed organisms, such as many invertebrates (Vinson and Hawkins 1998; Clarke et al. 2008).

Theoretical models and existing comparative data are congruent in identifying the importance of river network structure on diversity patterns (e.g., studies done in North America, Europe and Asia, Muneepeerakul et al. 2008; Vorosmarty et al. 2010; Altermatt et al. 2013). A major challenge is to extend these comparative studies to further river networks, including tropical systems, and to incorporate effects of anthropogenic river alterations (e.g., Grant et al. 2012). Furthermore, we are still at the very beginning in experimentally disentangling the causality between different factors such as network structure, directionally biased dispersal and species interactions on diversity patterns in dendritic networks (but see Carrara et al. 2012, 2013).

A major challenge is to address the effects of different dispersal rates or dispersal directionalities on diversity and community composition. Theoretical models suggest a contrasting effect of dispersal rate on diversity pattern in dendritic systems compared to two-dimensional lattice systems, such that increased dispersal reduces local diversity, but does not affect among-community diversity (Muneepeerakul et al. 2008; Rodriguez-Iturbe et al. 2009). Models also predict that regional coexistence of species is promoted by either asymmetric dispersal (Levine 2003) or dendritic landscape structure (Labonne et al. 2008; Morrissey and de Kerckhove 2009), but the relative significance of these two factors is unclear. These models need to be tested experimentally and to be compared to empirical data of natural river systems.

Finally, a largely unexplored question is how dendritic networks influence the spread of invasive species (Grant et al. 2007). Worldwide, river systems are among the most commonly invaded habitats, and invasive species can completely alter the composition of freshwater communities (Leuven et al. 2009; Vorosmarty et al. 2010). Only a few comparative studies addressed the effect of the dendritic structure of habitats on invasion success. For example, Fong and Culver (1994) found different colonization patterns of aquatic crustaceans invading a cave network. The invasion of one species (*Gammarus minus*) happened from the main cave branch through

upwelling, while the other species (*Caecidotea holsingeri*) repeatedly invaded the tips of the cave network. It is of general interest to understand whether the directionality of invasions in dendritic systems affects the outcome of the spread, and whether individual headwaters offer refuge habitats for native species (Lowe et al. 2006; Grant et al. 2007).

Conclusions

The recent application of network theory to riverine ecosystems has changed the way theoretical ecologists understand the origin and maintenance of diversity in rivers. Theory suggests that genetic diversity, heterozygosity and species richness are higher in dendritic systems compared to linear or two-dimensional landscapes (Muneepeerakul et al. 2007; Morrissey and de Kerckhove 2009). While migration into headwater populations is limited, such populations can act as reservoirs for unique alleles or competitively inferior species. In dendritic landscapes, one finds, by definition, more isolated patches (branches) than highly connected patches (confluences) compared to other types of landscapes (Rodríguez-Iturbe et al. 2009). Consequently, a higher overall diversity is maintained in metacommunities inhabiting dendritic networks (Morrissey and de Kerckhove 2009). Compared to other landscape types, however, the sources of diversity in dendritic systems, that is, individual headwater populations, are genetically homogeneous within each headwater (Morrissey and de Kerckhove 2009), but different among headwaters.

It is now timely that empiricists and conservation practitioners are applying these findings. Many studies on diversity in riverine ecosystems are, however, still focusing on a local perspective, ignoring dispersal and the specific network connectivity. Viewing riverine ecosystems in a spatially explicit perspective may not only improve our understanding on the origin of diversity, but can also be used to protect and restore communities in river systems. In terrestrial systems, the application of a spatially explicit perspective has been fruitful for conservation projects, either to specifically install corridors or to prevent fragmentation. A similar approach in river networks is needed to reverse the large-scale losses of aquatic diversity in rivers worldwide (Vorosmarty et al. 2010). Water pollution, hydroelectric dams and interbasin water

transfer (Vorosmarty et al. 2010; Grant et al. 2012) are negative anthropogenic effects affecting whole river networks. Therefore, the spatial scale to understand, prevent and ultimately reverse these changes must be the whole river network as well.

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