SPECIAL ISSUE

The role of dispersal in river network metacommunities: Patterns, processes, and pathways

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Abstract

1. River networks are hierarchical dendritic habitats embedded within the terrestrial landscape, with varying connectivity between sites depending on their positions along the network. This physical organisation influences the dispersal of organisms, which ultimately affects metacommunity dynamics and biodiversity patterns.

2. We provide a conceptual synthesis of the role of river networks in structuring metacommunities in relation to dispersal processes in riverine ecosystems. We explore where the river network best explains observed metacommunity structure compared to other measurements of physical connectivity. We mostly focus on invertebrates, but also consider other taxonomic groups, including microbes, fishes, plants, and amphibians.

3. Synthesising studies that compared multiple spatial distance metrics, we found that the importance of the river network itself in explaining metacommunity patterns depended on a variety of factors, including dispersal mode (aquatic versus aerial versus terrestrial) and landscape type (arid versus mesic), as well as location-specific factors, such as network connectivity, land use, topographic heterogeneity, and biotic interactions. The river network appears to be less important for strong aerial dispersers and insects in arid systems than for other groups and biomes, but there is considerable variability. Borrowing from other literature, particularly landscape genetics, we developed a conceptual model that predicts that the explanatory power of the river network peaks in mesic systems for obligate aquatic dispersers.

4. We propose directions of future avenues of research, including the use of manipulative field and laboratory experiments that test metacommunity theory in river networks. While field and laboratory experiments have their own benefits and drawbacks (e.g. reality, control, cost), both are powerful approaches for understanding the mechanisms structuring metacommunities, by teasing apart dispersal and niche-related factors.

5. Finally, improving our knowledge of dispersal in river networks will benefit from expanding the breadth of cost-distance modelling to better infer dispersal from observational data; an improved understanding of life-history strategies rather than relying on independent traits; exploring individual-level variation in dispersal through detailed genetic studies; detailed studies on fine-scale environmental

(e.g. daily hydrology) and organismal spatiotemporal variability; and synthesising comparative, experimental, and theoretical work. Expanding in these areas will help to push the current state of the science from a largely pattern-detection mode into a new phase of more mechanistically driven research.

1 | INTRODUCTION

Riverine ecosystems possess many unique physical properties that allow a disproportionately high biodiversity to flourish for the area they occupy on Earth's surface (Dudgeon et al., 2006). Most notably, rivers are organised into hierarchical dendritic networks embedded within the terrestrial matrix, with energy moving through networks predominantly downstream (Allan & Castillo, 2007). Habitats within rivers are connected longitudinally to varying extents depending on their position within the network and the overall structure of the landscape (Figure 1). Pioneering research emphasised the linearity of rivers (Vannote, Minshall, Cummins, Sedell, & Cushing, 1980), but it is now clear that understanding the spatial and dispersal dynamics regulating biodiversity in riverine ecosystems is enhanced by considering rivers as dendritic networks (reviewed in Altermatt, 2013).

The study of metacommunity ecology, which considers the combined roles of local and regional processes in community assembly (Holyoak, Leibold, & Holt, 2005; Leibold et al., 2004), has greatly accelerated our understanding of the factors governing spatial variation among communities. The branching organisation of river systems (Rodríguez-Iturbe & Rinaldo, 2001) can exert strong controls on metapopulation and metacommunity dynamics, ultimately shaping patterns of biodiversity (Altermatt & Fronhofer, 2017; Campbell Grant, Lowe, & Fagan, 2007; Fausch, Torgersen, Baxter, & Li, 2002; Rodriguez-Iturbe, Muneepeerakul, Bertuzzo, Levin, & Rinaldo, 2009), particularly through regulating the extent and rates of dispersal within the river network. Isolation can occur in river networks at much finer spatial scales than in other systems, particularly when localities are not highly connected via the river network (Hughes, Schmidt, & Finn, 2009). For instance, headwaters are less open to new arrivals of individuals of species primarily dispersing within the network and are therefore more isolated than locations downstream (Brown & Swan, 2010; Clarke, Mac Nally, Bond, & Lake, 2008; Schmera et al., 2017). As a result, much of river network biodiversity is supported in headwaters through a greater turnover of species among sites, and potentially greater evolutionary divergence (Boumans, Hogner, Brittain, & Johnsen, 2016; Leys, Keller, Robinson, & Räsänen, 2017), despite lower mean local richness than in mainstem reaches (but see Clarke, Nally, Bond, & Lake, 2010); a general pattern that has empirical, experimental, and theoretical support (Carrara, Altermatt, Rodriguez-Iturbe, & Rinaldo, 2012; Finn, Bonada, Múrria, & Hughes, 2011; Muneepeerakul et al., 2008; Seymour, Fronhofer, & Altermatt, 2015). Central and peripheral locations within a network can also exhibit divergent

dynamics. Recent work highlighted that nodes connected to headwaters in experimental networks supported the greatest population densities compared to other locations in the network including headwaters and central nodes (Altermatt & Fronhofer, 2017). Indeed, many aspects of river network structure can influence the spatial arrangement of biodiversity, such as connectivity, centrality, and drainage density (Altermatt, 2013; Altermatt, Seymour, & Martinez, 2013), and these physical controls can extend to ecosystem processes (Helton, Hall, & Bertuzzo, 2017), and disease transmission (Carraro, Mari, Gatto, Rinaldo, & Bertuzzo, 2017).

Organisms are constrained in different ways by the branching structure of rivers depending on their mode of dispersal. Benthic invertebrates (Petersen, Masters, Hildrew, & Ormerod, 2004), fishes (Dias, Cornu, Oberdorff, Lasso, & Tedesco, 2013; Olden, Jackson, & Peres-Neto, 2001), and plants (Schmiedel & Tackenberg, 2013) use stream corridors for dispersal, but many wind-dispersed plants, crayfishes, amphibians, and the flying adult stages of some insects may instead be able to disperse overland (Bunn & Hughes, 1997; Lancaster & Downes, 2013). Species that disperse within riverine corridors are likely to be more influenced by the structure of the network compared to those that disperse overland (Box 1 outlines four models of ecological connectivity in river networks relating to their dendritic structure). As a result, the dendritic structuring of rivers can be a primary determinant of fish (Muneepeerakul et al., 2008) and hydrochoric plant (Johansson, Nilsson, & Nilsson, 1996) distributions. Researchers examining both population genetic and metacommunity structure have found varying importance of the river network in explaining observed population- and community-level patterns (Cañedo-Argüelles et al., 2015; Göthe, Angeler, & Sandin, 2013; Kärnä et al., 2015; Phillipsen et al., 2015). Multiple factors can lead to this variability, both in the importance of the river network and also in the relative roles of dispersal and species sorting in shaping metacommunities, many of which we explore below.

Here, we provide a conceptual synthesis of the role that the river network plays in structuring metacommunities in riverine ecosystems in different geographical and environmental settings. We explore where the river network is best able to explain observed metacommunity dynamics compared to other descriptors of geographic connectivity. In examining how river network structure influences metacommunities, we are focusing on the dispersal (spatial) component of metacommunity theory and not the role of species sorting. We incorporate single-species research to bolster our understanding of multi-species metacommunity processes. Our review seeks to

BOX 1   Models of connectivity in river networks

Four general models have been detailed to describe ecological connectivity within and among river networks (Finn, Blouin, & Lytle, 2007; Hughes et al., 2009). Although the models were developed to describe population genetic patterns of individual species, we propose that they can be up-scaled to the metacommunity if paired with an understanding of the relative dominance of various dispersal traits represented by the species comprising communities of interest (Figure I); see section 3 for a justification of scaling these models from the population genetic to metacommunity level. First, the stream hierarchy model (SHM) (Meffe & Vrijenhoek, 1988) predicts that connectivity among localities in streams reflects the dendritic nature of river networks, such that hierarchically nested drainage basins internally connected by surface hydrology experience more frequent exchange of organisms at the smallest levels of spatial nesting. The SHM assumes minimal out-of-network dispersal and hence applies best to organisms with obligate aquatic dispersal (and to those with terrestrial dispersal primarily confined to stream corridors such as riparian forests). At the metacommunity level, the SHM might apply to fish assemblages and to other types of communities in which obligate aquatic dispersal dominates. Second, the Death Valley model (DVM) (Meffe & Vrijenhoek, 1988) also was developed for species that are aquatic at all life stages but that are unlikely to disperse great distances, either because of extreme isolation of small aquatic habitats (e.g. spring pools in Death Valley) or because of extreme habitat specificity (e.g. macroinvertebrates restricted to lake outlets with unique characteristics). At the metacommunity level, the DVM might apply when a majority of the assemblage consists of taxa with similar traits of limited dispersal capacity and high habitat specificity on unique ecological settings (species sorting). Third, the headwater model (HWM) (Finn et al., 2007) predicts essentially the opposite of the SHM, with more connectivity among nearby small streams, regardless of hydrologic connectivity, than throughout nested drainage basins. The HWM applies primarily to species that specialise on certain types of headwater stream habitat, but that also have some capacity for terrestrial dispersal (crawling or weak flight) during at least one stage of the life cycle. Similar to the previous models, the HWM might apply at the metacommunity level for assemblages with habitat specialisation (species sorting) and a majority of taxa having limited overland dispersal capacity. Finally, the widespread gene flow (WGF) model predicts high connectivity within and among stream networks, at least at some specified regional scale. That is, dispersal occurs regularly enough across the sample region, regardless of network structure, that populations are panmictic. The WGF applies to species with a strong capacity for overland dispersal and low habitat specificity. Applied to metacommunities, "WGF" could be changed to the broader "widespread dispersal model" (WDM) and represent metacommunities predominantly structured by mass effects.
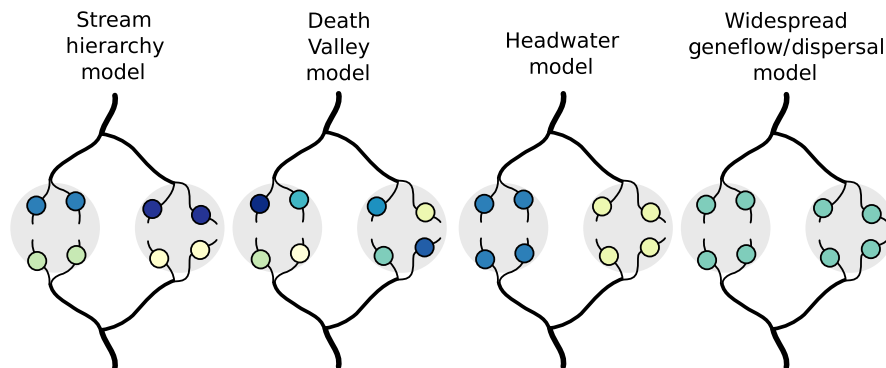

Stream hierarchy model   Death Valley model   Headwater model   Widespread geneflow/dispersal model

Figure I: The four models of population connectivity also applicable to metacommunity connectivity. Each panel represents a different connectivity model based on the same physical arrangement of sites: two adjacent but unconnected catchments with headwaters originating from the same high elevation locations (grey circles). The original terms (developed by Finn et al., 2007; Hughes et al., 2009) for genetic patterns can also be applied to metacommunities except for the more appropriate "widespread dispersal model". See the associated text for an explanation of each model and how it translates to metacommunities. The foundation of the models remains essentially the same. Modified from Finn et al. (2007) and Hughes et al. (2009).

illuminate the role of dispersal in river networks from a metacommunity perspective and identifies which dispersal proxies are best suited for a variety of contexts and a range of organisms. Improving our mechanistic understanding of how dispersal and river network structure interact is not only important for the development of basic riverine metacommunity ecology, but also allows for improved monitoring, management, conservation, and restoration in river networks (Brown et al., 2011; Economo, 2011; Heino, 2013; Siqueira, Bini, Roque, & Cottenie, 2012; Tonkin, Stoll, Sundermann, & Haase, 2014). We therefore conclude by providing a prospectus of
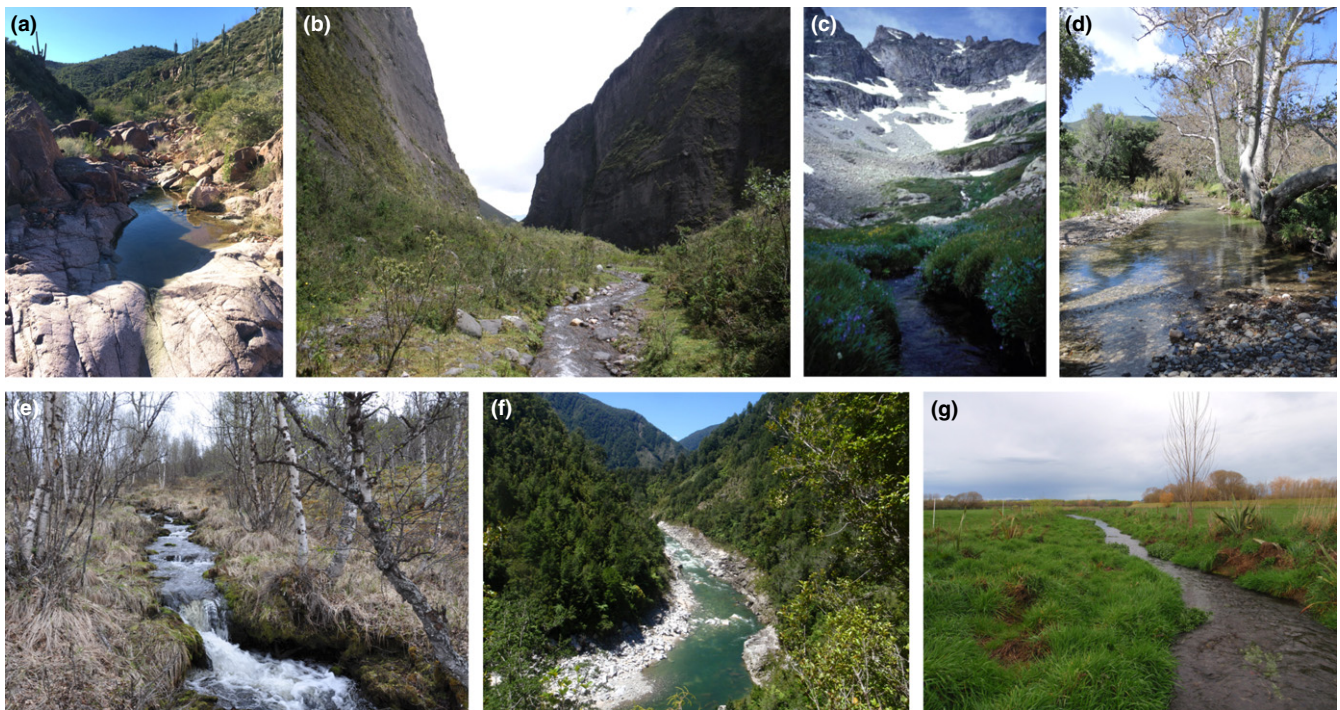
FIGURE 1 Reaches lying within river networks with different levels of network and overland connectivity, and importance for dispersing organisms. In no particular order, these span a gradient from arid to mesic (low to high river connectivity), open to forested, and low to high topographic relief. (a) A small intermittent stream in Saguaro National Park, AZ, U.S.A. with limited connectivity (credit: M. T. Bogan). (b) Cotopaxi stream, Ecuador bordered by overland dispersal barriers (credit: D. Finn). (c) A topographically isolated headwater Rocky Mountain, U.S.A. stream (credit: D. Finn). (d) The Nacimiento River, CA, U.S.A., a stream with limited topographic and forest-cover constraints but temporary longitudinal fragmentation, being partially intermittent and situated in an open oak savannah with low topographic relief (credit: J. D. Tonkin). (e) A small stream enclosed by forest but not topography in the Tenojoki basin in northern Finland (credit: M Grönroos). (f) The Mokihinui River gorge in Westland, New Zealand, a large river with relatively steep valley walls representing potential overland dispersal barriers (credit: J. D. Tonkin). (g) A small open pasture tributary of the Tukipo River in Hawkes Bay, New Zealand with no obvious constraints to overland dispersal except for potentially lacking favourable habitat (credit: J. D. Tonkin) [Colour figure can be viewed at wileyonlinelibrary.com]

methodological strategies likely to advance this rapidly emerging area of investigation.

2 | WHAT FACTORS INFLUENCE DISPERSAL IN RIVERINE METACOMMUNITIES?

From a metacommunity perspective, dispersal regulates the relative role of species sorting (Table 1). At one extreme, dispersal can limit species' ability to track their preferred environmental conditions (dispersal limitation; Table 1), and at the other, high dispersal rates can override local habitat control (mass effects; Table 1). At intermediate rates of dispersal, species are assumed to be best sorted according to their preferred environmental conditions (Leibold et al., 2004; Winegardner, Jones, Ng, Siqueira, & Cottenie, 2012). Consequently, dispersal can lead to departures from local community patterns that would be expected when modelling community structure based solely on environmental niches. The relative roles of species sorting, mass effects, and dispersal limitation may also depend on spatial extent and organisms' dispersal traits (Heino, Melo, Siqueira, et al., 2015), but empirical evidence supporting

these ideas remains limited (but see Declerck, Coronel, Legendre, & Brendonck, 2011).

Despite recent progress, ecologists continue to struggle to quantify the importance of dispersal in metacommunity processes, which largely results from the difficulty of quantifying dispersal for entire species assemblages (Jacobson & Peres-Neto, 2009). Given this challenge, freshwater research has typically used pairwise physical distances between sites (spatial dispersal proxies; most commonly Euclidean and watercourse distances) and associated distance-based modelling methods to infer dispersal processes and understand lateral and longitudinal connectivity (Box 2) (Altermatt, 2013; Heino et al., 2017; Kärnä et al., 2015; Olden et al., 2001). Although studies comparing physical and environmental distances have often suggested that species sorting is dominant in river systems (Erős, Takács, Specziár, Schmera, & Sály, 2017; Göthe et al., 2013; Jamoneau, Passy, Soininen, Leboucher, & Tison-Roseberry, 2017; Kärnä et al., 2015; Siqueira et al., 2012), there is evidence to suggest that the role of species sorting and dispersal effects is geographically dependent. That is, species correspond to their preferred environmental conditions more readily in headwaters than in mainstems, since higher connectivity in mainstems leads to species spill-over into sub-optimal habitats (i.e.

TABLE 1 Definitions of the important terms used in the paper

Term	Definition
Metacommunity	A set of local communities connected by dispersal (Leibold et al., 2004). Structured by the interplay between local and regional processes (Logue, Mouquet, Peter, & Hillebrand, 2011)
"Big Four" metacommunity paradigms	Coined by Brown, Sokol, Skelton, and Tornwall (2017) to refer to the four original metacommunity paradigms specified in Leibold et al. (2004). These consist of species sorting, mass effects, patch dynamics, and the neutral model
Species sorting	A metacommunity paradigm where species are filtered by the environment into environmentally suitable locations. Dispersal rates needs to be sufficient for species to track preferred environmental conditions (Leibold et al., 2004)
Mass effects	A metacommunity paradigm where species sorting is obscured by high dispersal rates between localities to the point where communities may become homogenised (Leibold et al., 2004). Species may spill over into sub-optimal environmental conditions
Dispersal limitation	Inadequate dispersal limits species reaching suitable sites due to being too distant (i.e. prevents species sorting)
Connectivity	"The degree to which the landscape facilitates or impedes movement among resource patches" (Taylor, Fahrig, Henein, & Merriam, 1993)
Euclidean distance	Straight-line distance between two sites ("as the crow flies")
Watercourse distance	The distance between two sites along the watercourse or river network ("as the fish swims")
Cost distance	A method using resistance maps to calculate the best route between two locations (Box 2). The least-cost path is that with the lowest resistance to movement (i.e. the path of least resistance). Pairwise resistance is the sum of each pixel's resistance along a path, with high values representing high cost or resistance to movement
Flow-connected distance	Distance along the network between two sites that are connected by flow. Can include bidirectional, and upstream and downstream biased connectivity. A special case of watercourse distance
Dispersal proxy	A proxy inferring dispersal between two sites. In distance-based modelling approaches, this is a distance matrix calculated from pairwise distances between sites (e.g. Euclidean, watercourse)

mass effects) (Brown & Swan, 2010; Schmera et al., 2017). When testing whether increasing network connectivity in river networks led to a reduction in site-based ecological uniqueness of assemblages, Tonkin, Heino, Sundermann, Haase, and Jähnig (2016) found high spatiotemporal variability across different watersheds. Such context dependency is widespread in the study of riverine metacommunities (Heino, Grönroos, Soininen, Virtanen, & Muotka, 2012; Heino, Melo, Bini, et al., 2015; Tonkin, Heino, et al., 2016; Tonkin, Shah, et al., 2017), which may result from differences in environmental conditions, heterogeneity, and ranges (through variation in species sorting processes), but may also be contributed by differences in the river network configurations between drainage basins.

We outline two major factors that dominate the regulation of dispersal in river networks: dispersal traits (mode and ability) of organisms, and the physical structure of networks within the surrounding landscape. These factors are primary predictors of geographic isolation and the degree of connectivity among populations of single, stream-dwelling species (e.g. Hughes et al., 2009; Box 1) and should likewise apply to understanding patterns of multi-species assemblage structure (Figure 2). We suggest this connectivity-dispersal relationship is interactive in that the importance of the river network in explaining diversity patterns depends on both its overall connectivity and the dispersal mode or strategy of an organism. We also briefly touch on several other factors that are important in dispersal processes occurring either along the network or overland. Given the considerable contingency that is introduced in the forms of research we review (e.g. through the various analytical

methodologies deployed, geographies examined, and trait databases used, among other factors), our approach in this review is mostly narrative.

2.1 | Dispersal mode and ability

Given the wealth of dispersal traits that can be represented within metacommunities, the mechanisms and directions of dispersal of species within any given assemblage are likely to be highly variable. For example, Alp, Keller, Westram, and Robinson (2012) found that Euclidean distance best explained patterns of gene flow for the mayfly *Baetis rhodani* with a terrestrial adult stage, whereas the obligate aquatic amphipod *Gammarus fossarum* was best explained by a combination of watercourse and Euclidean distance. This variability can also occur within species. For instance, most aquatic insects with adult flying stages are restricted to the aquatic environment during larval stages, but may disperse both along river networks and overland between branches and catchments during the adult stage (Bilton, Freeland, & Okamura, 2001; Bohonak & Jenkins, 2003). Understanding the modes of dispersal of species can therefore bolster our understanding of how the river network maintains functional connectivity of populations, and species traits may provide an opportunity for advancing the mechanistic basis of metacommunity dynamics (Cañedo-Argüelles et al., 2015; Datry, Bonada, & Heino, 2016; Kärnä et al., 2015).

One approach to explore the role of dispersal in river networks is to focus on subsets of the metacommunity that comprise organisms with similar dispersal traits (e.g. adult fliers versus in-stream

BOX 2   **The various approaches to examining pairwise spatial and physical distances between sites in river networks**

Often studies of connectivity in river networks use Euclidean (Figure IA; straight-line distance) and watercourse distance (Figure IC; the physical distance following the river network between two sites) as proxies of dispersal (Heino et al., 2017). Increasingly more detailed distance measures, such as cost distances, are incorporating more complex landscape features that influence the dispersal of organisms. Euclidean distance can also be expanded relatively easily into forms of straight-line resistances, such as topographic distance (Figure IB), which includes any rise and fall in elevation along a straight line path (Tonkin, Shah, et al., 2017). However, several other distances can be calculated. In addition to the symmetric distance along the river network, where there is no restriction on where an organism can disperse in the network, one can consider two sites connected only when they are flow connected (Figure ID). These can be calculated using asymmetric eigenvector maps (Blanchet, Legendre, & Borcard, 2008). Studies have employed directionally biased metrics to consider downstream movement only, assuming an important role of drift of aquatic invertebrates (Muller, 1982) or fish of specific stages (Olden et al., 2001), but also with an upstream bias, focusing on upstream dispersal during the adult stage of flying insects or migratory stages of fishes (Olden et al., 2001).

Cost-distance modelling (Figure IB) is a particularly fruitful approach, where resistance maps are created and least-cost paths are calculated for particular surfaces. Isolation by resistance approaches are used in many fields (McRae, 2006), and there are many different approaches to calculating landscape resistances (Spear, Balkenhol, Fortin, McRae, & Scribner, 2010; Zeller, McGarigal, & Whiteley, 2012). Essentially a cost distance is a path of least resistance over a landscape, depending on what surface is used for the resistance. This approach uses calculations of resistance of the landscape between pairs of sites, allowing for multiple pathways. Pairwise resistance is the sum of each pixel's resistance along a path, with high values representing high cost or resistance to movement. Most commonly, landscape topography is used, with higher costs assigned to convex areas, and low costs to concave areas.

These resistance surfaces can be tailored to the question at hand. For instance, a surface of land cover may be weighted favourably for open landscapes and unfavourably for dense forest, when considering an overland disperser that does not require shelter along the path. In contrast, in arid landscapes, forest may be weighted favourably to provide shade and rest spots for dispersers.

A good example of the use of cost-distance modelling comes from Phillipsen and Lytle (2013), who examined population connectivity of a giant waterbug in an arid landscape. They calculated six landscape cost variables: canopy cover, where they assigned low resistance values to map pixels with high percent canopy cover; landscape curvature, with concave structures having low resistance and convex high; elevation, where low elevation equalled low resistance; perennial habitats, where low resistance was assigned to patches of perennial freshwater habitats and high resistance to the matrix between patches; and, in addition to typical watercourse distance (the only course available), they also calculated a stream-resistance layer, where the stream network was assigned low resistance and outside of the stream, high resistance. Having such detailed cost distances can help to gain a better understanding of the intricacies of dispersal in complex landscapes.
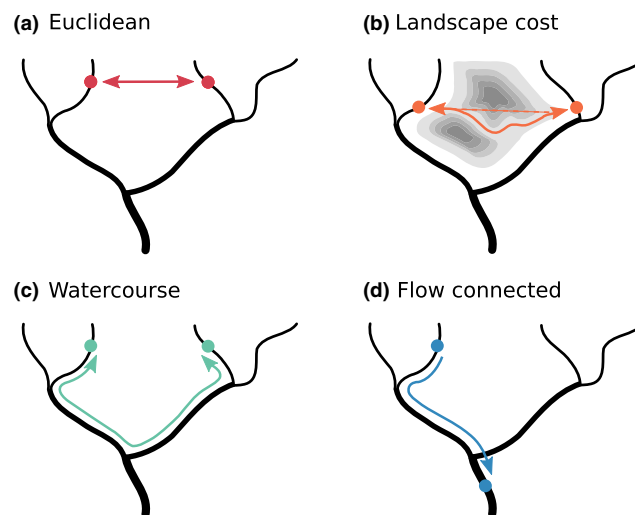
(a) Euclidean   **(b)** Landscape cost

(c) Watercourse   **(d)** Flow connected

Figure I: The main types of physical distances employed in a stream metacommunity study. Note that landscape cost distances can be calculated for whatever resistance surface is of interest, such as canopy cover, elevation, and specific land uses. The dashed line in B represents straight-line "resistance" methods, such as topographic distance, as mentioned in the text. Flow-connected distances, or asymmetric distances, can also be calculated in either direction to account for different dispersal direction at different life stages (i.e. downstream larval drift versus upstream adult flight).
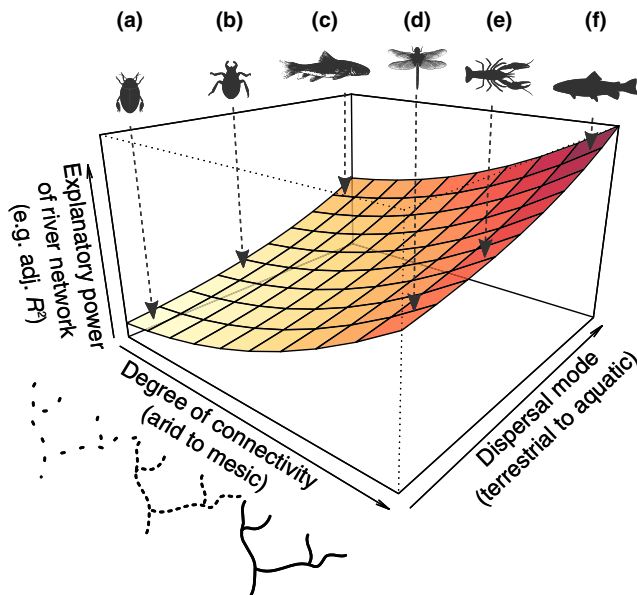
FIGURE 2 Conceptual relationship between the degree of physical connectivity of rivers in the landscape, dispersal mode, and the explanatory power of the river network for explaining patterns of biodiversity. The river network features as a more important dispersal pathway in longitudinally connected networks (e.g. in mesic regions) and for obligate aquatic organisms. In arid environments, where networks tend to be more fragmented, the network is less important for population and community connectivity than various overland routes. The relationship assumes an interactive effect between connectivity and dispersal mode (e.g. an aerial disperser may follow the river network more regularly in connected mesic networks than disconnected arid networks). Explanatory power could be the adjusted R^2 from variance partitioning or a Mantel r value. An alternative value may be the relative difference between adjusted R^2 values, using Euclidean and river network distances. Connectivity of the river network increases from arid to mesic areas. Example taxa along gradients of dispersal mode in arid and mesic environments: (a) diving beetle, *Boreonectes aequinoctialis*; (b) giant waterbug, *Abedus herberti*; (c) desert sucker, *Catostomus clarki*; (d) dragonfly, *Ophiogomphus occidentis*; (e) crayfish, *Pacifastacus leniusculus*; (f) rainbow trout, *Oncorhynchus mykiss* [Colour figure can be viewed at wileyonlinelibrary.com]

dispersers). Such a bottom-up approach (see Box 1) (Heino & Peckarsky, 2014; Marquet, Fernandez, Navarrete, & Valdovinos, 2004) has been widely applied in riverine metacommunity studies, often with promising results in comparison to studies focusing on more complete metacommunities (Cañedo-Argüelles et al., 2015; Göthe et al., 2013; Grönroos et al., 2013; Thompson & Townsend, 2006). In the broadest sense, body size can regulate the relative role of dispersal limitation in aquatic organisms, with a threshold between invertebrates and vertebrates (Shurin, Cottenie, & Hillebrand, 2009), and the importance of overland versus watercourse distances depending on the particular mode of dispersal. Watercourse distance (and the stream hierarchy model, SHM; Box 1) is more intuitively appropriate for obligate aquatic organisms (Le Pichon, Gorges, Baudry, Goreaud, & Boet, 2009), and incorporating flow directionality in watercourse distances can improve predictability (Olden et al., 2001).

Challenges remain in harnessing the apparent strengths of current trait-based approaches for prediction (Verberk, Siepel, & Esselink, 2008; Verberk, van Noordwijk, & Hildrew, 2013). For instance, relying on species dispersal traits that are developed based on morphology alone without consideration of establishment success may be misleading if they are interpreted incorrectly (Lancaster & Downes, 2017a). Morphological traits may indeed represent real dispersal ability (e.g. larger winged species disperse further), but not their ability to recruit or reproduce locally. Rather than considering traits independently, considering trait interactions, combinations, and life-history strategies that incorporate trade-offs (i.e. body size, development time, wing size, reproductive capacity) associated with such traits and strategies will likely improve the predictive ability of traits (Poff, 1997; Verberk et al., 2008, 2013).

Across large spatial extents, the movements of freshwater fishes are limited by their inability to cross oceans, high mountain ranges, or expansive deserts (Olden et al., 2010), although extreme events may override typical dispersal barriers (discussed in section on aquatic dispersers). Therefore, although they vary considerably in dispersal ability (Radinger & Wolter, 2014), river network distance is generally an appropriate metric (and SHM the appropriate model) to examine fish community structure within a drainage basin. Studies have corroborated this by finding a stronger ability of pairwise network distances to explain variation in fish community structure and overland distances to explain that of invertebrates (Landeiro, Magnusson, Melo, Espírito-Santo, & Bini, 2011; Olden et al., 2001). Padial et al. (2014) examined a broad range of taxonomic groups in the Upper Parana River and its floodplain in Brazil, including phytoplankton, zooplankton, periphyton, benthic macroinvertebrates, sedentary fishes, migratory fishes, and macrophytes. In general, they found that watercourse distances were stronger predictors than overland distances, and this became greater for organisms that relied more heavily on the river network for dispersal (e.g. fishes and macrophytes).

Dispersal strength or capacity is often employed as a composite metric representing mobility strength in general (Cañedo-Argüelles et al., 2015; Li, Sundermann, Stoll, & Haase, 2015; Thompson & Townsend, 2006; Tonkin, Death, Muotka, Astorga, & Lytle, 2016). Core dispersal traits that are available in trait databases commonly include: dispersal mode (aquatic active, aquatic passive, aerial active, and aerial passive), female and adult flight, occurrence in drift, crawling rate, and swimming ability for aquatic insects (Poff et al., 2006; Schmidt-Kloiber & Hering, 2015; Schriever et al., 2015; Tachet, Richoux, Bournaud, & Usseglio-Polatera, 2000); floating ability of seeds for plants (Schmiedel & Tackenberg, 2013); and body size and shape, fin morphology, and diadromy life-history for fishes (Mims, Olden, Shattuck, & Poff, 2010; Radinger & Wolter, 2014). However, such trait databases often do not capture the intricacies of dispersal, such as whether a species uses a vector for dispersal (e.g. zoochory) or phenological dependencies, and there are also other forms of non-aquatic dispersal such as overland crawling by insects and crayfishes. Where dispersal traits are well known, comparative multi-species-level assessments of population genetic structure, particularly if

coupled with observational data, can help to build our understanding of how organisms move within and among river networks (Baggiano, Schmidt, Sheldon, & Hughes, 2011; Chester, Miller, Valenzuela, Wickson, & Robson, 2015; Miller, Blinn, & Keim, 2002; Mims et al., 2015; Murphy, Guzik, & Wilmer, 2010; Short & Caterino, 2009). Below, we consider how different dispersal modes affect the use of different dispersal pathways (but not the relative role of dispersal and niche processes) and how this alters our understanding of metacommunity structuring. We also build a qualitative conceptual model describing the potential explanatory power of the river network for different dispersers in different landscape contexts (Figure 2).

2.1.1 | Aquatic

Many aquatic organisms use the river channel as a conduit to access diverse habitats to complete their life cycles, whether these are in the river itself, the river floodplain, estuaries, or marine environment (Junk, Bayley, & Sparks, 1989). Metacommunity structure for organisms that are aquatic at all life stages should therefore reflect river network structure more strongly than Euclidean distance (Olden et al., 2001) (Figure 2c,f; SHM), even in arid systems where the river network is rarely connected by surface flow. An exception to this pattern might occur at finer spatial scales in floodplain ecosystems. In such cases, seasonal flooding can connect previously unconnected habitats (Morán-Ordóñez et al., 2015; Razeng et al., 2016), and lead to overland dispersal routes; although the degree of lateral connectivity may vary longitudinally (Couto, Zuanon, Olden, & Ferraz, 2017). Extreme events like large-scale floods, which are set to play an increasingly strong role in river ecosystems (Woodward et al., 2016), may override many of these dispersal constraints that network-constrained dispersers face. Extreme flood events may increase connectivity, leading to movement of organisms between locations that would not occur under baseflow conditions, particularly in arid systems (Murphy, Pavlova, Thompson, Davis, & Sunnucks, 2015). Mossop et al. (2015) found greater than expected gene flow between dispersal limited populations of the desert goby, *Chlamydogobius eremius*, which they attributed to flood-driven dispersal.

Evidence is mounting that points to the utility of biogeographic and landscape genetic approaches to disentangle the role of historical events in maintaining population connectivity. For instance, despite occupying a highly fragmented arid region, Australia's most widespread inland fish species *Leipotherapon unicolor* has been shown to have little genetic divergence, indicating effective dispersal in the relatively recent past (Bostock, Adams, Laurenson, & Austin, 2006). At smaller scales, however, patterns of landscape genetics may require accompanying detail on the natural history of the organism of interest to tease apart multiple competing hypotheses explaining observed patterns (Leys et al., 2017; Shama, Kubow, Jokela, & Robinson, 2011). In such cases, observations of dispersal can help interpretation of results from landscape genetic studies (Miller et al., 2002).

Non-dispersing species that occupy isolated desert river waterholes—"Permanent Refugial" organisms—may not disperse even

under flowing conditions, resulting in genetic structure not associated with the river network (in line with the Death Valley model; DVM) (Phillipsen et al., 2015; Sheldon et al., 2010). In less extreme cases, such as alluvial rivers where flow ceases periodically, the primary source of recruitment following drying may be the hyporheic zone rather than upstream (i.e. drift) or elsewhere (i.e. oviposition) (Vander Vorste, Malard, & Datry, 2016). The relative extent of dispersal by lotic organisms that occurs in the hyporheic zone remains poorly understood; however, it is likely to be substantial, particularly in alluvial river networks where the interaction between groundwater and surface water is extensive (Stanford & Ward, 1993; Ward & Palmer, 1994). In fact, traversing the boundary between the lotic and hyporheic zone may involve life stage-specific use of different zones (Stanford & Ward, 1988). The role that less predominant and difficult-to-measure pathways of dispersal, such as movement through the groundwater (e.g. aquifers, or sub-surface networks as in karstic landscapes), play in structuring metacommunities is also an area open for future research (see section 4).

Due to the predominantly downstream direction of movement, downstream-biased distance metrics should better describe passive than active aquatic dispersers. Therefore, incorporating the potential effects of flow directionality may also provide added understanding of spatial structuring of biodiversity (Morrissey & De Kerckhove, 2009; Olden et al., 2001). Indeed, spatial models that incorporate flow direction in addition to stream distance have been shown to be more accurate than those using just watercourse distance (Peterson, Theobald, & Ver Hoef, 2007; Ver Hoef, Peterson, & Theobald, 2006). For fishes, this bias can depend on larval drift downstream or upstream migrations (Olden et al., 2001). For invertebrates, downstream movement via drift is also one of the primary mechanisms of within-network movement (Brittain & Eikeland, 1988; Downes & Lancaster, 2010; Lancaster & Downes, 2017b), and flow directionality has been found to be more important than environmental conditions in predicting diatom metacommunity structure (Dong et al., 2016). However, even for supposedly drift-prone invertebrate species, there is considerable variability between species in terms of the role that drift can play in their population densities and the ability to model their distributions based on flow and upstream population densities (Downes & Lancaster, 2010).

Upstream-biased dispersal by flying adults compensates, at least in part, for the downstream-biased dispersal of insect larvae (the "colonisation cycle") (Hershey, Pastor, Peterson, & Kling, 1993; Muller, 1954, 1982). Downstream directional bias also applies directly to many stream and riparian plant species distributions, with seed dispersal downstream via the flow of water (hydrochory) being an important means of dispersal. Kuglerova, Jansson, Sponseller, Laudon, and Malm-Renöfält (2015) found that species richness of plants with water transport capability increased with stream size, which was related the unidirectional flow of rivers providing a constant flux of propagules from upstream. Nevertheless, aerial dispersal via hosts or wind is a common phenomenon in stream and riparian plants (Coughlan, Kelly, Davenport, & Jansen, 2017; Wubs et al., 2016), which may reduce the strength of such relationships.

2.1.2 | Aerial

In theory, aerial dispersers are able to disperse overland between different branches of the river network, leading to higher predictive prowess of overland dispersal metrics (Figure 2a,d; Box 1). However, the likelihood of overland dispersal mostly depends on dispersal ability, and varies greatly both within and among taxa. For instance, dispersal distance can be sex dependent (Kuusela & Huusko, 1996; Theissinger et al., 2013), and some individuals of common aerial dispersers like caddisflies and stoneflies can disperse much greater distances overland than the population mean dispersal distance (Collier & Smith, 1998; Finn & Poff, 2008; Wiberg-Larsen, 2004). Many stoneflies, for example, remain close to their natal site, with few individuals travelling among streams, but a single long-distance dispersal event by a gravid female can be enough to colonise a new site. This process can be favoured by long-winged females in species with apterous or brachyopterous males (e.g. Teslenko, 2012). Nonetheless, despite the potential for long overland individual dispersal events in relatively weak-flying taxa such as stoneflies, the dominant dispersal route appears to be upstream along the river network, often close to the water surface (Figure 2e) (Macneale, Peckarsky, & Likens, 2005; Petersen et al., 1999, 2004).

Most aquatic insects with a flight stage have a short window for aerial dispersal compared to their aquatic phase, often with only short-lived adult stages outside of the aquatic zone. Exceptions to this generalisation include adult aquatic beetles with the ability to emerge, fly and re-enter the aquatic zone, and others such as various odonates that spend a comparatively greater proportion of the life cycle as terrestrial adults. Using genetic approaches, Razeng et al. (2017) found that strong-flying dragonflies were able to maintain geneflow between two regions separated by large tracts of predominantly dune desert (c. 1,500 km). By contrast, weaker flying mayfly species only maintained geneflow within single drainage basins harbouring networks of perennial pools. Coupled with a strong flight ability, these taxa are more likely to move long distances overland compared to smaller counterparts with weaker flight ability and shorter adult stages (Figure 2a), but still may also use the river network as their main channel of dispersal in many instances. These two cases represent endpoints of a continuum in flight ability; intermediate examples may include longer-lived caddisflies with a relatively strong flight ability. For instance, the montane caddisfly *Drusus discolor* has been shown to be unrestricted by catchment boundaries in headwater streams, with clear evidence of short-distance (<20 km) overland dispersal (Geismar, Haase, Nowak, Sauer, & Pauls, 2015), but limited long-distance dispersal across lowland regions between mountains (Pauls, Lumbsch, & Haase, 2006). Thus, the species-specific use of the river network as a pathway for movement during major dispersal events is also highly context dependent, and better knowledge is needed with regard to the interaction between dispersal distances and recruitment success (Lancaster & Downes, 2017a).

Passive aerial dispersers are likely to be much less deterministic in their frequency and direction of dispersal. For example, many

molluscs and some other invertebrates disperse via bird hosts (Coughlan et al., 2017; Dillon, 2004; Van Leeuwen et al., 2013; Walther et al., 2008), as can stream and riparian plants (Coughlan et al., 2017; Wubs et al., 2016). Smaller passive dispersers such as species of diatoms and poorly flying aerial dispersers will be heavily controlled by predominant weather systems like prevailing winds. The use of cost-distance modelling that accounts for such influences may prove useful in such cases (Box 2).

2.1.3 | Terrestrial (non-flying)

Some aquatic species without a flying stage can disperse overland by crawling or other means, such as the giant waterbug *Abedus herberti* (Boersma & Lytle, 2014; Lytle, 1999) and some crayfishes (Marques, Banha, Águas, & Anastácio, 2015; Ramalho & Anastácio, 2014). However, these dispersal events are probably rare occurrences given risks of exposure such as desiccation and increased predation pressure in the terrestrial landscape (Lytle & Poff, 2004). Benefits of overland crawling rarely outweigh the costs, such as in response to rainfall cues to escape catastrophic flood conditions (Lytle, 1999; Lytle, Bogan, & Finn, 2008) or in response to drought (Boersma & Lytle, 2014). In such cases, dispersal is likely to follow landscape contours including dry river beds and low passes separating drainage basins (Figure 2b) (Phillipsen & Lytle, 2013; Phillipsen et al., 2015). Aquatic animals that are able to disperse by short-distance crawling over the terrestrial landscape are those most likely to fit the headwater model (HWM; Box 1). This pattern is also apparent for some crayfish species (Ponniah & Hughes, 2004, 2006) and salamanders (Miller, Snodgrass, & Gasparich, 2015).

2.2 | Degree of physical connectivity

The degree of connectivity of the river network, represented by flowing surface water, should impart strong controls on the types of organisms present within a river network and the manner in which those organisms disperse. Connectivity may be associated with a climatic gradient from arid to mesic. All else equal, streams and rivers in mesic areas tend to be highly connected longitudinally, with the exception of many natural and man-made barriers (see section 2.3.2 below). By contrast, river networks in arid regions may comprise highly isolated patches of permanent water (Figure 1). Although these systems may connect seasonally, connectivity generally tends to be low (Jaeger & Olden, 2012). It is likely therefore that the ecoregion of a landscape will regulate the relative influence of the structure of the river network on dispersal. Specifically, as aridity increases, the river network may explain increasingly less of the spatial structuring of populations and communities due to dispersal relying less on the river channel for movement. In a study of six relictual headwater species in a drying landscape, Chester et al. (2015) found only one of six species exhibited dispersal via the stream channel, and the genetic structure of this species fit the DVM. By contrast, species with adult flight modes exhibited less evidence of isolation, supporting the contention that species with dispersal methods not

reliant on flow will more readily persist in dry environments. In the same set of streams, Chester et al. (2014) showed that fish, which must disperse via the stream channel, had managed to persist through a decadal drought except in those streams that were regulated. Regulation reduced longitudinal connectivity, which prevented dispersal and led to extinction of all native fish species, but the non-dispersing crayfish persisted. At the extreme end of the spectrum of aridity, the most likely model of ecological connectivity operating in desert systems is the DVM, with isolated patches of available water extremely functionally isolated. However, a review of connectivity of obligate aquatic fauna in desert systems found that many models of connectivity fit depending on species traits and hydrologic connectivity (Murphy et al., 2015). Species that are able to disperse well overland, either actively or passively, may overcome this isolation that emerges through fragmentation of the river network. For instance, Murphy et al. (2010) found no genetic structure for ostracods and snails across fragmented springs in the Great Artesian Basin of Australia, which they attribute to regular passive aerial dispersal (most likely via animal vectors; phoresy). By contrast, amphipods and isopods, which are less likely to be passively dispersed, showed increasing genetic structuring with decreasing dispersal ability.

Research from arid systems indicates that the river network plays a relatively minor role in the structuring of aquatic insect biodiversity, as demonstrated in the arid southwest US (Cañedo-Argüelles et al., 2015; Phillipsen & Lytle, 2013; Phillipsen et al., 2015). However, patterns for non-insects are less clear, and in some instances amphibians appear to move via the river network regardless of their relative reliance on permanent water (Mims et al., 2015). Using observational community data in arid but perennial central Australian streams, Razeng et al. (2016) inferred overland routes to be the most important pathway for dispersal of aquatic invertebrates, with rainfall events collecting in landscape depressions and facilitating movement. These studies highlight the importance of employing multiple approaches to measuring the potential role of overland dispersal (Box 2), including cost-distance modelling (Cañedo-Argüelles et al., 2015; Morán-Ordóñez et al., 2015; Phillipsen & Lytle, 2013; Phillipsen et al., 2015; Razeng et al., 2016). Landscape genetics, coupled with multiple landscape cost distances, revealed that landscape concavity, including dry stream beds, gullies, and low saddles between catchments, was the best predictor of gene flow between populations of the giant waterbug *Abedus herberti* (Phillipsen & Lytle, 2013). Thus, aquatic metacommunities that inhabit disjunct patches of perennial habitat characteristic of aridland habitats appear to rely on dispersal modes that are not strictly confined to river networks. In a direct comparison between arid and mesic streams, Datry, Melo, et al. (2016) found the role of environmental and spatial structuring depended on aridity. Under moderately harsh mesic environmental conditions they found that metacommunity structuring of fish was best explained by watercourse distances, whereas that of invertebrates was best explained by overland distance (Datry, Melo, et al., 2016). At the extremes (mesic—low harshness, and arid—high harshness), however, no pure spatial structuring was apparent.

2.3 | Other factors

2.3.1 | Topographic heterogeneity

Increasing topographic complexity of landscapes also restricts overland movement between river branches (Figures 1 and 2). In these cases, the river network becomes increasingly important as a pathway for dispersal of both aquatic and terrestrial dispersers (Finn, Encalada, & Hampel, 2016; Finn, Theobald, Black, & Poff, 2006). For instance, Tonkin, Shah, et al. (2017) found greater dispersal limitation in metacommunities with individual communities split across different branches separated by clear overland dispersal barriers in Himalayan streams. This was despite the fact that the majority of organisms had an aerial dispersal mode, highlighting the role that the overall topographic variation, landscape complexity, and structure can have on dispersal within riverine metacommunities. The same pattern can be seen at the level of individual species, as observed among hydropsychid caddisflies in the same region (Hoppeler et al., 2016). Dispersal along the river network in these cases involved much longer dispersal than direct line dispersal, but the mountains presented clear impediments to overland movement. A similar result was shown for diatoms in high mountain streams of southwestern China (Dong et al., 2016).

This may not be the case in less topographically extreme environments and highlights the role that increasing landscape complexity can have in promoting segregation in river networks (Finn et al., 2011; Wilcock, Bruford, Nichols, & Hildrew, 2007). Wilcock et al. (2007) found greater differentiation at a more confined spatial scale (*c.* 40 km) in upland compared to lowland (*c.* 100 km) streams in the caddisfly *Plectrocnemia conspersa*; whereas the dispersal of the caddisfly *D. discolor* is not limited by topographic features (Geismar et al., 2015). These studies also highlight the importance of considering the appropriate spatial scale of a study, as there is a strong interaction between dispersal ability and spatial scale of study. Studies across small spatial extents may fail to resolve population or metacommunity structure for all but poor dispersers, whereas at large scales, landscape-level patterns will be obscured by genetic drift or dispersal limitation. For example, Geismar et al. (2015) inferred panmictic populations of the caddisfly *D. discolor* at local scales, whereas Pauls et al. (2006) revealed clear dispersal limitation among regions in *D. discolor*.

2.3.2 | Land use and habitat connectivity

While the evidence is limited, land use also influences the amount of overland dispersal between river branches. In heavily forested landscapes, overland dispersal of aerially dispersing insects may be limited (e.g. Collier & Smith, 1998) compared to an open agricultural landscape, although the reverse may also occur for species that require forest cover (Alexander, Hawthorne, Palmer, & Lamp, 2011; Khazan, 2014). Nevertheless, many overland dispersers often fly at elevations above where sampling tends to occur, particularly in dense forest, leading to underestimating their numbers in

TABLE 2 Importance of different physical distances in explaining metacommunity structure of benthic invertebrates grouped by dispersal mode and landscape type. Only studies that compared multiple distance metrics were included. Given the level of contingency in different studies, including the analytical methods and selected environmental variables, we focused on relative differences between different distance metrics, rather than reporting values

Study	Grouping	Location	Distances used	Best metric and main findings
Mesic				
Brown and Swan (2010)	Female dispersers, adult fliers; each grouped into weak and strong dispersers	Maryland, U.S.A.	Euclidean, watercourse	Weak dispersers: both female dispersers and adult fliers best explained by network. Strong dispersers: only female dispersers explained by network. All patterns only apparent in mainstems, not headwaters
Campbell (2010)	Community	Canterbury, New Zealand	Euclidean, watercourse, downstream-biased flow-connected, upstream-biased flow-connected, downstream-biased flow-connected weighted by velocity	Varied between four catchments. Symmetric watercourse distance, upstream-biased flow-connected, downstream-biased flow-connected weighted by velocity most important in different catchments
Landeiro et al. (2011)	All caddisflies	Brazilian Amazon	Euclidean, watercourse	Euclidean
Maloney and Munguia (2011)	Community	Maryland, U.S.A.	Euclidean, watercourse	Euclidean at multiple spatial scales
Altermatt et al. (2013)	Community	Switzerland	Euclidean, watercourse	Watercourse marginally better
Göthe et al. (2013)	Community, low and high female dispersal, and adult flying strength	Sweden	Euclidean, watercourse, downstream-biased flow-connected	Often neither Euclidean or watercourse were important, but where there was spatial structuring, Euclidean was better than watercourse
Grönroos et al. (2013)	Community, active and passive aquatic and aerial dispersers	North and central Finland	Euclidean, watercourse	No clear difference. Slight variation between three drainage basins
Padial et al. (2014)	Community	Brazil	Euclidean, various watercourse incorporating complex flows, flow directionally-biased	Watercourse better than Euclidean, and asymmetric distance better than symmetric. Note this is a non-dendritic floodplain system, with complex bi-directional flows between main and side channels
Zhang et al. (2014)	Community	Southern China	Euclidean, downstream flow-connected	No clear difference
Kärnä et al. (2015)	Community, active and passive dispersers, body size groups	Northern Finland	Euclidean, watercourse, landscape cost (curvature)	Curvature, but minor difference. Slight variations between traits. Curvature most clearly important for small-bodied organisms, but least important for full community
Tonkin, Shah, et al. (2017)	Community, niche position, niche breadth	Nepalese Himalaya	Euclidean, topographic, watercourse	Variable between three datasets depending on spatial arrangement of sites. Topographic or watercourse
Schmera et al. (2017)	Community, flying and non-flying	Hungary	Euclidean, watercourse	Neither important in small streams, and similar in large rivers for full community. Euclidean, but not watercourse, distance important for flying macroinvertebrates in large rivers, but neither important in small streams for both flying and non-flying

(Continues)

TABLE 2 (Continued)

Study	Grouping	Location	Distances used	Best metric and main findings
Arid and mesic				
Datry, Melo, et al. (2016)	Community	Bolivia	Euclidean, watercourse	Euclidean at moderate environmental harshness (mesic). Neither at low and high harshness (mesic and arid)
Arid				
Cañedo-Argüelles et al. (2015)	Weak, local, moderate, and strong dispersers	Arizona, U.S.A.	Euclidean, watercourse, curvature (cost), perennial (cost)	Varied between dispersal capacities. Strongest findings were: strong = Euclidean, and moderate = curvature and perennial
Morán-Ordóñez et al. (2015)	Community, obligate aquatics, passive aerial dispersers, animals moving by aerial phoresy, weak and strong fliers	North-western Australia	Euclidean, multiple landscape resistance distances based on the spatial distribution of the river network accounting for both longitudinal and lateral connectivity	Varied between five watersheds and trait groups. In watersheds with lower topographic complexity, the network structure was a better predictor of trait groups, but geographic and least-cost path distances generally were poor predictors of communities
Razeng et al. (2016)	Community, obligate aquatic, aerial passive, weak flying, strong flying dispersers	Central Australia	Euclidean, watercourse, landscape concavity, various network connectivity models under different flood scenarios	Highly variable between multiple datasets and traits. However, evidence for importance of both landscape concavity and various network connectivity models for full community and various dispersal trait groups. Obligate aquatics best explained by landscape concavity

observational studies (Didham et al., 2012). Passive aerial dispersers may be more readily transported between adjacent streams overland in open landscapes by wind dispersal than in forested landscapes. Consequently, prevailing weather systems and the mode of dispersal will also likely regulate the extent of longitudinal dispersal along major rivers (Briers, Cariss, & Gee, 2003; Tonkin, Stoll, Jähnig, Haase, 2016).

Fragmentation of river networks can have profound implications on the way in which organisms can disperse (Dias et al., 2013). Fragmentation can be both natural (e.g. waterfalls, drying events, beaver dams) and man-made, including habitat loss, dams, culverts and weirs, river regulation, habitat modification, and climate change (Crook et al., 2015). Although most ecosystems harbour multiple pathways for movement of organisms between different locations, the dendritic nature of rivers can amplify the effects of artificial barriers on the movement of aquatic organisms (Olden, 2016). For organisms that require the network for movement and dispersal, it plays a central role in maintaining their functional connectivity, and for metacommunities, the network can regulate the relative role of dispersal in governing species sorting (Brown & Swan, 2010; Sarremejane, Mykrä, Bonada, Aroviita, & Muotka, 2017; Tonkin, Sundermann, Jähnig, & Haase, 2015). Therefore, anthropogenic fragmentation can alter the predicted importance of the river network we present here based on landscape structure and dispersal mode (Figure 2).

2.3.3 | Climate change

Maintaining connectivity and dispersal can help to maintain current communities and species interaction networks under climate change (O'Connor, Selig, Pinsky, & Altermatt, 2012; Thompson & Gonzalez, 2017). Species range displacement is one of the many ways that climate change can affect biodiversity, and the most directly related to dispersal (Garcia, Cabeza, Rahbek, & Araújo, 2014). Under range displacement scenarios, poor dispersers are among the most threatened organisms by climate change given their inability to effectively track shifting climatic conditions (Hering et al., 2009). All else equal, and assuming adaptive potential is low, species restricted to the network for movement are in most cases more at risk of extinction from climate change because their ability to shift poleward or towards higher elevations will be more restricted than an overland disperser (Bush & Hoskins, 2017). This can ultimately lead to extinction by a summit trap effect (Sauer, Domisch, Nowak, & Haase, 2011), especially in cold-adapted species (Bálint et al., 2011). Research in central Europe has shown benthic invertebrates have so far been able to keep up with climate warming, but the movement in response to changing temperatures has been mostly up river and in elevation, rather than in latitude (Haase et al., 2015). This response will eventually lose its effectiveness if the SHM is at play (dispersal restricted to the river network). However, this is not necessarily as problematic for organisms that can disperse overland and pass between catchments as for those relying on aquatic connections between sites, regardless of whether a species can fly overland or not (e.g. see Razeng et al., 2017 for comparison between strong and weak fliers).

With increasing aridity, as expected in many regions globally (IPCC, 2013), the amount of aquatic habitat will decrease, and populations will thus become more sparsely connected. Populations of aquatic organisms occupying arid regions are often already

naturally fragmented, but connectivity will decrease even more in the near future (Jaeger, Olden, & Pelland, 2014); potentially shifting the best model describing functional connectivity from the HWM to the DVM (Crook et al., 2015). Increases in aridity and associated decreases in hydrologic connectivity will have severe effects on native fish populations over the next century, with projections indicating reductions in network-wide hydrologic connectivity of 6%–9% on an annual basis and up to 12%–18% during spring spawning season in the Verde River Basin, United States (Jaeger et al., 2014).

2.3.4 | Biotic interactions

It is well recognised that predation risk plays an important role in shaping behavioural decisions made by organisms, including the choice to disperse between habitats (Lima & Dill, 1990). For instance, early research pointed to the possibility that high densities of piscivorous fishes may reduce movement of small-bodied fishes among tributaries due to the risk of predation (Townsend & Crowl, 1991) or alternatively, promote movement by inducing dispersal of individuals from side pools and channels (Fraser, Gilliam, MacGowan, Arcaro, & Guillozet, 1999). In a seminal study, Gilliam and Fraser (2001) found that killifish (*Rivulus hartii*) in Trinidad rivers showed greater movement along the river in the presence of the predator—wolf fish (*Hoplias malabaricus*); a result that was supported by a complementary mesocosm experiment. By contrast, field and laboratory studies found reduced movement of juvenile instars of an aquatic heteropteran (*Notonecta hoffmanni*) in the presence of adult conspecifics (Sih, 1982). Understanding the manner in which prey alter their immigration and emigration rates out of and into habitat patches, respectively, in response to predators, is important for advancing the study of metacommunities in river networks.

2.4 | Comparing multiple distance metrics simultaneously

Given the broad array of dispersal modes of benthic invertebrates, it makes sense to compare different distance metrics representing potential overland and watercourse dispersal. Many researchers have relied on Euclidean distances to examine metacommunity structure of benthic invertebrates (Heino, Melo, Bini, et al., 2015; Heino & Mykrä, 2008; Thompson & Townsend, 2006) often based on the fact that comparisons of Euclidean and watercourse distances have revealed little difference (see below). However, new approaches pertaining to cost-distance modelling have opened up interesting possibilities in recent years. In Table 2 and below, we summarise a suite of research specifically examining the metacommunity structure of benthic invertebrates where multiple spatial distance metrics were employed.

Typically, differences in the amount of variance explained in invertebrate metacommunity structure between watercourse and Euclidean distances have been marginal (Grönroos et al., 2013;

Zhang et al., 2014), but some studies have favoured Euclidean distance (Datry, Melo, et al. (2016); Landeiro et al., 2011; Maloney & Munguia, 2011), and some watercourse (Altermatt et al., 2013; Brown & Swan, 2010; Padial et al., 2014). Incorporating cost-distance modelling has improved explanatory power of overland dispersal in some instances (e.g. landscape curvature) (Cañedo-Argüelles et al., 2015; Razeng et al., 2016), as has incorporating flow directionality into watercourse distances (Padial et al., 2014), but again it appears to be strongly context dependent (Campbell, 2010). That is, the importance of dispersal pathways appear to vary within and among studies, and between different catchments, dispersal modes, and other various trait groups (e.g. Cañedo-Argüelles et al., 2015; Kärnä et al., 2015; Tonkin, Shah, et al., 2017).

While context dependency certainly arises from differences in biology and landscape setting, some may arise from the extensive contingency that is introduced at multiple points in the analytical process. These analysis decisions include trait assignment and lack of detailed understanding of dispersal (see section 4.3) (Lancaster & Downes, 2017a), data transformation, variable and site selection, and analytical approach. For instance, in variance partitioning alone there are multiple partially subjective choices that are required to be made in the multi-step process, including use of presence-absence or abundance data, and data transformation (e.g. Hellinger, Bray-Curtis); the choice of ordination methodology (e.g. RDA, CCA, dbRDA); selection of environmental variables to include in initial procedure; inclusion or exclusion of autocorrelated predictors (also requires an arbitrary threshold of the VIF value); the approach for variable forward selection (e.g. ordistep, ordiR2step functions from the R package vegan; also requires inclusion and exclusion thresholds); and whether to report adj. R^2 values if the overall ordination is non-significant. All of these choices introduce contingency in the potential results, which hampers quantitative comparisons and syntheses. These points suggest a need for consistent methodologies across studies, which will allow controlled comparisons. We emphasise many of these shortfalls in current methodological approaches and potential alternatives in section 4.

3 | COMPLEMENTARY APPROACHES SUPPORT A MORE COMPREHENSIVE UNDERSTANDING OF RIVER NETWORKS

In general, community ecology should be more informative about contemporary factors, and population genetics should provide better insights into historical factors shaping biodiversity, with much of the observed genetic structure seen under present-day conditions representing historical conditions (Bonada et al., 2009). Despite this, the processes that shape genetic structure of populations (selection, drift, mutation, and dispersal) can be mirrored at the community level, where dispersal, selection, drift and speciation are acting in similar ways, resulting in hypothesised correlations between population genetic and community patterns (Vellend, 2005, 2010). Just as gene flow and drift can interact at the regional scale through a

scale-dependent influence of dispersal, so can dispersal regulate the strength of species sorting (Heino, Melo, Siqueira, et al., 2015). Population genetics can therefore be used to test alternative explanations of community-level patterns. For instance, distinguishing between environmental filtering and dispersal barriers in explaining spatially disjunct patterns can be assisted by examining intraspecific genetic diversity and gene flow in some species. A good example of this can be found from the terrestrial literature; Dexter, Terborgh, and Cunningham (2012) used population genetics to disentangle a distance-decay of community dissimilarity gradient in Amazonian forest communities. Rather than species sorting along the environmental gradient, which would be assumed under conventional metacommunity approaches, using population genetics they were able to identify two historically separated assemblages that have recently come in contact producing a zone of high turnover. Differentiating historical processes such as these can only be done using population genetic approaches. Thus, many posited gradients of species sorting or dispersal limitation assumed through conventional metacommunity examinations may in fact represent undiscovered historical processes. Such complementary approaches should benefit studies in complex river networks, as we demonstrate in the case study below.

3.1 | Paired examinations of population genetic and metacommunity structure within river networks

The unifying role of the broader landscape structure on different organisational levels of biodiversity has been demonstrated in two studies on stream insects, one at the population genetic (Phillipsen et al., 2015) and one at the metacommunity (Cañedo-Argüelles et al., 2015) level, in the southwestern United States. By focusing on a gradient of species- and community-level dispersal ability, and employing multiple dispersal proxies characterising regional habitat structure, these studies found that only intermediate dispersers were significantly affected by landscape-level variables that characterised distance between sites. Examining population genetic structure, Phillipsen et al. (2015) found that dispersal ability regulated the regional balance of gene flow and genetic drift. A weak disperser (*Abedus herberti*) indicated populations under strong genetic drift with little or no among-population connectivity and no coherent landscape-level population genetic pattern. A strong-flying disperser (*Boreonectes aequinoctialis*) also showed no consistent landscape patterns, suggesting that panmixia overwhelmed landscape-level population structure. An intermediate disperser (*Mesocapnia arizonensis*), however, showed a classic isolation-by-distance pattern, with population genetic patterns well-explained by landscape variables. This hump-shaped relationship between dispersal ability and the explanatory power of landscape structure was mirrored by the metacommunity study of Cañedo-Argüelles et al. (2015), which found that landscape-level factors explained patterns for intermediate dispersers, but not for the strong or weak-dispersing members of the community. In agreement with our conceptual understanding (Figure 2), neither study found support for the river network as an important

explanatory variable, likely due to the fragmented nature of these aridland streams.

The effect of river network structure in shaping diversity patterns at different levels (from genes through species to communities), may not be as straightforward and universal as postulated in some cases. For instance, some studies have found similarity between genetic and species or community level data, such as population genetic and community data under neutral theory in highly isolated streams (Finn & Poff, 2011), and higher beta and gamma diversity at both species and genetic levels in headwaters than mainstems (Múrria, Bonada, Arnedo, Prat, & Vogler, 2013). By contrast, recent work on hundreds of communities of macroinvertebrates and fishes found no consistent signal of network structure on genetic and species level diversity (Fourtune, Paz-Vinas, Loot, Prunier, & Blanchet, 2016; Seymour, Seppala, Machler, & Altermatt, 2016). These studies found no strong correlation between alpha diversity at the level of allelic richness versus species or family level richness in macroinvertebrates (Seymour et al., 2016), and only weak positive species-genetic diversity correlations at the alpha diversity level but not at the beta-diversity level for fishes (Fourtune et al., 2016). Thus, although there have been several studies examining how river network structure shapes diversity patterns and genetic structure (e.g. Blanchet, Helmus, Brosse, & Grenouillet, 2013; Fronhofer & Altermatt, 2017), the empirical evidence is mixed and no consistent pattern has emerged yet. Most likely is that the significance of dispersal and gene flow versus species (or gene) sorting is highly system dependent, and may inconsistently affect the demography of different organisms.

In summary, although assessing patterns at different levels of biological organisation are beneficial to testing competing hypotheses, it remains unclear if species and genetic levels of diversity are shaped by the same or different mechanisms across spatiotemporal scales. Detailed studies of this nature would benefit from paired examinations across multiple river networks with differing network structure and landscape characteristics. We therefore identify the strong need for further studies addressing genetic and higher taxonomic richness patterns across the same river networks, and eventually meta-analyses integrating all these data in search of common patterns.

4 | FUTURE ADVANCES IN METHODOLOGICAL APPROACHES

Separating environmental filtering from dispersal processes is highly dependent on the method applied, as most environmental processes are spatially autocorrelated (Tuomisto & Ruokolainen, 2006). Consequently, there are now countless tools available for stream ecologists to examine metacommunity structure both in the laboratory and the field, including microcosm experiments, graph theory, simulations, neutral metacommunity models, manipulative experiments, spatial statistical modelling, and several methods based on the use of distance matrices, such as distance decay relationships, Mantel tests,

and multiple regression on distance matrices. The topology and uni-directionality of stream networks provides a unique situation for statistical modelling of spatial relationships (Peterson et al., 2013; Ver Hoef et al., 2006), and the modelling methods that account for directionally biased dispersal have proven useful for understanding complex directional dispersal in river networks.

Understanding the spatial organisation of communities was advanced substantially through developments of modelling approaches using constrained ordination techniques (Legendre, Borcard, & Peres-Neto, 2005). The reliance on ordination and distance-based methods to infer dispersal in metacommunity research results from the difficulty of measuring dispersal directly. However, approaches such as variance partitioning have come under scrutiny for their ability to truly infer the effects of dispersal (Vellend et al., 2014). Alternative approaches are increasingly being applied. For instance, Downes, Lancaster, Glaister, and Bovill (2017) developed a multi-step process involving combinatorics and found a strong role of dispersal in structuring communities in a human-altered stream. Moreover, questions can arise with regard to the adequacy of the included range of sampling sites that are included to create spatial distance matrices, as these may only represent a small proportion of available localities of colonists in the surrounding species pool (Sarremejane et al., 2017). Null models can help to overcome some of these data constraints, enabling testing the role of dispersal and niche processes at different positions along the stream network without relying on available sampling data (Sarremejane et al., 2017). Coupled with this focus on variance partitioning is an often mistaken reliance on grouping metacommunities into one of the prevailing "Big Four" paradigms (Brown, Sokol, et al., 2017) (Table 1). Although these potential issues can be avoided with well-designed experiments, there remains a need to advance methodologies to improve our understanding of how metacommunities are structured in river networks, particularly at a more mechanistic level.

Taken together, our review suggests that the river network features as a more important dispersal pathway in longitudinally connected networks and for obligate aquatic organisms. In arid environments, where networks tend to be more fragmented, the network is less important for population and community connectivity than various overland routes. Nevertheless, our review also highlights just how context-dependent the role of the river network is in influencing the way in which organisms disperse and metacommunities are structured. Improving our ability to accurately compare the role of the river network in structuring biodiversity clearly needs further methodological development. Without such improvement, progress in understanding and managing river network biodiversity will be stalled, and we may be left dealing with the contingency that has bothered community ecologists for decades (Lawton, 1999). In addition to improving methodological and analytical consistency, compiling a unified set of methodological approaches will help improve our understanding of how metacommunities are structured across a landscape, and potentially our ability to quantitatively compare and synthesise findings across studies. We see several fruitful avenues to explore or expand upon to increase our mechanistic understanding of how dispersal and river network structuring interact to determine biodiversity, which we outline below.

4.1 | Gaining new insights using manipulative field- and laboratory-based experiments

Well-designed manipulative field experiments allow direct insight into the processes structuring communities (Brown, Wahl, & Swan, 2017). However, these can be time and cost prohibitive and not easily replicated, and are thus not often used in riverine metacommunity studies. Given the uncertainty of many of the spatial and physical distance-based approaches to examining metacommunity processes in streams and rivers, it is heartening to see novel experimental approaches being used. Lancaster and Downes (2017b) recently performed a replicated (multiple sites and multiple temporal replicates up to 12 months) field experiment revealing the importance of dispersal in a resource-limited benthic invertebrate metacommunity in southern Australia. They found that by experimentally increasing the amount of detritus retained in stream reaches, invertebrate diversity increased locally, suggesting that dispersal was widespread and not limited in their study catchment and organisms were able to respond to local improvements in conditions. Of course, such an approach is not likely to be possible at large spatiotemporal scales, limiting its application across a wide range of situations. However, we believe stream metacommunity research in general, and also specific to questions related to network structure, will be bolstered by more of these classical manipulative experiments at the metacommunity scale.

An alternative to field experiments is laboratory-based experiments using microcosms. These experiments can be seen as a link between natural systems and theoretical models, and there has been a recent spate of such experiments to address conceptual questions in the context of riverine metacommunities (e.g. Carrara, Rinaldo, Giometto, & Altermatt, 2014; Carrara et al., 2012; Seymour et al., 2015). A common theme of these experiments is that dispersal itself can shape diversity patterns along dendritic networks even in the complete absence of any environmental heterogeneity. The goal of such experiments is to mechanistically test specific aspects hypothesised to be of relevance for shaping riverine metacommunities, such as effects of topological network structure, species interactions, or neutral dynamics on biodiversity patterns. Such microcosm experiments have a long tradition in ecology (Altermatt et al., 2015), and they capture elements of theoretical models but also add some true biological complexity. Such experiments look at components like dispersal limitation, dispersal directionality, network topography, or evolutionary processes. Their strength is not only their closeness to mathematical or simulation models, but also their ability to completely control individual factors, deduce causalities, and to replicate at the level of whole metacommunities. However, it should be noted that these experiments are not designed to capture all realism of natural metacommunities, and they cannot necessarily incorporate the level of biological complexity inherent to some larger or long-lived organisms.

4.2 | Practising creative and comparative cost-distance modelling

Recent application of cost-distance modelling has uncovered a deeper understanding of the intricacies of dispersal processes in riverine metacommunities (see Box 2). Incorporating more detailed environmental information and natural history into these approaches may be a fruitful avenue to explore, such as the role of overland flooding in connecting lowland systems or the role thermal and hydrologic patchiness in arid environments (Cañedo-Argüelles et al., 2015; Phillipsen et al., 2015; Razeng et al., 2016). Approaches that seek to quantify functional connectivity, as opposed to structural connectivity, continue to be essential in advancing the field. Future research should strive to match appropriate physical distances with appropriate species traits, or better, life history strategies, to disentangle the intricacies of dispersal across complex landscapes. Thus, although improving distance modelling approaches is critical for more mechanistic distance-based examinations of riverine metacommunities, these developments will not be complete without building more comprehensive species trait databases.

4.3 | Enhanced quantification of dispersal to inform models

Even for well-studied vertebrate groups such as fishes, the quantification of dispersal remains limited (Radinger & Wolter, 2014), and we generally know less about dispersal of other riverine organisms, including crayfishes and aquatic insects (Heino & Peckarsky, 2014). This is because of the difficulty of studying dispersal of such small organisms, with such complex life cycles of which there are often dozens of species at a single sampling site; hence the reliance on proxies for quantifying dispersal (Heino et al., 2017). Stable isotopes and whole-stream enrichments have proven useful for tracking individuals (Briers, Gee, Cariss, & Geoghegan, 2004; Macneale et al., 2005), but examining broader metacommunity dynamics remains out of reach for such an approach. Although it is currently time- and cost-prohibitive, population genetics are likely to develop to a level where individuals can be traced and individual-level dispersal can be inferred. Regardless, there is a clear need for increasing our understanding of dispersal in rivers, including instream, overland, and in groundwater, via direct methods (Jacobson & Peres-Neto, 2009); but this remains an ongoing challenge (Heino, Melo, Siqueira, et al., 2015).

Another interesting area to explore is the relationship between actual and effective dispersal (Lancaster & Downes, 2017a). Examining six species in the caddisfly genus *Ecnomus*, Lancaster and Downes (2017a) found that wing morphology was associated with actual dispersal but not effective dispersal. That is, itinerant species (those found with flying adults only) had larger wings than resident species (those found with both juveniles and adults), and therefore a greater capacity to disperse, which was observed in greater distances travelled. However, this greater dispersal did not lead to new individuals being added to populations. Unless accompanied by further information on which species contribute new individuals to populations, dispersal capacity alone, may not contribute to our understanding of metacommunity dynamics in streams. In sum, we need more detailed studies that couple morphological traits associated with dispersal with multi-site observations of recruitment or reproduction success (i.e. itinerancy versus residency). Such studies will better inform our understanding of dispersal in streams, providing the tools required for stronger tests of metacommunity theory in river networks.

4.4 | Estimation of individual-level variation in dispersal

Dispersal of individuals is driven by both intrinsic (e.g. morphological, physiological and genetic) and extrinsic (e.g. biotic interactions, habitat conditions or barriers) factors at the time of a dispersal event (e.g. Bilton et al., 2001; Fronhofer, Klecka, Melián, & Altermatt, 2015). An overarching concept integrating the relative roles of intrinsic and extrinsic drivers for dispersal of individuals, species, and taxonomic groups is missing. Importantly, we know very little regarding the level of intra-specific variation in dispersal within a population. For example, flight muscle mass, aspect ratio of the wings or fins, sex, fecundity status, number of completed reproduction events, and nutritional status are all potential intrinsic factors that vary between individuals of a population and may influence whether a long-distance or short-distance dispersal event is triggered under the prevailing environmental conditions. Simply put, intra-specific trait variability matters (Bolnick et al., 2011). Importantly, the variability in these factors is likely determined by an individual's genotype and may reveal a genetic precondition for "dispersers" versus "non-dispersers" in populations. Dispersal distances are thus likely determined by both intrinsic condition and the environment. Studying intraspecific variation of intrinsic factors and dispersal distances will likely lead to fundamental advances in our conceptual thinking regarding dispersal in freshwater systems and beyond.

4.5 | Finer spatiotemporal scaled analyses

To better understand the processes operating at the metacommunity level in river networks and the spatial use of and interchange between different locations within these systems, we need better spatiotemporal examination at the metacommunity level. Studies with any temporal resolution often place the replication focus at the annual scale to represent among-year variability. We believe within-year variability at the month-to-month scale in small catchments would open up a more mechanistic understanding of the processes structuring these systems (i.e. the interaction between environmental variability and dispersal and colonisation). For instance, seasonality is a fundamental component of ecosystems worldwide. However, the relative magnitude of seasonality varies globally, which can in turn regulate the amount of within-year temporal turnover in communities (Tonkin, Bogan, Bonada, Ríos-Touma, & Lytle, 2017). Understanding how this variability influences the annual shifts in

metacommunities in river networks and the use of different locations within networks will provide a much greater insight into the factors regulating dispersal and species sorting in highly complex river networks. In stochastic environments like New Zealand streams, this lack of climatic predictability is likely the primary mechanism behind the high level of context dependency at the metacommunity level (Tonkin, Death, et al., 2016). This calls for a much greater level of temporal replication to enable a better understanding of how climatic fluctuations regulate the dynamics and structuring of metacommunities.

4.6 | Integrating comparative and experimental research

An important finding from our review has been that there has been a great recent advance in comparative, experimental, and theoretical work with respect to metacommunity dynamics in river networks. However, the integration of these different approaches could be strengthened. At present, there is mostly a few microcosm experiments that technically link theoretical and comparative findings, while theoretical work is often still quite conceptual and system unspecific, and comparative work often lacks replication and testable theoretical predictions. In this context, we argue for a better integration of these three approaches.

Many empirical studies on riverine metacommunities assume theoretical concepts based on a patch-based structure, whereby the landscape is seen as a series of discrete communities linked by dispersal. For natural systems, this structure may be much less clear and gradual, and the extent and even definition of these patches may vary strongly between organisms. Discretising a river network into (often arbitrary) smaller sections does not make it automatically a metacommunity; it can be a spatially structured community, without the dynamics inherent to metacommunities (see above). Thus, metacommunity dynamics not only include a physical patchy structure, but also a subdivision of the communities, a decoupling from local versus regional dynamics, and subsequently a possible effect of dispersal on local dynamics. Recent theoretical works indeed show this and highlight why we expect metapopulation and metacommunity dynamics more frequently in river networks than in other landscape types (Fronhofer & Altermatt, 2017). Thus, we advocate that the definition of metacommunities used in individual studies should be clarified to separate "real" metacommunities and metacommunity dynamics from spatially discrete, but completely decoupled communities, or from spatially structured but completely homogenised communities (see also Box 1).

4.7 | Adopting life-history strategies rather than species traits

Traits do not operate individually, but they are interrelated, and should be viewed as such; that is, as life-history strategies (Olden, Poff, & Bestgen, 2006; Poff et al., 2006; Verberk et al., 2008, 2013; Winemiller & Rose, 1992). The reliance on traits or trait modalities as a means to group species into different dispersal modes and abilities may be hampering our ability to understand metacommunity dynamics in river networks. For instance, dispersal tends to be interrelated with reproductive and developmental traits, and passive dispersal is most likely associated with large egg numbers to offset the low potential of reaching favourable habitats (Verberk et al., 2008). One of the most common approaches in stream metacommunity studies is to split the full community into different groups based on their dispersal trait modalities. This approach lends itself well to the life-history approach; life-history studies often focus on comparisons between strategies rather than thinking along a continuum. We suggest that focusing on dispersal life-history strategies will produce a more complete view of the role that dispersal plays in shaping communities across river networks. The previously mentioned study of Lancaster and Downes (2017a) demonstrates this point clearly; while strong dispersers do indeed disperse further, they do not contribute to populations due to an inability to establish. Considering life history strategies instead will enable a better grouping of species based on life-history trade-offs associated with certain strategies. A good starting point for this is to consider Verberk et al. (2008) who outline three different dispersal life-history strategies.

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