a0010 Dispersal in Stream Networks: Meta-populations and Meta-communities[☆]

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Glossary

dt0010 **Dendritic network** The landscape of stream networks are dendritic, mimicking the dendrites of animal nervous systems. In a dendritic network, there are no discrete nodes or patches; habitat is contiguous throughout the network. The branching nature of dendritic networks affects how materials and information move along the network between sites. In a similar fashion, the dendritic nature of stream networks affects how organisms move between locations within the network.

dt0015 **Dispersal** Dispersal is the movement of organisms between populations and communities. Dispersal may be an active behavior or a passive process.

dt0020 **Drift dispersal** The active or passive dispersal by aquatic organisms as they become entrained in the water column and carried downstream.

dt0025 **Drift Paradox** Due to the downstream drift of aquatic insects and the lack of upstream sources of recolonization, logic suggests that upstream reaches could be left devoid of individuals. Experimental work has demonstrated that aerial upstream flight by adult life stages allows for recolonization of upstream areas.

dt0030 **Graph-based dispersal proxy** A proxy based on the distance between populations and communities within the stream network. There are numerous ways to measure this distance, including overland dispersal between sites as well as stream network distance between sites.

dt0035 **In-network dispersal (IND)** This dispersal is limited to the confines of the aquatic habitat of the stream network. The dispersal of obligate aquatic taxa, such as fish and some macroinvertebrates, is restricted to the aquatic habitat of streams.

dt0040 **Meta-community** An extension of meta-populations, a meta-community is a network of communities connected by the dispersal of organisms between communities.

dt0045 **Meta-population** A network of populations on a landscape connected by dispersal.

dt0050 **Network Position Hypothesis** Suggests that the position within a stream network affects patterns of biodiversity and community assembly. As you move across a stream network, levels of dispersal, habitat conditions, and species interactions may vary, and this variation may produce predictable patterns based on network location.

dt0055 **Organismal-based dispersal proxy** A proxy based on an organismal attribute or trait. These traits may be directly measured, such as body size, or categorical, such as dispersal ability (weak versus strong).

dt0060 **Out-of-network dispersal (OND)** Dispersal that occurs outside the aquatic habitat of the stream network. For instance, salamanders and crayfish may disperse overland between headwater streams and adult aquatic insects may fly between adjacent streams and networks.

dt0065 **Radio telemetry** A technique to monitor dispersal that relies on the generation and detection of radio waves to identify the location of aquatic organisms. Common methods utilize PIT tags (passive integrated transponder tags).

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s0010 Introduction

s0015 Meta-approaches in ecology

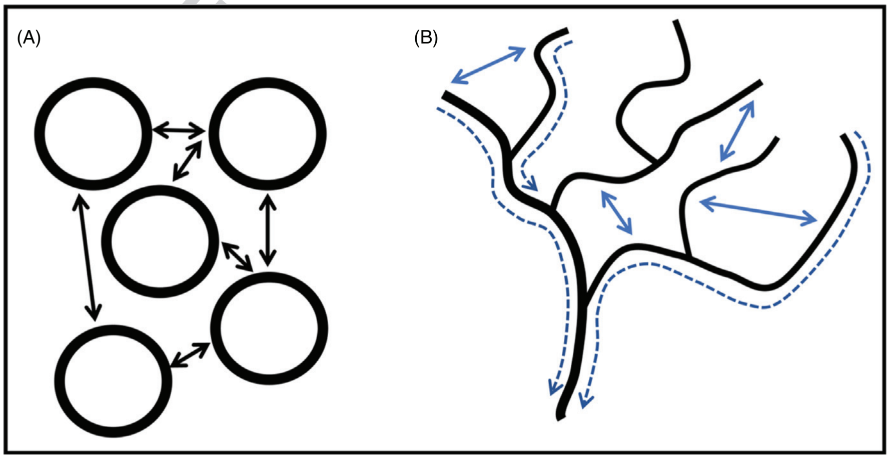
p0010 The substantial variation in dispersal that exists between organisms contributes to the structuring of ecological populations and communities in space and time. Most organisms find a way to get around on a landscape, including sessile organisms like plants and corals that use their reproductive stages as a major vehicle for dispersal. The influences of dispersal were included in a number of approaches aimed at understanding the distributions and diversity of species, including the Island Theory of Biogeography (MacArthur and Wilson, 1967), and Supply Side Ecology (Sale, 1977), but these approaches addressed the influence of dispersal at very large and very small scales, respectively. However, the influence of dispersal at a landscape or meso-scale has historically been one of the underappreciated aspects of the ecology of organisms, populations, and communities.

p0015 Two bodies of theory, meta-population ecology and meta-community ecology, emphasized the incorporation of meso-scale dispersal of organisms into the study of the distributions and abundances of species. A meta-population is a spatially separated group of populations connected on a landscape by the dispersal of individuals (Hanski and Gilpin, 1997). The multi-species extension of this idea, a meta-community, is a group of multi-species communities connected on a landscape by the dispersal of one or more species (Leibold et al., 2004). These ideas are conceptually linked in that they (1) emphasize the importance of dispersal in structuring populations and communities and (2) necessitate a multi-scale approach in their investigation. Local scales are defined by the structure and dynamics of a single population or a single community on a landscape, while regional scales are the aggregate properties of all local populations or local communities on a landscape.

p0020 Both meta-population and meta-community theory have had profound impacts on the field of ecology, by presenting testable predictions for empiricists and catalyzing research that includes mathematical theory, simulation studies, survey approaches, and experimental manipulations. Virtually every subfield of ecology has benefitted from the insight of meta-approaches, including the study of diversity in stream and river networks. However, the study of meta-patterns in riverine ecosystems presents challenges and opportunities that are quite unique.

s0020 Meta-approaches in stream networks

p0025 By their very nature, stream networks present challenges to meta-scale approaches. Prototype meta-populations and meta-communities were defined as distinct populations or communities on a landscape that are connected by dispersal (Fig. 1). The populations and communities within these networks exist in habitat patches with discrete boundaries, such as a forest patch in a grassland. In contrast, riverine systems are constructed dendritically (Fagan, 2002; Grant et al., 2007). Dendritic systems—so named because of their structural similarity to the dendrites of animal nervous systems—are linear, hierarchically-branching continuous habitat (Fig. 1); thus there are no discrete patches in dendritic systems (Fagan, 2002; Grant et al., 2007). The lack of distinct patches also leads to the lack of distinct boundaries by which to define the populations and communities that are members of a meta-population or meta-community. A second challenge is that, while much of the theory constructed from meta-approaches assumes that organisms disperse randomly, dispersal in river networks is often strongly directionally oriented. Fish, amphibians, and both the larval and adult stages of aquatic insects have been found to move in fairly specific and repeatable directions relative to the downstream flow of water (Mackay, 1992; Hershey et al., 1993; Skalski and Gilliam, 2000; Lowe, 2003; Petersen et al., 2004;



f0010 **Fig. 1** Schematic examples of aquatic networks. (A) A "classic" aquatic meta-community in which habitat patches are fairly discrete entities like ponds, and dispersal of species occurs among those patches. (B) A stream dendritic network in which there are two modes of dispersal: In Network Dispersal (IND), represented by dotted arrows, is dispersal via waterway within the network and that often has a distinct downstream bias, and Out of Network Dispersal (OND) represented by solid arrows occurs when organisms walk, crawl, or fly overland to other points in the aquatic network.

Finn et al., 2006). However, while these two properties of river networks initially challenged the utility of meta-population and meta-community approaches in riverine systems, both sets of theory have proven to be adaptable and broadly applicable for understanding the diversity, distribution, and abundances of species in river networks.

p0030 Even though meta-populations and meta-communities are often conceived and visualized as sets of discrete patches (Fig. 1), this particular depiction does not reflect an actual requirement of meta-approaches. Delineating "patches," even in continuous habitat, allows the application of the same theory and approaches that are applied in landscapes with spatially distinct patches. This tactic is particularly effective in networks where habitat characteristics are expected to differ depending on location in the network. Although stream networks are continuous dendritic habitat, that habitat is not uniform throughout. This foundational principle was codified by the River Continuum Concept which details how a large number of environmental parameters predictably change from the smallest headwater streams to progressively larger streams and rivers (Vannote et al., 1980). Along this gradient, stream size and discharge increase, while stream gradient and average substrate particle size decrease. The base of the stream food web also shifts progressively from leaf-litter decomposition to increasing amounts of algal primary production (Vannote et al., 1980). While these changes in stream environmental characteristics occur gradually down the length of a stream network, delineating spatially separated "patches" within this network allows an investigator to not only apply meta-approaches to river networks, but is also likely capture the environmental heterogeneity that creates unique conditions in different parts of river networks. Additionally, environmental conditions are not the only predictable differences between sections of stream networks; dispersal abilities and propensities vary predictably with network location.

s0025 Dispersal in stream networks

p0035 The dispersal of stream organisms is highly variable among taxa, and one major difference among taxa is whether or not their dispersal is restricted to inundated sections of the stream network. Fish and snails, for example, are strictly limited to in-stream dispersal, while a number of aquatic taxa including crayfish, amphibians, and some aquatic insect larvae have the ability to make limited journeys across land. Thus, in stream networks, there are two major dispersal modes: in-network dispersal (IND), and out-of-network dispersal (OND) (Fig. 1). Aquatic insects, the most commonly studied organisms in streams, actually use both IND and OND during their life cycles. In their larval forms, most aquatic insects are limited to IND by either crawling or allowing themselves to be swept along in stream current, a process termed "drift." Initially, drifting by macroinvertebrates was thought to be accidental or passive and that entry into the drift was the product of organisms losing purchase on benthic substrate and being swept away by current. While such passive drift entry certainly occurs, especially in high flow conditions, subsequent investigations have revealed that drift entry is most often an active process used to change foraging locations or escape predation (e.g., Kohler and McPeek, 1989). However, as stream insects meta-morphose into reproductive adults, most aquatic insects possess wings that allow them considerable freedom for OND. The typical life cycle of an aquatic insect is a prolonged larval stage, followed by a short-lived winged adult stage that quickly reproduces and then deposits eggs in or near a stream. These winged flying stages not only allow OND, but may be a primary mechanism for recolonizing upstream sites, especially headwaters, whose populations have been denuded by constant downstream drift (Hershey et al., 1993, but see Anholt (1995) for alternative resolution to the so-called Drift Paradox).

p0040 As with environmental conditions, dispersal dynamics of organisms may change with network position. With highly mobile organisms like fish, dispersal is rarely limited by the physical ability of a species to move between stream networks and river basins. However, a number of abiotic factors limit the ranges of fish in stream systems. For example, fish are often excluded from upstream sections of stream networks because of perennial drying or lack of adequate depth, or they may be excluded from some sections of stream networks because the stream thermal regime lies outside of a species' tolerance range. The effect of network location on benthic invertebrates may be even more profound. The major IND mode of benthic macroinvertebrates is drifting, which has been measured to occur over two kilometers (Hershey et al., 1993), and drift dispersal is unidirectional because water flows downhill. Additionally, drift propensity and distance are related to discharge, stream substrate, and local densities of similar species (James et al., 2009). Taken together, these factors suggest that dispersal has a considerably stronger influence on macroinvertebrate diversity and distributions in larger streams when compared to smaller, headwater streams (Brown and Swan, 2010). This conclusion has profound implications for the factors that dictate diversity and distributions of species in river networks.

p0045 The Network Position Hypothesis (NPH; from Schmera et al., 2018, based on hypotheses presented in Brown and Swan, 2010) suggests that the factors that control diversity and distributions of organisms in stream networks depend on the position of a population or community within a river network. Based on the NPH, the influence of IND is expected to increase from smaller to larger streams within a river network, thus the structuring forces on a population or community are predicted to shift from more local factors like environment and species interactions, to more regional controls driven by the movement of organisms. The NPH has been evaluated in a large number of studies primarily focusing on benthic invertebrates and fish. The results of these investigations have been mixed, with some studies strongly supporting the NPH (e.g., Wilson and McTammany, 2014; Tornwall et al., 2017; Brown et al., 2018), some studies producing results counter the NPH (e.g., He et al., 2020), and some studies showing mixed or equivocal results (e.g., Schmera et al., 2018; Henriques-Silva et al., 2019). Taken together, these studies suggest that the NPH does capture a fundamental pattern in river network systems, but that the overall model may be strongly modified by context. Those contexts include the life histories and dispersal abilities of organisms involved, the spatial heterogeneity captured in a river network, and human modifications to stream networks.

p0050 Meta-approaches have had a strong influence on the study of stream biodiversity. Not only have they provided new theoretical foundations for understanding the biodiversity of organisms in running waters (e.g., Brown and Swan, 2010; Holt and Chesson, 2018), but they have also provided empirical tests of these theories (e.g., Swan and Brown, 2017; Tornwall et al., 2017) and described new patterns of biodiversity in river networks. Additionally, they have informed management of threatened native species (e.g. White and Wagner, 2021). Foundational to applying meta-approaches is the study of organismal dispersal in river networks.

s0030 Studying organism dispersal in streams

s0035 Challenges to studying dispersal in streams

p0055 Studying dispersal in a meaningful way is difficult for many organisms (Heino et al., 2017). Some organisms like fish and amphibians can be marked, tagged, or tracked using various individual marking techniques, radio transponders, or passive integrated transponder (PIT) tags, and there are numerous examples of studies that use such techniques to infer dispersal behavior (e.g., Bubb et al., 2002; Hedden and Gido, 2020). However, invertebrates are the most commonly studied organisms in stream and river networks (Tornwall et al., 2015), and to date, no practical method has been developed to directly monitor the movement of benthic invertebrates with the possible exception of PIT tagging in large macroinvertebrates like crayfish (Bubb et al., 2002). For smaller benthic invertebrates like aquatic insects that make up the vast majority of benthic biomass and diversity, such marking or tagging is either methodologically impossible or impractical for three reasons. The first is the limitation imposed by the small size of most benthic macroinvertebrates, many of which are <1 mm in length and which rarely exceed 2 cm in length, a size that prohibits the use of radio or PIT tagging. Secondly, there is a low probability of recapture of marked organisms. Smaller invertebrates could conceivably be marked using a surficial marking like latex paint. However, due to the small size and high densities of these organisms, the probability of recapturing organisms marked in such a manner would be quite low. Additionally, great care would be necessary when marking these small organisms to prevent the marking compound from hindering organism function by coating gills or sensory structures. Third, insects molt, and some taxa molt frequently. Each molt would shed the exoskeleton and thus any superficial marks on the organism.

p0060 Given these limitations, there has been a considerable amount of creative science devoted to inferring the dispersal behavior of stream organisms. For larger organisms, the methods are often more direct. However, for smaller organisms like stream insects, investigators rely on inferential methods that include estimating species dispersal pattern by their abundances in drift samples, isotopic tracing of labeled populations, scaling-up based on the results of small-scale controlled studies, and modeling studies that predict dispersal based on known organism traits. Below we categorize and describe the major ways that the dispersal of aquatic organisms is either directly studied or indirectly inferred.

s0040 Approaches for studying the influence of dispersal in river networks

s0045 *Movement monitored*

p0065 Capture-mark-recapture work in stream meta-populations has mainly relied on radio telemetry. These approaches have been used to study the dispersal of larger stream organisms, predominantly fish, but also crayfish and salamanders, and even river otters. After stream organisms are captured and radiotagged, radio transponders may be placed along the stream bank to detect organisms as they move, or organisms may be detected within the stream itself by more active recapture or tracking techniques. For example, Hedden and Gido (2020) used mark-recapture methods to investigate the effects of stream drying on fish communities in stream networks. Deploying PIT antennas upstream and downstream of a perennial stream, the researchers found that stream fishes recolonized rewetted reaches. White and Wagner (2021) also used radio telemetry to monitor the dispersal of wild brook trout (*Salvelinus fontinalis*) in a small network in Pennsylvania (United States). They tracked the movement of the trout by actively monitoring them through the stream network to find that half of the tagged fish were sedentary. The mobile fish that dispersed moved over a short duration of time, and this behavior may be important for maintaining connectivity within the stream network.

p0070 For smaller organisms, tagging with radiotags is not currently possible. For stream insects, researchers have marked aquatic larvae by enriching the stream benthos with stable isotopes. As aquatic insect larvae feed on stream periphyton (i.e., algae and attached organic detritus), they too are marked with the stable isotope. The insect larvae can then be caught in stream drift nets. To understand the drift dynamics of stream insects, Hershey et al. (1993) captured drifting *Baetis* may fly larvae along the Kuparuk River in Alaska, determining that the larvae drifted at least 2.1 km downstream over the course of the Arctic summer.

p0075 Stable isotope enrichment has also been used to understand the aerial flight dynamics of adult stream insects. After enriching the stream benthos, researchers have set up nets at locations within and across stream networks to capture the marked insects. Briers et al. (2003) used this approach to understand the dispersal dynamics of stonefly populations (*Leuctra inermis*) in Wales, becoming the first to show insect dispersal between streams. Macneale et al. (2005) used a similar approach at Hubbard Brook Experimental Forest, New Hampshire (United States), where they added enriched nitrogen to streams before capturing adult stoneflies (*Leuctra ferruginea*) to identify their dispersal patterns. Their work demonstrated that stonefly populations can be connected across catchments within one generation via aerial dispersal.

p0080 To detect trends in species movement, there are a variety of traps and nets that may be used to capture stream organisms as they move within and across networks. Researchers often use Malaise traps to capture adult insects, drift nets for larval stream insects, and various traps, such as minnow traps, for fishes (Baxter et al., 2017). Malaise traps are set up along stream corridors and various distances from streams to capture flying adults as they move around stream networks. Petersen et al. (2004) trapped adult insects in malaise traps within a stream network and identified the crucial role that the stream corridor can play in the dispersal of adult aquatic insects. Likewise, traps have also been used to extensively estimate the movement of flying adult insects in urban stream corridors (Smith et al., 2015a, 2015b). Drift nets are deployed to catch the larval stages of aquatic insects as they drift in the current downstream, and they have been used in a large number of studies to produce estimates of dispersing aquatic insects and to infer how this dispersal behavior influences meta-population and meta-community patterns (e.g., Lancaster and Downes, 2017a, 2017b). Similar techniques can also be used for fish, including weir traps. For example, Schlosser (1998) used weir traps to demonstrate that the creation of beaver ponds was the primary factor driving the dispersal of fish to upstream reaches.

p0085 However, the measures of organism movement derived from the use of nets and traps have to be interpreted with extreme caution for two reasons. First, temporal variability in movement patterns can be profound. For example, aquatic insect drift density changes on a diel cycle, with the majority of drift occurring at night (Waters, 1965), so studies need to integrate both diel and diurnal movements. The second concern is that some organisms may actively avoid traps, so trapping may be an underestimate of actual dispersal behavior.

s0050 *Organismal-based proxies*

p0090 Due to the limitations of directly monitoring the dispersal of stream organisms within and between stream networks, researchers often turn to organismal-based proxies to infer dispersal. These proxies may include traits-based approaches that utilize organismal attributes relating to size, dispersal ability, and dispersal mode, as well as approaches that examine the population genetic structure and the natural isotope abundance of stream organisms. For symbiotic stream organisms, the dispersal of the host may also be used to understand symbiont dispersal.

p0095 Traits relating to size, such as body size, wing size, or fin size, are commonly used as proxies for dispersal ability. Wing morphology is also used as a proxy to understand dispersal dynamics in stream networks. Over the course of 3 years, Lancaster and Downes (2017a, 2017b) measured the size and shape of the wings of *Ecnomus* caddisflies. Pairing this information with data from benthic samples that allowed them to categorize individuals as residents or immigrants, they were able to determine that wing morphology may serve as a proxy for dispersal ability.

p0100 For aquatic insects, researchers often rely on the dispersal traits available in published trait databases to examine the role of dispersal in community assembly. Brown and Swan (2010) used a traits-based approach to examine how the dispersal ability and mode of stream macroinvertebrates affected patterns of community assembly across three Maryland (United States) stream meta-communities. Using traits for both adult and larval dispersal, they determined that dispersal-driven dynamics were more important in well-connected mainstem sites within the river network, while more isolated headwater sites were driven by local conditions.

p0105 Grönroos et al. (2013) applied a similar approach to investigate how the dispersal mode of aquatic insects affected community assembly of stream macroinvertebrates. They grouped the macroinvertebrates based on whether the larval stages of the organisms were active or passive dispersers and whether the adult stage was aquatic or terrestrial. They found that macroinvertebrates with an active larval dispersal stage and a terrestrial flying adult stage were more likely to be affected by the environmental conditions of the stream network (such as sediment size and flow conditions), suggesting that those organisms may be better able to track environmental conditions.

p0110 Examining the population genetic structure of stream organisms can be used as a proxy for dispersal as it may provide insight into gene flow between stream populations. Alp et al. (2012) examined the population genetics of two aquatic species with different dispersal strategies, a baetid mayfly (*Baetis rhodani*) and an amphipod (*Gammarus fossarum*). This work revealed that the mayfly, with its overland dispersal capabilities and its generalist niche, had little genetic structure across the river network. The population genetic structure of the amphipod, on the other hand, was impacted by its dispersal limitation within the stream network.

p0115 Historically, population genetics work has examined processes that occur over larger spatiotemporal scales. Recently, including within the freshwater ecology literature, researchers have been using population genetics studies to understand community assembly and processes at finer spatial scales. Yaegashi et al. (2014) used a population genetics approach to investigate the population genetic structure of the caddisfly *Stenopsyche marmorata* across four stream networks. Through this approach, the researchers found that the dispersal distances inferred from genetic work were similar to those distances measured for one generation in the field. Kelson et al. (2015) also used a fine-scale genetics approach to examine the genetic structure of brook trout (*S. fontinalis*) within a New Hampshire stream network. This study revealed the effects of isolation due to waterfalls on the genetic structure of the meta-population as well as the dispersal of highly migratory individuals across the network. As demonstrated by Kelson et al., population genetics studies at fine scales within river networks can reveal insights that may improve conservation and management strategies.

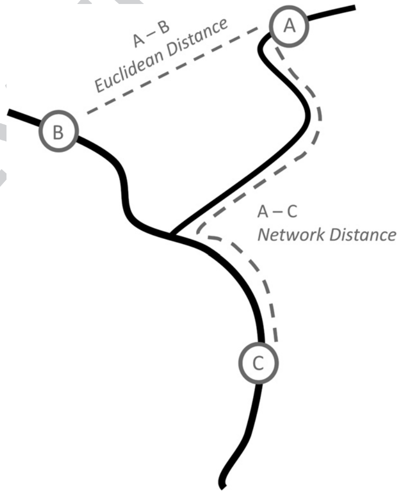
p0120 The stable isotopic signatures of species may provide clues to their dispersal in stream networks. Cook et al. (2007) analyzed isotopic data alongside the population genetics of the southern pygmy perch (*Nannoperca australis*) to examine dispersal across a stream network. This approach allowed them to determine that at least half of the fish sampled were residents of the stream where they were captured, suggesting little population connectivity within the network.

p0125 For freshwater species that participate in symbioses, one way to understand the dispersal of the symbiont is to determine the dispersal of its host. Terui and Miyazaki (2015) studied the dispersal of the freshwater mussel *Margaritifera laevis* based on the dispersal of its host fish, *Oncorhynchus masou masou*. After identifying the location of mussel beds within the river network, the researchers conducted fish sampling during the seasons of symbiont larval attachment and detachment periods. With this approach, they found that fish that were "tagged" with mussel larvae dispersed over four kilometers, demonstrating the importance of the host for symbiont dispersal across the river network.

s0055 *Graph-based proxies*

p0130 To understand the role of dispersal in stream networks, researchers often use graph-based proxies to infer dispersal based on the distance between populations and communities (Heino et al., 2017). These proxies differ based on which metric is used to quantify distances between sites in the network (Fig. 2). Often, ecologists will utilize more than one graph-based proxy in their study and compare how the various distance methods better describe dispersal within and between networks. In addition, certain proxies may be better suited for certain taxa or life stages. For instance, Euclidean distance, or the overland, straight-line distance between sites, may be a more appropriate proxy for taxa with both aquatic and terrestrial life stages or for the adult life stages of aquatic insects. On the other hand, for taxa that passively disperse with the current, dispersal distance may be better described with network distance, a graph-based proxy that relies on the contours of the stream network and/or flow distance, which accounts for the direction of dispersal based on streamflow (upstream versus downstream). To study community assembly dynamics in a Swedish stream meta-community, Göthe et al. (2013) employed all three of these graph-based proxies: overland (Euclidean) dispersal, network (along-stream) dispersal, and flow (directional downstream) dispersal. This approach, coupled with their traits-based analysis, allowed them to identify the role of these different dispersal strategies in structuring stream communities and how this role changed with taxa, season, and spatial scale.

p0135 In addition to relying on linear distances for graph-based proxies, stream ecologists have developed proxies that utilize circuit theory to study dispersal (Cañedo-Argüelles et al., 2015). For instance, the topographical distance between study sites can be used to account for the effect of landscape features on dispersal, with species traveling downhill facing lower resistance to movement between sites. Stream organisms also have to contend with the intermittency of aquatic habitats in stream networks. This circuit theory-based approach can also be extended to intermittent networks. Here, species traveling between sites that are separated by perennial flows face lower resistance to dispersal.



f0015 **Fig. 2** Illustration of measures of distance in river networks using three hypothetical sampling points, A, B, and C. Euclidean distance is the shortest distance between two points, illustrated by the distance between sites A and B. Network distance is the distance between points, following the contours of the river network, illustrated by the distance between sites A and C.

s0060 *Experimental approaches*

p0140 Experimental approaches can be used to disentangle the role of dispersal in driving patterns of biodiversity and community assembly in river networks (Fig. 3). Microcosm experiments have been effectively used to test meta-population and meta-community theory in dendritic systems. Using protozoan and rotifer communities, Carrara et al. (2012) created meta-community networks with different levels of connectivity and examined how network configuration affected patterns of diversity. With this approach, they were able to experimentally demonstrate that the dendritic connectivity of stream networks can produce different patterns of biodiversity than in networks with higher levels of connectivity. Altermatt and Fronhofer (2018) also used a microcosm approach to test how population densities varied within a dendritic network based on network configuration and position within the network. This work confirmed previous theory that communities connected to both headwaters and central nodes emerged as those with the highest population densities.

p0145 Investigating the dispersal dynamics of stream organisms is not only important for understanding biodiversity patterns and community assembly, but also for developing a knowledge base for how stream communities will respond to certain management strategies, such as stream restoration. A growing body of recent literature has set out to understand how communities at different locations within stream networks respond to disturbance and habitat manipulation and what role dispersal plays in the resulting community assembly dynamics. Tornwall et al. (2017) manipulated stream habitat complexity within headwater streams and at mainstem sites within stream networks. Only the communities of the headwater streams were affected by the manipulation, providing evidence in favor of the NPH. Similarly, Lancaster and Downes (2017b) manipulated the retention of detritus in a stream to disentangle the roles of environmental condition and dispersal in structuring macroinvertebrate communities. The manipulation revealed an interaction between resource levels and dispersal in which areas with augmented resources were quickly colonized by species not present before the manipulation.

f0020 **Fig. 3** Representative experimental methods for investigating dispersal in stream meta-communities. (A) Microcosms consisting of eight protist species. Network architecture was controlled by the transfer of medium between "connected" local communities. From Carrara et al. (2012), photo by Florian Altermatt; (B) Microcosms consisting of 14 protist species and 1 rotifer species in physical networks of tubing. From Seymour et al., 2016; photo by Florian Altermatt; (C) Replicated flume systems. Each flume set consisted of four recirculating flumes colonized by macroinvertebrates from local streams. Brown et al., 2018 used eight sets of these flumes to test the influence of dispersal and community source pool. Photo by Chris Swan; (D) In-stream flume system. Flumes are actually located in stream beds but the flumes can be manipulated. In this case, nets over the outflow valves (not shown in this picture) reduced in-network dispersal, while screens over some of the channels (not shown in this picture) prevented aerial dispersal. This research is currently in-progress. Photo by Bryan L. Brown.

p0150 Stream ecologists are also experimentally investigating how dispersal mode influences community dynamics and stability. Baumgartner and Robinson (2017) used a field experiment to investigate how upstream active dispersal modes (swimming and crawling) and aerial dispersal dynamics influenced the recovery of agricultural streams following disturbance. After disturbing the uppermost reaches of the streams, the researchers blocked aerial dispersal from half of the stream to differentiate the role of aquatic and aerial dispersal in the colonization dynamics of stream macroinvertebrates. While they didn't find an influence from aerial dispersal, they did find that aquatic, upstream dispersal allowed for the stream benthos to recover rapidly following disturbance.

s0065 *Theoretical modeling*

p0155 Modeling based on theoretical principles is a longstanding tradition in ecology. The primary utility of theoretical modeling is that it allows for "tests" of hypotheses that cannot be performed practically, often because of methodological or temporal limitations. Accordingly, theoretical models have strongly influenced thinking on the consequences of dispersal in stream meta-populations and communities.

p0160 Early contributions of theoretical modeling in stream networks addressed the so-called "Drift Paradox." The Drift Paradox recognized that, despite empirical measures of large numbers of organisms drifting in a downstream direction, the small headwaters of streams did not become depopulated through time. Initial resolutions to the paradox theorized that adult insect flight was upstream-biased and promoted recolonization of headwaters, and these theories were supported by numerous observations of upstream-biased flight (Hershey et al., 1993; Williams and Williams, 1993). However, such bias was not observed for all stream insects, and the hypothesis did not explain the persistence of non-flying headwater species like amphipods. Modeling studies of the Drift Paradox suggested that an upstream bias in adult flight was an unnecessary condition for promoting persistence in headwaters. Rather, a combination of random or unbiased dispersal and density dependence of populations could theoretically account for persistence (Anholt, 1995; Kopp and Allen, 2021).

p0165 Theoretical modeling has also been largely responsible for the appreciation of the effects of dendritic structure on organism dispersal in stream networks. Meta-population modeling of organisms in dendritic networks suggested that the size and architecture of stream dendritic networks strongly affected meta-population persistence and gene flow, and that fragmentation in dendritic networks could have highly variable effects that depended on the specifics of network architecture (Fagan, 2002; Chaput-Bardy et al., 2009; Grant, 2011). Other work extended similar concepts to multi-species communities in dendritic networks. Insights from this work include elucidating the role network architecture and dispersal tradeoffs between species create patterns of community composition in river networks (Auerbach and Poff, 2011). In addition, modeling work has shown that that network structure affects the spread of Proliferative Kidney Disease in salmon (Carrara et al., 2012) and that the stability of communities in river networks is promoted by asynchronous fluctuations in populations at different parts of a network (Anderson and Hayes, 2018). Species coexistence in river networks largely depends on the spatial heterogeneity of environmental conditions in a network and how that heterogeneity interacts with effects of the network on species' dispersal (Holt and Chesson, 2018).

s0070 Conclusion

p0170 Meta-approaches have permeated much of the theory and practice of ecology in the last few decades, first through the introduction of meta-population theory (Hanski and Gilpin, 1997) and later through meta-community theory (Leibold et al., 2004). Both of these concepts link local-scale patterns, like those occurring in a single stream reach, to larger-scale patterns that occur at the scale of multiple stream reaches, whole watersheds, or even entire river drainages (Schindler et al., 2010). The link between those scales is the dispersal of organisms. The growing influence of meta-frameworks highlights the importance of being able to accurately measure or estimate the dispersal of aquatic organisms.

s0075 Case studies

Case studies of scientific investigations of dispersal in stream networks.

Investigative Method	*Technique*	*Method III*	*Taxa*	*Biological scale*	*Name of site*	*Country*	*Source*
Movement monitored	Capture-mark-recapture	Radio telemetry	Crayfish	NA	Rivers Wharfe and Urfe	England	Bubb et al. (2002)
			Fish	NA	Johns Creek network	Virginia, United States	Albanese et al. (2003)
			Fish	Metacommunity	Kings Creek	Kansas, United States	Hedden and Gido (2020)
			Fish	Metapopulation	Loyalsock Creek	Pennsylvania, United States	White and Wagner (2021)
		Red latex dye	Fish	Metapopulation	Mill River	Massachusetts, United States	McLain and Ross (2005)
		Elastomer tags	Fish	Metapopulation	Leslie Tributary and Berczy Creek	Ontario, Canada	Poos and Jackson (2012)
		NA	Salamanders	Metapopulation	Shenandoah National Park	Virginia, United States	Campball Grant (2011)
	Mark-recapture	Stable isotope enrichment	Aquatic insects	NA	Kuparuk River	Alaska, United States	Hershey et al. (1993)
			Aquatic insects	Metapopulation	The headwater streams of the Rivers Severn and Wye	Wales, United Kingdom	Briers et al. (2003)
			Aquatic insects	Metapopulation	Hubbard Brook Experimental Forest	New Hampshire, United States	Macneale et al. (2005)
	Traps	Malaise traps	Aquatic insects	NA	Detroit River and Lake St. Clair	Ontario, Canada	Kovats et al. (1996)
			Aquatic insects	NA	Llyn Brianne reservoir	Wales, United Kingdom	Petersen et al. (2004)
		Weir traps	Fish	Metapopulation	Gould Creek	Minnesota, United States	Schlosser (1998)
Proxy	Organismal-based proxy	Body size	Fish	Metapopulation	West Brook	Massachusetts, United States	Letcher et al. (2007)
		Wing size	Aquatic insects	NA	Hughes Creek	Victoria, Australia	Lancaster and Downes (2017a, 2017b)
		Dispersal ability	Aquatic insects	Metacommunity	Youghiogheny, Savage, and Casselman River basins	Maryland, United States	Brown and Swan (2010)
			Aquatic insects	Metacommunity	Chiricahua Mountains	Arizona, United States	Bogan and Boersma (2012)
			Aquatic insects	Metacommunity	Lower West Branch of the Susquehanna River	Pennsylvania, United States	Wilson and McTammany (2016)
		Dispersal mode	Aquatic insects	Metacommunity	Streams within Iijoki, Koutajoki, and Tenojoki basins	Finland	Grönroos et al. (2013)
			Aquatic insects	Metacommunity	NA	Germany	Li et al. (2016)
			Benthic macroinvertebrates	Metacommunity	NA	Germany	Li et al. (2018)
		Host dispersal	Bivalves	Metapopulation	Mill River	Massachusetts, United States	McLain and Ross (2005)
			Bivalves	Metacommunity	Ontario	Canada	Schwalb et al. (2011)
			Bivalves	NA	Shubuto River	Japan	Terui and Miyazaki (2015)
		Natural abundance of stable isotopes	Fish	NA	Connecticut River	Massachusetts, United States	Kennedy et al. (2002)
			Fish	Metapopulation	Granite Creeks	Australia	Cook et al. (2007)
		Population genetic structure	Aquatic insects	Metacommunity	Rocky Mountain National Park	Colorado, United States	Finn and Poff (2011)
			Aquatic insects	NA	River Sense	Switzerland	Alp et al. (2012)

(*Continued*)

(Continued)

Investigative Method	*Technique*	*Method III*	*Taxa*	*Biological scale*	*Name of site*	*Country*	*Source*
			Aquatic insects	NA	Ou Mountains	Japan	Yaegashi et al. (2014)
			Aquatic insects	NA	Victoria Range, Grampians National Park	Australia	Chester et al. (2015)
			Crayfish	Metapopulation	Bear Creek and Cahaba River drainages	Alabama, United States	Barnett et al. (2020)
			Fish	Metapopulation	Lahontan Basin	Nevada, United States	Neville et al. (2006)
			Fish	Metapopulation	Granite Creeks	Australia	Cook et al. (2007)
			Fish	NA	Fridley Gap	Virginia, United States	Hudy et al. (2010)
			Fish	NA	Kent Falls Brook, Jefferson Hill Brook, and Spruce Brook	Connecticut, United States	Kanno et al. (2011)
			Fish	Metapopulation	Arkansas River watershed	Colorado, United States	Fitzpatrick et al. (2014)
			Fish	Metapopulation	Diamond River watershed	New Hampshire, United States	Kelson et al. (2014)
			Frogs	NA	Mount Kilimanjaro	Tanzania	Zancolli et al. (2014)
			River otter	NA	Alentejo Region	Portugal	Quaglietta et al. (2013)
			Salamander	NA	Hubbard Brook Watershed	New Hampshire, United States	Lowe et al. (2006)
			Salamander	NA	St. Regis, St. Joe, and Locha river basins	Idaho and Montana, United States	Mullen et al. (2010)
	Graph-based proxy	Dendritic network distance	Bacteria	Metacommunity	Lookout Creek watershed, H.J. Andrews Experimental Forest	Oregon, United States	Wisnoski and Lennon (2020)
		Flow distance	Bivalves	Metapopulation	Shubuto River basin	Japan	Terui et al. (2014)
		Network distance	Aquatic insects	Metacommunity	lower West Branch of the Susquehanna River	Pennsylvania, United States	Wilson and McTammany (2014)
			Benthic macroinvertebrates	Metacommunity	South Island (Six stream networks)	New Zealand	Campbell et al. (2015)
			Bivalves	Metapopulation	Neosho River basin	Kansas, United States	Smith et al. (2015a, 2015b)
			Fish	Metapopulation	Boise River basin	Idaho, United States	Dunham and Rieman (1999)
			Fish	Metapopulation	Sorachi River basin	Hokkaido, Japan	Koizumi and Maekawa (2004)
			Fish	NA	Kent Falls Brook, Jefferson Hill Brook, and Spruce Brook	Connecticut, United States	Kanno et al. (2011b)
			Fish	Metacommunity	Lake Balaton catchment	Hungary	EROS et al. (2012)
		Overland (Euclidean) distance	Aquatic insects	Metacommunity	Central Amazonia	Brazil	Landeiro et al. (2012)
		Overland (Euclidean) distance and network distance	Aquatic insects	Metacommunity	Youghiogheny, Savage, and Casselman River basins	Maryland, United States	Brown and Swan (2010)
			Plant	Metacommunity	Krycklan watershed	Sweden	Kuglerová et al. (2019)
		Overland (Euclidean) distance, network distance, and flow distance	Benthic macroinvertebrates and periphyton diatoms	NA	River Don watershed	United Kingdom	Rouquette et al. (2013)
			Diatoms	Metacommunity	Dalalven River catchment	Sweden	Göthe et al. (2013)

		Overland (Euclidean) distance, network distance, and fragmentation-based distance	Benthic macroinvertebrates	Metacommunity	10 stream networks	France	Gauthier et al. (2020)
		Overland (Euclidean) distance, network distance, topographical distance, and perennial distance	Aquatic insects	Metacommunity	Upper San Pedro River basin	Arizona, United States	Cañedo-Arguelles et al. (2015)
		Overland (Euclidean) distance, watercourse distance, and flow distance	Benthic macroinvertebrates	Metacommunity	Ecological Reserve of Antisana	Ecuador	Cauvy-Fraunié et al. (2015)
	Experimental approach	Dispersal manipulation	Aquatic insects	NA	Eygues River	France	Vander Vorste et al. (2016)
			Aquatic insects	Metacommunity	Maryland	United States	Brown et al. (2018)
			Aquatic insects	Metacommunity	Río Fardes	Spain	López-Rodríguez et al. (2021)
			Benthic macroinvertebrates	NA	Hombrechtikon and Volketswil streams	Switzerland	Baumgartner and Robinson (2017)
		Habitat manipulation	Benthic macroinvertebrates	Metacommunity	Jefferson National Forest	Virginia, United States	Tornwall et al. (2017)
		Microcosm experiment	Protists and rotifers	Metacommunity	–		Carrara et al. (2012)
			Protist	Metacommunity			Altermatt and Fronhofer (2018)
Theoretical modelling	Metapopulation model	–		Metapopulation	–		Anholt (1995) Kopp et al. (2001) Fagan (2002) Lowe (2002) Chaput-Bardy et al. (2009) Morrissey and de Kerckhove (2009) Campbell Grant (2011) Mari et al. (2014) Streib et al. (2020)
	Metacommunity model	–		Metacommunity	–		Auerbach and Poff (2011) Anderson and Hayes (2018) Carraro et al. (2018) Holt and Chesson (2018)

References

Albanese B, Angermeier PL, and Gowan C (2003) Designing mark–recapture studies to reduce effects of distance weighting on movement distance distributions of stream fishes. *Transactions of the American Fisheries Society* 132: 925–939.

Alp M, Keller I, Westram AM, and Robinson CT (2012) How river structure and biological traits influence gene flow: A population genetic study of two stream invertebrates with differing dispersal abilities. *Freshwater Biology* 57: 969–981.

Altermatt F and Fronhofer EA (2018) Dispersal in dendritic networks: Ecological consequences on the spatial distribution of population densities. *Freshwater Biology* 63: 22–32.

Anderson KE and Hayes SM (2018) The effects of dispersal and river spatial structure on asynchrony in consumer–resource metacommunities. *Freshwater Biology* 63: 100–113.

Anholt BR (1995) Density dependence resolves the stream drift paradox. *Ecology* 76: 2235–2239.

Auerbach DA and Poff NL (2011) Spatiotemporal controls of simulated metacommunity dynamics in dendritic networks. *Journal of the North American Benthological Society* 30: 235–251.

Barnett ZC, Adams SB, Ochs CA, and Garrick RC (2020) Crayfish populations genetically fragmented in streams impounded for 36–104 years. *Freshwater Biology* 65: 768–785.

Baumgartner SD and Robinson CT (2017) Short-term colonization dynamics of macroinvertebrates in restored channelized streams. *Hydrobiologia* 784: 321–335.

Baxter CV, Kennedy TA, Miller SW, Muehlbauer JD, and Smock LA (2017) Macroinvertebrate drift, adult insect emergence and oviposition. In: Hauer FR and Lamberti GA (eds.) *Methods in Stream Ecology*. 3rd edn, vol. 1, pp. 435–456. Boston: Academic Press. ch. 21.

Bogan MT and Boersma KS (2012) Aerial dispersal of aquatic invertebrates along and away from arid-land streams. *Freshwater Science* 31: 1131–1144.

Briers RA, Cariss HM, and Gee JHR (2003) Flight activity of adult stoneflies in relation to weather. *Ecological Entomology* 28: 31–40.

Brown BL and Swan CM (2010) Dendritic network structure constrains metacommunity properties in riverine ecosystems. *Journal of Animal Ecology* 79: 571–580.

Brown BL, Wahl C, and Swan CM (2018) Experimentally disentangling the influence of dispersal and habitat filtering on benthic invertebrate community structure. *Freshwater Biology* 63: 48–61.

Bubb DH, Lucas MC, Thom TJ, and Rycroft P (2002) The potential use of PIT telemetry for identifying and tracking crayfish in their natural environment. *Hydrobiologia* 483: 225–230.

Campball Grant EH (2011) Structural complexity, movement bias, and metapopulation extinction risk in dendritic ecological networks. *Journal of the North American Benthological Society* 30: 252–258.

Campbell Grant EH (2011) Structural complexity, movement bias, and metapopulation extinction risk in dendritic ecological networks. *Journal of the North American Benthological Society* 30: 252–258.

Campbell RE, Winterbourn MJ, Cochrane TA, and McIntosh AR (2015) Flow-related disturbance creates a gradient of metacommunity types within stream networks. *Landscape Ecology* 30: 667–680.

Cañedo-Arguelles M, Boersma KS, Bogan MT, Olden JD, Phillipsen IC, Schriever TA, and Lytle DA (2015) Dispersal strength determines meta-community structure in a dendritic riverine network. *Journal of Biogeography* 42: 778–790.

Cañedo-Argüelles M, Boersma KS, Bogan MT, Olden JD, Phillipsen IC, Schriever TA, and Lytle DA (2015) Dispersal strength determines meta-community structure in a dendritic riverine network. *Journal of Biogeography* 42: 778–790.

Carrara F, Altermatt F, Rodriguez-Iturbe I, and Rinaldo A (2012) Dendritic connectivity controls biodiversity patterns in experimental metacommunities. *Proceedings of the National Academy of Sciences* 109: 5761–5766.

Carraro L, Mari L, Gatto M, Rinaldo A, and Bertuzzo E (2018) Spread of proliferative kidney disease in fish along stream networks: A spatial metacommunity framework. *Freshwater Biology* 63: 114–127.

Cauvy-Fraunié S, Espinosa R, Andino P, Jacobsen D, and Dangles O (2015) Invertebrate metacommunity structure and dynamics in an Andean glacial stream network facing climate change. *PLoS One* 10: 1–19.

Chaput-Bardy A, Fleurant C, Lemaire C, and Secondi J (2009) Modelling the effect of in-stream and overland dispersal on gene flow in river networks. *Ecological Modelling* 220: 3589–3598.

Chester ET, Miller AD, Valenzuela I, Wickson SJ, and Robson BJ (2015) Drought survival strategies, dispersal potential and persistence of invertebrate species in an intermittent stream landscape. *Freshwater Biology* 60: 2066–2083.

Cook BD, Bunn SE, and Hughes JM (2007) Molecular genetic and stable isotope signatures reveal complementary patterns of population connectivity in the regionally vulnerable southern pygmy perch (Nannoperca australis). *Biological Conservation* 138: 60–72.

Dunham JB and Rieman BE (1999) Metapopulation structure of bull trout: Influences of physical, biotic, and geometrical landscape characteristics. *Ecological Applications* 9: 642–655.

EROS T, Sály P, Takács P, Specziár A, and Bíró P (2012) Temporal variability in the spatial and environmental determinants of functional metacommunity organization—Stream fish in a human-modified landscape. *Freshwater Biology* 57: 1914–1928.

Fagan WF (2002) Connectivity, fragmentation, and extinction risk in dendritic metapopulations. *Ecology* 83: 3243–3249.

Finn DS and Poff NL (2011) Examining spatial concordance of genetic and species diversity patterns to evaluate the role of dispersal limitation in structuring headwater metacommunities. *Journal of the North American Benthological Society* 30: 273–283.

Finn DS, Theobald DM, Black WC, and Poff NL (2006) Spatial population genetic structure and limited dispersal in a Rocky Mountain alpine stream insect. *Molecular Ecology* 15: 3553–3566.

Fitzpatrick SW, Crockett H, and Funk WC (2014) Water availability strongly impacts population genetic patterns of an imperiled Great Plains endemic fish. *Conservation Genetics* 15: 771–788.

Gauthier M, Launay B, Le Goff G, Pella H, Douady CJ, and Datry T (2020) Fragmentation promotes the role of dispersal in determining 10 intermittent headwater stream metacommunities. *Freshwater Biology* 65: 2169–2185.

Göthe E, Angeler DG, and Sandin L (2013) Metacommunity structure in a small boreal stream network. *Journal of Animal Ecology* 82: 449–458.

Grant EHC (2011) Structural complexity, movement bias, and metapopulation extinction risk in dendritic ecological networks. *Journal of the North American Benthological Society* 30: 252–258.

Grant EHC, Lowe WH, and Fagan WF (2007) Living in the branches: Population dynamics and ecological processes in dendritic networks. *Ecology Letters* 10: 165–175.

Grönroos M, Heino J, Siqueira T, Landeiro VL, Kotanen J, and Bini LM (2013) Metacommunity structuring in stream networks: Roles of dispersal mode, distance type, and regional environmental context. *Ecology and Evolution* 3: 4473–4487.

Hanski IA and Gilpin ME (eds.) (1997) *Metapopulation Biology: Ecology, Genetics, and Evolution*. San Diego: Academic Press.

He S, Soininen J, Chen K, and Wang B (2020) Environmental factors override dispersal-related factors in shaping diatom and macroinvertebrate communities within Stream Networks in China. *Frontiers in Ecology and Evolution* 8. https://doi.org/10.3389/fevo.2020.00141.

Hedden SC and Gido KB (2020) Dispersal drives changes in fish community abundance in intermittent stream networks. *River Research and Applications* 36: 797–806.

Heino J, Alahuhta J, Ala-Hulkko T, Antikainen H, Bini LM, Bonada N, Datry T, Erös T, Hjort J, Kotavaara O, Melo AS, and Soininen J (2017) Integrating dispersal proxies in ecological and environmental research in the freshwater realm. In: *Environmental Reviews*, pp. 334–349. Canadian Science Publishing.

Henriques-Silva R, Logez M, Reynaud N, Tedesco PA, Brosse S, Januchowski-Hartley SR, Oberdorff T, and Argillier C (2019) A comprehensive examination of the network position hypothesis across multiple river metacommunities. *Ecography* 42: 284–294.

Hershey AE, Pastor J, Peterson BJ, and Kling GW (1993) Stable isotopes resolve the drift paradox for *Baetis* mayflies in an Arctic river. *Ecology* 74: 2315–2325.

Holt G and Chesson P (2018) The role of branching in the maintenance of diversity in watersheds. *Freshwater Science* 37: 712–730.

Hudy M, Coombs JA, Niwslow KH, and Letcher BH (2010) Dispersal and within-stream spatial population structure of brook trout revealed by pedigree reconstruction analysis. *Transactions of the American Fisheries Society* 139: 1276–1287.

James ABW, Dewson ZS, and Death RG (2009) The influence of flow reduction on macroinvertebrate drift density and distance in three New Zealand streams. *Journal of the North American Benthological Society* 28: 220–232.

Kanno Y, Vokoun JC, and Letcher BH (2011) Fine-scale population structure and riverscape genetics of brook trout (Salvelinus fontinalis) distributed continuously along headwater channel networks. *Molecular Ecology* 20: 3711–3729.

Kelson SJ, Kapuscinski AR, Timmins D, and Ardren WR (2014) Fine-scale genetic structure of brook trout in a dendritic stream network. *Conservation Genetics* 16: 31–42.

Kelson SJ, Kapuscinski AR, Timmins D, and Ardren WR (2015) Fine-scale genetic structure of brook trout in a dendritic stream network. *Conservation Genetics* 16: 31–42.

Kennedy BP, Klaue A, Blum JD, Folt CL, and Nislow KH (2002) Reconstructing the lives of fish using Sr isotopes in otoliths. *Canadian Journal of Fisheries and Aquatic Sciences* 59: 925–929.

Kohler SL and McPeek MA (1989) Predation risk and the foraging behavior of competing stream insects. *Ecology* 70: 1811–1825.

Koizumi I and Maekawa K (2004) Metapopulation structure of stream-dwelling Dolly Varden charr inferred from patterns of occurrence in the Sorachi River basin, Hokkaido, Japan. *Freshwater Biology* 49: 973–981.

Kopp D and Allen D (2021) Trait–environment relationships could alter the spatial and temporal characteristics of aquatic insect subsidies at the macrospatial scale. *Ecography* 44: 391–402.

Kopp M, Jeschke JM, and Gabriel W (2001) Exact compensation of stream drift as an evolutionarily stable strategy. *Oikos* 92: 522–530.

Kovats Z, Ciborowski JAN, and Corkum L (1996) Inland dispersal of adult aquatic insects. *Freshwater Biology* 36: 265–276.

Kuglerová L, Kielstra BW, Moore RD, and Richardson JS (2019) Importance of scale, land-use, and stream network properties for riparian plant communities along an urban gradient. *Freshwater Biology* 64: 587–600.

Lancaster J and Downes BJ (2017a) Dispersal traits may reflect dispersal distances, but dispersers may not connect populations demographically. *Oecologia* 184: 171–182.

Lancaster J and Downes BJ (2017b) A landscape-scale field experiment reveals the importance of dispersal in a resource-limited metacommunity. *Ecology* 98: 565–575.

Landeiro VL, Bini LM, Melo AS, Oliveira Pes AM, and Magnusson WE (2012) The roles of dispersal limitation and environmental conditions in controlling caddisfly (Trichoptera) assemblages. *Freshwater Biology* 57: 1554–1564.

Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, Hoopes MF, Holt RD, Shurin JB, Law R, Tilman D, Loreau M, and Gonzalez A (2004) The metacommunity concept: A framework for multi-scale community ecology. *Ecology Letters* 7: 601–613.

Letcher BH, Nislow KH, Coombs JA, O'Donnell MJ, and Dubreuil TL (2007) Population response to habitat fragmentation in a stream-dwelling brook trout population. *PLoS One* 2.

Li F, Sundermann A, Stoll S, and Haase P (2016) A newly developed dispersal metric indicates the succession of benthic invertebrates in restored rivers. *Science of the Total Environment* 569–570: 1570–1578.

Li F, Tonkin JD, and Haase P (2018) Dispersal capacity and broad-scale landscape structure shape benthic invertebrate communities along stream networks. *Limnologica* 71: 68–74.

López-Rodríguez MJ, Paz Moreno I, Peralta-Maraver I, Pérez-Martínez C, and Tierno de Figueroa JM (2021) Experimental evaluation of biodiversity response to dispersal barriers and patch primary producer biomass in Mediterranean streams. *Aquatic Sciences* 83: 1–10.

Lowe WH (2002) Landscape-scale spatial population dynamics in human-impacted stream systems. *Environmental Management* 30: 225–233.

Lowe WH (2003) Linking dispersal to local population dynamics: A case study using a headwater salamander system. *Ecology* 84: 2145–2154.

Lowe WH, Likens GE, McPeek MA, and Buso DC (2006) Linking direct and indirect data on dispersal: Isolation by slope in a headwater stream salamander. *Ecology* 87: 334–339.

MacArthur RH and Wilson EO (1967) *The Theory of Island Biogeography*. Princeton, NJ: Princeton University Press.

Mackay RJ (1992) Colonization by lotic macroinvertebrates: A review of processes and patterns. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 617–628.

Macneale KH, Peckarsky BL, and Likens GE (2005) Stable isotopes identify dispersal patterns of stonefly populations living along stream corridors. *Freshwater Biology* 50: 1117–1130.

Mari L, Casagrandi R, Bertuzzo E, Rinaldo A, and Gatto M (2014) Metapopulation persistence and species spread in river networks. *Ecology Letters* 17: 426–434.

McLain DC and Ross MR (2005) Reproduction based on local patch size of Alasmidonta heterodon and dispersal by its darter host in the Mill River, Massachusetts, USA. *Journal of the North American Benthological Society* 24: 139–147.

Morrissey MB and de Kerckhove DT (2009) The maintenance of genetic variation due to asymmetric gene flow in dendritic metapopulations. *American Naturalist* 174: 875–889.

Mullen LB, Woods HA, Schwartz MK, Sepulveda AJ, and Lowe WH (2010) Scale-dependent genetic structure of the Idaho giant salamander (Dicamptodon aterrimus) in stream networks. *Molecular Ecology* 19: 898–909.

Neville HM, Dunham JB, and Peacock MM (2006) Landscape attributes and life history variability shape genetic structure of trout populations in a stream network. *Landscape Ecology* 21: 901–916.

Petersen I, Masters Z, Hildrew AG, and Ormerod SJ (2004) Dispersal of adult aquatic insects in catchments of differing land use. *Journal of Applied Ecology* 41: 934–950.

Poos MS and Jackson DA (2012) Impact of species-specific dispersal and regional stochasticity on estimates of population viability in stream metapopulations. *Landscape Ecology* 27: 405–416.

Quaglietta L, Fonseca VC, Hájková P, Mira A, and Boitani L (2013) Fine-scale population genetic structure and short-range sex-biased dispersal in a solitary carnivore, Lutra lutra. *Journal of Mammalogy* 94: 561–571.

Rouquette JR, Dallimer M, Armsworth PR, Gaston KJ, Maltby L, and Warren PH (2013) Species turnover and geographic distance in an urban river network. *Diversity and Distributions* 19: 1429–1439.

Sale P (1977) Maintenance of high diversity in coral reef fish communities. *The American Naturalist* 111: 337–359.

Schindler D, Hilborn R, Chasco B, Boatright C, Quinn T, Rogers L, and Webster M (2010) Population diversity and the portfolio effect in an exploited species. *Nature* 465: 609–612.

Schlosser IJ (1998) Fish recruitment, dispersal and trophic interactions in a heterogeneous lotic environment. *Oecologia* 113: 260–268.

Schmera D, Árva D, Boda P, Bódis E, Bolgovics Á, Borics G, Csercsa A, Deák C, Krasznai EÁ, Lukács BA, Mauchart P, Móra A, Sály P, Specziár A, Süveges K, Szivák I, Takács P, Tóth M, Várbíró G, Vojtkó AE, and Erős T (2018) Does isolation influence the relative role of environmental and dispersal-related processes in stream networks? An empirical test of the network position hypothesis using multiple taxa. *Freshwater Biology* 63: 74–85.

Schwalb A, Poos M, and Ackerman J (2011) Movement of logperch-the obligate host fish for endangered snuffbox mussels: Implications for mussel dispersal. *Aquatic Sciences* 73: 223–231.

Seymour M, Deiner K, and Altermatt F (2016) Scale and scope matter when explaining varying patterns of community diversity in riverine metacommunities. *Basic and Applied Ecology* 17: 134–144.

Skalski GT and Gilliam JF (2000) Modeling diffusive spread in a heterogeneous population: A movement study with stream fish. *Ecology* 81: 1685–1700.

Smith BR, Edds DR, and Goeckler JM (2015a) Lowhead dams and the downstream dispersal of zebra mussels. *Hydrobiologia* 755: 1–12.

Smith RF, Venugopal PD, Baker ME, and Lamp WO (2015b) Habitat filtering and adult dispersal determine the taxonomic composition of stream insects in an urbanizing landscape. *Freshwater Biology* 60: 1740–1754.

Streib L, Kattwinkel M, Heer H, Ruzika S, and Schäfer RB (2020) How does habitat connectivity influence the colonization success of a hemimetabolous aquatic insect? - A modeling approach. *Ecological Modelling* 416: 108909.

Swan CM and Brown BL (2017) Metacommunity theory meets restoration: Isolation may mediate how ecological communities respond to stream restoration. *Ecological Applications* 27: 2209–2219.

Terui A and Miyazaki Y (2015) A "parasite-tag" approach reveals long-distance dispersal of the riverine mussel Margaritifera laevis by its host fish. *Hydrobiologia* 760: 189–196.

Terui A, Miyazaki Y, Yoshioka A, Kaifu K, Matsuzaki SIS, and Washitani I (2014) Asymmetric dispersal structures a riverine metapopulation of the freshwater pearl mussel Margaritifera laevis. *Ecology and Evolution* 4: 3004–3014.

Tornwall B, Sokol ER, Skelton J, and Brown BL (2015) Trends in stream biodiversity research since the river continuum concept. *Diversity* 7: 16–35.

Tornwall BM, Swan CM, and Brown BL (2017) Manipulation of local environment produces different diversity outcomes depending on location within a river network. *Oecologia* 184: 663–674.

Vander Vorste R, Malard F, and Datry T (2016) Is drift the primary process promoting the resilience of river invertebrate communities? A manipulative field experiment in an intermittent alluvial river. *Freshwater Biology* 61: 1276–1292.

Vannote RL, Minshall GW, Cummins KW, Sedell JR, and Cushing DH (1980) The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37: 130–137.

Waters TF (1965) Interpretation of invertebrate drift in streams. *Ecology* 46: 327–334.

White SL and Wagner T (2021) Behaviour at short temporal scales drives dispersal dynamics and survival in a metapopulation of brook trout (Salvelinus fontinalis). *Freshwater Biology* 66: 278–285.

Williams DD and Williams NE (1993) The upstream/downstream movement paradox of lotic invertebrates: Quantitative evidence from a welsh mountain stream. *Freshwater Biology* 30: 199–218.

Wilson MJ and McTammany ME (2014) Tributary and mainstem benthic macroinvertebrate communities linked by direct dispersal and indirect habitat alteration. *Hydrobiologia* 738: 75–85.

Wilson MJ and McTammany ME (2016) Spatial scale and dispersal influence metacommunity dynamics of benthic invertebrates in a large river. *Freshwater Science* 35: 738–747.

Wisnoski NI and Lennon JT (2020) Microbial community assembly in a multi-layer dendritic metacommunity. *Oecologia* 195: 13–24.

Yaegashi S, Watanabe K, Monaghan MT, and Omura T (2014) Fine-scale dispersal in a stream caddisfly inferred from spatial autocorrelation of microsatellite markers. *Freshwater Science* 33: 172–180.

Zancolli G, Rödel MO, Steffan-Dewenter I, and Storfer A (2014) Comparative landscape genetics of two river frog species occurring at different elevations on Mount Kilimanjaro. *Molecular Ecology* 23: 4989–5002.

Further reading

Brown BL, Swan CM, Auerbach DA, Campbell Grant EH, Hitt NP, Maloney KO, and Patrick C (2011) Metacommunity theory as a multispecies, multiscale framework for studying the influence of river network structure on riverine communities and ecosystems. *Journal of the North American Benthological Society* 30: 310–327.

Heino J, Melo AS, Siqueira T, Soininen J, Valanko S, and Bini LM (2015) Metacommunity organisation, spatial extent and dispersal in aquatic systems: Patterns, processes and prospects. *Freshwater Biology* 60: 845–869.

Tonkin JD, Altermatt F, Finn DS, Heino J, Olden JD, Pauls SU, and Lytle DA (2018) The role of dispersal in river network metacommunities: Patterns, processes, and pathways. *Freshwater Biology* 63: 141–163.

Non-Print Items

Abstract:

Meta-approaches to understanding diversity, including meta-populations and meta-communities, have created a paradigm shift in ecological research, including in stream ecosystems. Both of these frameworks emphasize the major role that organismal dispersal plays in generating and maintaining biodiversity patterns because dispersal links processes at local scales to processes at larger spatial scales. Fundamental to the application of meta-approaches is an understanding of dispersal. Ecologists working in stream systems use various methods to measure or estimate the dispersal of aquatic organisms. More direct measures include mark-recapture techniques and the use of various nets and traps. Due to the difficulty of directly monitoring the dispersal of aquatic organisms, particularly smaller taxa, organismal-based dispersal proxies such as traits-based approaches and population genetics can be used to infer dispersal patterns. Graph-based proxies that rely on the spatial distribution of sampling sites can also be used to infer dispersal in stream networks. While experimental approaches—including the direct manipulation of dispersal—have been employed less often than observational approaches, they have been able to mechanistically link dispersal rates and patterns to patterns in observed biodiversity. Likewise, theoretical approaches that include mathematical and simulation modeling have been able to conduct in silico experiments to test scenarios that are impractical or impossible to conduct in real-world systems. Here we provide a brief introduction to these techniques, highlight some of the insights that they have enabled, and discuss their importance in bringing meta-approaches to the study of stream ecosystems.

In this chapter, we provide an introduction to the study of dispersal from the perspective of its importance for meta-approaches in stream ecology that briefly touches on the conceptual importance of studying dispersal and on the techniques used to measure or estimate dispersal. In reviewing literature to include in this article, we chose to focus on fine-scale work performed at a maximum scale of a few adjacent watersheds because these studies best illustrate the approaches and techniques for the study of dispersal. However, a considerable amount of work also exists that applies meta-population and meta-community theory to large-scale biogeographic biodiversity patterns. Thus, our work here is not meant to be an exhaustive review of the literature on dispersal in stream networks, but to serve as an introduction to the various techniques used to understand the dispersal of stream organisms. Additionally, while the focus of this article is mainly dispersal in stream meta-populations and meta-communities, these are relatively new fields of study. Multiple foundational papers on dispersal in stream networks that we included here do not directly address meta-population or meta-communities. These older works are, however, crucial for an introduction to the topic, and the study of dispersal would be much diminished without the groundwork that these works provided.

Keywords: Benthic macroinvertebrate; Dispersal; Drift; Graph-based proxy; Meta-community; Meta-population; Organismal-based proxy; Radiotelemetry; Stream