



BIOTA CONNECT AQUATIC HABITATS THROUGHOUT FRESHWATER ECOSYSTEM MOSAICS¹

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ABSTRACT: Freshwater ecosystems are linked at various spatial and temporal scales by movements of biota adapted to life in water. We review the literature on movements of aquatic organisms that connect different types of freshwater habitats, focusing on linkages from streams and wetlands to downstream waters. Here, streams, wetlands, rivers, lakes, ponds, and other freshwater habitats are viewed as dynamic freshwater ecosystem mosaics (FEMs) that collectively provide the resources needed to sustain aquatic life. Based on existing evidence, it is clear that biotic linkages throughout FEMs have important consequences for biological integrity and biodiversity. All aquatic organisms move within and among FEM components, but differ in the mode, frequency, distance, and timing of their movements. These movements allow biota to recolonize habitats, avoid inbreeding, escape stressors, locate mates, and acquire resources. Cumulatively, these individual movements connect populations within and among FEMs and contribute to local and regional diversity, resilience to disturbance, and persistence of aquatic species in the face of environmental change. Thus, the biological connections established by movement of biota among streams, wetlands, and downstream waters are critical to the ecological integrity of these systems. Future research will help advance our understanding of the movements that link FEMs and their cumulative effects on downstream waters.

(KEY TERMS: aquatic ecology; biotic integrity; connectivity; rivers/streams; wetlands.)

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INTRODUCTION

Spatial and temporal connections created by flows of energy, materials, and organisms within and among habitats are needed to sustain ecosystem

structure and function. In aquatic ecosystems, large rivers, lakes, and coastal waters depend on flows of physical and chemical (i.e., nonliving) materials, such as water, nutrients, organic matter, and sediment, from upstream ecosystems (see Fritz et al. 2018; Lane et al. 2018, for discussion of physical and

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chemical connections). These physicochemical flows support and interact with biological connections created by the active or passive movements of living aquatic and semiaquatic organisms or their propagules, moving in diverse ways, across different spatial and temporal scales (Gounand et al. 2018). Because biological connections among aquatic habitats have important and long-lasting effects on species distributions (Dias et al. 2014), population and community dynamics (Perkin and Gido 2012; Crook et al. 2015), biodiversity (Jeltsch et al. 2013), water quality (Vaughn 2017), and ecosystem function (Lundberg and Moberg 2003), they are an integral part of all aquatic ecosystems.

In this paper, we review and synthesize the literature on biological connections between small or temporary streams, wetlands, and downstream waters such as rivers, lakes, and coastal waters. This subset of freshwater ecosystem connections was the focus of the United States (U.S.) Environmental Protection Agency's recent review and synthesis (USEPA 2015; Alexander et al. 2018). The overall objective of the Clean Water Act (CWA) is to restore and maintain the chemical, physical, and biological integrity of the nation's waters. When the CWA was enacted in 1972, ecosystem integrity was a relatively new concept and aquatic ecology still a young science. Research and monitoring over the next decade made it increasingly clear that, despite gains in chemical water quality under the CWA, water quality standards that considered only chemical pollutant concentrations were insufficient to restore or maintain aquatic ecological integrity, defined as the sum of chemical, physical, and biological integrity of aquatic ecosystems (Karr and Dudley 1981; Karr 1993). These findings helped to motivate new research into factors affecting aquatic ecological integrity. A key factor that has emerged from this research is the importance of structural and functional connectivity of streams, wetlands, and downstream waters (Alexander et al. 2018).

This review summarizes how movements of biota link streams, riparian and floodplain wetlands, and nonfloodplain wetlands to downstream waters, and why these connections are important. Together with lakes, ponds, and other freshwater habitats, streams and wetlands collectively make up dynamic freshwater ecosystem mosaics (FEMs) of watersheds — that is, the diverse collection of integrated freshwater habitats needed to sustain aquatic life and the ecological integrity of these systems (Karr and Dudley 1981; Karr 1995). Many aquatic species either require or facultatively use resources derived from different habitat types in these mosaics, which vary spatially and temporally in response to seasonal, decadal, or episodic changes in environmental conditions (Pickett and Cadenasso 1995; Stanford et al. 2005; Mushet

et al. 2013; Datry et al. 2016). Heterogeneous habitat mosaics depend on exchanges of different types of materials, energy, and organisms across ecosystem boundaries. These exchanges form, in effect, metaecosystems with potential for feedbacks between habitat diversity, biological diversity, and ecosystem function at different spatial and temporal scales (Loreau et al. 2003; Alsterberg et al. 2017).

We first present an overview of biological connectivity (Figure 1; Table 1), in terms of the pathways, modes, purposes, and taxa involved in movements and the key factors that determine the degree and scales (e.g., distances, frequencies, and rates) at which these movements occur. We present examples of biological connections along stream networks and between stream channels and riparian/floodplain and nonfloodplain wetlands (Table 1). We then consider how these connections affect the structure and function of downstream waters, and discuss areas of future research that will provide new insights into the role of biological connectivity in the integrity of freshwater ecosystems.

Although this review is focused on biological connections among freshwater habitats, we recognize that ecologically important biological connections also exist between aquatic habitats and other ecosystems, including terrestrial (Nakano and Murakami 2001; Gibbons 2003; Baxter et al. 2004; Rine et al. 2016) and marine (Schindler et al. 2005; Rine et al. 2016) systems. We also recognize that biological connections affect physical and chemical connections (and vice versa). For example, biota play critical roles in maintaining physical and chemical connections to downstream waters, through their effects on organic matter breakdown (Wallace and Webster 1996), algal productivity and microbial activity (Feminella and Hawkins 1995), sediment mobilization (Hassan et al. 2008; Statzner 2012), and storage, transport, and release of nutrients and contaminants (Krümmel et al. 2003; Walters et al. 2008; Popova et al. 2016). Any comprehensive examination of overall connectivity among these systems must consider physical, chemical, and biological connections, both within FEMs and between FEMs and other ecosystems. For the purposes of this review, however, we focus solely on how the movements of biota create biological connections throughout FEMs.

DESCRIBING BIOLOGICAL CONNECTIONS

How and Why Aquatic Organisms Move

Biological connections result from the active or passive movement of living organisms or their

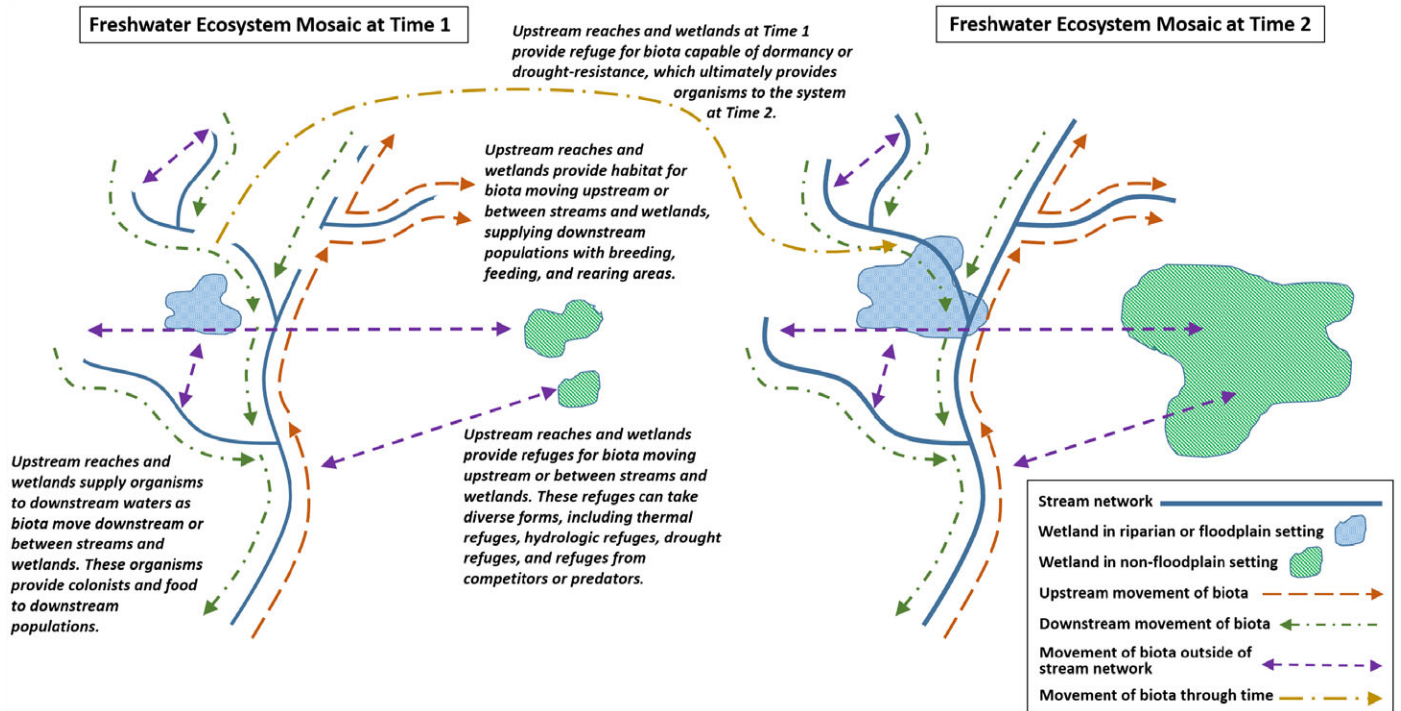


FIGURE 1. Schematic illustrating how upstream reaches, riparian and floodplain wetlands, and nonfloodplain wetlands influence the integrity of downstream waters via movement of aquatic and semiaquatic biota throughout the freshwater ecosystem mosaic, in both space and time. For illustrative purposes, upstream movements are shown on the right side of the stream network; downstream movements are shown on the left side of the stream network. Although not shown in this schematic, these movements can also occur vertically (i.e., to and from the hyporheic zone) and across watershed boundaries. Modified from Meyer et al. (2007).

reproductive materials (e.g., seeds, eggs, genes) through space (e.g., via dispersal or migration) or time (e.g., via dormancy). All aquatic and semiaquatic organisms — including microbes, algae, plants, invertebrates, and vertebrates (Table 1) — move within and among components of the FEM. These movements may occur for multiple reasons, including dispersal (permanent, undirected movement away from an existing population or breeding habitat); migration (periodic, directed movements away from and returning to an existing population or habitat); persistence in time through dormancy (Auffret et al. 2015); or localized movements within and between FEM components that allow organisms to acquire resources (e.g., food, protection from predators, mates) (Smock 1994; Lamoureux and Madison 1999). In some cases, these localized movements may be required, such as when a species obligately uses different habitat types at different life cycle stages (Huryn and Gibbs 1999; Gibbons et al. 2006; Subalusky, Fitzgerald, et al. 2009); in other cases, species may move facultatively within and among habitats throughout their life cycles.

Biological connections are established via multiple pathways (Figure 1; Table 1), and can be measured in several ways. Spatially, these pathways include the passive transport of aquatic and semiaquatic biota by water, wind, or “hitchhiking” on other

organisms, and the active movement of biota through water, over land (for organisms with semiaquatic or terrestrial life stages), or through air (for birds or insects) (Table 1). Key parameters used to quantify or describe biological connections include the *distance* an organism or propagule can move (or *duration*, when considering movement through time); the *frequency* with which these movements occur (e.g., once a generation vs. multiple times over a life span); the *rate* at which these movements occur (e.g., in terms of number of individuals or amount of biomass per unit time); and the *timing* of these movements (e.g., seasonally vs. randomly throughout year).

Even within a single species, organisms often move via more than one pathway (e.g., aquatic invertebrates with flight-capable adults; plants with seeds that can be dispersed by water, wind, and/or animals), and individuals can vary in their movement patterns (e.g., Rasmussen and Belk 2017). For organisms that move only via water, biological connections coincide with hydrologic flowpaths (Fritz et al. 2018; Lane et al. 2018). However, many species are capable of overland movement, via either passive transport or active movement. Overland movements establish important biological connections that can cross both ecosystem and watershed boundaries, even when surface hydrologic flowpaths are disrupted or absent

TABLE 1. Examples of biological connections along stream networks, between stream networks and riparian/floodplain wetlands, and between stream networks, riparian/floodplain wetlands, and nonfloodplain wetlands.

Pathway	Mode of transport	Examples		
		Along stream network	Between stream network and riparian/floodplain wetlands	Between stream network, riparian/floodplain wetlands, and nonfloodplain wetlands
With water	Active	<p><i>Invertebrates</i>: Significant net upstream movement was observed for multiple snail taxa, with individuals moving a maximum of 200 m upstream (Huryn and Denny 1997).</p> <p><i>Fish</i>: Intermittent streams provided rearing habitat for coho salmon, and smolts that overwintered in these streams were larger than smolts that overwintered in perennial streams (Wigington et al. 2006).</p> <p><i>Amphibians</i>: Two stream salamander species tend to move in an upstream direction within the stream network (Grant et al. 2010).</p>	<p><i>Invertebrates</i>: Aquatic invertebrates crawled from headwater stream channels, along stream bottoms and across channel boundaries to forested floodplains (Smock 1994).</p> <p><i>Fish</i>: During the spring flood pulse, spotted gar moved a median distance of roughly 130 m per day among diverse aquatic habitats across the floodplain (Snedden et al. 1999).</p>	<p><i>Invertebrates</i>: Nonflying and flight-capable invertebrates dispersed with equal frequency via pond fill-and-spill through temporary channels or overland flow (Van de Meutter et al. 2006).</p> <p><i>Fish</i>: Fishes dispersed between lakes and seasonal wetlands via transient hydrologic connections (Hohausová et al. 2010).</p>
	Passive	<p><i>Microorganisms</i>: Hydrologic connectivity between high- and low-elevation stream sites increased the incidence of frog infection by a chytrid fungus (Sapsford et al. 2013).</p> <p><i>Algae</i>: Stream corridors provided the primary dispersal pathway for benthic diatoms (Dong et al. 2016).</p> <p><i>Plants</i>: Downstream dispersal along stream networks influenced the structure of forest plant communities, even for plants not adapted for water dispersal of seeds (Honnay et al. 2001).</p> <p><i>Invertebrates</i>: 167 aquatic invertebrate taxa were collected in springtime drift samples, at total drift densities of 0.26–26.04 m⁻³ day⁻¹ (Pond et al. 2016).</p> <p><i>Fish</i>: Eggs of pelagic-spawning prairie fishes were estimated to be transported up to 177 km downstream before hatching (Platania and Altenbach 1998).</p>	<p><i>Algae</i>: Floodplain habitat contributed to fourfold increases in phytoplankton biomass and higher percentages of diatoms and green algae (Lehman et al. 2008).</p> <p><i>Plants</i>: Dispersal of riparian plant seeds by water resulted in a 36%–58% increase in the pool of plant species colonizing flooded riparian areas (Jansson et al. 2005).</p> <p><i>Invertebrates</i>: Aquatic invertebrates drifted with waterflow from headwater stream channels to forested floodplains (Smock 1994).</p>	<p><i>Plants</i>: For two wetland plant species that disperse via both wind and water, water dispersal results in the transport of more seeds over longer distances (Soomers et al. 2013).</p> <p><i>Invertebrates</i>: Genetic analyses of an invasive aquatic snail species indicated that the snail disperses readily via water throughout flooded rice fields (Van Leeuwen et al. 2013).</p>
Over land	Active	<p><i>Invertebrates</i>: Adults of 15 caddisfly species (out of 26 species considered) flew at least 1.5 km away (the farthest distance evaluated in the study) from permanent water (Graham et al. 2017).</p> <p><i>Amphibians</i>: Two stream salamander species move over land between adjacent headwater streams (Grant et al. 2010).</p> <p><i>Reptiles</i>: Reptiles moved both upstream and downstream</p>	<p><i>Reptiles</i>: Two turtle species used a variety of aquatic and terrestrial habitats throughout a river floodplain, with 95% of population movements occurring within a riparian zone 449 m from the river (Bodie and Semlitsch 2000).</p> <p><i>Mammals</i>: River otters use a variety of aquatic habitats, including streams and rivers, wetlands, and open waters (Newman and Griffin 1994).</p>	<p><i>Amphibians</i>: Columbia spotted frogs occupy widely distributed wetlands in summer, then migrate over land to deeper lakes to overwinter (Pilliod et al. 2002).</p> <p><i>Reptiles</i>: American alligators use hydrologically isolated seasonal wetlands for nesting and nursery habitat and riverine systems for nonnesting habitat (Subalusky, Fitzgerald, et al. 2009).</p> <p><i>Mammals</i>: Translocated river otters ranged from 1.2 to 54.0 km,</p>

(continued)

TABLE 1. (continued)

Pathway	Mode of transport	Examples		
		Along stream network	Between stream network and riparian/floodplain wetlands	Between stream network, riparian/floodplain wetlands, and nonfloodplain wetlands
In air	Active	along dry riverbeds (Sánchez-Montoya et al. 2016). <i>Mammals</i> : Mammals moved both upstream and downstream along dry riverbeds (Sánchez-Montoya et al. 2016).		from riverine habitats to isolated aquatic habitats throughout the landscape (Spinola et al. 2008).
	Passive	<i>Invertebrates</i> : Up to roughly one-half of an adult mayfly population flew upstream along the stream network upon emergence (Hershey et al. 1993).	<i>Invertebrates</i> : Stream insects and noninsect invertebrates aeriually colonized temporary floodplain aquatic habitats (Tronstad et al. 2007). <i>Birds</i> : The Rocky Mountain population of sandhill cranes overwinters and breeds in both riverine and wetland habitats (Pacific Flyway Council and Central Flyway Council 2016).	<i>Invertebrates</i> : Numerous flight-capable insects use both streams and nonfloodplain wetlands (Williams 1996). <i>Birds</i> : Abundance of migratory waterbirds was positively related to the area of semipermanent wetlands within 10 km of each study wetland (Webb et al. 2010).
With other organisms	Active	<i>Microorganisms</i> : At least 30 viable taxa of protozoans have been sampled atmospherically (Schlichting 1969). <i>Algae</i> : At least 150 viable taxa of algae have been sampled atmospherically (Schlichting 1969).	<i>Plants</i> : Many wetland plant species adapted to wind dispersal (37%–46% of all species) are found in wetlands that rely on rainwater and groundwater inputs (Soons 2006).	<i>Plants</i> : Wind-dispersed wetland plant species made up 45%–50% of all species in more terrestrial wetland types (Soons 2006). <i>Invertebrates</i> : 7 of 51 rotifer species and 5 of 25 microcrustacean species that colonized temporary pond habitats only reached those ponds via airborne dispersal (Lopes et al. 2016).
	Passive	<i>Algae</i> : Numerous diatom genera (including the nuisance species <i>Didymosphenia geminata</i>) were found on the fur of minks surveyed in two Patagonian streams (Leone et al. 2014). <i>Plants</i> : Via consumption, internal transport, and egestion, fish provided a means for upstream dispersal of the seeds they consume (Horn 1997). <i>Invertebrates</i> : The distribution of unionid freshwater mussels was determined by distribution of the mussels' host fishes, which they rely on for dispersal (Schwalb et al. 2013).	<i>Microorganisms</i> : Up to 19 genera of protozoans were found on insects collected from ponds, including insects known to frequent streams (Stewart and Schlichting 1966). <i>Algae</i> : Up to 25 genera of algae were found on insects collected from ponds, including insects known to frequent streams (Stewart and Schlichting 1966). <i>Plants</i> : Common carp consume and egest viable unbranched bur-reed seeds, creating the potential to internally transport seeds up to 27 km (Pollux et al. 2007).	<i>Microorganisms</i> : Approximately 15% of 397 wild geese screened for a chytrid fungus were found to carry the fungus on their feet (Garmyn et al. 2012). <i>Plants</i> : Approximately 7% of seeds ingested by ducks remained viable after passing through their digestive tracts, making it possible for ducks to internally transport wetland plant seeds up to 1,400 km (Mueller and van der Valk 2002). <i>Invertebrates</i> : Waterbird movements across North America contributed significantly to gene flow among cladoceran and bryozoan populations (Figuerola et al. 2005).

Note: Examples are presented in terms of the pathways by which organisms move (with water, over land, in air, or “hitchhiking” on other organisms), mode of transport (active or passive), and type of organism. We present only one example per category, although in many cases numerous examples have been documented.

(Figure 1) (Hughes et al. 2009). Species also may create biological connections within and among FEM components through time, via dormancy or drying-resistant stages (Figure 1).

The variety of movements that organisms undertake reflects the multitude of life history strategies (and their inherent tradeoffs; Stearns 1989) that species have evolved to optimize survival and reproductive

fitness within FEMs. These movements allow organisms to recolonize habitats, avoid inbreeding, escape biotic or abiotic stressors, locate mates, and acquire the resources needed to survive and reproduce. They also connect populations and communities throughout the FEM and contribute to species persistence and resilience to disturbance and environmental change (Labbe and Fausch 2000; Fagan 2002; Bohonak and Jenkins 2003).

Cumulatively, these movements enhance and sustain biodiversity at all levels of biological organization, from genes to ecosystems. Dispersal and migration contribute to population and species persistence through the maintenance of genetic diversity (e.g., Waples 2010); location of mates and breeding habitats (Semlitsch 2008); rescue of small populations threatened with local extinction (Brown and Kodric-Brown 1977); and colonization of new habitats (e.g., Hecnar and McLoskey 1996; Tronstad et al. 2007). The functions of dispersal (e.g., to avoid kin competition, limit inbreeding, colonize new habitat patches) are also determinants of the distance over which an organism will actually move, which has consequences for local and regional aquatic biodiversity (Duputié and Massol 2013). Thus, these movements, and the biological connections they establish, are critical to the structure and function of aquatic ecosystems (Bornette et al. 1998; Steiger et al. 2005; Meyer et al. 2007).

Biological connectivity occurs along spatial and temporal gradients, from highly isolated habitats with relatively little or no movement of biota into or out of the system to highly connected habitats with extensive movement of biota into and out of the system, and all conditions between these extremes. These gradients of connectivity are important for maintaining ecosystem integrity, as different types and scales of movement can have unique effects. For example, mass river insect migrations into headwater streams provide food subsidies to support young-of-year fish (Uno and Power 2015), including diadromous salmon (Bramblett et al. 2002). On the other hand, lower rates of movement between more isolated habitats can decrease the spread of pathogens (e.g., Hess 1996) and invasive species (e.g., Bodamer and Bossenbroek 2008) and increase regional genetic diversity through local adaptation (e.g., Fraser et al. 2011).

Key Factors That Affect Biotic Movements

Key factors affecting the movement of biota through FEMs include: (1) climate and other environmental conditions that determine the distribution, relative abundance, and quality of aquatic habitats

within the FEM; (2) physical features that facilitate or impede the movement of species between aquatic habitats; and (3) traits and behaviors of the species present in the system. These factors are not independent of each other, and interact in complex ways. For example, even though passively dispersing organisms can control the timing of their movements to some extent, passive dispersal tends to be riskier than active dispersal when there is unsuitable intervening habitat (Bonte et al. 2012). Each factor also can be altered by human activities that enhance or restrict biological connections (Crook et al. 2015). Some human activities create physical features that impede movement (e.g., by damming stream networks); other activities may create physical features that facilitate movement (e.g., by creating drainage ditches from wetlands to streams).

For biota that move only in water, any factors that influence water storage and flowpaths (i.e., hydrologic connections; Leibowitz et al. 2018) also will influence biological connections. Climate is a key determinant of hydrologic connectivity, as well as the relative size, density, and spatial arrangement of FEM components. In physiographic regions such as formerly glaciated portions of North America's Great Plains Ecoregion, seasonal or longer term climate cycles have dramatic effects on surface water storage and flowpaths, and thus on resources available to aquatic biota (Figure 2; Vanderhoof et al. 2016). Hydrologic connections are enhanced in wet years, and distances between habitat components decrease; in dry years, these hydrologic connections are diminished and habitat components are farther apart.

These types of cycles result in flood pulse dynamics (Junk et al. 1989); wetland fill-and-spill dynamics (Tromp-van Meerveld and McDonnell 2006; Shaw et al. 2013); wetland-lake-stream fill-and-merge dynamics (Leibowitz et al. 2016; Vanderhoof and Alexander 2016; Vanderhoof et al. 2016); and high-volume stormflows in arid streams (Stanley et al. 1997; Goodrich et al. 2018). For example, drought-to-deluge climate cycles dramatically affect stream and wetland densities in the Prairie Pothole Region (Vanderhoof et al. 2016). Movements of biota throughout FEMs in response to these spatial or temporal changes in the number, extent, arrangement, and quality of the component aquatic habitats are thus highly variable in both space and time (Figure 1), and reflect the strong selection pressure these dynamics exert on aquatic species (Grant 2011; Mushet et al. 2013).

Physical barriers between different aquatic habitats, such as steep gradients, waterfalls, mountain ranges, dams, or intervening inhospitable habitats, can restrict movements needed to establish or

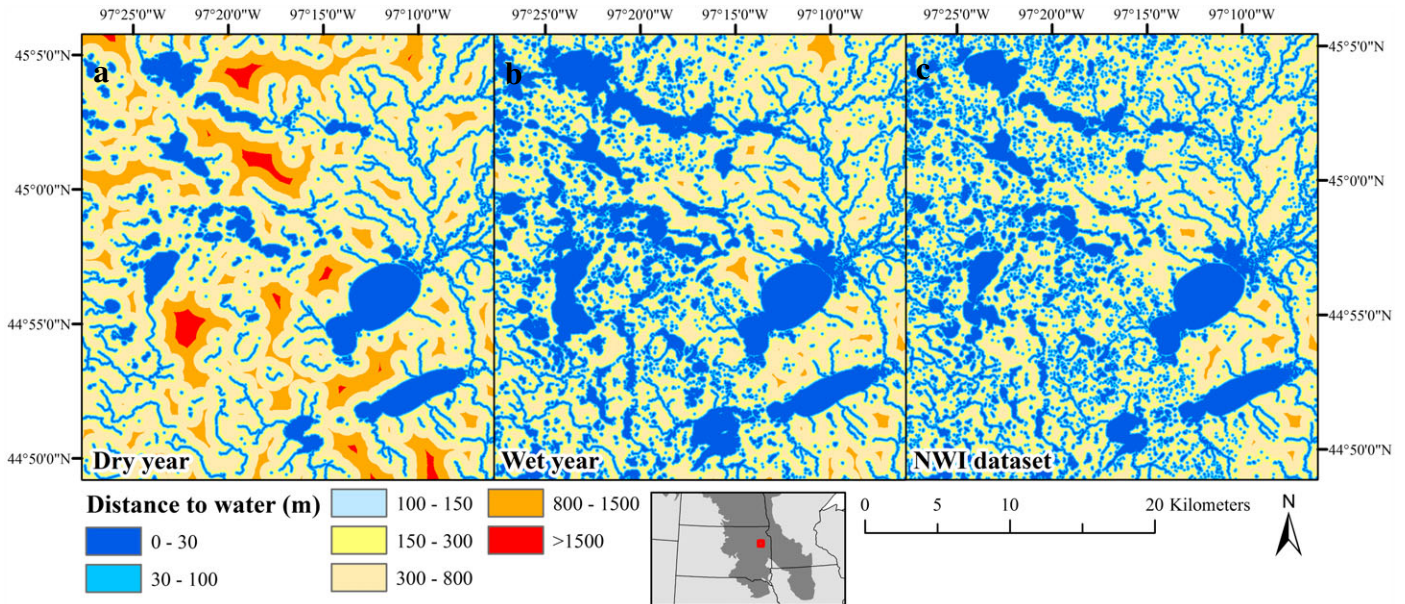


FIGURE 2. Euclidean distance to nearest water changes depending on how and when wetland/lake extent is defined. Euclidean distance to nearest water using: (a) wetland/lake extent during a dry year (1990, day of year 130), as defined by Landsat imagery; (b) wetland/lake extent during a wet year (2011, day of year 156), as defined by Landsat imagery; and (c) wetland/lake extent, as defined by the National Wetlands Inventory (NWI) dataset, included here for reference.

maintain biological connectivity (e.g., Greathouse et al. 2006; Hanfling and Weetman 2006; Hall et al. 2011). When all other factors (e.g., climate, topography, geology) are equal, large, high-quality aquatic habitats separated by shorter distances are more likely to be biologically connected, due to greater carrying capacity and lower costs associated with movement (MacArthur and Wilson 1967; Hanski 1999). During dry years, organisms moving between aquatic habitats must traverse greater distances via aerial or overland movement (Figure 2). Greater spatial distance between suitable habitats may increase the number and variety of intervening landscape patches through which organisms must move, decreasing the probability of traversing them successfully (Bonte et al. 2012). Mortality due to predators or natural hazards (e.g., adverse environmental conditions) generally increases with the distance an organism must travel to reach another habitat (Bowler and Benton 2009).

Ultimately, biological connections depend on the biota present in the system. The physical structure of the FEM determines the system's structural connectivity; the species present (or potentially present) determine how structural connectivity is translated into actual or functional connectivity (Calabrese and Fagan 2004; Wainwright et al. 2011). Species traits and individual behaviors, such as dispersal mode, dispersal propensity, life cycle requirements, and responses to disturbance or environmental cues, arise

over time in response to abiotic and biotic selection pressures. In turn, these determine why, when, how, and how far organisms move throughout the FEM — and thus the potential for biological connectivity.

BIOLOGICAL CONNECTIVITY THROUGHOUT FEMs

The establishment of biological connections throughout a FEM depends on the movement of living organisms (or their propagules) between the discrete habitats that the FEM comprises. These movements can occur longitudinally, along stream networks; laterally, between stream networks, riparian/floodplain wetlands, and nonfloodplain wetlands; vertically, between streams and wetlands and their hyporheic zones; or through time (Ward 1989). Although vertical and temporal movements can have important effects on aquatic ecosystems (Hairston 1996; Stubbington 2012; Vander Vorste et al. 2016), we focus here on longitudinal and lateral connections that directly or indirectly (e.g., through “stepping-stone” movements) affect downstream waters.

In the following sections, we summarize evidence that demonstrates how and why biota move along stream networks and between stream networks and wetlands. We provide specific examples illustrating

the different pathways, modes of transport, and types of organisms involved in Table 1. In Figures 3 through 6, we illustrate biological connections with example organisms, using the visual framework laid out in Figure 1.

Movement of Biota Along Stream Networks

Biological connections are clearly evident along stream networks, as organisms travel downstream with the flow of water. A diverse collection of organisms (e.g., microbes, algae, aquatic invertebrates, fishes) are passively transported or actively move downstream along hydrologically connected stream channels (Table 1). These movements establish biological connections between upstream habitats and downstream waters.

Many aquatic and semiaquatic species inhabit headwater streams (Meyer et al. 2007). These species are often found throughout a range of stream sizes (Hall et al. 2001; Freeman et al. 2007) and flow durations (Schlosser 1987; Feminella 1996; Labbe and Fausch 2000), and move into and out of headwater

streams at different points in their life cycles (Horwitz 1978; Ebersole et al. 2006; Meyer et al. 2007). For certain taxa, headwater streams — including intermittent and ephemeral streams — support highly diverse communities (e.g., Besemer et al. 2013) and provide critical habitat at one or more stages of their life cycles (Koizumi et al. 2017; Woelfle-Erskine et al. 2017).

The use of headwater streams as habitat is especially evident for diadromous species that migrate between headwater streams and marine environments during their life cycles, such as Pacific and Atlantic salmon, American eels, and certain neotropical shrimps (Figure 3). Many of these taxa are either obligate or facultative users of headwater streams (Erman and Hawthorne 1976; Ebersole et al. 2006; Wigington et al. 2006; Hitt et al. 2012), but over their life cycles they travel the entire length of the river network. Thus, the presence of diadromous taxa provides robust evidence of biological connections along stream networks.

Biological connections are not reliant on diadromy, however, as nondiadromous organisms are also capable of significant movement along river networks.

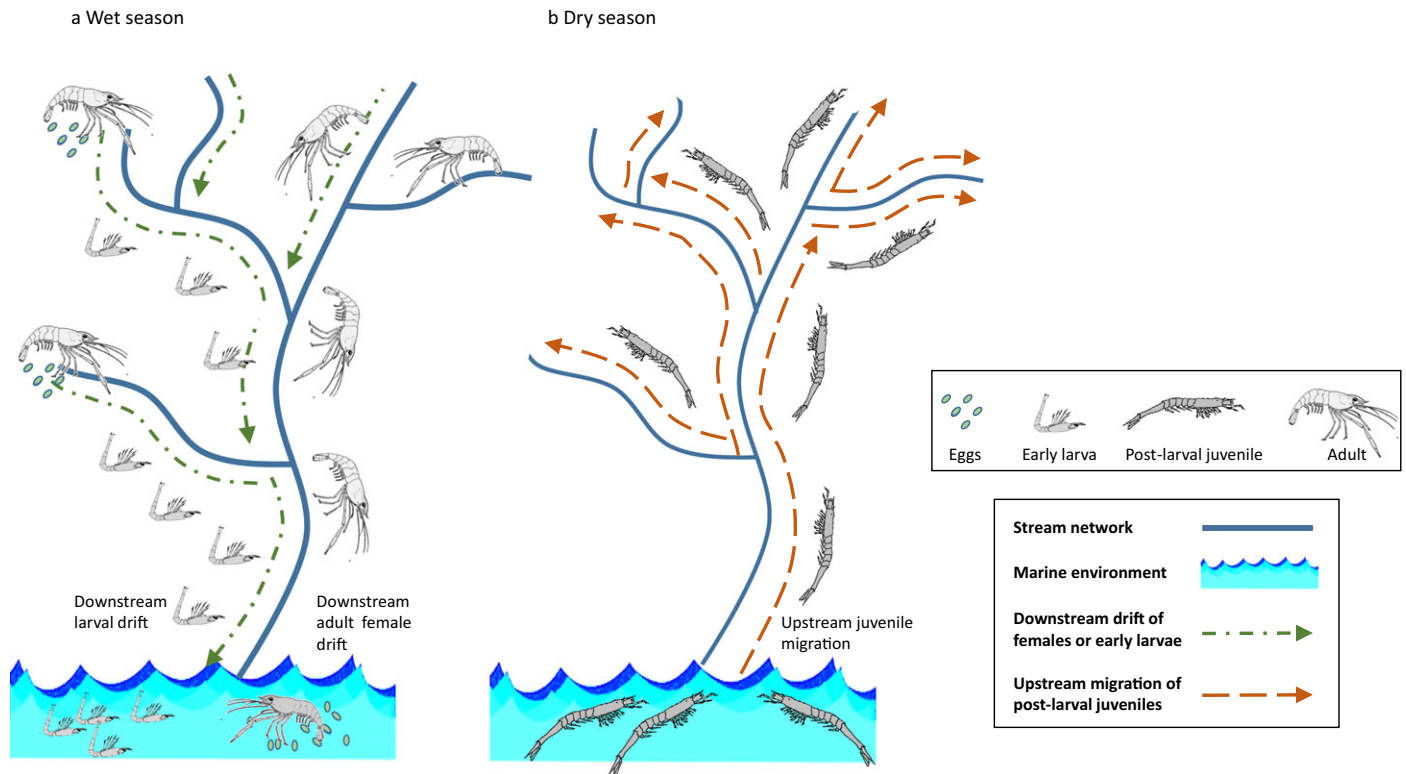


FIGURE 3. Migration of freshwater shrimps (modified from Bauer 2013). Caridean shrimps are found on every continent except Antarctica, move actively and passively within and between diverse habitats, and are important food sources for other aquatic organisms. Some caridean shrimps are commercially valuable, and many are amphidromous. (a) Biological connections during the wet season. In many amphidromous species, adult females spawn in streams and early-stage larvae drift downstream to develop in marine waters. In other species, adult females drift downstream to spawn in marine environments. (b) Biological connections during the dry season. Post-larval juveniles migrate back upstream to mature in freshwater habitats.

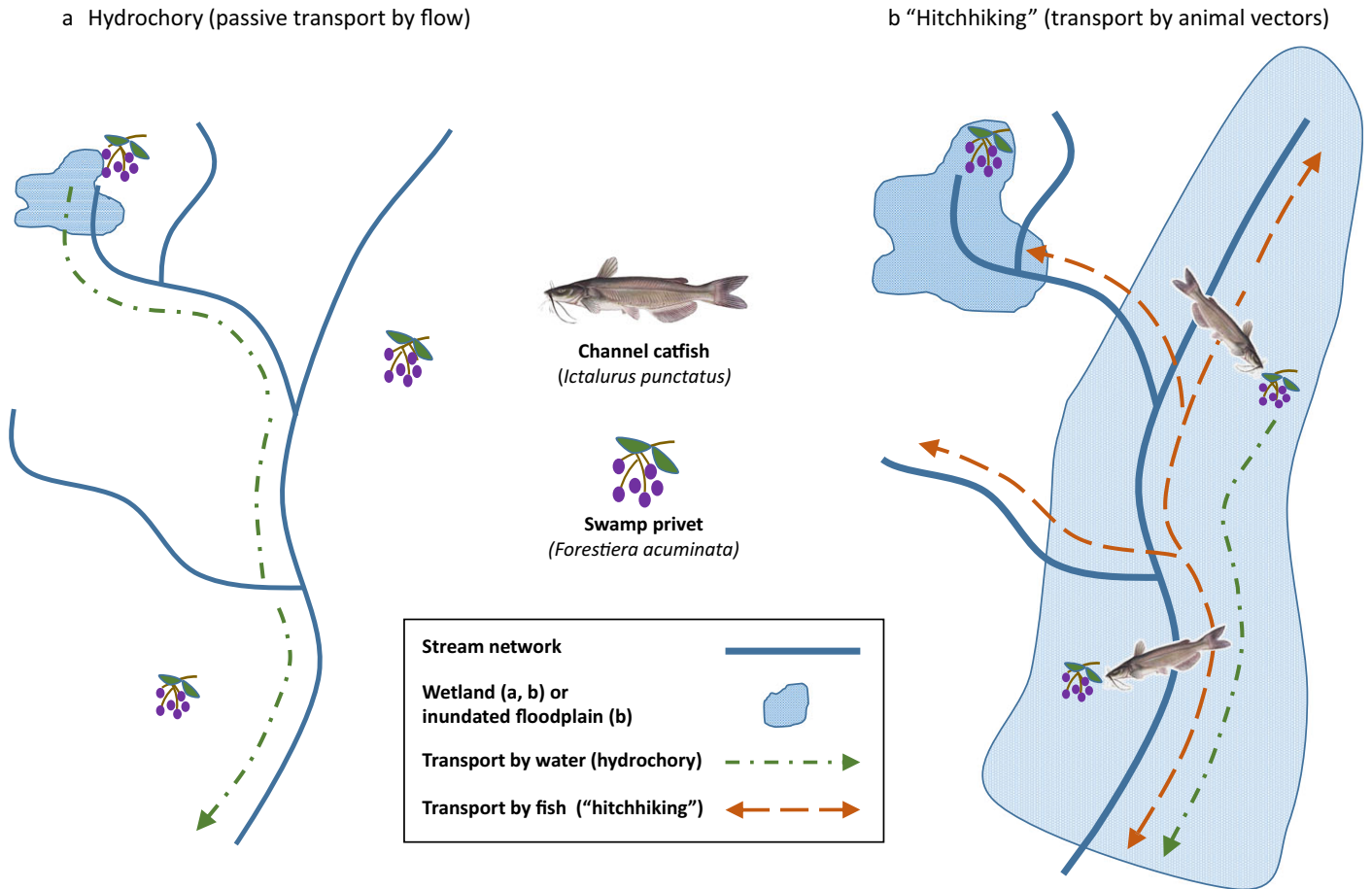
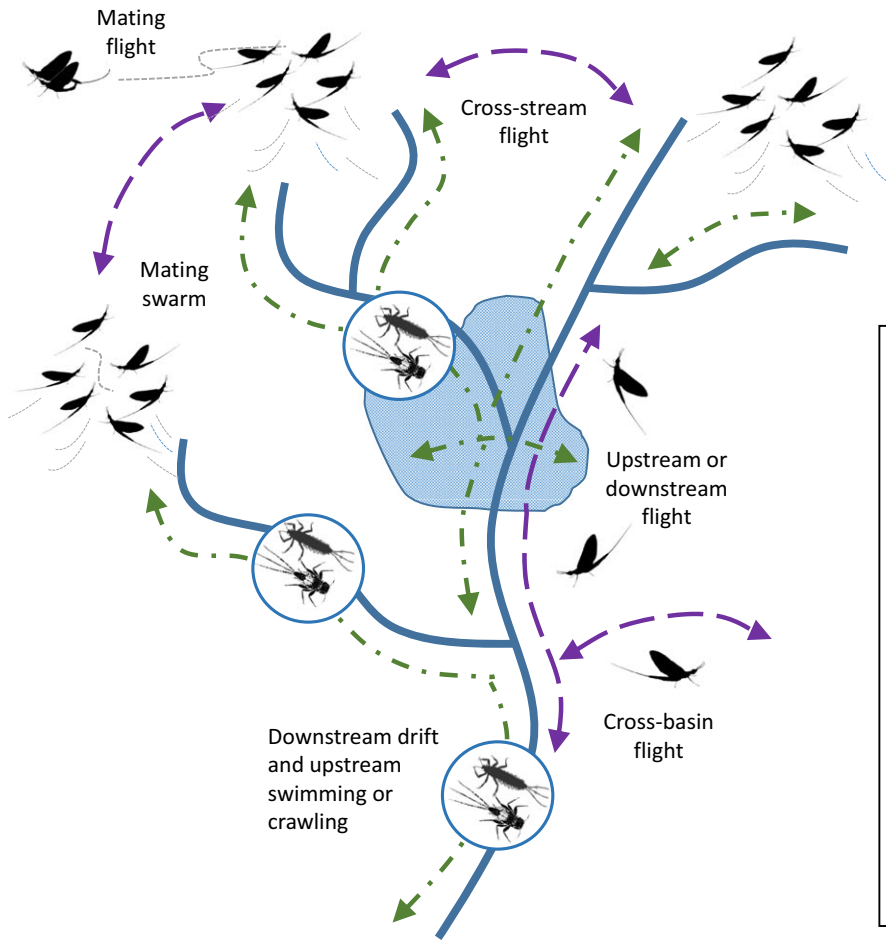


FIGURE 4. Aquatic plant dispersal via hydrochory and "hitchhiking." Aquatic plants can disperse passively by wind or moving water, actively by animal vectors, or both. (a) Streamflow carries propagules — here, mature fruits of swamp privets — from headwater wetlands to downstream wetlands, where seeds settle and germinate (Nilsson et al. 2010). (b) Plants can also disperse by "hitchhiking" on animal vectors. Here, frugivorous channel catfish move into seasonally inundated floodplains to feed on mature fruits of off-channel swamp privets (Chick et al. 2003). Dispersal is accomplished by transport, excretion, and germination of viable seeds in habitats throughout the river-floodplain network.

Many fishes require different habitats during different life stages, and move significant distances both upstream and downstream throughout their life cycles (e.g., Gorman 1986; Labbe and Fausch 2000; Hitt and Angermeier 2008; Falke et al. 2010; Kanno et al. 2014). For example, Schrank and Rahel (2004) found that Bonneville cutthroat trout moved from <1 to more than 80 km after spawning. Many fish spawn in headwater streams, including those with intermittent flow (Erman and Hawthorne 1976; Schrank and Rahel 2004; Ebersole et al. 2006). For example, Wigington et al. (2006) found that intermittent streams were an important source of coho salmon smolts in Oregon, where juveniles survived dry periods in residual pools located within intermittent stream channels. Many salmonids also rear in headwater streams (Brown and Hartman 1988; Curry et al. 1997; Bramblett et al. 2002), and these habitats can provide higher quality habitat for juvenile fish, as evidenced by increased growth, size, and overwinter

survival in these habitats (Ebersole et al. 2006; Ebersole et al. 2009). Coho salmon smolts that overwintered in intermittent Oregon streams were larger than those from perennial streams (Wigington et al. 2006). Fishes also can transport other organisms (e.g., seeds, pathogens, glochidia), carrying them against flow or extending their dispersal distances (e.g., Chick et al. 2003; Senderovich et al. 2010; Schwalb et al. 2013) as they move through stream networks (Figure 4). For example, Schwalb et al. (2011) estimated that host fishes could disperse freshwater mussel larvae from 8 to 1,645 km, depending on host fish species.

Prairie fishes provide another clear demonstration of biological connections along the river network. Many prairie fishes release their eggs into the water column, and eggs develop as they are transported downstream with water flow (Fausch and Bestgen 1997; Platania and Altenbach 1998; Durham and Wilde 2006). When unimpeded (e.g., by dams),



Adult male mayfly (*Ephemera invaria*)

Stream network	
Wetland in floodplain	
Aquatic movement	
Aerial movement (active flight)	
Mayfly nymphs (aquatic)	
Mayfly adult (terrestrial)	
Mayfly mating swarm (terrestrial; females return to waters to oviposit)	

FIGURE 5. Movements associated with the aquatic and terrestrial life stages of a mayfly. Mayflies are found in freshwater and brackish habitats on all continents except Antarctica, and are important food sources for a wide range of aquatic and terrestrial organisms. Despite a reputation as “weak” fliers, mayflies can disperse over very long distances (up to 700 km; Sartori and Brittain 2015). Mayfly nymphs are relatively long-lived (typically up to a year) and fully aquatic. They swim, crawl, or drift in streamflow to find food and shelter, avoid predators, escape unfavorable conditions, and colonize new underwater habitats (green dot-dashed lines). In contrast, adult mayflies are short-lived (typically 24–48 h) and fully terrestrial. Adult mayflies move actively to disperse, reproduce, and oviposit in streams or wetlands (purple dashed lines).

downstream transport of these drifting eggs and larvae can be extensive (e.g., more than 350 km; Platania and Altenbach 1998). Adult fishes, which are capable of long-distance migrations, then move upstream prior to egg release (Fausch and Bestgen 1997; Durham and Wilde 2006). Maintenance of prairie fish populations thus depends on these bidirectional biological connections along river networks (Fausch and Bestgen 1997; Durham and Wilde 2006). Pelagic-spawning mussels create similar biological connections along stream networks, via downstream drift and upstream movement attached to host fishes (Schwalb et al. 2010).

Headwater streams also provide habitat for diverse and abundant stream invertebrates (Meyer et al. 2007) and serve as collection areas for terrestrial and riparian invertebrates that fall into them (Kawaguchi and Nakano 2001; Eberle and Stanford 2010). These

aquatic and terrestrial invertebrates can be transported downstream with water flow (Figures 3 and 5) (Elliott 1971; Müller 1982; Brittain and Eikeland 1988; Reynolds et al. 2014). Cumulatively, export of invertebrates from numerous headwater streams within a single network to downstream waters can be substantial (Wipfli and Gregovich 2002), especially in intermittent and ephemeral streams, as terrestrial invertebrates accumulate in these channels during dry periods and are then transported downstream upon channel rewetting (Corti and Datry 2012; Rosado et al. 2015).

To compensate for loss of individuals to downstream drift, invertebrate populations in headwater streams are maintained and replenished through processes such as high productivity and upstream dispersal (Figures 3 and 5) (Hershey et al. 1993; Humphries and Ruxton 2002). For organisms capable

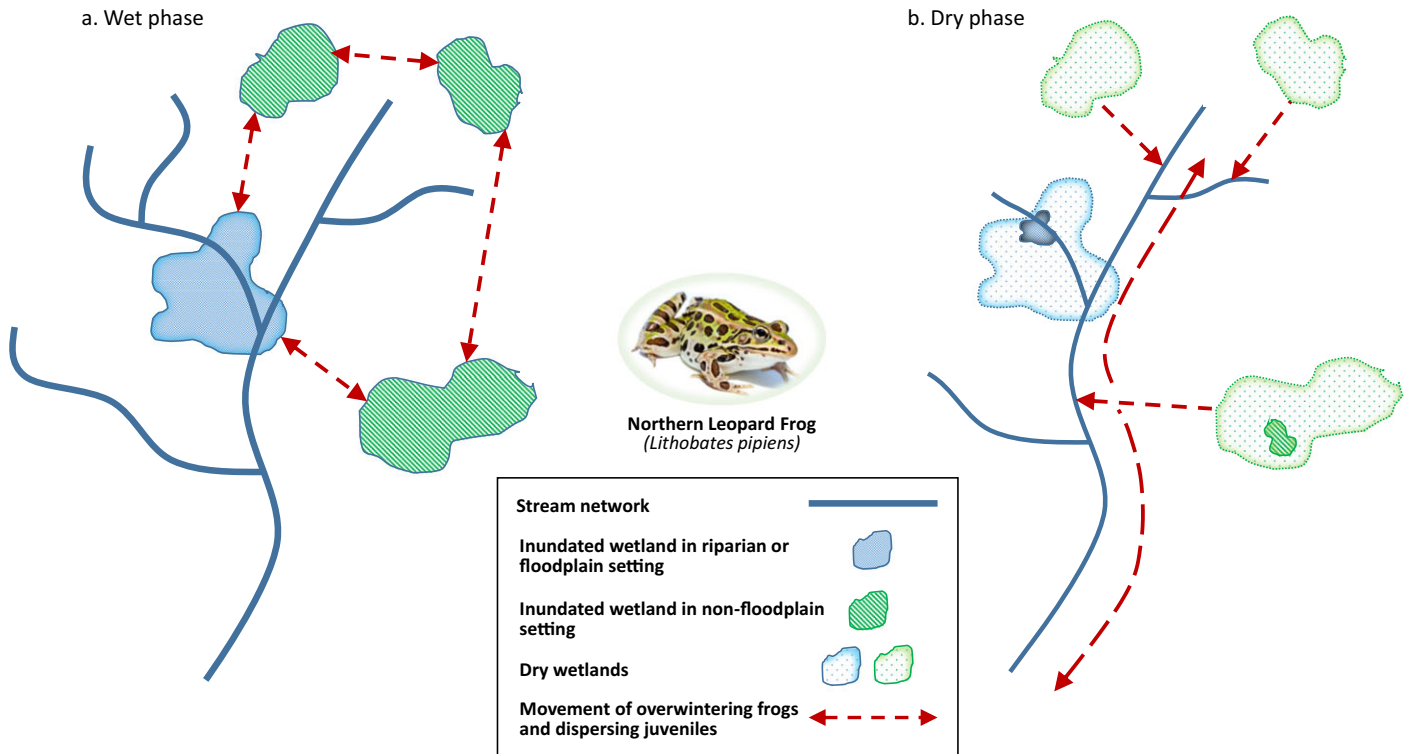


FIGURE 6. Habitat complementarity in amphibians. Amphibians (frogs, salamanders, and caecilians) are globally distributed except in Antarctica and Greenland, with particularly high concentrations in neotropical regions. Adults often inhabit terrestrial habitats but require moist environments; eggs must be deposited in water and immature stages are often fully aquatic. Northeastern populations of the northern leopard frog (NLF) exhibit uncharacteristically high levels of genetic diversity, which has been attributed to large stable populations inhabiting landscapes with high densities of wetlands (a). Under drought conditions, NLFs move into streams, then disperse rapidly to recolonize wetlands when drought conditions end (b) (Mushet et al. 2013). Because NLFs are not freeze-tolerant, they move into deep wetlands or flowing water to survive harsh northern winters.

of directed movement over long distances (e.g., winged adult forms of aquatic insects), these downstream-to-upstream connections can occur over significant network distances. In addition, these connections are often not dependent on hydrologic connections (Figure 5). Upstream and downstream movements along, but not necessarily within, streams (e.g., dispersal over land or aurally) further strengthen linkages between upstream habitats and downstream waters (Grant et al. 2010). For example, dry stream channels can serve as dispersal corridors for terrestrial adult forms (Bogan and Boersma 2012; Steward et al. 2012), and stream networks can create transportation corridors for terrestrial and semi-aquatic fauna (Sánchez-Montoya et al. 2016; Goodrich et al. 2018).

Movement of Biota between Stream Networks and Wetlands

In addition to the longitudinal connections described above, biota also create lateral connections throughout FEMs as organisms move from the river

network into riparian/floodplain and nonfloodplain wetlands (Figure 1). These movements occur via the same pathways as longitudinal movements (Table 1), although the relative importance of different pathways may vary. Hydrologic connections between stream networks and wetlands are typically more variable than hydrologic connections between upstream and downstream areas of stream networks, particularly in perennially flowing systems. Nonfloodplain wetlands are generally more spatially distant from (and thus typically less hydrologically connected to) stream channels than riparian/floodplain wetlands, and may lack even intermittent surface water connections. As a result, movements via nonwater pathways tend to increase in prevalence and importance for these lateral connections.

Research has clearly demonstrated that organisms move laterally between river networks and wetlands, thereby establishing biological connections throughout FEMs. Wetlands support diverse communities of aquatic, amphibious, and terrestrial plant and animal species, which are adapted to the periodic or episodic inundation of these habitats (Galat et al. 1998; Robinson et al. 2002; Rooney et al. 2013; Granado

and Henry 2014). Adaptations of stream-dwelling organisms to variable moisture conditions, as well as their ability to rapidly disperse and exploit temporary or seasonal hydrologic connections, provide strong evidence that biological connections exist between rivers and other aquatic habitats over relatively long time frames.

When overbank flow causes rivers to expand laterally, surface hydrologic connections between the river network and adjacent wetland habitats are created (Figures 1 and 4) (Junk et al. 1989). Aquatic biota can move into these newly flooded wetland habitats (Junk et al. 1989; Smock 1994; Tockner et al. 2000; Robinson et al. 2002; Tronstad et al. 2007), and then eventually return to the river network when flooding recedes (Copp 1989; Smock 1994; Richardson et al. 2005). In unregulated rivers, floodplain inundation greatly increases the area and diversity of aquatic habitats, and these habitats often have high primary productivity (Junk et al. 1989; Tockner et al. 1999; Tockner et al. 2000; Brooks and Serfass 2013). As a result, floodplains are important habitats for fish (Copp 1989; Snedden et al. 1999; Bestgen et al. 2000; Schramm and Eggleton 2006; Alford and Walker 2013), aquatic life stages of amphibians (Richardson et al. 2005), and aquatic invertebrates (Smock et al. 1992; Smock 1994).

There is abundant evidence that fishes move between the main river channel and wetlands when these habitats are hydrologically connected (Table 1). Many fish species disperse into riparian/floodplain wetlands to feed, reproduce, rear young, and seek refuge from harsh conditions (e.g., Copp 1989; Mathe-ney and Rabeni 1995; King et al. 2003; Crook and Gillanders 2006; Pease et al. 2006; Henning et al. 2007; Jeffres et al. 2008; Zeug et al. 2009; Burgess et al. 2013). Fishes can also carry other organisms with them as they move. For example, channel catfish that move into seasonally inundated floodplains can consume and transport viable swamp privet seeds to downstream floodplains (Figure 4) (Chick et al. 2003).

Oxbow lakes can be important fish feeding and rearing habitats (Baranyi et al. 2002; Zeug et al. 2005; Shoup and Wahl 2009; Zeug et al. 2009). For example, isotopic analysis of gizzard shad in the Brazos River, Texas, showed that isotopic signatures of both juvenile and adult fish varied between main channel and oxbow habitats (Zeug et al. 2009). The isotopic signatures of adult fish were more variable in oxbows, indicating that these individuals fed in main channel vs. oxbow habitats to varying degrees (Zeug et al. 2009). Fish also move between lacustrine wetlands (wetlands associated with lakes) and large lakes when hydrologic connections exist (Jude and Pappas 1992; Miyazono et al. 2010).

The presence of fish in nonfloodplain wetlands clearly demonstrates that these wetlands are biologically as well as hydrologically connected to other waters, even if those hydrologic connections are intermittent. For example, fish were present in 21% of 63 Carolina bays surveyed, even though many of the bays dried out during part of the year. Fish travelled up to 4 km from a Florida lake into seasonal wetlands, eventually colonizing 9 of the 25 temporary habitats sampled (Hohausová et al. 2010). If non-floodplain wetlands are periodically connected to other aquatic habitats by surficial water flows, fish, other swimming organisms, and organisms transported by flowing water (e.g., invertebrates, seeds) can move into nonfloodplain wetlands via hydrologic connections (Baber et al. 2002; Hulsmans et al. 2007; Herwig et al. 2010).

Stream invertebrates (e.g., insects, crayfish, mussels, cladocerans, copepods, rotifers, and gastropods) also move into wetlands during seasonal or episodic periods of hydrologic connectivity (Junk et al. 1989; Ilg et al. 2008). Even in small headwater streams, thousands of invertebrates can drift or crawl between streams and riparian wetlands per day (Smock 1994). Many invertebrate species have evolved life history strategies to exploit these habitats, such as the ability to rapidly colonize newly flooded areas, short life cycles that allow them to complete their life cycles before floodplains dry again, and the use of aquatic refuges or dormant life stages to persist (sometimes for many years) until wetlands are re-inundated (Tronstad et al. 2007).

Biological connections are also established by organisms typically thought of as less mobile. Primary producers, including phytoplankton and aquatic and emergent plants, are capable of moving between the river network and wetlands, as seeds, plant fragments, and whole organisms are transported back and forth between these habitats via multiple pathways (Table 1; Figure 4) (e.g., Barrat-Segretain 1996; Middleton 2000; Soons 2006; Angeler et al. 2010; Nilsson et al. 2010). Seeds from vegetation within the channel or from upstream wetlands can be transported with water flow and deposited on bordering or downstream riparian areas and floodplains (Gurnell 2007; Boudell and Stromberg 2008; Gurnell et al. 2008; Nilsson et al. 2010). Lateral expansion of the river network can dislodge viable plant fragments in riparian/floodplain wetlands, which can then be transported down the river network and reestablish in downstream waters (e.g., Truscott et al. 2006).

As the examples above illustrate, hydrologic connections establish multiple biological connections. Biological connections do not require hydrologic connections, however. Particularly for habitats that are less

frequently connected via surface water flowpaths (e.g., nonfloodplain wetlands), biological connections often depend on nonwater-mediated movements of biota. Aquatic and semiaquatic species have evolved numerous strategies to survive and thrive in landscapes that often lack surface hydrologic connections (Bohonak and Jenkins 2003). Although movements via crawling, flying, wind, "hitchhiking," and dormancy can be cryptic, sporadic, or asymmetric, and thus difficult to observe directly, these connections are common (Table 1).

Many aquatic species require or facultatively use resources in more than one habitat type to complete their life cycles or to persist when preferred habitats are scarce (Figure 6) (Skagen and Knopf 1993; Ribera 2008; Mushet et al. 2013). Numerous flight-capable insects, including mayflies, caddisflies, diving beetles, backswimmers, whirligig beetles, water striders, water boatmen, scavenger beetles, crane flies, and nonbiting midges, use both streams and nonfloodplain wetlands (Williams 1996). In a survey of 150 aquatic insect species in the orders Coleoptera (beetles) and Hemiptera (true bugs) in perennial stream pools, cattle troughs, and seasonal ponds, Bogan et al. (2013) reported that 46 species (31%) were generalists occurring in at least two of the three habitats sampled. Many nonfloodplain wetlands (e.g., western vernal pools, Carolina and Delmarva bays) support generalist invertebrate and amphibian species that also inhabit streams, lakes, or riparian/floodplain wetlands (Hudson et al. 1990; Leeper and Taylor 1998; Zedler 2003). Observations that nonfloodplain wetlands such as prairie potholes often lack endemic biota (i.e., biota restricted to a small geographic area) suggest that these habitats are not isolated over sufficiently long time frames to allow local speciation, and thus have been or currently are biologically connected to other aquatic habitats (van der Valk and Pederson 2003).

Seeds and invertebrates can be passively dispersed among nonfloodplain wetlands by wind (Galatowitsch and van der Valk 1996). This pathway can be particularly important in seasonal wetlands, as large numbers of transportable seeds, resting eggs, cysts, diapausing larvae, and adults can be picked up from dry-phase soils and dispersed. Some invertebrate species colonizing temporary pond habitats rely solely on airborne dispersal (Table 1) (Lopes et al. 2016). Vanschoenwinkel et al. (2009) collected 850 viable dormant eggs, larvae, and adults, from 17 aquatic invertebrate taxa, in windsocks erected near temporary rock pools. Wind-dispersed wetland plant species make up a high percentage (45%–50%) of all species in more terrestrial wetland types (Soons 2006).

Active overland dispersal throughout FEMs is also common, as insects, amphibians, reptiles, birds, and mammals can move among wetlands and stream networks on the ground or in the air (Table 1)

(Lamoureux and Madison 1999; Clark 2000; Milam and Melvin 2001; Gibbons et al. 2006, Attum et al. 2007; Spinola et al. 2008; Subalusky, Fitzgerald, et al. 2009; Subalusky, Smith, et al. 2009). Aerial dispersal of individuals from multiple taxonomic orders and phyla is a significant source of stream invertebrate colonists in newly inundated floodplain habitats (Tronstad et al. 2007; Vanschoenwinkel et al. 2009). For example, Tronstad et al. (2007) investigated aerial insect colonization of floodplains in an unregulated coastal plain river, and reported high densities (maximum $\approx 80,000$ individuals m^{-2}) in floating trays placed in floodplain waters, as well as high densities (21,291 individuals m^{-2}) of passively dispersing (e.g., via wind or animal vectors) microcrustaceans. Bogan et al. (2013) determined that several aquatic insect species occurring only in stream pools are either flightless or have weak dispersal abilities, whereas species occurring only in seasonal ponds are capable of frequent and long-distance dispersal. These findings suggest that biota occupying nonfloodplain wetlands may actually be better long-distance dispersers than biota occupying other aquatic habitats.

Overland biotic movements also create biological connections between wetlands and the river network (e.g., Newman and Griffin 1994; Swimley et al. 1999; Bodie and Semlitsch 2000) that are independent of hydrologic connections. Many amphibian species move between wetlands and streams throughout their life cycles (Figure 6) (Lamoureux and Madison 1999; Babbitt et al. 2003; Green 2005; Petranka and Holbrook 2006; Mushet et al. 2013), and numerous studies have demonstrated that amphibians commonly disperse in nonfloodplain wetland landscapes, often in large numbers. For example, Gibbons et al. (2006) documented more than 360,000 juvenile amphibians, from 24 species, emigrating from one Carolina bay during a single breeding season; more than 95% of the biomass (about 1,330 kg) came from juveniles of the southern leopard frog, which is known to use both stream and wetland habitats (Pope et al. 2000; Mushet et al. 2013). Riverine turtles can move hundreds of meters between rivers and wetlands to find suitable foraging, mating, nesting, rearing, and overwintering habitat throughout the year (Bodie and Semlitsch 2000; Bodie 2001). River-dwelling mammals such as river otters also move between rivers and wetlands (Newman and Griffin 1994; Swimley et al. 1999).

The movement of migratory water- and shorebirds (e.g., ducks, geese, cranes) provides perhaps the most extensive example of biological connections throughout FEMs. Wetlands are often critical habitats for these species, and used by large numbers of birds. For example, Webb et al. (2010) observed more than 1.6 million birds, representing 72 migratory bird species, actively using roughly 40 playas (shallow,

wind-formed wetland depressions) in Nebraska during a three-year spring migration study. Many of these migratory water- and shorebirds have been documented to use multiple aquatic habitats (e.g., streams, wetlands, estuaries) throughout their life cycles (Krapu et al. 1984; LaGrange and Dinsmore 1989; Folk and Tacha 1990; Adair et al. 1996; Austin and Richert 2005; Ballard et al. 2010). Use of these different habitats is often opportunistic, and dispersal among them varies with temporal and spatial changes in habitat availability (Farmer and Parent 1997; Haig et al. 1998; Ballard et al. 2010). Because these birds cover large distances with their migrations, they create biological connections that can link aquatic habitats over large spatial scales.

Because many organisms disperse to and from riparian/floodplain and nonfloodplain wetlands as “hitchhikers” on actively dispersing fauna (Table 1), the biological connections established by one taxon can frequently be transformed into multiple potential connections. For example, seeds of aquatic and riparian plants can be actively dispersed between riverine and riparian/floodplain wetlands when they are consumed by fish (Figure 4) (Pollux et al. 2007). Viable seeds and vegetative plant parts can travel great distances within the guts of or externally attached to migratory birds (Murkin and Caldwell 2000; Amezaga et al. 2002; Figuerola and Green 2002), which move between wetlands and river networks depending on temporally dynamic habitat availability (Murkin and Caldwell 2000; Haukos et al. 2006). Recent evidence also suggests that invertebrates are commonly transported by birds, as well as mammals (Figuerola and Green 2002; Figuerola et al. 2005; Allen 2007; Frisch et al. 2007). Because migratory birds can fly such long distances during their migrations, maximum dispersal distances for hitchhiking organisms have been estimated at 1,400 km (Mueller and van der Valk 2002). Invertebrates can also serve as the transport vector for smaller organisms, such as algae and protozoa (Table 1).

WHY BIOLOGICAL CONNECTIONS THROUGHOUT FEMs MATTER

The examples detailed above provide strong evidence of the movements of diverse biota along stream networks and between streams and wetlands. Taken together, these movements create the incredible diversity, variability, and complexity of biological connections in FEMs. Assessing the effects of these connections, however, is even more challenging than documenting the occurrence of movement among habitats. Despite these challenges, an increasing

number of studies are explicitly addressing both the occurrence and the importance of biological connections that affect the structure and function of downstream waters.

In this section, we discuss how biotic movements affect FEM structure and function. We first consider these effects in terms of the functions by which upstream habitats can influence population and community structure in downstream waters (Leibowitz et al. 2018): as sources of organisms to downstream waters; as sinks that retain organisms and reduce their provision to downstream waters; as refuges that support persistence of populations and biodiversity in downstream waters; as lags that temporarily “store” organisms or propagules (e.g., seeds) before providing them to downstream waters; and as transformers that provide resources needed for the development of individuals to different forms (e.g., different life stages) and for the evolution of locally adapted populations. Because each of these functions exerts effects at multiple levels of biological organization, from genes to ecosystems, we also find it useful to discuss biological connections in terms of how connections among streams, wetlands, and downstream waters affect individuals, populations, and communities throughout the entire FEM.

Although we are primarily focused on upstream-to-downstream connections and resulting effects on downstream waters, it is important to note that these functions and effects often depend on bidirectional movements — that is, biological connections in a downgradient direction, and their resulting effects on downstream waters, often rely at least in part on biological connections in an upgradient direction. For example, biota must be able to reach upstream refuges under adverse conditions, and then recolonize newly habitable downstream habitats when adverse conditions abate. Ultimately, then, the ecological integrity of FEMs requires that the full complexity of biological connections, in all dimensions and directions, be considered.

Biological Connections and the Functions of Streams and Wetlands

All three of the habitat types considered here — streams (including perennially and intermittently flowing channels), riparian/floodplain wetlands, and nonfloodplain wetlands — can function as sources, sinks, refuges, lags, and transformers of biota for downstream waters. As defined here, these functions are not necessarily independent and discrete, and can work synergistically. For example, growth of an organism in a headwater stream or wetland, and subsequent movement into downstream waters, could

arguably be considered a source, refuge, and/or transformer function of the upstream habitat.

Existing evidence clearly supports the idea that streams and wetlands commonly serve essential source and refuge functions for downstream waters. Streams and wetlands are sources of organisms and propagules, which then can serve as food or colonists in downstream waters (e.g., Thorp and Delong 2002; Bunn et al. 2003; Hein et al. 2003; Keckeis et al. 2003; Gurnell et al. 2008). This provision of organisms occurs via multiple pathways, including active or passive movements in water, over land, aerially, or attached to other organisms (Table 1; Figure 1). The source function served by tributaries and wetlands often stems from the refuge function served by these habitats. Under adverse abiotic or biotic conditions in downstream waters, streams and wetlands can serve as refuge habitats (Meyer et al. 2004; Chester and Robson 2011; Bogan et al. 2013; Cañedo-Argüelles et al. 2015); when biota leave these refuges and return to downstream waters, these habitats may then act as sources of individuals to downstream waters.

Streams and wetlands also function as sinks, lags, and transformers via numerous biological connections to downstream waters. For example, wetlands serve as sinks for seeds and plant fragments that remain in these habitats but do not germinate (Middleton 2000), or for fish that are stranded when wetlands are no longer connected via surface water pathways (Nagrodski et al. 2012). Lags can occur when movement from wetlands back to the stream network is delayed (e.g., by dormancy or by temporary drying of hydrologic flowpaths) (e.g., Smock 1994; Tronstad et al. 2007). When used as spawning or rearing habitats, streams and wetlands can be considered transformers that allow organisms to “transform” from one stage of development to another; this function is particularly evident for species that undergo ontogenetic habitat shifts between different FEM components (Huryn and Gibbs 1999, Gibbons et al. 2006). For example, American alligators in southern Georgia use seasonal wetlands for nesting and nursery areas and riverine habitats for nonnesting habitat (Subalusky, Fitzgerald, et al. 2009).

Biological Connections at the Organismal Level

At the organismal level, biological connections throughout FEMs provide individuals in downstream waters access to two key resources: food and habitat. Movement of organisms throughout FEMs creates biological connections that supply food for other organisms and that allow organisms to access suitable habitats.

Along stream networks, there is clear evidence that upstream areas provide food to downstream waters. Many fish feed on drifting insects (e.g., Nakano and Murakami 2001; Wipfli and Gregovich 2002), so the biological connections created by invertebrate drift provide food resources for downstream fish (Figure 5). Wipfli and Gregovich (2002) estimated that drifting insects and detritus from fishless headwater streams in Alaska supported between 100 and 2,000 young-of-year salmonids per kilometer in a large, salmon-bearing stream. Increased invertebrate drift has also been associated with increased fish growth (Wilzbach et al. 1986; Nielsen 1992; Rosenfeld and Raeburn 2009), indicating that drift provides a valuable food resource, particularly when food is limiting (Boss and Richardson 2002).

Wetlands also contribute food resources to downstream waters. Phytoplankton communities in river networks can be enhanced by conditions that promote high productivity in temporarily connected floodplain wetlands (Hein et al. 2003). This pattern holds even when little flow passes through floodplains relative to total flows through the main channel (Lehman et al. 2008). High production of algal biomass in floodplains ultimately contributes high-quality food resources (e.g., in terms of labile carbon and essential fatty acids) to downstream waters (Thorp and Delong 2002; Bunn et al. 2003; Lehman et al. 2008), which then supports downstream fisheries.

Similarly, invertebrates emerging from wetlands (Leeper and Taylor 1998) can become important food sources for fishes and other biota in nearby streams, particularly when one considers cumulative emergence from numerous wetlands across the landscape. The biota inhabiting wetlands convert organic matter in those wetlands into biomass, which then can subsidize other aquatic and terrestrial components of the ecosystem (Semlitsch and Bodie 1998; Brooks 2000; Gibbons et al. 2006).

Nonfloodplain wetlands such as Carolina and Delmarva bays are often immensely productive amphibian breeding habitats, and are critical for the persistence of pond-breeding amphibian populations that can move to other water bodies (Sharitz and Gibbons 1982; see Biological Connections at the Population Level, below). Given the proximity of many Carolina and Delmarva bays to tributaries (12%–19% of Carolina bays within 100 m, roughly 90% within 1.6 km; Sharitz 2003), amphibians emigrating from these bays could transfer large amounts of energy and organic matter into rivers and streams.

In addition to food, streams and wetlands provide organisms in downstream waters access to additional habitats; under adverse conditions in downstream waters, these habitats may serve as refuges. This provision of habitat is particularly evident for fishes

that can actively move into upstream habitats. For example, headwater streams and small tributaries can provide fishes refuge from flow (Wigington et al. 2006; Koizumi et al. 2013) and temperature extremes (Peterson and Rabeni 1996; Curry et al. 1997; Baxter and Hauer 2000; Labbe and Fausch 2000; Bradford et al. 2001). Use of these refuge habitats can result in increased food availability, growth, and average egg size (Peterson and Rabeni 1996), demonstrating that these upstream areas can provide downstream organisms with high-quality habitats that influence individual reproductive success and survival (e.g., Ebersole et al. 2009).

The refuge function served by upstream habitats can be especially important in intermittent streams, where perennial habitats (e.g., permanent pools) can serve as refuges during drying for fish (Pires et al. 1999; Labbe and Fausch 2000; Fritz and Dodds 2002; May and Lee 2004; Wigington et al. 2006) and invertebrates (Fritz and Dodds 2004). In other cases, intermittent channels themselves may serve as refuges, by allowing species adapted to drying conditions to persist (Meyer et al. 2004).

Biological Connections at the Population Level

As discussed above, the movement of biota throughout FEMs provides organisms access to food and habitat. Ultimately, these biological connections and their effects at the organismal level have repercussions at the population level, most notably in terms of population persistence and genetic diversity. Biological connections allow stream biotic assemblages to recolonize both downstream and upstream habitats following disturbances (Fritz et al. 2002; Franssen et al. 2006; Chester and Robson 2011). For many biota, upstream areas are a source of colonists for downstream reaches (Meyer and Wallace 2001; Hanfling and Weetman 2006), allowing organisms to persist and recolonize downstream areas once adverse conditions have abated (Meyer and Wallace 2001; Meyer et al. 2004; Huryn et al. 2005; Bogan et al. 2013; Cañedo-Argüelles et al. 2015). Particularly in streams subject to alternating periods of flooding and drying, populations depend on dispersal out of intermittent reaches before drying occurs, and subsequent recolonization of these habitats once water flow resumes. Prairie stream fishes provide a good example of this, as they can quickly move upstream or downstream into newly available habitat — including previously dry, rewetted channels — during and after floods (Harrell et al. 1967; Fritz et al. 2002; Franssen et al. 2006).

The persistence of prairie stream fish populations requires biological connections along entire stream

networks. Many studies have documented significant associations between impoundment of prairie streams and loss of native fishes (Winston et al. 1991; Luttrell et al. 1999; Falke and Gido 2006; Matthews and Marsh-Matthews 2007). Prairie stream fishes can require more than 100 km of undisrupted stream channel (i.e., channels with no impoundments or drying associated with water withdrawals) to support persistent populations (Perkin and Gido 2011), and impoundments can disrupt both downstream transport of developing eggs and larvae and upstream and downstream movement of adult fish. Fragmentation of river networks also has consistently been related to local extinction of salmonid populations (Morita and Yamamoto 2002; Letcher et al. 2007).

Biological connections among wetlands and downstream waters also can be important for population persistence in these downstream habitats. Riparian/floodplain wetland habitats can be significant sources of fish recruitment in streams and rivers (Brown and Hartman 1988; Crook and Gillanders 2006; Pease et al. 2006). For example, Crook and Gillanders (2006) analyzed otolith chemical signatures to show that floodplain lakes were estimated to be the source of 98% of the young-of-year carp for areas 140 km downstream of the floodplain lakes, illustrating that upstream habitats can have significant effects on downstream populations.

Loss of hydrologic connectivity between wetlands and stream networks eliminates feeding, breeding, rearing, and refuge habitat for the many fully aquatic species that use wetlands for these purposes. If species do not demonstrate plasticity in behavior, habitat preference, or life cycle requirements, loss of access to these wetlands can result in local extirpation (Crook et al. 2015). In the Missouri River, flow regulation and disconnection of the river from its historical floodplain has coincided with declines in many species that rely on floodplain wetlands (e.g., fish, plants, insects, mussels, reptiles, birds, and mammals) (Galat et al. 1998). Biodiversity increased when these wetlands were reconnected to the river during major flood events (Galat et al. 1998).

The importance of streams and wetlands for populations in downstream waters is not limited to biota capable of active movement. Establishment and reproduction of refuge floodplain populations can provide important wetland seed sources for the river network, especially when catastrophic flooding scours streambed vegetation and seed banks (Gurnell et al. 2008). Many taxa with limited mobility can be moved over longer distances via “hitchhiking” on more mobile organisms, with resulting population-level effects across extensive spatial scales. For example, winter migration of waterbirds can be an important mechanism for spring colonization of aquatic habitats

separated by hundreds or even thousands of kilometers (Frisch et al. 2007). Figuerola et al. (2005) found that, for three of four invertebrate species examined, movement of waterbirds explained a significant amount of gene flow between populations located across North America.

These population-level effects can also be examined in terms of the maintenance of genetic connectivity and diversity. Genetic connectivity results from biotic dispersal and subsequent reproduction and gene flow. This gene flow connects spatially subdivided populations (e.g., headwater vs. downstream populations, populations in spatially distant wetlands), making it more likely that populations will retain higher levels of within-population genetic diversity and enhancing both population persistence and adaptive capacity in changing environments (Lande and Shannon 1996; Ishiyama et al. 2015). Floods that periodically connect different parts of the river network generate the potential for gene flow across time and space by mixing individuals from different locations (e.g., upstream/downstream, river channel/floodplain) and different years (e.g., eggs that might have diapaused for tens or even hundreds of years) (Jenkins and Boulton 2003; Frisch and Threlkeld 2005). The combination of organismal movement and different life history strategies supports gene flow for individual species, as well as overall biodiversity in FEMs (see Biological Connections at the Community Level, below). In general, genetic connectivity decreases with increasing spatial distance (Wright 1943). In river networks, it is also strongly influenced by the hierarchical structure of the network, the direction of dispersal (upstream, downstream, or both), dispersal modes and pathways used (e.g., swimming, flying), and species' life histories (Morrissey and de Kerckhove 2009; Hudy et al. 2010). Species that disperse frequently or over long distances tend to have higher within-population genetic diversity (Fer and Hroudova 2008; Mullen et al. 2010).

Individual species behavior can also profoundly affect observed genetic patterns, via out-of-network gene flow (e.g., aerial or terrestrial dispersal by insects or amphibians) (Grant et al. 2010; Alexander et al. 2011), very high levels of within-network gene flow (e.g., fish that move and reproduce throughout the network) (Chaput-Bardy et al. 2009), or use of complementary habitats (Figure 6) (Mushet et al. 2013). For example, in a microsatellite analysis of northern leopard frog populations that recolonized wetland habitats after an extended drought, Mushet et al. (2013) observed high levels of genetic diversity and low population genetic structure (F_{ST} 0.0–0.05) among populations in wetlands separated by distances up to 65 km. These results indicate that dispersing juveniles of this frog, which breeds in

seasonal wetlands and overwinters in deep or flowing waters to avoid the subfreezing temperatures, connect FEM habitats over long distances in the northern Great Plains (Figure 6).

Population-level effects of streams and wetlands on downstream waters can be closely related to where along the connectivity-isolation continuum these habitats fall. For native populations, persistence may depend on isolation, rather than connectivity (Letcher et al. 2007; Cook et al. 2010). Both natural and artificial physical barriers, which reduce connectivity and increase isolation, can protect headwater habitats and populations by isolating them from colonization by, and hybridization with, invasive species (Freeman et al. 2007; Fausch et al. 2009). These effects are also reflected in the genetic structure of populations, as illustrated by the fact that most genetically pure cutthroat trout populations are confined to small, high-elevation streams that are naturally or anthropogenically isolated (Cook et al. 2010). However, this isolation can also adversely affect native species via reduced genetic connectivity potentially leading to reduced reproductive fitness and increased risk of local extinction. Barriers to fish movement can result in increased genetic divergence between headwater and downstream populations, as well as loss of headwater genetic diversity (Wofford et al. 2005; Hanfling and Weetman 2006; Deiner et al. 2007; Fausch et al. 2009; Gomez-Uchida et al. 2009).

Biological Connections at the Community Level

In addition to effects at the organismal and population levels, biological connections between streams, wetlands, and downstream waters also affect the structure of biotic communities. Fish assemblages among connected streams tend to have more species in common (Matthews and Robinson 1998; Hitt et al. 2003; Grenouillet et al. 2004), and measures of river network structure (e.g., link magnitude) can be significantly related to fish assemblage structure (e.g., Osborne and Wiley 1992; Smith and Kraft 2005). Perkin and Gido (2012) demonstrated the importance of biological connections in structuring fish communities by examining the effects of stream network fragmentation. In 12 Kansas stream networks, fragmentation by road crossings affected both alpha diversity (species richness) and beta diversity (dissimilarity): fish species richness decreased in isolated segments, whereas dissimilarity to downstream sites increased (Perkin and Gido 2012).

Community-level effects of biological connections are also evident for invertebrates. Fritz and Dodds (2002, 2004) examined invertebrate assemblages before and after drying in intermittent prairie streams

and reported that initial recovery of invertebrate richness, richness of invertebrate drift, and richness of aerially colonizing insects were negatively related to distance from upstream perennial water (i.e., upstream refuge habitats). Recovery from disturbance in these intermittent streams appears to depend on biological connections via both downstream drift of colonizers and downstream (and potentially upstream) movement of aerially dispersing, egg-depositing adults (Miller and Golladay 1996; Dodds et al. 2004). Communities in downstream waters also are affected by wetlands. For example, variability in wetland habitat availability and condition both within and across years enables multiple fish species with specific habitat requirements or preferences to reproduce and rear young (Robinson et al. 2002), thereby contributing to the maintenance of fish diversity throughout river networks (Shoup and Wahl 2009).

This pattern of movements between different habitats allowing for the persistence of different species is true for invertebrates, as well. For example, initial microinvertebrate colonizers of newly flooded riparian habitats in one arid system were washed downstream from distant upstream reaches of the river network, illustrating biological connections along the entire stream network, including ephemeral and intermittent streams (Jenkins and Boulton 2003). In just a few days, species hatching from diapausing eggs in transported sediments greatly increased size and diversity of the downstream microinvertebrate community (Jenkins and Boulton 2003).

Lateral biological connections between the river channel and riparian/floodplain wetlands and open waters such as oxbow lakes are integral to the viability of many riverine species (Bunn and Arthington 2002; Shoup and Wahl 2009) and increase overall levels of species productivity and biodiversity in river systems (Junk et al. 1989). In a five-year study of fish in floodplain lakes, Shoup and Wahl (2009) found that hydrology and water chemistry differed across individual oxbow lakes, which thus varied in suitability for different fish species; they concluded that the entire floodplain should be considered a single functioning unit that supports the overall biological integrity of the river. Hydrologic connectivity between channels and riparian/floodplain wetlands can significantly enhance riparian vegetation diversity (Jansson et al. 2005) and determine floodplain wetland community structure (Boschilia et al. 2008). These connections can significantly influence macroinvertebrate community structure in riparian areas, as well (Obolewski et al. 2009; Paillex et al. 2009), and can help support invertebrate diversity throughout the river system (Reckendorfer et al. 2006). For example, composition of floodplain invertebrate assemblages in the Rhône River, France, was

strongly related to hydrologic connectivity between floodplain habitats and the main river channel, in part due to increased voltinism (i.e., shorter life cycles) with increased hydrologic connectivity (Paillex et al. 2007). Fish assemblages in riparian wetlands along the semiarid region of the Murray River, Australia, similarly showed a large decline in diversity when those wetlands were disconnected from the river through hydrologic modifications, a trend which was reversed when connections were restored (Vilizzi et al. 2013).

Biotic movement, both within nonfloodplain wetland habitats and between these habitats and other FEM components, has well-documented effects on community structure and biodiversity of these mosaics, particularly for amphibians (e.g., Wellborn et al. 1996; Snodgrass et al. 2000; Julian et al. 2013). Similarity between spatially separated populations and communities — measured in terms of genetic or community structure — provides additional evidence of biological connectivity between nonfloodplain wetlands and river networks (Ivey and Richards 2001; Capers et al. 2010). For example, Capers et al. (2010) determined that aquatic habitats (small isolated wetlands to large lakes) located more closely together had more similar plant communities, regardless of habitat type and local determinants of community structure (e.g., rainfall and soil type).

Isolation of nonfloodplain wetlands can also contribute to the long-term genetic diversity of populations (King et al. 1996). For example, present-day Pacific vernal pool wetland communities are characterized by endemic species that have evolved within globally distributed genera (King et al. 1996; Keeley and Zedler 1998; Zedler 2003). Over geologic time, passively dispersing species colonized, then became locally adapted to, spatially isolated vernal pool landscapes. In these wetland ecosystems, relatively infrequent biological connections have resulted in the creation of new, endemic species from the rootstock of ancient, widespread lineages. Despite their relatively high spatial isolation, Pacific vernal pools are now rich reservoirs of genetic and species diversity (Zedler 2003). The existence and periodic connectivity of such reserves are especially important at a time when changing environmental conditions are threatening biodiversity of aquatic species worldwide (Carpenter et al. 2011).

SYNTHESIS AND IMPLICATIONS

Based on existing scientific evidence, biota clearly link FEMs via movements within and among their aquatic habitat components. Even freshwater habitats

that appear to be hydrologically isolated are connected by movements of biota that affect all levels of biological organization, from genes to ecosystems. For species that are only capable of moving via water (e.g., most fish, many aquatic invertebrates), biological connections largely depend on hydrologic connections. The hydrologic flowpaths used by biota do not need to be permanent, as water-dependent life stages and movements (e.g., juvenile dispersal, adult migration) are timed to coincide with intermittent flows or take advantage of ephemeral or episodic flows. Furthermore, downgradient flow does not restrict biota to downstream movement, as biota can actively move with or against the direction of hydrologic flows. Even greater flexibility is present in aquatic species that are also capable of moving overland. This group includes many fully aquatic organisms (e.g., algae, invertebrates with no terrestrial life stage) that nonetheless have evolved mechanisms for terrestrial movement between aquatic habitats via flying, walking, crawling, hopping, “hitchhiking,” drifting in wind, or some combination of these (Table 1). The diverse nature of biotic movements reflects aquatic species’ many adaptations to life in dynamic freshwater ecosystems. As a result of their remarkable diversity, biological connections are far more widespread, complex, and variable than hydrologic connections in aquatic ecosystems.

The temporal and spatial scales over which physical pathways for movement (structural connectivity) and actual movements (functional connectivity) link aquatic habitats vary with the environmental conditions and species assemblages present in them (Baguette et al. 2013). A complete discussion of the biotic and abiotic factors that influence biological connectivity in freshwater ecosystems, including the evolutionary tradeoffs in species traits associated with growth, reproduction, and survival (Bonte et al. 2012; Kubisch et al. 2014), is beyond the scope of this paper. However, existing and emerging information on the effects of surface water dynamics (e.g., Figure 2) on habitat stability can provide new insights into aquatic species’ distributions (Williams 2006), biodiversity (Marten et al. 2006; Dehling et al. 2010), range sizes (Ribera and Vogler 2000; Hjalmarsson et al. 2015), metapopulation and metacommunity dynamics (Larned et al. 2010), and dispersal (Hof et al. 2012).

The diversity of habitats and species in FEMs makes them ideal systems for investigating scales of biological connectivity, and the relationships between habitat heterogeneity, habitat stability, and biodiversity (Jeltsch et al. 2013). Future research to advance our understanding of the timing, rate, frequency, and distance of movements can build upon past work by focusing not on model species, but rather on assemblages with the range of life histories representing

species’ adaptations to conditions in different FEM landscape settings. It will come as no surprise that data availability still poses the critical limitation to quantifying biological connectivity (Calabrese and Fagan 2004; Bergsten and Zetterberg 2013). Actual movement is challenging to measure at any scale, and is particularly difficult to observe and quantify for small or cryptic organisms and infrequent, long-distance dispersal events that have ecologically and evolutionarily significant consequences (e.g., Ishiyama et al. 2015).

While challenging to obtain, these data are needed to improve the accuracy of connectivity metrics and the performance of models to predict connectivity. Our understanding of biological connections has been advanced by explicit consideration of landscape-scale habitat structure, for example dendritic stream networks (Fagan 2002; Grant et al. 2007) and wetland habitat modularity (Fletcher et al. 2013). Modeling methods capable of incorporating local- to macro-scale connectivity of streams, wetlands, lakes, and ponds with specific information about habitats, focal species, and species–landscape interactions (e.g., habitat area or quality, population abundance) and connectivity attributes (e.g., Euclidean distance, landscape resistance, direction of movement) are now available (Galpern et al. 2011). Recent advances in the theory and application of multilayer networks to ecological systems are also forwarding the development of analytical methods that can evaluate biological connectivity across species, over multiple spatial and temporal scales, and in response to diverse ecological and socio-ecological processes (Kivelä et al. 2014; Pulosof et al. 2017).

For practical reasons, research into biological connections is often conducted in single systems, looking at individual species, assemblages, or ecosystem types. In reality, biological connectivity is the cumulative effects of multiple species moving, via multiple pathways and across multiple habitat types, to make use of the full range of resources occurring throughout heterogeneous FEMs (Figure 1). The movements of organisms, and the materials they transport, are essential to the functions of streams and wetlands, which in turn provide critical functions to downstream waters by serving as sources of colonists, food, and genetic diversity; as sinks for organisms; as transformers via organism growth and development and subsequent return to downstream waters; and as lags via dormancy and temporary isolation. Thus, the diverse biological connections among different components of FEMs, which vary in space and time, across species and even across individuals within a species, are needed to sustain aquatic life and maintain the ecological integrity of downstream waters.

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DISCLOSURE

Former JAWRA Editor Kenneth J. Lanfear served as acting editor in chief for all articles in this featured collection. Parker J. Wigington, Jr., an author on some of the collection papers and who was JAWRA editor in chief at the time the collection was submitted, had no role in the review or editorial decisions for any part of the collection.

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