Differing Modes of Biotic Connectivity within Freshwater Ecosystem Mosaics

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Research Impact Statement: Fully including aquatic, wetland, and terrestrial habitats facilitates adoption of next-generation, individual-based, models that integrate principles of population, community, and ecosystem ecology.

ABSTRACT: We describe a collection of aquatic and wetland habitats in an inland landscape, and their occurrence within a terrestrial matrix, as a “freshwater ecosystem mosaic” (FEM). Aquatic and wetland habitats in any FEM can vary widely, from permanently ponded lakes, to ephemerally ponded wetlands, to groundwater-fed springs, to flowing rivers and streams. The terrestrial matrix can also vary, including in its influence on flows of energy, materials, and organisms among ecosystems. Biota occurring in a specific region are adapted to the unique opportunities and challenges presented by spatial and temporal patterns of habitat types inherent to each FEM. To persist in any given landscape, most species move to recolonize habitats and maintain mixtures of genetic materials. Species also connect habitats through time if they possess needed morphological, physiological, or behavioral traits to persist in a habitat through periods of unfavorable environmental conditions. By examining key spatial and temporal patterns underlying FEMs, and species-specific adaptations to these patterns, a better understanding of the structural and functional connectivity of a landscape can be obtained. Fully including aquatic, wetland, and terrestrial habitats in FEMs facilitates adoption of the next generation of individual-based models that integrate the principles of population, community, and ecosystem ecology.

(KEYWORDS: aquatic ecology; biotic connectivity; functional connectivity; landscape connectivity; mosaics; sustainability; wetlands.)

INTRODUCTION

Ecologists have postulated that understanding movements and interactions of individuals within an ecosystem context is necessary to unify ecological theory (Huston et al. 1988). However, progress integrating individual-based approaches (e.g., DeAngelis and Grimm 2014) with ecosystem-based approaches (e.g., Walters et al. 2000) in ecology has been slow (Grimm et al. 2017). The next generation of individual-based models (Grimm et al. 2003) requires simulation of not just flows of individual organisms across a landscape from a population- and community-ecology perspective, but also flows of energy and materials from an ecosystem-ecology perspective. Consideration of...
aquatic and wetland habitats in inland landscapes as pieces of a complete mosaic rather than as islands separated by inhospitable environments is an approach that meshes directly with these next-generation models designed to integrate the principles of population, community, and ecosystem ecology.

Here we use the term “connectivity” to describe linkages among habitat patches through the flow of energy, materials, or organisms. Connectivity can be divided into structural connectivity that refers to the spatial distribution and arrangement of habitat patches in a landscape, and functional connectivity that refers to the actual movement of energy, materials, or organisms across the landscape (Baudry and Merriam 1988). Thus, structural connectivity describes the underlying physical foundation, or matrix, upon which functional connectivity can occur. Temporal connectivity refers to how habitat patches can be connected through time. For example, if the environment of a patch varies between favorable and unfavorable conditions, an organism might connect the patch through time if it has a mechanism to persist through periods of unfavorable conditions. Therefore, temporal changes in environmental conditions must be considered when identifying the overall structural connectivity of a landscape. Likewise, physiological, morphological, and behavioral traits that allow individual organisms to persist during periods of unfavorable conditions must be considered when determining the overall functional connectivity of that same landscape.

The movement of organisms among aquatic, wetland, and terrestrial habitats, and flows of energy and materials associated with these movements, can be modeled and quantified through explicit consideration of interactions between structure and function. Additionally, flows of materials and energy between habitats (e.g., terrestrial to wetland, wetland to terrestrial, wetland to aquatic) and the influence of these flows on individual organisms and communities can be incorporated. Only when all components of a landscape are considered as integrated and inseparable parts of a mosaic (sensu Sayer 2014) can important influences of ecosystem flows be fully considered and incorporated into models that link population, community, and ecological theory.

To explore the relationship between structural and functional connectivity of landscapes and to facilitate the integration of population, community, and ecosystem models, we set out to (1) define the concept of freshwater ecosystem mosaics (FEM: pronounced “fem”); (2) link the concept to existing ecological frameworks; (3) demonstrate the usefulness of the FEM concept for assessing structural and functional components of biotic connectivity; and (4) illustrate, through specific examples, a range of different FEM types to which we hypothesize species are likely to be differently adapted, via specific physiological, morphological, and behavioral traits.

FEMS DEFINED

Most inland (i.e., nonoceanic or coastal) landscapes consist of some combination of aquatic (both lotic and lentic) and terrestrial habitats, with wetlands as transitional areas (Cowardin et al. 1979), although wetlands also occur as distinct landscape features without transition to either an aquatic or a terrestrial habitat, and as transitions between inland and coastal ecosystems. Therefore, a perspective that adopts the view of an inland landscape as a mosaic (e.g., Wiens et al. 1993) consisting of aquatic and wetland habitats interspersed within a terrestrial matrix provides a foundation upon which to describe a landscape and the underlying structural connectivity to which biota must adapt to persist. For inland landscapes, we describe a collection of aquatic and wetland habitats, and their variable spatial and temporal patterns of occurrence within a terrestrial matrix, as a “FEM.”

When viewing an art mosaic of individual tiles of different colors and shapes set within a mortar matrix, the full pattern of tile and mortar must be considered to see a complete vision of the artist’s work and appreciate it in its entirety. Similarly, the size, type, and spatial arrangement of aquatic and wetland habitats must be considered in conjunction with the terrestrial matrix in which they exist in order to get a complete vision of any FEM (Figure 1). However, unlike an art mosaic, FEMS are not set in stone — they are constantly shifting over time, and those shifts have repercussions for movement of organisms. Additionally, humans undoubtedly can alter FEMS, and the need to consider the entire mosaic holds in both natural and human altered landscapes. In fact, including the effects of human alterations to the tiles (aquatic and wetland habitats) and the mortar (terrestrial landscapes) can greatly influence the structural and functional connectivity of the FEM.

Often, the space between “tiles” is viewed by ecologists as an inhospitable environment across which organisms must cross. This is the view promulgated within island biogeography theory and is often the case for true islands (MacArthur and Wilson 1967). However, inland aquatic and wetland habitats are only partially or superficially analogous to oceanic islands (e.g., Smith and Green 2005). The terrestrial environment, either natural or altered, may or may not be an inhospitable habitat that acts as a barrier to movement, and the differences in its effects on movement are often seasonal and species-specific.
Just as with habitats, species occur along a continuous gradient from fully aquatic to fully terrestrial (e.g., Allen et al. 2014). Additionally, the flows of energy and materials between aquatic habitats and the terrestrial matrix must be considered. When a landscape is viewed as a mosaic, the role that the surrounding terrestrial matrix plays as another (or multiple) habitat type(s) becomes apparent as an integral part of the complete picture of species–landscape and ecosystem interactions. As an example, to fishes, the terrestrial environment separating two aquatic habitats is, under most circumstances, an inhospitable barrier. In contrast, an amphibian might require that same terrestrial environment as essential foraging habitat. A mallard, on the other hand, might not directly interact with the terrestrial matrix at all as it flies overhead but may rely on it later to provide essential nesting habitat. This view of FEMs as landscapes within which all habitat types, including those of the terrestrial matrix, are potentially connected provides context for not just flows of organisms, but also flows of abiotic energy, inorganic nutrients, and detritus among various ecosystem types. These flows can come directly from the movement of organisms or through abiotic processes such as runoff, erosion, and nutrient transport. Loreau et al. (2003) defined a meta-ecosystem as “a set of ecosystems connected by spatial flows of energy, materials and organisms across ecosystem boundaries.” The meta-ecosystem concept moves us away from considering aquatic and wetland habitats as metaphorical “islands” separated by inhospitable terrestrial environments. Instead, the meta-ecosystem concept necessitates consideration of functional interactions between the “islands” and the matrix in which they exist when considering spatial flows among habitats. The FEMs we define here are fully compatible with the meta-ecosystem concept and facilitate its incorporation into connectivity assessments and combined population, community, and ecosystem modeling efforts.

MOVEMENTS WITHIN FEMS

Movement of organisms among aquatic, wetland, and terrestrial habitats within a FEM occurs via diverse means in multiple directions, including longitudinal (up- and downgradient), lateral (across), vertical (surface, subsurface), and temporal dimensions (Ward 1997). Therefore, biotic connectivity within a FEM includes not only movements through the water column and over intervening land surfaces but also through the atmosphere (e.g., Beisner et al. 2006) and through underlying groundwater and sediments. In dry seasons or droughts, for example, many organisms typically found in surface waters survive by moving into underlying sediments within wetlands or hyporheic zones in stream networks, which provide refuge and alternative pathways for movement (e.g., Sedell et al. 1990; DiSalvo and Haynes 2015). In many cases, the movement of water is unidirectional.
over and through the landscape (Malard et al. 2002; seiche and tidal influenced waters, and wetland-to-
wetland and stream-to-wetland flows are exceptions); however, many organisms are capable of multidi-
tensional movement along longitudinal, lateral, and ver-
tical routes over their life spans. Riverine stonofly larvae, for example, can move over long distances
through floodplain aquifers (~2 km laterally and
~10 m vertically from surface channels, Stanford and
Gaufin 1974; Stanford and Ward 1988) to take advan-
tage of nutrient-rich hyporheic habitats. In many
landscapes, surface waters are highly dynamic (e.g.,
Lang et al. 2012; Vanderhoof et al. 2016) such that
availability and spatial arrangement of habitats and
resources can vary dramatically over an individual’s
lifetime or across multiple generations (Roshier and
Reid 2003). Flows of energy and materials greatly
affect the condition of habitats and resources encoun-
tered by moving organisms. Changes in this avail-
ability, arrangement, and condition of habitats influence
movements of biota both directly and indirectly by
affecting flows of resources, environmental cues and
stressors (e.g., Gaston et al. 2013; Shannon et al.
2016).

CONTINUOUS GRADIENTS WITHIN FEMS

Vannote et al. (1980) introduced the River Contin-
uum Concept to describe the continuous gradient of
physical conditions along the length of a river; the
predictable effects of those conditions on biological
communities; and the consistent patterns of organic
matter loading, transport, utilization, and storage
that result. Key to the River Continuum Concept is
the realization that patterns of inputs from habitats
outside the river environment are needed to explain
longitudinal patterns in stream habitat conditions.
Similarly, Euliss et al. (2004) introduced the Wetland
Continuum Concept to describe the influence of atmo-
spheric water and groundwater flows on differing pat-
terns of community structure in wetland ecosystems.
While the focus on flow types differs (primarily sur-
face water in the River Continuum vs. surface, atmo-
spheric, and groundwater flows in the Wetland
Continuum), the concepts can be viewed as working
in tandem, with flows that emanate from wetlands
ultimately influencing the concentration and net flux
of chemicals, including nutrients, in flows that extend
to rivers and streams.

The FEM concept provides a framework within
which a more unifying approach that links the River
Continuum Concept, the Wetland Continuum Con-
cept, and other important conceptual models (e.g.,
Kratz et al. 1997) can be developed. A FEM view of a
landscape requires acknowledgment of a complete
picture of flows that includes flows to and from ter-
restrial habitats in addition to aquatic and wetland
habitats. Both the River Continuum and Wetland
Continuum Concepts implicitly include flows to and
from surrounding, often terrestrial, habitats. How-
ever, interactions between wetlands, especially non-
riverine wetlands, and water, energy, and material
flows in rivers have been poorly represented (USEPA
2015). Consideration of the landscape as a mosaic of
aquatic and wetland habitats bound together by a
terrestrial matrix incorporates the often-overlooked
interactions among differing freshwater and terres-
trial ecosystem types.

STRUCTURAL CONNECTIVITY OF FEMS

Water runoff from the terrestrial matrix during
rain events or snowmelt often is a major input of
water into the aquatic and wetland habitats of a
FEM. This surface-water inflow also transports nutri-
ents, energy, and organic and inorganic particles
from surrounding terrestrial lands. Additionally, in
many FEMs, the composition of soils and bedrock
influences groundwater inputs to and outflows from
aquatic and wetland ecosystems (Winter 2001). Both
surface and groundwater flows work in conjunction
with biogeochemical and physical processes (Cohen
et al. 2016) to help form the abiotic environment to
which biota must be adapted to persist in a particular
habitat (Southwood 1988; Euliss et al. 2004). How-
ever, the number, size, shape, arrangement, and
hydrology of aquatic and wetland habitats on the
landscape are parameters of the structural connectiv-
ity to which organisms must also be adapted. These
factors determine the distance to another favorable
environment, setting a minimum threshold distance
beyond which individuals must be able to move to
connect populations, communities, habitats, and
ecosystems. The surface-water permanence of a habi-
tat can place a temporal limit on how often move-
ments must be made; for example, if a stream or
wetland habitat dries seasonally, organisms living
there must either move seasonally or have a life-his-
tory form (e.g., desiccation resistant eggs) that allows
them to survive periods without ponded or flowing
surface water. For species restricted to aquatic envi-
nvironments (e.g., fishes), a spatially continuous sur-
facer-water connection is typically required for unassisted
movement among habitats. For organisms that can
traverse terrestrial lands (e.g., amphibians, mam-
mals, many insects), the distance they must be
capable of traveling may be a straight-line distance between favorable habitats; however, often dispersal requires movement over longer distances along favorable pathways (e.g., along riparian corridors) or through risky environments.

While the number, size, shape, arrangement, and permanence among landscape features set the underlying structural connectivity in a FEM, the diverse adaptations of organisms in terms of morphological, physiological, and behavioral traits that influence movement abilities ultimately determine biotic movement, and this functional connectivity. Therefore, to identify the functional biotic connectivity of a landscape, the underlying structural connectivity must first be understood; adoption of a FEM perspective facilitates development of such an understanding.

BIOTIC ADAPTATIONS: TRANSLATING STRUCTURAL CONNECTIVITY INTO FUNCTIONAL CONNECTIVITY

Ecosystem and community ecology can only be fully and mechanistically integrated when we revert to their building blocks and acknowledge individual organisms and their traits and adaptive behaviors. (Grimm et al. 2017)

Freshwater ecosystems in any given landscape can be connected to and influence each other in diverse ways (USEPA 2015). One key way is through the movement of organisms among ecosystems (Schofield et al. 2018). In many cases, individuals must move for populations to persist. This movement can take many forms, both active and passive, and includes seeds dispersed by the wind, fish swimming among aquatic systems, amphibians traveling through uplands, birds flying along migratory pathways, and freshwater invertebrates clinging to the feathers of ducks. As put by Tiner (2003), “...most, if not all, wetland scientists would agree that there is no such thing as an isolated wetland from an ecological standpoint.” Thus, to truly understand any ecosystem, the movement needs and abilities, and therefore the traits and adaptive behaviors, of the individual species within these systems must be considered (Table 1).

The arrangement and variability of aquatic and wetland habitats within a FEM will influence the traits and behaviors of the organisms that persist there. In a FEM where aquatic or wetland habitats are separated by short distances, traits needed to traverse intervening terrestrial habitats may differ from traits needed for a species to persist in a FEM in which favorable habitats are situated far apart. Similarly, in FEMs where surface water is ephemeral, the need to move will be different than in FEMs with sustained surface-water permanence. Flowing-water habitats often offer linear pathways through which species can move, but typically these systems can also be connected to other aquatic or wetland habitats in a FEM through movements of biota across the terrestrial matrix.

The community-wide composition of traits that facilitate movement evolves as a result of interactions between species and the environments in which they occur (Loreau 2010). Therefore, more heterogeneous habitats theoretically could support more diverse species pools, representing a greater diversity of movement traits and capabilities. Additionally, communities in landscapes with greater degrees of structural connectivity could also increase biotic diversity simply by allowing for multiple spatially based classes of dispersers. For example, in a landscape with a high density of aquatic and wetland habitats, species capable of short-distance movements would flourish; however, species capable of long-distance travel (through water, overland or aerially) could also occur. But if required habitats are widely dispersed or highly ephemeral, species that can move only short distances and lack adaptations to dry conditions would likely be excluded from resultant communities, or not persist for long. Decreasing structural connectivity has a filtering effect (Figure 2), limiting communities to some hierarchically reduced sets of traits as the degree of habitat connectedness decreases (Poff 1997). Therefore, understanding the traits of species that exist in any FEM will indicate the degree of habitat connectivity within, integrated over time. However, the influence of energy and material flows on condition of the habitats, and ultimately the functional connectivity of a landscape, cannot be ignored.

EXAMPLE FEMS

While the structural connectivity of a region from a biotic perspective undoubtedly incorporates factors beyond an area’s hydrologic landscape, the hydrologic landscape principles and maps of Winter (2001) and Wolock et al. (2004) provide a useful classification framework for exploring biotic structural connectivity in the absence of mapping products derived specifically to delineate FEMs. Wolock et al. (2004) identified 20 noncontiguous, hydrologic landscape regions
### TABLE 1. Examples of traits facilitating movement within FEMs, and FEM conditions promoting each movement type.

| Movement type                                           | Morphological and physiological traits                                                                 | Behavioral traits                                                                                      | FEM conditions promoting movement type                                                                 | Example biota                                                                                   |
|---------------------------------------------------------|-------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------|
| Active or passive, short- or long-distance, freshwater movement (underwater or on the water surface) | Morphology adapted for swimming (e.g., fins, webbed feet), floating (e.g., air-filled tissues), skating (e.g., long legs, hydrophobic hairs), or crawling on underwater substrates (e.g., claws); hydrodynamic shape (e.g., streamlined body case); muscles for locomotion; respiratory organs and structures (e.g., gills, breathing tubes, plastrons); migration or dispersal synchronized with flow and thermal regimes (e.g., summer or winter flows) | Behaviors that exploit downstream and lateral flow (e.g., passive drift, behavioral drift, movement into inundated floodplains) or that resist flow (e.g., active swimming, positive rheotaxis; burrowing through soft substrates or interstitial spaces); underwater dispersal triggered by changes in habitat condition (e.g., drying, warming, low dissolved oxygen, stormflow); behaviors for the display or release of seeds or propagules (e.g., glochidia) that promote transfer to dispersing hosts | High density of streams and rivers, in networks that provide a variety of stream sizes, flow regimes, and in-stream habitat types | Most fishes and lotic insects; most riverine plants, amphibians, reptiles, and mammals; some riverine birds; some freshwater molluscs and crustaceans |
| Active or passive, short-distance, overland movements | Presence of a terrestrial phase or life stage; lungs, spiracles, and tracheal tubes, or other mechanisms for air-breathing; variable body size; ambulatory limbs (e.g., jointed legs for jumping, walking, or crawling; wings) | Moisture preservation behaviors; aerial or terrestrial dispersal triggered by changes in habitat condition (e.g., drying, warming, shifts in dissolved oxygen or ion levels, stormflow), population density, or community structure | High density of all freshwater habitats, or high density of wetlands but lower stream/river density; or arid streams; or high density headwaters with ephemeral streams | Many amphibians and aquatic reptiles; some flightless aquatic insects (e.g., Abedus herberti, Belostomatidae); some crustaceans and aquatic mammals |
| Active or passive, long-distance, overland movement | Same as above, also: large body size; large energy reserves; large limbs and musculature for movement; eggs or seeds that can survive desiccation or passage through gut of mammals; clinging seeds or propagules; broad niche breadth | Same as above, also: behaviors that increase odds of being ingested (e.g., release of seeds when and where migratory seed-and fruit-eating animals are mostly likely to be present) | Low density of all freshwater habitats or high density of ephemeral ponds and/or intermittent streams/ rivers | Most aquatic mammals; many amphibians and aquatic reptiles; phoretic meiofauna; zoochoric aquatic plants |
| Active or passive, short-distance, through sediment movement | Narrow body (anguilliform); spade-like head, limbs, or structures (e.g., sclerotized tusk) for digging or anchoring; protective structures (e.g., gill plates); tolerance of low oxygen or anaerobic conditions; dormant phase or life stage | Burrowing into soft substrates or interstitial spaces constructing; well-defined tubes or other structures to facilitate flow for respiration or filter feeding | Low density of all freshwater habitats, or high density of ephemeral ponds and/or intermittent streams/ rivers | Burrowing aquatic insects (e.g., Ephemeroidea) and bivalves (Unionidae); meiofauna (e.g., some copepods); many fungal and bacterial species |
| Active or passive, short-distance, aerial movement | Aerodynamic form; variable body size; wings; winged or clinging seeds or propagules | Clinging, skimming, flight; behavioral response to change in habitat conditions (e.g., drying down), population density, or community structure | High density of all freshwater habitats, or high density of wetlands (including seasonal wetlands) but lower stream/river density; or | Many aquatic insects that have a terrestrial adult stage; some fully aquatic diving beetles (Dytiscidae), water boatmen (Corixidae) and |
HLRs in the continental United States (U.S.) based on similarities of multiple land-surface-form, geologic, and climate characteristics. Here we discuss five of these HLRs (Figure 3), the structural characteristics that we expect to occur in each, and the functional traits and biotic adaptations that would be needed by biota to convert structural connectivity of the mosaic into functional connectivity required for population persistence. The five HLRs we have selected as examples are: desert washes with a low average density of wetlands and seasonal springs (HLR 14; Figure 3, inset 5); arid playa landscapes with a moderate average wetland density and low stream density (HLR 10; Figure 3, inset 4); semiarid prairie potholes with a high average wetland density and low stream density (HLR 8; Figure 3, inset 3); subhumid plains with a high average density of streams and riparian wetlands and high influence by subsurface flows (HLR 1; Figure 3, inset 1); and humid plains with a high average density of streams and wetlands (HLR 2; Figure 3, inset 2). Until FEMs are more explicitly mapped, the HLRs of Wolock et al. (2004), and other HLR classifications (e.g., Wigington et al. 2013), can facilitate exploration of physiological, morphological, and behavioral adaptations of organisms to the unique structural connectivity within differing landscapes.

Wolock et al. (2004) described HLR 10 as “arid plateaus with impermeable soils and permeable bedrock.” The hydrology of this area is dominated by overland flows and deep groundwater. While these groundwater flows support deep aquifers (e.g., the Ogallala Aquifer), overland flows on impermeable soils result in the development of the numerous playa lakes and wetlands that define this region. Thus, this

### TABLE 1. (continued)

| Movement type                        | Morphological and physiological traits                                                      | Behavioral traits                                                                 | FEM conditions promoting movement type                                      | Example biota                                                                 |
|--------------------------------------|------------------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------|-------------------------------------------------------------------------------|-------------------------------------------------------------------------------|
| Active or passive, long-distance,    | Same as above, also: large body size, strong wings and musculature, large energy reserves,    | Life stage for long-distance migration or dispersal from natal sites to breeding or| High density of small (headwater) streams                                    | Backswimmers (Notonectidae)                                                      |
| aerial movement                      | eggs or seeds that can survive passage through gut of birds, light wind-blown seeds, ballooning | oviposition sites; behaviors that increase odds of being ingested (see above);    | Low density of all freshwater habitats, or high density of ephemeral ponded   | Water birds; zooplankton, seeds, or  |
| Connectivity                        | Drought-resistant resting eggs, dormant phase, propagules (statoblasts, gemmules, cysts), shell | escaping predators or harsh conditions                                             | wetlands and/or intermittent streams/rivers                                  | many dragonflies and damselves (Odonata)                                      |
| through time                         | or protective case, seedbank, eggbank, anhydribiosis, cryptobiosis, short freshwater life stage(s), |                                                                                   |                                                                              |                                                                               |
|                                      | atmospheric respiration                                                                      | Life stage for long-distance migration or dispersal from natal sites to breeding or |                                                                              |                                                                               |
|                                      |                                                                                                | oviposition sites; behaviors that increase odds of being ingested (see above);    |                                                                              |                                                                               |
|                                      |                                                                                                | escaping predators or harsh conditions                                             |                                                                              |                                                                               |

Note: While not comprehensive, these examples illustrate the diversity of traits and strategies that aquatic and semiaquatic species have evolved for movement within and among habitats.
HLR is typified by aquatic and wetland habitats that, as a result of the region’s arid climate, often go dry and are separated by relatively large distances. Consequently, biota without a mechanism to survive drying would be minimal or absent in a FEM within HLR 10 (although these taxa could persist in the few streams or rivers that pass through the HLR). The primary characteristics of the region are conducive to long-distance dispersers (e.g., damselflies [Zygoptera], waterfowl) or those that can survive long dry periods (e.g., clam shrimp [Eulimnadia]; Great Plains toad [Anaxyrus cognatus]; McCay et al. 1990; Anderson and Smith 2004).

HLR 8 is described as semiarid plains. Overland flow (primarily from snowmelt) drives the hydrology of the numerous wetlands on relatively impermeable glacial till within this HLR. The wetter climate of HLR 8 contributes to a greater density of wetlands on the landscape than under the arid climate of HLR 10, but flowing water and permanent lakes are largely absent in the region. Therefore, fishes were not historically a significant component of the region’s biota (McLean et al. 2016). The FEMs in this region are amenable to species capable of short-distance overland and aerial movements (e.g., painted turtles [Chrysemys picta], Griffin 2007; some midges [Chironomidae], Bataille and Baldassarre 1993), while still supporting long-distance dispersers (e.g., waterfowl) and some species with resistance traits due to longer term periodic drought (e.g., some cladocerans [Gleason et al. 2004]). Additionally, species that may outwardly appear to be capable of only short-distance movements (e.g., many seeds, small freshwater crustaceans) may be capable of long-distance dispersal if they have adaptive traits allowing for ecto or endo-zoochory or phoresy (i.e., “hitch-hiking” on or within dispersing hosts).
In contrast to HLR 8, HLR 1 is underlain by permeable soils and bedrock, and aquatic and wetland ecosystems are primarily driven by groundwater flows rather than overland runoff. In the mosaics of HLR 1, we find a larger number of flowing-water systems supported by groundwater inputs. There is also a greater number of riparian wetlands supported by bidirectional connections with stream networks, and upland embedded wetlands, also influenced by groundwater inputs through the permeable substrates. Biotic communities within FEMs characteristic of HLR 1 would be much more likely to contain fishes and other organisms with adaptive traits that facilitate movements along stream channels and riparian corridors. Conversely, organisms exhibiting drought-resistant traits would be less prominent here than in either HLR 8 or 10.

In areas designated as HLR 2, the climate is very wet and an even greater abundance of flowing-water and permanent-water systems exist in this region. Therefore, the landscape is conducive to dominance by physiological, morphological, and behavioral traits facilitating linear movements along continuous aquatic or wetland habitats such as fishes and many stream-dwelling amphibians. Also, generalists that can live in both streams and wetlands are likely to occur given the conditions present in HLR 2.

At the opposite extreme of HLR 2 are the arid plateaus with permeable soils and bedrock found in HLR 14. A FEM within HLR 14 is expected to be dominated by the terrestrial matrix. The few aquatic or wetland habitats would be streams or rivers that originated in distant mountains or spring-fed habitats supported by groundwater flows through the permeable substrates. The great distances between lake and wetland habitats would tend to result in high levels of endemism (e.g., the many endemic pupfish such as Desert Pupfish [Cyprinodon macularius]), except for those species with traits that make them capable of moving long distances between suitable habitat patches (e.g., waterfowl).

CONCLUSIONS

The FEM perspective views aquatic and wetland habitats as integral components of a mosaic with terrestrial habitats as the mortar that binds together, rather than separates, landscape components. This perspective reflects the underlying reality stated by John Muir (1911, 110), “when we try to pick out anything by itself, we find it hitched to everything else in the Universe.” FEMs adopt the interconnected view of inland landscapes and facilitate the merging of aquatic, wetland, and terrestrial perspectives of hydrology, biogeochemistry, and ecology consistent with the next generation of simulation models that combine concepts of population, community, and ecosystem ecology. A FEM perspective also acknowledges flows of nutrients, energy, particles, and organisms among ecosystems, consistent with the functioning of meta-ecosystems.

Viewing aquatic, wetland, and terrestrial ecosystems from a FEM perspective serves to facilitate their study and management given the inherent integration of natural landscapes. For example, wetlands outside of floodplains, along with ephemeral, intermittent, and seasonally flowing streams, have been defined as vulnerable waters due to their susceptibility to degradation and destruction from anthropogenic activities such as agricultural development and urban expansion (Creed et al. 2017). From a FEM perspective, these vulnerable waters are critical as they are typically the first water feature to interact with terrestrial solute and particle fluxes (Alexander et al. 2007). If such a perspective is adopted, concepts such as the “geographic isolation” of wetlands (Tiner 2003) lose their validity and relevance (Mushet et al. 2015; Calhoun et al. 2017), because geographic connections of aquatic and wetland habitats to terrestrial habitats are recognized as integral parts of the system. Additionally, from a FEM perspective, the continuum of wetlands may be characterized as transitional lands between aquatic and terrestrial habitats rather than aggregated with aquatic ecosystems and divorced from terrestrial systems. Placement of wetlands, including vulnerable waters, back into their important transitional position more fully acknowledges the role that they play in a fully functional landscape. Given the myriad species and associated physiological, morphological, and behavioral traits that exist in any ecosystem, a perspective that acknowledges the interconnected nature of terrestrial, aquatic, and transitional ecosystems as the default position, and integrative models that can be tailored to different representations of landscape mosaics, will lead to improved understanding of freshwater ecosystems through the integration of population, community, and ecosystem ecology.

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