esa ECOSPHERE

CONCEPTS & THEORY

On the multiple ecological roles of water in river networks

Ryan A. Sponseller,[1,]† James B. Heffernan,[2] and Stuart G. Fisher[3]

[1]*Department of Forest Ecology and Management, Swedish University of Agricultural Sciences (SLU), SE-901 8 Umeå, Sweden*
[2]*Nicholas School of the Environment, Duke University, Durham, North Carolina 27708 USA*
[3]*School of Life Sciences, Arizona State University, Tempe, Arizona 85287 USA*

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Abstract. The distribution and movement of water can influence the state and dynamics of terrestrial and aquatic ecosystems through a diversity of mechanisms. These mechanisms can be organized into three general categories wherein water acts as (1) a resource or habitat for biota, (2) a vector for connectivity and exchange of energy, materials, and organisms, and (3) as an agent of geomorphic change and disturbance. These latter two roles are highlighted in current models, which emphasize hydrologic connectivity and geomorphic change as determinants of the spatial and temporal distributions of species and processes in river systems. Water availability, on the other hand, has received less attention as a driver of ecological pattern, despite the prevalence of intermittent streams, and strong potential for environmental change to alter the spatial extent of drying in many regions. Here we summarize long-term research from a Sonoran Desert watershed to illustrate how spatial patterns of ecosystem structure and functioning reflect shifts in the relative importance of different 'roles of water' across scales of drainage size. These roles are distributed and interact hierarchically in the landscape, and for the bulk of the drainage network it is the duration of water availability that represents the primary determinant of ecological processes. Only for the largest catchments, with the most permanent flow regimes, do flood-associated disturbances and hydrologic exchange emerge as important drivers of local dynamics. While desert basins represent an extreme case, the diversity of mechanisms by which the availability and flow of water influence ecosystem structure and functioning are general. Predicting how river ecosystems may respond to future environmental pressures will require clear understanding of how changes in the spatial extent and relative overlap of these different roles of water shape ecological patterns.

Key words: disturbance; drought; ecohydrology; flooding; landscapes; river continuum.

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† **E-mail:** ryan.sponseller@slu.se

INTRODUCTION

The distribution and movement of water across landscapes influence a broad suite of ecological, biogeochemical, and geomorphological processes. Most obviously, water is a critical resource, necessary to support biological processes (Noy-Meir 1973, 1974, McCluney and Sabo 2009) and provide habitat for aquatic and riparian species (Stanley et al. 1997). Accordingly, the inputs and flows of water at broad scales drive landscape, regional, and global patterns of metabolism (D'Odorico et al. 2010, Schwalm et al. 2011), as well as the basic life history traits of plants and animals on land (e.g., Schwinning and Sala 2004) and in water (Lytle and Poff 2004). In addition, water serves as a major vector for transport and connectivity in landscapes (Fisher et al. 2004), regulating the passive movement of dissolved and suspended materials (e.g., energy and nutrients) and facilitating the active dispersal of aquatic organisms. Finally, hydrologic flow acts physically on landforms and organisms (Fisher et al. 1982, Montgomery 1999, Corenblit et al. 2009), shaping landscapes through erosional processes that disturb and displace biota, reset ecological communities at varying frequencies, and govern the long-term physical and geometric structure of habitats.

These general 'roles of water'—as a resource/habitat, a vector for connectivity, and an agent of physical disturbance and geomorphic change—can operate to varying degrees within a given ecosystem (e.g., Doyle et al. 2005). Among ecosystems, the relative strength or importance of these different roles can vary according to landscape position, underlying geologic and geomorphic structure, and prevailing climate. Our central hypothesis is that these differences in turn determine what kinds of processes drive the ecological or biogeochemical dynamics at any given time or place. A comprehensive understanding of ecohydrological systems thus requires a framework that integrates these roles and the different models that characterize their ecological influences. Our goal is to develop such a framework and apply it towards a conceptual model for running-water ecosystems that addresses ecological patterns within drainage networks, and among river systems in different climatic settings.

ECOLOGICAL PATTERNS IN RIVER NETWORKS

Research in freshwater science has long sought to explain ecological changes observed from headwater streams to large rivers. The influential 'River Continuum Concept' (RCC: Vannote et al. 1980) described how downstream change in channel geometry, together with the transport and processing of organic and inorganic resources, explains longitudinal patterns in aquatic community structure and ecosystem functioning (Minshall et al. 1985). Similar models address riparian plant community structure and diversity, based on predictable changes in flood frequency and power with drainage size (e.g., Gupta et al. 1994) and the influence of hydrologic dispersal on the distribution of riparian species (e.g., Nilsson et al. 2010). In response to these drivers, riparian communities are also thought to change predictably with longitudinal position in the network (Nilsson et al. 1989, Bendix 1997, Tabacchi et al. 1998). More recent conceptual models of river networks emphasize discontinuities and non-linearities in ecological pattern, which may emerge from man-made impoundments (Ward and Stanford 1983), tributary junctions (Benda et al. 2004), and abrupt changes in geomorphic structure and processes (Montgomery 1999, Poole 2002, Finlay et al. 2011). While specific predictions from the RCC and similar models are not always met, their importance lies in the recognition of an underlying set of factors (channel geometry, flood disturbance, and hydrologic connectivity) that determine ecological patterns and processes within river systems (Webster 2007, Thompson and Lake 2010).

Existing models of longitudinal change in rivers have been developed mostly in mesic and montane environments and thus highlight the role of water as an agent of physical disturbance and vector for connectivity, but largely ignore water availability per se as a driver of ecological pattern. This omission is striking given the obvious relevance of water to biological processes, the global coverage of arid, semi-arid, and dry sub-humid lands, and an increasingly large body of research describing the ecological consequences and legacies of drying and drought for the ecology of streams and riparian zones (Stromberg et al. 2007, Larned et al. 2010*a*, Lake 2011). Intermittent and ephemeral streams are dominant features of drainage systems worldwide, even in mesic settings (Dodds 1997). Moreover, the direct and indirect effects of human activities, including the extraction of surface and groundwater (e.g., Gleick and Palaniappan 2010, Sabo et al. 2010), land-use and land-cover shifts (e.g., Scanlon et al. 2007), and changes in air temperature (Seager et al. 2007) all could alter the frequency and spatial extent of intermittency and drought within drainage networks globally.

Here we describe a framework for understanding ecological patterns in river systems that accounts for how the roles of water as a resource, vector for connectivity, and agent of physical disturbance are distributed and interact within drainage networks. The integration of these three roles has the potential to provide a model for understanding the spatial organization of species and processes that is applicable across a broad range of climatic settings (e.g., from mesic to xeric biomes), and is essential if we are to predict how ecological responses to future hydrologic change may be propagated through river networks. We focus on the longitudinal changes along a well-studied upper Sonoran Desert channel continuum (Sycamore Creek, USA) to illustrate how the importance of water as a resource, *relative* to its roles as an agent of flood disturbance or vector for connectivity, varies with catchment size and local geomorphology. In this context, arid and semi-arid landscapes represent extreme cases in that the importance of water as a resource is particularly obvious and evident from the distribution of vegetation among different upland and riparian habitats. Nonetheless, such systems are useful as end members, against which spatial patterns in other biomes may be compared, and from which we might gain insight into future ecological changes in river networks that could arise from climate and/or land use change.

Ecological Patterns in a Desert Stream Network

Sycamore Creek drains a 505-km^2 basin located 52 km northeast of Phoenix, Arizona in the Mazatzal Mountains, receives about 40 cm of rainfall annually and has been the focus of ecosystem research since the late 1970s. Hydrologic patterns within the Sycamore Creek drainage basin are extremely variable in space and time (Stanley et al. 1997), and the rainfall regime and subsequent hydrologic routing have consequences for ecological patterns at multiple scales, in both terrestrial and aquatic environments. Our conceptual model for understanding longitudinal change in this system recognizes three scaling domains (sensu Wiens 1989), or distinct ranges in drainage size, within which ecological pattern and process are driven by similar 'roles of water' (Fig. 1): the *pulse domain*, in which hydrologic flow through ephemeral channels occurs only in response to rain events; the *seasonal domain*, where alluvial storage may support flow for weeks to a months; and the *perennial domain*, where near-permanent flow occurs during most years. This organizational framework is conceptually analogous to the process-domain concept (Montgomery 1999), but instead of focusing on geomorphic processes, we address the scaling domains that arise from the distribution and flow of water across landscapes. Importantly, the relative importance of, and interactions among, the different roles of water shift among these domains, and the scale breaks separating them correspond to the emergence of ecological systems with fundamentally different properties and underlying dynamics.

Pulse domain (PLD)

As in other desert basins, ephemeral rills and washes account for most of the channel length in the Sycamore Creek catchment. Hydrologic flow in these channels coincides with precipitation and may persist from minutes to weeks, depending on drainage size and rainfall characteristics (e.g., storm size, intensity, and frequency; Welter 2004). Channels within the pulse domain are thus usually dry and represent primary habitat for few organisms with turnover times greater than that of microbes. In response to rainfall, however, these rills and washes receive nutrient-rich water from the surrounding uplands, and rates of microbial activity in sediments can increase rapidly upon rewetting (Welter 2004). Accordingly, across a broad range of drainage sizes within the pulse domain (e.g., all catchments <1 km^2), longitudinal patterns of biological activity are determined by the size and intensity of rain events and the downstream extent of water flow and associated transport of resources (Belnap et al. 2005).

Long-term rainfall and runoff patterns also drive the development and productivity of riparian zones within the pulse domain. As rills transition into larger washes, the most obvious changes in plant structure include an increase in overall cover and a greater relative dominance by facultative riparian species, like velvet mesquite (*Prosopis velutina*; Stromberg et al. 1996, Sponseller and Fisher 2006). As is the case in adjacent uplands, plant growth along channels with ephemeral flow regimes is closely linked to

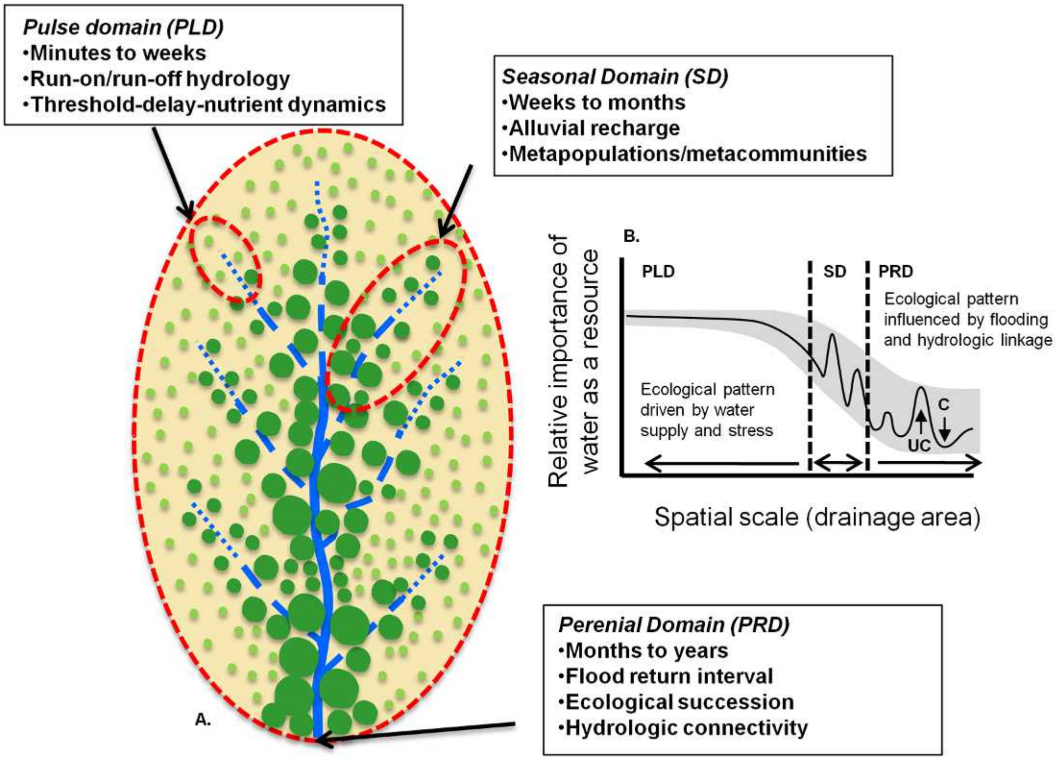

Fig. 1. (A) Representation of longitudinal patterns and scaling domains described for the Sycamore Creek drainage network. Each scaling domain represents a range of drainage sizes within which ecological pattern and process are linked to similar 'roles of water'. Boxes indicate the general time scale of wetted conditions, identify key hydrological processes, and provide examples of dominant ecological frameworks that characterize each domain. The overall longitudinal pattern that emerges (inset B) reflects non-linear shifts across scaling domains where the overwhelming importance of water as resource/habitat gives way to additional roles (e.g., flooding and vector for connectivity) as flow permanence increases. This longitudinal pattern is not continuous, but is instead modified and disrupted at smaller scales by variation in geomorphic structure (e.g., in constrained (C) versus unconstrained (UC) segments) that can influence local surface and subsurface water availability.

seasonal precipitation; however, where rainfall is sufficient to generate run-off, water lost vertically and laterally can augment the productivity of vegetation along washes (Ludwig 1987). Overall, the ecological models that are most useful for understanding and predicting the dynamics in both channel and riparian habitats within the pulse domain borrow from terrestrial and ecohydrological perspectives, including pulse dynamics (Austin et al. 2004, Welter et al. 2005), threshold-delay models of plant growth (Ogle and Reynolds 2004), and hillslope-hydrologic processes that redistribute water and materials in landscapes (e.g., Ludwig et al. 2005).

Seasonal domain (SD)

The structure and dynamics of stream and riparian ecosystems associated with the intermittent and often-isolated reaches within the seasonal domain are less well studied than either upstream washes, which have fallen largely in the realm of terrestrial ecology and hydrology, or downstream perennial reaches, where aquatic research has most often focused. For stream biota, the presence/absence of water will represent a first-order constraint to biotic distributions (Stanley et al. 1994), but we expect that ecological dynamics within this domain are also captured by conceptual models that emphasize spatial processes, including island biogeography, source-sink dynamics, and metapopulation and metacommunity models (Larned et al. 2010*a*). Controls on biogeochemical processes and transport are likely to shift from runoff-driven, pulse dynamics during dry periods to surface-subsurface hydrologic interactions characteristic of more permanent channels during periods of sustained flow.

Within the seasonal domain, surface and subsurface drainage from low-order catchments and high-elevation water sources recharge downstream alluvial aquifers, supporting stream flow in larger channels for extended periods of time (e.g., weeks to months) through the winter, spring, and early summer. While there is a general increase in surface and/or subsurface permanence with drainage size, there is also important spatial variation in flow within this domain that is associated with local geomorphic setting, including valley floor width and distance to bedrock (Stanley et al. 1997). Channels with increasingly permanent flow support characteristically 'aquatic' biota, like benthic and hyporheic invertebrates and algae (e.g., Clinton et al. 1996). Flow permanence, the nature of hydrologic connection with downstream habitats (e.g., surface vs. subsurface), and distance from propagule sources interact with organismal life history traits (e.g., growth rate, dispersal mode and capability) to determine the local composition of invertebrate assemblages. Tributaries that sustain brief periods of surface flow support benthic taxa with short life cycles and/or air-breathing adult insects with strong dispersal abilities (Gray 1980, Gray 1981). In contrast, large tributaries characterized by longer periods of surface and subsurface flow may share many of the aquatic taxa that are common to the main stem of Sycamore Creek (Stanley 1993). Annual drying of even these larger tributaries, however, generally excludes slower-growing benthic invertebrate and fish species that are found in downstream habitats within the network.

Riparian vegetation in the seasonal domain is dominated by facultative tree species whose groundwater use generally increases with drainage area, leading to increasing size, cover, and productivity (Stromberg et al. 1996, Snyder and Williams 2000, Sponseller and Fisher 2006). This access to groundwater reduces the sensitivity of riparian vegetation growth to precipitation pulses, but heterotrophic processes in surface soils are still strongly subject to wetting-drying cycles (Williams et al. 2006). Spatial and temporal hydrologic intermittency in this domain may promote greater long-term diversity for some riparian groups when compared to either pulse or perennial domains (e.g., herbaceous plants; Katz et al. 2011). Finally, longitudinal increases in plant growth correspond to greater accumulation of soil resources, as well as a fundamental shift in ecosystem patterning as individual 'plant islands' characteristic of desert uplands (Schlesinger et al. 1996) give way to larger multi-plant, riparian-forest galleries.

Perennial domain (PRD)

The main channel of Sycamore Creek experiences spatially-intermittent flow, with several bedrock- and valley floor-constrained segments that retain surface water even during dry periods. These nearly-permanent stream reaches support diverse benthic and hyporheic communities (Gray 1981, Boulton and Stanley 1995), with exceptionally high rates of primary (Busch and Fisher 1981) and secondary (Fisher and Gray 1983) production. Whereas channels in the pulse domain have sufficient hydrologic permanence to support organisms with generation times on the scale of hours (e.g., bacteria), stream reaches within the perennial domain may host aquatic macroinvertebrate taxa that require as much as a year to develop (Gray 1981), as well as several fish species that need months or even years to reach reproductive age (Fisher et al. 1981). These channels also provide habitat for several obligate riparian tree species (e.g., sycamore, *Platanus wrighti*; cottonwood, *Populus fremontii*; willow, *Salix goodingii*), smaller shrubs associated with parafluvial (sandbar) sediments (seepwillow; *Baccharis salicifolia*; Schade et al. 2001), and obligate wetland plants (which form 'ciénegas') that thrive under long hydroperiods (Heffernan 2008).

With the relative decrease in drying stress that accompanies greater catchment area, physical disturbance by floods and transport of resources by flow become correspondingly more important in both streams and riparian zones (Fisher et al. 1998). Within the perennial domain, frequent and severe flash floods mobilize channel sediments and displace algae and other stream organisms (Fisher et al. 1982). These flood pulses also deliver water, nutrients (Martí et al. 2000), and sediments (Sponseller and Fisher 2006) laterally to riparian zones and can mobilize resources stored in dry soils (Heffernan and Sponseller 2004). The temporal dynamics of population, community, and ecosystem processes in stream reaches within this domain are strongly influenced by the timing and magnitude of these high-flow events and the subsequent trajectories of ecological succession by primary producers and consumers (Grimm and Fisher 1989), which are further shaped by the transport and exchange of limiting resources across subsystems during recovery (Valett et al. 1994, Fisher et al. 1998).

The history of research at Sycamore Creek captures the dynamics for only a portion of the dryland river continuum. Larger river systems in arid and semi-arid regions typically share basic hydrological characteristics (Puckridge et al. 1998) and, like the perennial domain of Sycamore Creek, are subject to flooding and drying disturbances and have spatially intermittent flow regimes (e.g., Stromberg et al. 2007) that often include sections of perennial aquatic habitat (e.g., Bunn et al. 2006*a*). What is unique in many lowland river systems, however, is the development of wide, hydrologically-active floodplains (Lake et al. 2006), which include a diversity of aquatic habitats (e.g., oxbows lakes, sloughs, and wetlands) not observed in the Sycamore Creek basin. These water bodies themselves span gradients of hydrologic intermittency and degree of connectivity to the main stem and can encompass a continuum of lentic to lotic habitat characteristics (Sheldon et al. 2002). Floodplains of arid and semi-arid lands can be remarkably rich and productive ecosystems with notably diverse communities of invertebrates, fish, and waterfowl (e.g., Bunn et al. 2006*b*).

HIERARCHICAL STRUCTURE OF ROLES ACROSS SCALING DOMAINS

Observations made at Sycamore Creek illustrate the overwhelming importance of water availability as the driver of ecological pattern and process along the entire channel continuum and contrast strongly with comparable models derived from mesic settings (e.g., Minshall et al. 1985). The longitudinal gradient of hydrologic permanence that we describe for this system dictates the distribution of species and processes across the network, and only beyond a threshold in drainage size do flash flooding and subsequent succession (e.g., Fisher et al. 1982), vertical and lateral hydrologic exchange (i.e., connectivity; Valett et al. 1994, Henry and Fisher 2003), and nutrient limitation (Grimm and Fisher 1986) emerge as key drivers of ecological dynamics. Similarly, only in the most downstream reaches do the timing and magnitude of floods, and associated geomorphic changes, play a critical role in the structure, recruitment, and overall dynamics of riparian vegetation (e.g., Stromberg et al. 1993, Lite et al. 2005). This hierarchical structuring of the roles of water along the channel continuum is conceptually analogous to models of terrestrial ecosystem change with increasing rainfall, which similarly argue that water requirements must be met before other ecological drivers and interactions can emerge as significant (Schwinning and Sala 2004). We suggest that hydrologic flowpaths within catchments represent a spatial expression of this general principle and accordingly determine when and where other processes or interactions emerge as important ecological drivers within drainage systems.

Hierarchy of roles within the pulse domain (PLD)

In the pulse domain, water inputs and availability are obviously vital, and the potential hierarchical interactions with other roles of water are likely to be relatively weak. However, the transport of nutrients and sediments by hydrologic flow may nonetheless influence certain ecological patterns or processes over short time scales. For example, while precipitation is known to trigger biological activity in arid soils, rapid responses to water pulses, coupled with low resource availability, may lead to limitation by energy and/or nutrients during a single wetting cycle (Sponseller and Fisher 2008). Given this, the redistribution of resources via overland and rill flow (i.e., connectivity) has the potential to mediate the pattern, magnitude, and duration of local precipitation-driven pulses within the rainfall-runoff scaling domain (Belnap et al. 2005). Physical disturbance is potentially the least important ecological role of water within the pulse domain, as overland flow typically lacks the power to remove or disturb upland vegetation. Bank erosion of rills, however, may occasionally result in plant mortality, and over longer timescales, incision of arid uplands by the channel network shapes the characteristics of overland flow and thus patterns of water storage and loss (Chartier and Rostagno 2006).

Hierarchy of roles within the seasonal domain (SD)

Hierarchical interactions among of the roles of water within the seasonal domain are potentially strong and mediated by basin properties (e.g., valley floor width) that dictate local flow conditions. Stream reaches within this domain may be characterized by extended periods of time (weeks to months) where the constraints of water limitation are alleviated, allowing for other factors to emerge as drivers of local ecological dynamics. While pulse responses to water inputs to previously dry channel and riparian habitats are undoubtedly still important within this domain, prolonged subsurface flow and more reliable access to groundwater can begin to decouple some ecological processes (e.g., riparian plant productivity) from short-term climatic events (e.g., Williams et al. 2006). Because of these extended periods of flow, it is within this scaling domain that flooding first emerges with dual ecological roles. During dry periods, floods likely serve as a trigger for biotic activity (as in the pulse domain); however, following even a short period of sustained stream flow, the same events can act as a physical disturbance that decimates benthic communities and initiates community and ecosystem succession (Stanley et al. 2004). Despite this, the overarching importance of water availability is still clear within this domain. Longer-lived organisms that require surface-water connections (e.g., fish) are undoubtedly more challenged by the short duration of habitat availability and hydrologic connectivity than are organisms with very short generation times (e.g., microbes), or strategies for tolerating or avoiding drought (e.g., facultative phreatophytes, aquatic insects with highly mobile adult stages). For groups not filtered out by the duration of water availability, flood disturbance and mediation of chemical conditions by longitudinal and vertical hydrologic connectivity likely play a more significant role in shaping ecosystem properties during periods of sustained flow.

Hierarchy of roles within the perennial domain (PRD)

Within the perennial scaling domain, water increasingly acts as an agent of physical disturbance and vector for other resources, and the potential interactions among all three roles are more pronounced. For example, while early studies in Sycamore Creek documented rapid (1–2 month) recovery by benthic communities in response to flash flooding (Fisher et al. 1982), more recent compilations of time-series data in this system indicate that short-term community changes during post-flood succession are influenced by longer-term responses to antecedent drought in the system (Boulton et al. 1992, Sponseller et al. 2010). Within the same domain, extended periods of quiescent surface flow can promote the colonization of channel sediments by wetland plants (ciénegas), which profoundly alter the effects of subsequent floods. Ciénegas occur almost exclusively in constrained channels that sustain perennial surface water, while gravel-bed reaches predominate in wider alluvial valleys that support more intermittent flow (Heffernan et al. 2008). During dry years, alluvial volume drives variation in local surface water permanence and thus production of vegetation. Given sufficient biomass accrual, plants stabilize sediments and reduce shear stress, thereby conferring resilience of wetland patches to even large flash floods. This positive feedback creates alternative stable states (ciénega vs. gravel-bed reaches; Heffernan 2008) that differ markedly in their hydrologic, geomorphic, and biogeochemical structure (Heffernan et al. 2008). During wet years, surface water is more evenly distributed, but runoff and groundwater inputs (i.e., connectivity) may still be important because of their influence on N availability (Dent and Grimm 1999, Welter et al. 2005), which limits wetland plant production (Heffernan and Fisher 2012) and thereby the potential for local patches to cross thresholds in biomass sufficient to resist the effects of flash floods.

For larger dryland rivers, ecological and biogeochemical processes in lateral floodplains are also driven by hierarchical interactions among roles of water. As in other scaling domains, the availability of water remains a major organizer of floodplain communities and processes, through its role as a resource to consumers (McCluney and Sabo 2009), vegetation (Horner et al. 2009), and soil microbes (Harms and Grimm 2012) and as habitat for aquatic communities (e.g., Sheldon et al. 2002). Hydrologic connectivity, however, emerges as an increasingly important role for water for these ecosystems. Indeed, while floods represent major physical disturbances within the channels of mid-size reaches, these same events generally serve to replenish and re-connect floodplain habitats (Lake et al. 2006)—delivering water and associated nutrients (Valett et al. 2005, Harms and Grimm 2010), mobilizing resources in dry litter and soils (Baldwin and Mitchell 2000), triggering the development of organisms from dormant stages in dry sediments (Jenkins and Boulton 2003), and reestablishing hydrologic connectivity among the diverse water bodies. For aquatic habitats, this river-floodplain connectivity drives patterns of primary productivity (Bunn et al. 2006*b*, Gallardo et al. 2012) and shapes spatial variation in community composition (Sheldon et al. 2002, Leigh and Sheldon 2009).

Our model of interactions among the multiple roles of water in arid and semi-arid stream networks illustrates several characteristics that may also hold in more mesic settings. In particular, we find that the boundary between drying- and flood-dominated domains in this system is spatially and temporally indistinct. In other words, there is no precise channel size or drought frequency at which drying becomes unimportant or where flooding becomes the only significant driver. Instead, longitudinal patterns are characterized by shifts in the hierarchical interactions among these roles. In the driest upstream rills, as in their adjacent uplands, both short- and long-term dynamics are fundamentally linked to the availability of water. As water availability increases in larger drainage basins, flood disturbance and material re-distribution take primacy, but drying remains a significant mediator of longer-term trajectories in streams and riparian zones, even in dryland river systems much larger than Sycamore Creek (e.g., Stromberg et al. 2007). Thus, transitions between our proposed scaling domains may be best characterized by a shift in the timescales over which different roles of water exert the most significant influence.

REGIONAL PERSPECTIVES

Although water performs multiple ecological roles in all drainage basins, the spatial extent of different scaling domains is likely to vary as a function of regional climate, resulting in different 'river continuum' patterns among biomes (Fig. 2). This is particularly clear for the size of the pulse domain as the number and length of intermittent streams within drainage systems can differ by nearly an order of magnitude among regions (Dodds 1997). Channels that drain catchments as small as 0.1 km^2 may support perennial flow in temperate deciduous forests, yet hundreds of km^2 are required to sustain permanent aquatic habitat in some arid and semiarid landscapes. These regional differences in the drainage requirements for sustained flow determine the size of scaling domains within which other roles of water may influence ecological patterns. For example, the pulse domain may be constricted or absent from mesic/humid settings where systems are relatively less sensitive to water inputs (but see Lee et al. 2004), perennial streamflow begins in comparatively small drainages, and drought less frequently limits plant growth in riparian zones (Fig. 2A). Under such circumstances, longitudinal patterns likely conform to prevailing conceptual frameworks (e.g., the RCC), with relevant caveats (Poole 2002), and reflect downstream gradients in geomorphic structure (Finlay et al. 2011), and the coupling of in-stream processing with upstream-downstream hydrological linkage (Webster 2007). Similarly, for riparian zones in these environments, flooding, disturbance, and hydrologically-mediated dispersal (hydrochory) throughout the drainage system are likely to represent primary organizers of vegetation structure and function (Tabacchi et al. 1998, Montgomery 1999, Nilsson et al. 2010).

As increasingly dry regions are considered, the spatial extent of the pulse domain increases at the expense of domains that are strongly influenced by hydrologic disturbance and connectivity. For the driest regions, even the largest basins may only support sediment microbes and facultative riparian vegetation (Fig. 2C; e.g., Jacobson et al.

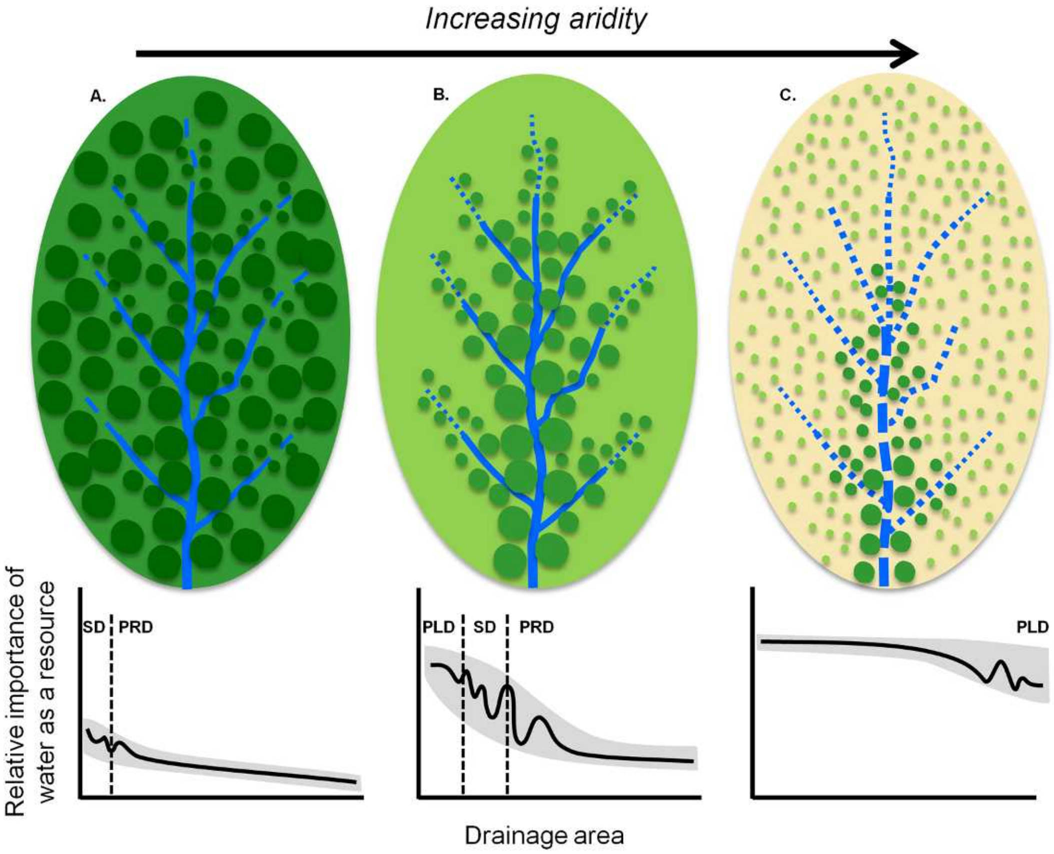

Fig. 2. Regional variation in longitudinal structure of river basins and hypothetical distribution of scaling domains organized (A–C) along a gradient of increasing aridity (abbreviations as in Fig. 1).

1999). Under these extreme circumstances, water largely plays the role of 'resource' across all scales. Between these humid and xeric end-members, thresholds between domains occur at intermediate drainage sizes. Such systems may be characterized by scaling domains that are particularly sensitive to geomorphic features that generate heterogeneity in surface water availability and are subject to relatively high variability in flow conditions (Fig. 2B). In regions with strong seasonal or inter-annual variation in precipitation and stream flow, the location of these thresholds may also shift in time (e.g., Larned et al. 2010*b*). Accordingly, hydrologic connectivity (i.e., aqueous transport of matter, energy, and organisms) may organize ecological pattern across a broad range of drainage sizes during the wet season, but this scaling domain may collapse to only include specific reaches or segments during the dry season. Furthermore, the location of these thresholds is likely to differ among response variables (taxonomic groups or processes) that vary in susceptibility to short-term water loss (Fig. 3). In particular, organisms which have strict requirements for surface water (e.g., most fish species) should respond to the longitudinal distribution of water availability in a much different way than those using hyporheic or groundwater habitats or sources, or species with aerial adults able to travel along spatially intermittent stream segments.

The conceptual model we present here addresses variation in the drivers of longitudinal pattern along river continua assuming a fairly simple hydrology, where drying is linked to the size of the upstream contributing area, and local constraints imposed by the valley floor width and distance to bedrock. Variation in aquifer geology (e.g., karst) and basin structure can also create diverse patterns of surface stream perma-

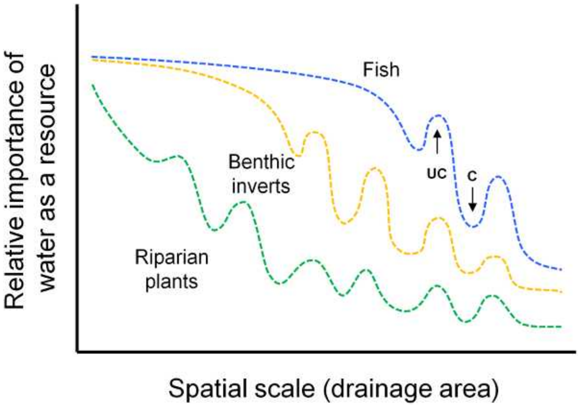

Fig. 3. Variation in the spatial extent at which water as resource may act as the primary determinant of longitudinal patterns for different vertebrate (blue), invertebrate (orange), and plant (green) groups within the same drainage basin. The different hypothetical curves arise from variation in life history characteristics that determine (1) the degree of hydrologic permanence necessary to sustain local populations, (2) the requirement for surface water connections to allow dispersal in the network, and (3) the ability to access water in deep soils or sediments for direct use or as habitat. Patterns here are intended to represent a system with a dry (semi-arid or Mediterranean) climate, where variation in the role of water is additionally influenced by valley floor constraints that influence local availability and flow (C and UC as in Fig. 1).

nence (Lake 2003, Steward et al. 2012). Overlain on these templates, human alterations such as groundwater extraction and channel impoundment can create novel patterns with clear ecological ramifications (e.g., Falke et al. 2011). The implications of these patterns may depend on the broader ecological and hydrogeologic context, as well as the specific variables of interest. For example, in mesic and/or floodplain settings, the presence of water may inhibit rather than stimulate some organisms and processes (e.g., through the development of anoxic conditions in soils, e.g., Silver et al. 1999). The framework presented here is not intended to generate specific predictions that apply to all landscapes, but rather to illustrate how ecological patterns in river systems can arise from the spatial distribution of water's differential influence as a resource and habitat, vector for connectivity, and agent of physical disturbance.

CONCLUSIONS

The challenge of broad-scale changes in water quantity and quality (Vorosmarty et al. 2010, Carpenter et al. 2011, Sabo et al. 2010) arises from and reflects the multiple roles that water plays in both minimally- and intensively-manipulated ecosystems. Changes in water quality and quantity may influence the hierarchical interactions among these roles (e.g., nutrient enrichment reducing the importance of surface-subsurface connectivity). Moreover, the number and character of these roles are very likely to expand when societal services such as power generation and recreation are considered (Guo et al. 2000, Brauman et al. 2007, Palmer et al. 2009). Global models that account for both climate and socio-economic factors project substantial variation in future discharge regimes (Alcamo et al. 2007): Some regions are expected to experience decreased flow and more frequent and severe drought (Seager et al. 2007); other areas may see increased discharge and flooding (Scanlon et al. 2007). These hydrologic changes will shift the scaling domains of the various ecological and socio-ecological roles of water within drainage basins; in turn, changes in ecological systems and services have the potential to feed back onto human decision making.

The ecological effects of future hydrologic changes on river continuum patterns will depend strongly on the degree to which these bring about novel conditions from an evolutionary perspective. Future changes may increase or decrease the spatial extent of already existing 'roles' within a given drainage system (e.g., altering the spatial extent of drought in an already xeric region). In this case, prior hydrologic conditions over evolutionary timescales generate a species pool able to take advantage of or at least accommodate such changes. For example, increasing the spatial extent of drying in a desert catchment may result in a shifting distribution of facultative riparian species that are already present in the landscape and are more competitive than obligate riparian taxa under a drier regime. On the other hand, future changes might involve the local emergence of 'roles' that historically have been non-existent or extremely reduced in spatial extent (e.g., widespread drought in a mesic region, or complete severing of longitudinal connectivity). In this case, the potential for biotic response to novel conditions may be limited by biogeographical constraints and the life history traits of the available species pool. Our ability to predict ecological responses to such novel stressors is particularly poor.

The importance of water's multiple functions within ecological systems is potentially relevant to a wide range of settings. Whether in wetlands, drylands, or mesic landscapes, water has the potential to act as a resource (or inhibitor), a vector for transport and connectivity, and an agent of physical disturbance—and in some cases may play other roles that shape community structure and ecosystem dynamics. The identity and character of these roles is likely to vary substantially depending on precipitation and temperature regime, and the relative importance of these roles will vary depending on the spatial and temporal scale of analysis (e.g., along upland catenas, within wetland complexes, or along regional land-use gradients). Here we have applied this water framework to understand the multi-scale drivers of ecological pattern and process along river continua, but we argue that an integrative view of the multiple roles of water is more generally fundamental to the development of a comprehensive and synthetic science of ecohydrology.

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