

Chapter 5. The Watershed Continuum: A Conceptual Model of Fluvial-Riparian Ecosystems

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Mountains of music swell in the rivers, hills of music billow in the creeks, and meadows of music murmur in the rills that ripple over the rocks. Altogether, it is a symphony of multitudinous melodies. All this is the music of waters ... sounds that span the diapason from tempest to tinkling raindrop, from cataract to bubbling fountain.

John Wesley Powell 1895: 394, 397

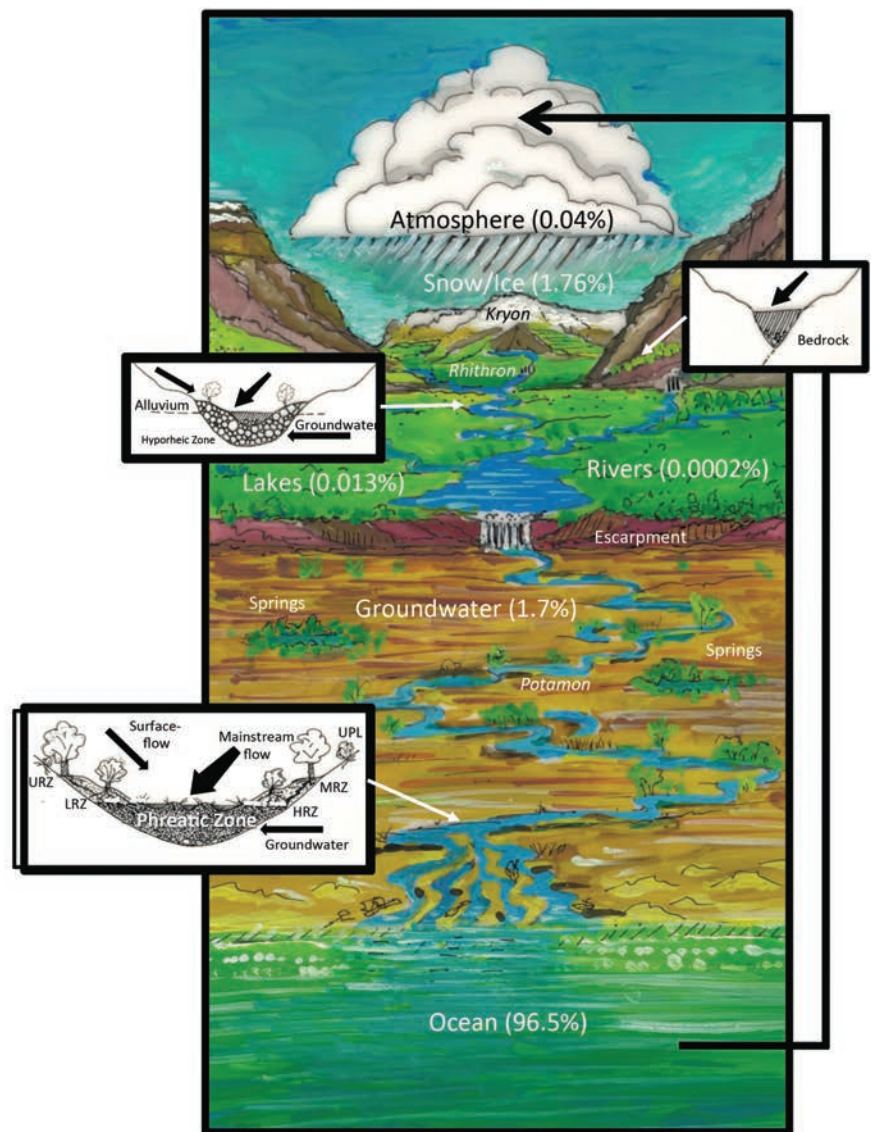
Introduction

Terrestrial fluvial-riparian ecosystems (FREs) are riverine landscapes that integrate aquatic, riparian, and upland domains within watersheds, linking physical, biological, and cultural-economic processes (Tockner et al. 2002). FRE characteristics and processes intergrade through the entire watershed, from the river's headwaters to its terminus into an endorheic basin or the sea, and can extend far out into the submarine environment (e.g., Canals et al. 2009; Vannote et al. 1980; Ward et al. 2018; fig. 10). FREs include all sources of water that contribute to the basin's riverine ecosystem, including springs, surface runoff, lakes, and atmospheric sources, such as humidity and fog. Only an average of 2,120 km³ (0.0002 percent) of the world's water exists in river systems at any given time (Shiklomanov 1993).

While rivers process only a tiny fraction of the Earth's fresh water and occupy only a minute proportion of the Earth's terrestrial surface, FREs are highly productive and ecologically interactive, often supporting diverse, densely packed biotic assemblages across short to vast time scales (Behrensmeyer et al. 1992; Sabo and Hagen 2012). Elevated biodiversity in FREs is linked to, and influenced by, many factors, including hydrogeomorphological, ecotonal, and shifting habitat mosaic effects (Gregory et al. 1991; Naiman and Décamps 1997; Naiman et al. 1987, 2005). Humans rely on FREs, and our species' evolutionary history and modern demography clearly demonstrate that reliance. As human domination of the Earth has progressed, rivers have been subjected to a host of anthropogenic alterations, including resource extraction, groundwater withdrawal, flow diversion and regulation, water quality degradation, and introduction of nonnative species. The need to integrate understanding of groundwater, fluvial, and lacustrine interactions within basins, and to sustainably manage rivers, has never been more urgent (Famiglietti 2014).

The natural dimensions and human impacts on FREs have stimulated a rich history of basic research, generating a vast literature, and prompting initiation of many local to international riparian research and stewardship organizations. Diverse ecohydrogeological models have been synthesized, tested, and predictively applied to FREs stewardship. Although sometimes biased by the expertise of the authors, these syntheses have advanced the collective understanding of FRE ecology. However, much remains to be learned. With the growing anthropogenic pressures on rivers and associated riparian ecosystems, we require an expansive, hierarchically organized conceptual framework to generate advanced understanding and management of FREs.

Figure 10—The hydrological cycle, emphasizing stream-order transition and lateral processes within watersheds between constrained, alluvial, and lentic reaches. Numbers are percent of Earth's water in different settings (Shiklomanov 1993). Illustration by Lawrence E. Stevens.



Here, we introduce the watershed continuum model (WCM) to expand interdisciplinary collaboration in ecological resource watershed system science and to improve science-based natural resource stewardship. The WCM describes matter, energy, and socio-values subsidy exchange within an entire FRE basin through the physical, ecological, and cultural processes that influence ecosystem geomorphology, biota, and society, across four-dimensional temporal and spatial scales. FRE connectivity extends from groundwater emergence and surface-derived flow, across the watershed, to the mouth, into the receiving basin or sea, and into the atmosphere. This integrative approach has been emphasized by Annear et al. (2004, 2009), Hynes (1975), Stanford (1998), Ward (1989), and others to interrelate physical hydrology, geochemistry, geomorphology, sedimentology, and aquatic and riparian domain linkage. We further advance this framework by linking aquatic and biological domains across stream order within watersheds (*sensu* Horton 1945; Strahler 1957) and over time.

We restrict our discussion in this chapter to natural, unmanipulated FRE processes and characteristics, independent of the many anthropogenic impacts affecting FRE

ecology. Anthropogenic impacts on rivers are widespread and merit much more scientific and societal attention, but we focus on natural processes and components to clarify and describe the interdisciplinary integration of hydrogeology, geomorphology, ecosystem ecology, and evolution. These components collectively interact within the watershed to generate FRE processes, assemblage structure, and stewardship decision-making. It is impossible here to do full justice to the broad array of FRE characteristics, themes, and models that contribute to this complex view; rather, we seek to provide a synthesis of patterns and insights, and to identify information gaps that affect FRE ecology and evolution. Collectively, the WCM couples multidirectional, trans-temporal material, and energy interchange from uplands to fluvial habitats throughout the basin, ultimately influencing the evolution of both aquatic and riparian FRE biota, as well as human cultures.

Although our focus is global, we draw on examples from western North America, especially the Colorado River basin in the American Southwest where we have done much of our work. We begin this chapter by summarizing basic fluvial-riparian concepts, and then we describe the physical, biological, and ecological elements that provide the basis for the WCM. Next, we review and discuss biologically focused FRE models using illustrated schema. Finally, we discuss issues that remain understudied or unresolved. Given the focus of this publication, and because integration of aquatic and terrestrial domains across scales within FRE ecology is complex and incomplete, we add additional emphasis on the riparian domain. We recommend further considerations and actions and discuss conceptual model dimensions and limitations.

We present the WCM to enhance ecological resource watershed system science and improve natural resources management. Full predictive capacity of the WCM is not likely to be soon forthcoming, because some components have not been measured, numerically modeled, or assessed in relation to process interactions. Nonetheless, we welcome insight and collaboration from all who are interested in expanding and refining this integration, and we hope to stimulate further research needed to advance FRE ecology and stewardship.

Physical FRE Elements and Processes

Overview

Many supporting models have been proposed to describe the array of physical processes associated with FREs. FREs are terrestrial dendritic surface-water flow paths transporting matter and energy downslope through their channels within watersheds, with flow contributed by groundwater and multiple surface water sources. Riverine processes and geomorphology vary in relation to the geologic setting, gradient, flow, channel bed material, and sediment loads (Hey et al. 1982; Leopold and Mattuck 1953; Li et al. 1976; Schumm 1985; Tinkler and Wohl 1998; Wohl 2010).

We initiate this discussion with a brief overview of physical flow and hydrogeomorphological models (HGMs). Early work in fluvial hydrogeomorphology focused on classification and process-based modeling at microsite to basin-wide spatial scales, and on understanding and describing the interrelationships between basin characteristics and climate-based flow on channel form, function, and development. These

HGM topics remain under intensive study and debate, particularly in relation to physical FRE management of rivers (e.g., Leopold et al. 1964; Leopold and Maddock 1953; Lewin 1978; Morisawa 1968; Schumm 1985). More recent emphases have shifted to tributary- and reach-based HGMs, with growing recognition that channel geomorphology and function depend on the extent of geologic constraint (Bellmore and Baxter 2014; Montgomery 1999; Sabo and Hagen 2012). In some situations, bio-ecological processes may reciprocally influence FRE geomorphology (e.g., Beschta and Ripple 2006). We follow this literature review with a description of how these elements relate in an integrated watershed approach.

Fluvial Hydrogeomorphology

While trophic cascades can influence fluvial geomorphology, study of “bottom-up” physical processes has stimulated a long history of HGMs and much ongoing effort to improve understanding and description of FREs. The initial foci of HGMs was on understanding channel landform organization and distribution and the processes that generate them (e.g., Buffington and Montgomery 2013; Knighton 1998; Rosgen 1994, 2008). HGMs were primarily considered in unconstrained alluvial rivers, but Rosgen (1996), Tinkler and Wohl (1998), Wohl (2010), and others extended channel formation description to constrained and bedrock-dominated settings. Additional focus has been placed on the extent of groundwater-dependence (Eamus and Froend 2006). The Committee on Riparian Zone Functioning and Strategies for Management (2002), Giller and Malmquist (1998), Malanson (1993), and Naiman and Décamps (1997) also emphasized the importance of lentic habitat (river-related lakes and wetlands) relationships to rivers. That discussion was expanded by the Instream Flow Council (Annear et al. 2004, 2009) to include variability in lateral and vertical flow in relation to instream flow assessment and management strategies, particularly for salmonid fish.

Discipline-based or regional specificity has limited the applicability of some HGMs. For example, Bennett and Simon (2004) focused on engineering-based analyses of riparian ecology, without considering the implications of evolutionary ecology, as discussed by Steiger et al. (2005) and Stromberg et al. (2004). Harvey and Gooseff (2015) recognized this difficulty and emphasized integration of physical and ecological models. However, increased interdisciplinary dialogue is needed to further integrate hydrogeomorphic models with fluvial engineering, aquatic and riparian ecosystem ecology, as well as socio-cultural, economic, and evolutionary models (e.g., Lubinski 1993).

The process domain concept (Bellmore and Baxter 2014; Montgomery 1999) shifted attention to FRE structure and process from the spatial scale of the basin to that of reaches. Alluvial reaches often support broader riparian zones and filter, store, and process organic matter from upstream (Nilsson and Svedmark 2002). In contrast, constrained reaches function more as conduits for material transport. At a coarse scale, Bellmore and Baxter (2014) compared aquatic-riparian organic matter dynamics in five confined versus five alluvial reaches, reporting that the former had twice the allochthonous (extrinsic) organic input, but had a reduced capacity to retain and process that material. As an across-scale approach, the process domain concept posits that spatial variation among geophysical processes shapes the disturbance regime, ecosystem structure, and ecosystem dynamics. This approach resolves some of the limitations of the river continuum

FRE structure is strongly dominated by physical processes operating in a bottom-up fashion to shape riverine landforms and the habitats on which aquatic and riparian assemblages develop (figs. 10, 11). The geologic context and climate of the watershed control basin position, geomorphology, topography (elevation), configuration, and the supporting aquifers are physical state variables. Collectively, those physical state variables regulate flow, hydrography, water quality, and sediment transport. They also generate the FRE templates that are organized through hierarchically flow-linked reaches (Fisher et al. 1998; Montgomery 1999; Vannote et al. 1980). Ecologically, nearly all terrestrial FREs exhibit four-dimensional subsidy exchange, including: (1) upslope eolian and zoochorous transport processes; (2) capillary rise of groundwater through fine sediments; (3) lateral and vertical transport through the watershed, often with subsurface or tidal influences at the confluence of tributaries, in parallel flow with head from adjacent rivers, in lowermost reaches, and into the atmosphere; and (4) artesian groundwater or, in very low-gradient reaches, downstream tributary flooding that initiates upstream-directed flow (Ward 1989; figs. 10, 11).

Time T_1

Geology & Tectonics - Climate

Aquifers and GW quality

Basin Geomorph. Regional Climate

Surface & Hyporheic Flow, WQ

Sediment Flux Hydrography

PAR Reach and X-section Geomorph.

PNAPP (P-R) Disturbance

FRE Biogeography (Colonization) Diversity (Extinction)

Autochthonous Allochthonous

Upland & Trib. Riparian

Mainstream River

Upland & Trib. Riparian: 3°C , 2°C , 1°C

Mainstream River: 1°P , 1°P

Tributary Input: 1°C , 2°C , 3°C

Decomposition, Nut. Spirals

Nutrient Flux, Spiraling

Soft bedrock (e.g., shale) $\rightarrow$ wide, shallow reaches, expanded floodplains and riparian habitat; lentic, possible lake habitat

Hard bedrock channel (e.g., granite) $\rightarrow$ narrow, deep reaches, limited riparian habitat

Stream Order (WQ Homogeneity)

0 (Headwater springs or lakes)

1

2

3

(Mouth)

Upstream X

dispersal, migration

Wide reach or endorheic Basin (Note: May be a losing system)

Wide or Lacustrine Reach

Narrow-width Reach

Narrow Reach

Terrestrial

Aquatic

Tributary effects

Microclimate: climate effects

Upstream estuarine (e.g., anadromy) or endorheic lake influences

A comprehensive FRE conceptual model must integrate these dimensions over time among aquatic, riparian, and upland domains within the watershed. It also must link independent and dependent physical, biological, and interacting ecosystem processes. All of these processes respond dynamically toward equilibration of fluvial boundary conditions, matter transport, and energy dynamics. Consequently, we depict FREs as primarily driven by physical factors. This emphasizes the foundational role of physical processes with dependent biotic composition, structure, function, and trophic interactions (figs. 10, 11). Although little-discussed in the RCC, lower stream order FRE changes often occur in a punctuated, stepped, or reach-boundary fashion, as flowing water emerges from groundwater and FREs receive tributary contributions. In contrast, higher order streams terminating at the confluence with the sea (but not those terminating in endorheic basins) generally change more gradually, both spatially and over time.

Fluvial Hydrogeology Model Elements

Overview

Hydrogeological influences on FREs vary in relation to latitude, elevation, season, stream order, and the derivation of reach source waters (e.g., precipitation and runoff, groundwater, springs, or lakes). This variation exists on scales ranging from microsite to local stream cross sections, among reaches, across entire basins, and through different climate/humidity regimes (figs. 10, 11). Impacts also vary as a result of differing regional and global tectonic histories. Hydrogeological FRE models have developed incrementally over the past century, building on each other without any major concept-changing epiphanies. Careful experimentation and analyses have gradually expanded the logic, empirical background, and predictive capabilities of groundwater and surface water models. However, additional research is needed to incorporate ecological and evolutionary concepts into fluvial ecohydrology.

Basin Geography

The geologic setting in which groundwater and surface water basins exist control FRE form and function. Tectonics, geography, sources, elevation range, basin structure, climate, parent rock stratigraphy, glacial rebound status, structural geology, and aspect all influence rivers to varying degrees (figs. 10, 11). Tectonic controls on river development were reviewed by Holbrook and Schumm (1999), but coarse-scale configuration of groundwater and surface water basins under different tectonic regimes needs further elucidation. Large, high order rivers typically interconnect intracontinental basins through periods of tectonic quiescence. Such periods of tectonic inactivity can persist across evolutionary and geologic time scales. Integration of large river systems across complex landscapes has involved 10+ million years in the Nile, Colorado, Rio Grande, and Mississippi River basins (Mack et al. 2006; Timmons and Karlstrom 2012; Wickert et al. 2013; Woodward et al. 2007).

Orogenies that dominate continental margins often produce abundant low to moderate stream order basins. In contrast, extensional terrains in East Africa and western North America generate streams of moderate order from high elevations that discharge into isolated, endorheic basins. While aquifers that develop in these landscapes often are assumed to be constrained by surface catchment boundaries (e.g., Springer et al. 2016),

such is not always the case. For example, groundwater passes more than 200 km beneath several endorheic basins in Nevada before emerging in the lower White River (Winograd and Thordarson 1975).

Tributary Effects

Tributary influences on mainstream rivers vary in relation to stream order and the extent of differences in hydrography, water quality, sediment loading, and biota (Benda et al. 2004b; Dye 2010; Rice et al. 2001; Thorpe and DeLong 1994; Ward and Stanford 1983). Habitat complexity at tributary confluences increases ecological productivity and biodiversity, and it sustains biogeographic habitat connectivity in four dimensions (Naiman et al. 1993; Rice et al. 2008; Sabo and Hagen 2012; Stevens and Ayers 2002; Thorpe and DeLong 1994). Tributary impacts on mainstream water quality are likely greatest when flows of the two are similar; however, differences in biota may follow the opposite pattern: aquatic macroinvertebrates in a small, springfed tributary may substantially differ from that in the large, adjacent mainstream. In figure 11, we depict the magnitude of tributary influences as dark triangles of varying size, but we also note that the impacts of large or influential tributaries occur across mainstream order.

Source Waters

Along with precipitation, snowmelt, and lake source contributions, springs play a far more important role in FRE ecology than has previously been recognized. Many of the world's major rivers arise from discrete springs, springfed marshes, or groundwater-fed lakes (Junghans 2016). Rivers with spring-sourced baseflow include the Amazon, Colorado, Mississippi, Rhine, Volga, Murray, and many others. For example, the Mississippi River heads in springfed Nicollet Creek and two tributaries of Elk Lake in Minnesota, as well as springfed Lake Itasca. The Missouri River heads at Browers Spring on the Montana-Idaho border. One of its major tributaries, the Yellowstone River, heads in the Absaroka Mountains in northwestern Wyoming, passes through Yellowstone Lake (which is partially springfed by biota-rich thermal vents; Morgan et al. 2007), and eventually joins the Missouri River. Both the Nile and Colorado Rivers head in springfed helocrene marshes. Lake Tahoe in the Sierra Nevada Mountains of California and Nevada receives about 0.05 km³/year from groundwater inflow (0.033 percent of its volume; Thedol 1997). That lake is the source of the Truckee River, which terminates in endorheic (and also partially springfed) Pyramid Lake in Nevada's Great Basin Desert. Both subaerial and subaqueous springs contribute to river flows, although subaqueous springs are difficult to quantify and study (Springer and Stevens 2009). Headwater springs often are distinctive habitats with unique water quality that may influence mainstream processes, such as imprinting among larval fish (Teeers 2016; but see Muller-Schwarze 2006), and they often provide headwater baseflow for rivers in non-ice-dominated regions.

FRE hydrologic models often assume that river baseflows arise from diffuse emergence of groundwater. Such a generalized assumption is questionable, because geologic structure usually brings groundwater to the surface at discrete points (springs), generating focused point-sources of groundwater. In 2016, the senior author found that the headwaters sources of the Fiume Tagliamento in northeastern Italy, the last undammed river in the Alps, arose from a suite of high-elevation rheocrene and hillslope springs, with some summertime flow augmented by snowfield runoff. This was despite reports

of its source flow arising from diffuse groundwater (Tockner et al. 2003). In addition, rivers often support infiltration, adding to groundwater supplies. However, the assumption that diffuse groundwater largely provides the baseflow sources of rivers has hampered integration of knowledge of groundwater-surface water interactions in FRE stewardship, obscured understanding of the contributions of springs to surface water, and biased river science and policy (e.g., U.S. Army Corps of Engineers and Environmental Protection Agency 2015).

Reaches and Stream Order

River drainage networks are often subdivided into segments and reaches, which are important organizational units of FREs. We define a river segment (*sensu* Stevens et al. 1997b) as one or a group of river reaches that are collectively subject to an abrupt change (usually) in one or more ecosystem characteristics (e.g., water temperature, geochemistry, suspended sediment load, or gamma diversity species assemblage). Such changes often are introduced by a tributary, thereby affecting downstream ecology (Bruns et al. 1984; Rice et al. 2008). Reaches lie within segments and are distinguished geomorphologically on the basis of differences in parent rock geology, shoreline erodibility, slope (gradient), and thalweg position. Schmidt and Graf (1990) analyzed several hundred cross sections to define the geomorphic reaches of the Colorado River in Grand Canyon in relation to bedrock geology. Thus, both segment and reach boundaries commonly occur at tributary confluences with the mainstream. Division of watersheds into sub-basins at various spatial scales (e.g., the hydrologic unit classification system used in the United States) may not well reflect reach geomorphology or segment configuration. Agreement on definition of these terms remains an important issue for further progress in FRE ecology.

FRE complexity is defined, in part, by stream order, which increases when two stream channels of the same magnitude meet (Horton 1945; Strahler 1957) (fig. 11). We regard springs as “zero order” streams, and springbrooks are typically first order channels. Stream order increases erratically downstream: the largest rivers can exceed a stream order of 10. For example, with more than 1,000 tributaries more than 1,000 km long, the Amazon River is considered to be a 12th order stream. FREs lacustrine reaches can occur at any order within a basin, through which limnological processes like thermal or chemical stratification can influence downstream flow and geochemistry.

Higher stream order FRE characteristics and processes vary primarily in relation to the extent of geologic constraint, stream order, and reach geometry (figs. 10, 11). In alluvial rivers, reach characteristics are generally influenced by stream order, exhibiting distinctive, sinuous meanders, or braiding. Shales and other soft bedrock strata allow reach width to expand in unconstrained river channels, resulting in less variation in flow dynamics, reduced responses to aspect and microhabitat effects, and reduced species extinction probability. Such streams usually have increased solar energy, productivity, and colonization potential. In contrast, in geologically constrained reaches, the bedrock geology and geologic structure exert stronger influences over reach geometry. Narrow reaches often form in harder bedrock, where their channels sustain greater variation in flow, stronger responses to aspect, reduced solar energy budgets and productivity, and decreased colonization potential coupled with increased species extinction probability. Riparian zones in narrow, constrained reaches typically exist in a state of perpetual succession, a process suspended by high disturbance intensity (Campbell and Green 1968).

Large rivers are typically high order streams, and the large quantity of water they transport exert unique ecological influences on their ecology, buffering changes in water temperature, geochemistry, and equilibration timing. Johnson et al. (1995) questioned whether the RCC that Vannote et al. (1980) applied to large (high order) rivers, due to the temporally and spatially nested hierarchical organization, the potentially increasing influences of physical bottom-up ecological controls, increased equilibration time, and the inadequacy of understanding and modeling physical process interactions.

Water Quality

River water quality varies across lithology, latitude, elevation, humidity province, season, and stream order within basins, and among reaches, and springs and lakes can influence river waters. Water quality characteristics transition over stream order and are important determinants of macrophyte composition and life history cues for aquatic macroinvertebrates, fish, and amphibians. In turn, they influence food web linkage (but see Heino et al. 2015) and riparian groundwater quality. Surface flow geochemistry generally dominates higher stream orders, with river water quality change occurring at tributary confluences (Dye 2010), and to a lesser extent in side channels and shallow, low-velocity shoreline habitats. Limnologically influenced water quality dominates lake-sourced rivers, but we know of little research on natural downriver responses to such alteration. River water trends toward a universal quality across stream order, creating relative similar geochemistry among the world's major rivers at their mouths. However, the contributions and evolution of FRE water quality depends in large measure on subbasin geology and the relative contributions of tributaries (e.g., Giller and Malmqvist 1998; Kabede et al. 2005).

As zero order streams, springs often exhibit strikingly different temperature and geochemical characteristics than those in the adjacent higher order streams with which they are confluent (e.g., Lowe and Likens 2005). The ecological transition from headwater springs into first order streams is highly individualistic, often occurring at a chemically and thermally discrete distance from the source (Morrison et al. 2013). The quantity and quality of riverside or in-stream springs, as well as seasonal flow changes driven by precipitation, also can affect stream channel geomorphology. For example, limestone (travertine)-depositing springs shape stream geomorphology by precipitation of calcium carbonate (CaCO_3), forming dams and creating pools similar to those behind beaver dams (Cantonati et al. 2016). Such springs have received global attention as important aquatic ecosystems, and often add much dissolved load to rivers. They also affect downstream channel landforms, morphology, and interstitial pore space in mainstream bed sediments.

Geothermal springs, such as those at Yellowstone National Park and Mammoth Hot Springs, often deposit travertine (Sorey 1991). CaCO_3 precipitation rates in Fossil Creek in central Arizona exceeded 0.11 g/L of discharging flow, actively depositing travertine that shapes channel geomorphology (Malusa et al. 2003). Travertine deposition appears to be facilitated by algal growth, a deposition process that quickly oxidizes organic carbon, either through microbial activity or through as-yet-unrecognized chemical processes, enhancing the role of travertine deposition in CO_2 release. Larger springs can dominate or strongly influence or dominate riverine water quality. For example, Silver Springs provides nearly 13 m³/sec of baseflow to the Silver River in Florida (Odum 1957), and the newly discovered Shanay-Timpishka River is a large geothermal river arising on the floor of the Amazon basin (Ruzo 2016).

Hydrography

Flow, stage, and flow variability are the primary physical factors affecting FRE geomorphology and ecological processes and components (e.g., Junk et al. 1989; Tockner et al. 2000; Topping et al. 2003). Flows of most temperate and many tropical rivers vary seasonally, and factors that regulate flow include drainage area, geographic position, humidity province, underlying lithology and groundwater hydrology, vegetation cover, seasonality, and regional climate. Two useful analyses for understanding individual FREs are annual hygrographs (plots of the average daily flow and variation across days of the year) and flow duration curves (plots of the annual frequency distribution of flows). These plots vary in relation to climate, basin structure, and location within the basin. Such analyses are most robust when data represent long time series, clearly displaying interannual variability among wet and dry years. Failure to incorporate a sufficient duration of flow data and the range of variation can lead to serious mis-management of water. For example, the Colorado River was famously over-allocated among basin States in 1922, based on an insufficiently long flow time series that overemphasized wet-year data.

Physical disturbance strongly influences FRE geomorphology and biotic assemblages, but how does disturbance intensity vary across the channel and across stream order? Magilligan (1992) used HEC-2 flood modeling to describe variation in channel boundary shear stress and unit stream power on an array of stream channels across 2- to 500-year floods. She included analyses of channel cross section and distance downstream through basins with varying lithology, noting at least three-fold variation in flood power through the basin due to valley width, which is largely controlled by lithology. Wide valleys with broad, alluvial channels were subject to lower flood power, because of reduced percent of channel conveyance during large magnitude floods and decreased rates of depth change.

In contrast, such events generated increased flood power in narrow valleys with constrained channels, a pattern influenced both by basin size and by local controls, such as dams. Magilligan estimated minimum shear stress and unit stream power for “catastrophic” floods in humid, alluvial channels of 300 W/m². Interestingly, she suggested that maximum flood impacts on channel geomorphology occur at discrete points in the reach or drainage and that such points are likely to shift over time (headward movement of such points seems most likely). Her insights suggest that geomorphic evolution of a drainage network occurs most intensively at a highly localized scale, affecting reach-based disturbance dynamics and FRE biotic assemblages.

Antecedent high flows exert lasting impacts on FRE structure and ecology. Foster et al. (1998) highlighted the importance of antecedent imprints from large, infrequent disturbances on ecosystem structure and function. Parsons et al. (2005) reported that large, infrequent floods following volcanic eruptions, wildfires, or hurricanes increased heterogeneity in fluvial riparian habitat, creating multiple trajectories for vegetation renewal along the Sabie River in Kruger National Park in South Africa and Mozambique. Thus, river geomorphology may continue to respond to flood impacts from the distant past—impacts that often are difficult to discern.

The frequency, duration, magnitude, and timing of low flows and dewatering events also are critical determinants of FRE ecology. If flows are sufficiently low, the river may become a series of pools, with limited connectivity, or may entirely desiccate. A full

dewatering event can eliminate FRE macroinvertebrate and fish species, and prolonged dewatering alters a host of geomorphic and ecological processes and characteristics. However, long-term flow data on droughts and their ecological effects are limited and difficult to correlate. These data challenges sometimes can be addressed through dendrochronology. Long-term flow modeling of dendrochronology within basins among a wide array of arid to humid environments around the world have provided insight into drought frequency and duration (e.g., Akkemik et al. 2004; Case and MacDonald 2003; D'Arrigo et al. 2009; Melo et al. 2012; Therrell and Bialecki 2015). Such studies have the advantage not only of evaluating wet years and extreme precipitation events, but also of drought characteristics that strongly affect water resource supplies management. The studies highlight the need for adaptive strategies to cope with climate change (e.g., U.S. Bureau of Reclamation 2012).

The impacts of natural, regular, short-term stage fluctuations in rivers are generally poorly known, but they are of great consequence in rivers impounded for hydroelectric power production (e.g., Kennedy et al. 2016). Natural semi-daily tidal bores are a common phenomenon in the lowermost reaches of low-gradient rivers that reach the sea, and less regular stage fluctuations may extend upstream into low-gradient streams that open into wind-influenced lakes. Daily variation in flow stage in such settings may desiccate or freeze macrophytes, or macroinvertebrate habitats, and eggs. It may also interrupt aquatic and riparian faunal feeding and other behaviors, leading to reduced or fluctuating primary and secondary consumer production. Given the frequency of hydropower-driven flow fluctuation impacts on regulated rivers, understanding the effects of natural fluctuating flows is an important topic for future FRE and WCM research.

Sedimentology

The erosion, and deposition, of bed, suspended, dissolved loads, and flotsam are related to watershed geology, aquifer properties, flow dynamics, and channel configuration. In addition, ice processes, upland wildfire, forest pest insect outbreaks, and overgrazing affect fluvial sedimentation and nutrient transport (e.g., Bormann and Likens 1979). Cumulatively, including anthropogenic materials, the world's rivers deposit about 20 billion metric tonnes of solid material into the sea each year (Gray and Simões 2008). However, rather than being solely a function of basin area, sediment deposition is disproportionately the result of discharge from thousands of small, relatively high-gradient rivers (i.e., drainage areas < 10,000 km²) that open directly into the ocean (Milliman and Syvinski 1992). Large rivers deposit proportionally less sediment due to subaqueous storage in deltas. Alluvial reaches often have relatively uniform bed materials and channel landform configuration, and often are closer to equilibrium than are constrained channels. Parent rock lithology, geologic structure, and less predictable gradients and bed loads control reach characteristics and channel geometry in constrained channels (e.g., Hey 1982; Schmidt and Graf 1990; Tinkler and Wohl 1998; Vogel 1981).

Models of sediment deposition and erosion are diverse (reviewed by Merritt et al. 2003, among others), and can provide adequate two-dimensional prediction of suspended sediment transport through channels with varying bed roughness, channel steepness, and sediment transport. Some two-dimensional models accurately predict flow and sediment transport for some rivers (e.g., the Glen and Grand Canyon reaches of the Colorado River) (Rueda 2015). However, most rivers have insufficient historical flow and hydrographic

resolution to permit high-precision modeling (Alley et al. 2013). Variation in turbulence, shear stress, transport capacity, and bed and suspended loads results in more highly variable channel landform and FRE habitat variation among bedrock-defined reaches. In addition, three-dimensional flow modeling is needed to relate discharge and sediment transport to sedimentation and channel landform development.

FRE suspended sediment transport is a power function of flow, increasing and varying dramatically during floods (e.g., Leopold et al. 1964; Topping et al. 2003, 2013). Suspended and bed load grain sizes vary from clay, silt, sand, and pea gravel to boulders and bedrock, typically with grain size negatively related to elevation and stream order. Fluvial sediment grain sizes are non-randomly erodible, with clay and cobble-to-larger sediments far less erodible than are silt or sand (Hjulstrøm 1939). Suspended sediments are actively redistributed by high flows and strongly influence FRE channel landforms and the availability and quality of germination and maturation microhabitats needed for riparian plant and faunal assemblages. Deposition of fine-grained sediments tends to occur on the falling limb of flood hydrographs and, in constrained reaches, at discrete microsites, commonly in relation to release of channel constrictions (e.g., Schmidt and Graf 1990; Topping et al. 2013).

FREs also transport extensive allochthonous (upland- and upstream-derived) and autochthonous dissolved and fine-to-coarse organic matter, depositing large quantities that may affect flow, channel geomorphology, and riparian habitat development (Stevens 1997; Tockner et al. 2003). A vast literature exists on the quantity, distribution, and ecological roles of woody debris (reviewed by Stevens 1997). For example, coarse woody debris provides refugia for aquatic macroinvertebrate larvae during upper Colorado River basin floods.

Channel Geometry

Geomorphologists have identified an array of river channel types based on the extent of geologic constraint: geologically unconfined (alluvial) and highly erodible channels and mobile beds differ geomorphically and ecologically from constrained (fixed shoreline to canyon-bound) channels with relatively immobile (low erodibility) margins and beds (e.g., Rosgen 1996; Tinkler and Wohl 1999) (figs. 10, 11). Alluvial streams often have relatively broad, meandering, lower gradient, shallow channels with highly mobile beds, and sometimes with anastomose channels. In contrast, geologically constrained rivers often have narrow, low-sinuosity channels with higher slopes, deep channels, and largely immobile beds. The primary variables of interest in understanding development of fluvial channels include: channel slope, the stage-to-discharge relationship, the hydrograph, bed materials, channel roughness, and the history and frequency of catastrophic disturbances (e.g., ice damming, earthquakes, volcanism and lava flows, and mass wasting slope failures) (Leopold et al. 1964).

Many channel classification systems have been proposed (reviewed by Buffington and Montgomery 2013), providing a robust description of channel types and ranging from non-symmetrical spring channels (e.g. Griffiths 2008) and bedrock channels (Tinkler and Wohl 1998), to a wide array of alluvial, highly sinuous, braided, or anastomosing channels (e.g., Rosgen 1996). From a stream ecology perspective, rivers can be divided into rhithron (headwaters) and potomon (lowland) zones.

Ward (1994) identified three low-order stream segment types in European headwater

alpine habitats. Kryal (icemelt) reaches were characterized by glacially sourced flows with low temperatures, variable discharge, and turbidity; limited and largely allochthonous food sources; and limited benthic assemblages. Rhithral (channel stream) reaches were dominated by snowmelt hydrograph, varying temperature, and more complex and variable stream invertebrate assemblages. Krenal (springbrook) segments were steadier-flow, groundwater-dependent reaches, with high water clarity and water quality, dominated in his study by calcium carbonate, and supporting a richer assemblage of benthic macroinvertebrate species derived from multiple sources. Rhithron and potomon segments can be either constrained or alluvial. However, few studies have quantified or modeled channel geometry across stream order within basins in different tectonic settings or across latitude and additional comparative studies are needed to reveal broader scales of channel geomorphological organization and the implications on FRE ecology.

Springs that emerge along river channels can increase the frequency of bank failure and redirect mainstream current direction (L.E. Stevens, unpublished observations). Hillslope springs along the edges of smaller perennial or many ephemeral FREs may exert feedback on channel geomorphology by increasing dense wetland plant cover or woody phreatophytic shrubs and trees (plants rooted in the water table or on the phreatic surface) along adjacent low-order mainstream channels. Such vegetation may be sufficiently extensive to reduce stream power during floods, causing local deposition and geomorphic alteration of channel geometry.

Fluvial Landforms

Channel landforms include pools, eddy deposits, debris and cobble islands, side channels, paleo- and contemporary terraces, and other features, whose development can be mapped but not yet reliably modeled. Predicting fluvial landform development and responses to flow events remains limited, due in part to divergence among turbulence physics equations. Post-flood flow subsidence sequentially exposes an array of draining shoreline habitats and generates terrace development along alluvial, sand-dominated channels. As flow stage declines, lateral channels change from being through-flow features to being open at the downstream end, and then becoming isolated pools. This annual flood cycle allows a progression of vegetation, invertebrates, and fish assemblages changes (e.g., Stella et al. 2011). In constrained, sand-dominated segments, return current channels are distinctive side channel features that form in recirculating zones and mouth upstream (Schmidt and Graf 1990). Under low flows, these features can undergo fluvial hydrarch succession into marshes and, with prolonged dewatering, into terrestrial habitats (Nilsson 1984; Stevens et al. 1995).

Riparian vegetation is often strongly zoned in response to stage (fluvial groundwater availability) and the return frequency and magnitude of flooding or ice scour disturbances. Although definition of riparian terrace structure and habitat has been attempted several times in various hydrological and ecological contexts over the past century (Carothers et al. 1979; Hupp and Osterkamp 1988, 1996; Johnson 1991; Nilsson 1983; U.S. Natural Resources Conservation Service 2013), there appears to be little consensus in the river science community about terrace lexicon and classification. For example, the phrases “first overbank terrace,” “geolittoral zone,” and “hydrologically active zone” all apply to what we refer to (below) as the “lower riparian zone.” Such lack of agreement on basic terminology impedes understanding of FRE landform and vegetation interactions. It also

hinders interdisciplinary collaboration. Here and in the figures, we describe and define physical and biological terminology and concepts to help clarify, assess, and descriptively model the WCM as the basis for proposing this FRE model. In general, we prefer the simplest, most intuitive landform descriptions, and therefore we propose the following stage-terrace definitions:

The aquatic zone (AQZ) is the wetted channel, downslope from the lowest stage elevation.

The hydrologically active zone (HAZ) is inundated and scoured one to many times/year, and it extends upward from the baseflow water's edge up to the bankfull stage. This zone, when vegetated, usually is occupied by wetland and flood-tolerant plant species.

The lower riparian zone (LRZ) is the first overbank terrace. It is usually flooded or scoured every 1-2 years and in the arid regions often is occupied by a combination of drought-tolerant deciduous species (e.g., clonal *Phragmites australis*) and shallow-rooted phreatophytes (e.g., *Acer negundo*, *Alnus*, *Platanus*, some *Fraxinus* and *Quercus* species, and various *Salicaceae* in the American Southwest) as well as deeply rooted, nonnative *Tamarix* and *Eleagnus*. In mesic regions of eastern North America, the LRZ often is occupied by riparian understory herbs and graminoids, as well as *Acer*, *Platanus*, *Quercus*, *Populus*, *Salix*, and other bottomland hardwoods, *Larix*, and other species. Patagonian LRZs often support *Salix* (Stevens, unpublished data). Australian LRZs also are occupied by a wide array of herb and woody species, depending on the region (Lukacs et al. 2008).

The middle riparian zone (MRZ), sometimes referred to as the second overbank terrace, is usually flooded or scoured every 2-10 years and in arid regions often is occupied both by moderately deeply rooted phreatophytes, and opportunistic and weedy upland species. In mesic regions, it often is dominated by upland species.

The upper riparian zone (URZ) is only flooded or scoured by large, rare (> 10 years) events, and in arid regions it is generally occupied by deeply rooted phreatophytes and both facultative and non-facultative upland-riparian plant species. In mesic regions, it usually is dominated by upland species.

The upland zone (UPL) occupies non-flooded/non-scoured stages above the river channel, and it is dominated by non-phreatophytic plant species.

FRE Soils

Organic riparian soils develop in relation to flood and saturation frequency, as well as organic litter deposition and decomposition. Those processes vary by humidity province, stage elevation (scour disturbance intensity and frequency), and microhabitat type. Because pedogenesis requires considerable time, riparian soil development is negatively related to flood and ice scour return frequency and may increase non-linearly with distance and elevation above the active floodplain. Soils differentially influence plant functional group distribution (e.g., Andrew et al. 2014). With sufficient time, geologic and climate conditions, geomorphology, and vegetation, riparian soils can develop into deep, fertile loams and serve as a sink for carbon fixation.

Riparian substrata, soils, and microhabitats affect germination niche availability and quality (Grubb 1977). Day et al. (1988) reported that soil fertility (as grain size and nutrient status) and flood scour decreased germination and growth of fluvial wetland plant species. Bagstad et al. (2006) examined soil-vegetation relationships along the San Pedro River in southeastern Arizona, reporting that electrical conductivity, silt content,

organic matter content, and biologically available phosphate all increased with patch age, as determined by the age of associated plants, although silt content more likely was a function of the geomorphic setting. Stevens (1989) experimentally demonstrated that germination and ecesis probabilities of common southwestern United States riparian plant species increased in relation to the concentration of silt in sandy shoreline sediments, due to reduced desiccation, susceptibility to flood scour, and increased nutrient availability. Jacobs et al. (2007) and Stella et al. (2011) reported that complex interactions among upland and river environmental variables, soils, microsite geomorphology, and large animal behavior all affected N and P processing in mesic and semiarid African riparian zones.

Soil salinity can be a strong organizing factor in riparian and lacustrine plant assemblages, influencing plant assemblage composition and structure. Brotherson (1987) identified five zones along the shore of saline Utah Lake in central Utah. The lowest elevation zone was occupied by halophilic saltgrass (*Distichlis spicata*) and dysclimax weeds, followed upslope (in order of increasing elevation) by saltgrass-alkaligrass, saltgrass-forb, saltgrass, and spikerush assemblages. Soluble salt concentration and soil pH decreased downslope, while moisture and organic matter increased. Forb distribution was correlated with micronutrient concentration.

Fluvial Microclimate

Fluvial climate is influenced by global- to local-scale phenomena, the latter including nocturnal cool air subsidence and upriver mountain valley wind patterns (e.g., Draught and Rubin 2006; Whiteman 1990), as well as local microclimate interactions. However, we know of few meso-scale studies of river influences on basin, reach, or local microclimates. Stevens (2012) and Yard et al. (2005), respectively, reported that riparian and in-stream interception of photosynthetically active radiation (PAR) varied temporally and by reach in the deep, narrow Colorado River in Grand Canyon, influencing in-canyon air temperature, relative humidity, aquatic and riparian production. Although not yet studied, variation in PAR flux also may influence slope failure frequency, cliff retreat, and canyon landform evolution.

At the local microclimate scale, Stanitski-Martin (1999) demonstrated that flow and channel aspect influenced cross-sectional fluvial solar energy flux, creating seasonally discrete patterns of diel temperature and relative humidity on the Colorado River in Arizona. In particular, she noted a discrete belt of humid air that developed over the river surface. This belt of humid air is evident because it conveys sound more effectively than less humid air farther above the surface. The humid air belt increased in thickness and extended into the riparian zone, particularly during nocturnal hours, and it often shrank during daytime. Occasionally visible as fog, it may positively influence riparian biotic productivity, particularly in arid regions. Such river-based microclimate patterns also affect riparian trophic dynamics. For example, increased riparian humidity was positively associated with avian species diversity in the Murray-Darling River basin in Australia (Selwood et al. 2016). Microclimate gradients and soil moisture availability contribute to the “riparian effect” in which the lowest elevation occurrences of aridlands upland shrub and tree species occur in ephemeral riparian channels.

Microsite variation in PAR flux and microclimate also may be a common phenomenon at tributary confluences, particularly in temperate constrained or canyon-

bound rivers, affecting FRE aquatic and terrestrial productivity. The confluences of east (E) or west (W)-flowing tributaries in temperate rivers that flow north (N) or south (S) may not receive any direct solar radiation during the winter months, particularly in deep canyons at latitudes greater than 23° (Stevens 2012). In contrast, in the northern hemisphere, the confluences of N-flowing tributaries on mainstream rivers that flow E or W are likely to receive a shaft of light throughout the year, potentially greatly increasing PAR, increasing ambient temperature, and reducing the duration of winter freezing, all of which add to productivity and habitat diversity at ecologically interactive tributary mouths. The opposite pattern (a south-flowing tributary confluent with an east- or west-flowing canyon-bound mainstream) should obtain in the southern hemisphere. Such solar radiation patterns clarify why tributary confluences can serve as biological hotspots (Thorpe and DeLong 1994).

Dynamic Geomorphological Equilibrium

Rare coarse-scale events, such as lava flows, peak flows, tectonic events, ice dam failures, fire, and other types of physical catastrophic events exert formative and long-lasting influences on channel establishment and development. Antecedent events, including the failure of natural dams or large paleofloods, are long-term drivers of fluvial geomorphology (Foster et al. 1998; Parsons et al. 2005). FRE channels undergo geomorphic transitions after destabilizing flows, moving toward spatially uniform energy dissipation, as described in Morisawa's (1968) dynamic equilibration model (DEM). The DEM is a cornerstone of our WCM, in which stream channel geomorphology and ecosystem development trend toward equilibrium but never reach that condition because destabilizing flooding and other disturbances are frequent, vary in intensity, and are erratic.

Variation in high flow return frequency (FRF) in rivers with erodible banks affects FRE channel geometry and geomorphology by creating or maintaining shoreline habitats, point bars, gravel and cobble islands, and terraces, all of which can support riparian assemblages. River landforms are maintained or readjusted through hydrographic time and change at rates ranging from instantaneous to the geological lifespan of the watershed (107 years or more), depending on FRE and the stage elevation of the landform. However, and in part due to the power function of suspended sediment load to flow rate (e.g., Gray and Simões 2008), discrete FRF intervals (particularly the bankfull 1.5-2.5 year interval) generate new channel bedforms and scour or reset riparian vegetation on hydrologically active and lower riparian terraces (Campbell and Green 1968). Channel geometry and landforms respond over long periods, with rare, large, antecedent floods exerting long-lasting impacts on channel landform distribution.

Physical Elements and Processes: Conclusions

Much widely divergent, interdisciplinary expertise is required to understand rivers as ecosystems, and the incomplete integration of physical science elements with ecological disciplines remains an impediment to FRE ecology and stewardship. The next steps in refining and testing HGM concepts are likely to involve intensified study. This includes improved modeling of groundwater-surface water interactions and interactions among reaches (including lentic and frozen landscape transitional reaches) among watersheds in relation to tectonic history and under changing climates. In addition, more refined

communications among FRE physical and ecological researchers may help clarify future science directions. This dialogue requires improved long-term monitoring data on hydrographic, hydrologic, and other physical and biological variables. Such emphases will enhance understanding of channel landform development, as well as the interactive spatial and temporal scales of hydrogeomorphological and ecological influences on FRE development.

Bio-Ecological FRE Concept Modeling

Historical Synthesis

Building on the abiotic processes discussion above, we review and discuss biological elements and processes of FRE ecology and evolution. In addition, we use a description of the details of figures 11 and 12. We examine continuity and other models of FRE processes and characteristics within the watershed across stream order and hierarchical frameworks of stream habitat classification (e.g., Frissell et al. 1986). Many river ecosystem models have been developed over the past several decades, including recent, highly integrative approaches. While many of these models have substantially advanced understanding of FRE structure and function, none are mutually exclusive, and many broadly but incompletely overlap.

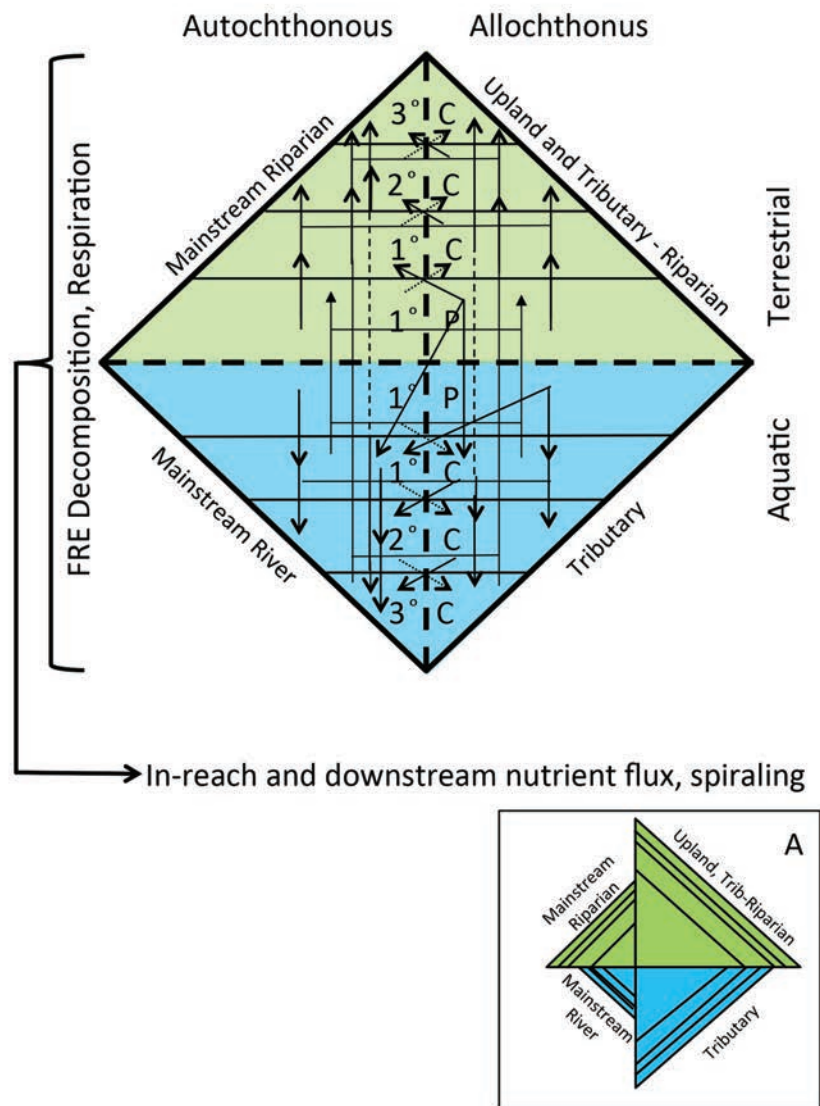
Hutchinson (1967) and Hynes (1970)

While G.E. Hutchinson (e.g., 1967) and his students and colleagues set the stage for much of modern ecology and limnology, the first comprehensive synthesis of flowing water ecology was presented by Hynes (1970). Hynes' *Ecology of Running Waters* was a pioneering compendium focused largely on biological elements and ecological processes associated with streams and smaller rivers. Hynes (1970) described and related many discrete biological studies of flowing water, and his subsequent work included consideration of the watershed spatial scale and groundwater influences, advancing both basic and applied research. Hynes' research included the role of the watershed, lakes, and ecological risk assessment in FRE ecology and management (e.g., Hynes 1974, 1975; Stanford 1998; Ward 1989). However, Hynes focused less attention on non-flowing watershed components, like the importance of the riparian zone or a unified FRE model. Wurtsbaugh et al. (2015) reported that focus on Hynsian (lotic) versus Hutchinsonian (lentic) freshwater limnology created differences in interpretation about the roles of habitat and biotic factors in fish population biology and freshwater aquatic research. Nonetheless, both Hutchinson's and Hynes' contributions initiated a rush of integrative thinking about FRE ecology that followed their 1970s work and continues today.

The River Continuum Concept (RCC)

Beginning in the 1970s, the RCC was developed in the 1970s by Cummins (1976) and Meehan et al. (1977), and was formalized by Vannote et al. (1980), integrating aquatic and riparian domains of FREs. The RCC "... described the entire fluvial system as a continuously integrated series of physical gradients and associated biotic adjustments as the river flows from headwater to mouth" (Annear et al. 2004: 9-10). The RCC described "... a series of responses within the constituent populations resulting in a continuum of biotic adjustments and consistent pattern of loading, transport, utilization and storage of

Figure 12—Expanded detail of linkage of the FRE, contrasting allochthonous (uplands and tributary) vs. autochthonous (mainstream) ecosystem energy inputs with aquatic vs. riparian domain interactions. Arrows indicate common energy pathways among trophic levels in the four FRE arenas. Not all interactions occur in every FRE, and other trophic interactions that are not depicted here may exist in some FREs. Inset A depicts spatial change in reach-based FRE structure and function in response to watershed changes. For example, upland fire can result in sediment, ash, and nutrient loading through tributaries, processes that may diminish FRE productivity and ecological role in the watershed. Similarly, reduction in precipitation or groundwater contribution through climate change or aquifer depletion may reduce mainstream and riparian function.



organic matter along the length of a river” (Vannote et al. 1980:130). The focus of the RCC was on lotic (riverine) processes supporting the aquatic ecology of invertebrates and fish and did not relate streams to groundwater and lentic sources or to potential hyporheic refugia (Palmer et al. 1992). Quickly recognized as a useful overall FRE model (Merriam 1984), the RCC was broadly supported by studies of low-medium order streams, primarily in mesic regions (e.g., Minshall 1988, Minshall et al. 1983, 1985). Applicability of the RCC to higher stream orders has been questioned (e.g., Sedell et al. 1989).

The RCC described perennial streams (AQZ) bordered by hydriparian (HRZ) to URZ ecosystems from headwaters to mouth (Johnson et al. 1984) and generally supporting large, important fish populations, particularly salmonids. Although concentrating on aquatic ecosystems, it emphasized interactions between aquatic and riparian domains. The RCC considers the riparian zone as a dependent contributor of organic matter, shade, and fish food, sourced from upstream reaches and adjacent uplands. Riparian zones provide important ecotonal interfaces between aquatic and terrestrial domains (reviewed in Committee on Riparian Zone Functioning and Strategies

for Management 2002). In addition to autochthonous primary productivity, FRE aquatic domains receive essential contributions of nutrients and bio-available leaf litter, wood, detritus, and dissolved organic carbon, as well as recalcitrant carbon from the adjacent riparian zone. The bio-available portions of those contributions are processed by stream microbes and macroinvertebrates, providing food resources for fish. In turn, the adjacent riparian ecosystem depends on subsurface water from the hyporheic zone, other groundwater, and surface flow events including overbank flooding. As originally described, the RCC did not explicitly extend into the hyporheic zone, but a plethora of FRE macroinvertebrates, such as Plecoptera (stoneflies) and amphipods, can occur there (Palmer et al. 1992), some being found in 10 m-deep wells as far as 2 km from the channel on the floodplain of the Flathead River, Montana (Stanford 1998; Stanford and Ward 1988; Annear et al. 2004).

The RCC quickly became the leading paradigm explaining FRE ecology, and it stimulated a vast wave of research, assessment, metrics development. It also encouraged policy relating water quality, aquatic macroinvertebrate feeding guilds, and fish populations as management indicators of stream health (Annear et al. 2004, 2009). This emphasis has included Karr's (1991, 1999) development of the index of biotic integrity (IBI), which assembles multiple layers of information to provide a quantifiable metric of stream ecosystem health to guide management and stream rehabilitation. Reviews of the success of IBI and other metrics by Merritt et al. (2008), and of the success in understanding gradient responses of aquatic macroinvertebrates by Heino et al. (2015), are somewhat reserved because of the growing recognition that these metrics and relationships often only weakly describe patterns of macroinvertebrate biodiversity and distribution. Interactions occur among physical and biotic variables, not to mention anthropogenic factors, operating at microsite to watershed scales. These interactions influence the ecological integrity of FRE aquatic habitats in sometimes incomprehensible ways.

The RCC champions the concept of ecological connectivity, which was recognized in the 1980s as "... maintenance of longitudinal, lateral, and vertical pathways for biological, hydrological, and physical processes" (Annear et al. 2004:215). However, spatial focus on watershed and river flow and geomorphology in the RCC has somewhat neglected the temporal dimension, which is integral to FRE development, function, and dynamic seasonal and interannual geomorphic adjustment (Morisawa 1968). Although connectivity is recognized as important to perennial streams and adjacent riparian zones, it also is applicable to ephemeral and intermittent streams and their adjacent riparian zones, as well as river source lakes, lentic zones, and groundwater sources, including springs (National Research Council 2002).

Subsequent to Hynes' (1970) work and formulation of the RCC, many FRE syntheses have been undertaken, including comprehensive edited volumes and reviews by: Annear et al. (2004); Bouwman et al. (2013); Fisher et al. (1998); Humphries et al. (2014); Johnson and Jones (1977); Johnson et al. (1985); Karr (1991, 1999); Karr and Chu (1999); Malanson (1993); Minshall et al. (1983, 1985, 1988); Naiman et al. (1998, 2005); National Research Council (2002); Sedell et al. 1989; Stanford (1998); and Thorp et al. (2006, 2008). While a full review of these syntheses is beyond the scope of this document, we note that each review has emphasized particular aspects of FRE ecology, somewhat to largely overlapping previous reviews, but sometimes shifting focus away from conceptual integration.

Contributing Ecological Models and Syntheses

During and since the initial formulation of the RCC, a number of important additional models have been proposed. These contributions appear to us and others (e.g., Sedell et al. 1989; Ward 1989) to refine FRE ecology as critically definitive axioms, corollary processes, and addenda to the RCC, although several offer alternative perspectives on FRE ecology.

The nutrient spiraling concept was formulated by Newbold et al. (1981; reviewed in Ensign and Doyle 2006) to describe the helical ecological pathways of material and nutrient processing through FREs. Autochthonous (endogenic) and allochthonous (exogenic) production is processed, released, and taken back up as water flows through uplands and tributaries into riparian zones and mainstream rivers. Nutrient spirals lengthen with stream order and with higher flows, thus, spiraling is a process that directly links upstream to downstream reaches, in addition to lateral shoreline habitats.

Although developed to describe the impacts of impoundment on regulated rivers, Ward and Stanford's (1983, 1995) serial discontinuity concept (SDC) illuminated the issue in many natural rivers of the roles and impacts of natural dams that form lacustrine reaches and affect FRE channel geomorphology, flow, and population dynamics, both upstream and downstream from the dam. Lacustrine reaches can occur anywhere in a basin as a result of tectonism, lava dams, slope failure, or glacier development, and the natural dams may persist for short to long durations. Lake Victoria in Uganda formed as a result of tectonic rifting, interrupting the flow of the Kagera and other Nile River headwater streams. Lago de Nicaragua (L. Cocibolca), the largest lake in Central America, formed as a result of tectonic uplift in the lower Tipitapa and San Juan River basins. Prominent examples of North American lava flow dams include the formation and collapse of basalt dams; large to enormous paleo-impoundments in lower Grand Canyon (Crow et al. 2008; Dalrymple and Hamblin 1998; Fenton et al. 2004); and in the Verde River basin in central Arizona (Elston et al. 1974). Costa and Schuster (1987) claimed that natural impoundments created by landslides, glacial ice, and glacial moraines constitute substantial threats to human life and property. They identified six types of slope failure dams around the world, ranging from relatively common single events that half-impounded a valley, to rare, simultaneous impoundment of multiple valleys, creating several to many natural lakes. The largest slope failure dams in the Colorado River basin in the American Southwest occurred in the Surprise Valley region in the middle of Grand Canyon (Rogers and Pyles 1980). Due to several triggering mechanisms among several events, nearly 15 km of the north rim failed (at least once catastrophically), slid into the canyon, and repeatedly dammed the river, causing it to shift its deeply incised course. Other large dam-forming landslides are known throughout Grand Canyon and elsewhere in the region, including a 0.3 km³ dam-forming landslide in the Virgin River Canyon downstream from Zion National Park (Castelton et al. 2016; Hereford et al. 1995). Enormous Pleistocene glacial dam outburst floods from Lake Missoula swept through the lower Columbia River drainage, creating scablands geomorphology (Benito and O'Connor 2003; Bretz 1923). Ice damming floods are well known on fjord rivers as well (e.g., Reeburgh and Neburt 1987).

Like anthropogenic dams, natural impoundments change river seasonal water quality and flow, hydrography, stage relations, velocity, habitat quality and distribution, and FRE

biogeography. The SDC posits that the location and size of a dam resets and influences downstream recovery of the FRE “normal” conditions through tributary contributions of flow, water quality, and biota (Dye 2010; Rice et al. 2008). Furthermore, the extent of river recovery from natural impoundment varies in relation to the number, size, and flow characteristics of downstream tributaries. Like large, influential tributaries, natural dams are not controlled by stream order (they can occur anywhere within a basin), and a large and persistent natural dam may exert long-term direct and antecedent impacts on FRE geomorphology and ecology. Like anthropogenic impoundments, natural dams also seasonally influence upstream FRE habitat quality and connectivity.

Also related to Ward and Stanford’s (1983) SDC, the discontinuity impacts of larger tributaries often are abrupt and generate multi-reach alterations of mainstream FRE ecology, as incorporated in the link discontinuity concept (LDC; Rice et al. 2001). The LDC posits that rivers are networks of tributary confluence nodes linked by the mainstream. This perspective was advanced in the network dynamics hypothesis (Benda et al. 2004b), which integrates drainage networks of channel and confluences, and proposes that the complexity of the overall basin shapes tributary contributions to the mainstream, resulting in minor to overwhelming influences on mainstream characteristics (Benda et al. 2004a,b; Clay et al. 2015).

The flood pulse concept (FPC; Junk et al. 1989; Tockner et al. 2000) added the importance of high flow pulses to the FRE function. Floods regularly restructure river landscapes, remove encroaching channel margin vegetation, transport and deposit large woody debris, trigger river biota life history events, and open new habitat for germination and establishment of fluvial and riparian biota. Floods vary in frequency, duration, timing, and magnitude, sometimes on catastrophic spatial scales (e.g., regular seasonal flooding), accounting for the state of suspended succession recognized as a common characteristic of natural riparian vegetation by Campbell and Green (1968).

Ward (1989) clarified four dimensions of spatial and temporal scale operating in most lotic ecosystems, including: (1) the “longitudinal” dimension up- and downstream through rivers; (2) across-channel, riparian-aquatic domain interactions; (3) vertical interactions with hyporheic habitats and groundwater; and (4) a broad temporal dimension (fig. 11). Dynamic interactions among all of these dimensions contribute to the individuality of character of FREs.

Ecosystem research and stewardship require detailed and long-term understanding of geologic, hydrographic, biota, and land use history within a basin. White (1979) emphasized this in relation to forest management, and Décamps et al. (1988) and Petts et al. (1989) described the relevance of such understanding in western European river basins.

Following Stanford (1998) and Ward et al. (1989, 1998, 2002), Malard et al. (2002) expanded discussion of the biodiversity and roles of FRE hyporheic exchange through microbial and macroinvertebrate distribution and activity (figs. 10, 11).

Focusing specifically on river riparian zones but related to Ward’s (1989) considerations, Nilsson and Svedmark (2002) recognized that four major processes or characteristics interactively function in FREs: (1) The flow regime (hydrograph) regulates FRE ecological and geomorphological processes, including riparian succession. (2) The channel provides a corridor for inorganic and organic transport, primarily downstream but also upstream, and including dispersal of propagules. (3) The riparian zone functions as a filter and boundary between upland and riverine processes. Naiman et al. (1993) and

Nilsson and Svedmark (2002) also recognized (4) that riparian zones are particularly rich in biodiversity and species interactions, and play important roles in watershed biodiversity.

From advances in nearshore marine ecology patch dynamics concept (e.g., Pringle et al. 1988; Townsend 1989), Thorp and DeLong (1994) proposed and refined the river productivity model (RPM), which posits that production, as well as decomposition, recruitment, and other important river processes are distributed nonrandomly within the channel. These processes occur at specific points or in specific zones in the channel, such as at tributary confluences, along shorelines, or in certain depositional settings. Thus, their RPM proposes that river ecosystems are mosaics of microhabitats with differing ecological functions. They and their colleagues subsequently expanded this description to more fully describe the complexity of river food webs (Thorp et al. 2006, 2008), and much subsequent research has proceeded from this area of inquiry.

Fisher et al. (1998) proposed the telescoping ecosystem model, in which the FRE includes nested, concentrically positioned subsystems of the stream, hyporheic zone, channel margins, and riparian zone. Collectively, these function like a telescope, extending or retracting in relation to flood disturbance. Their model implies stepped transitions at tributary confluences and reach boundaries across stream order.

Following the lead of Jacobs et al. (2013) and Meybeck (1982), Bouwman et al. (2013) emphasized the importance of integrated biogeochemistry in FRE conceptualization. Rather than regarding a river simply as a single thread of flow or as a coupled mainstream and floodplain landscape, they considered all parts of the flow system (river mainstems, floodplains, lakes, wetlands, etc.) as a biogeochemical retention and processing network.

The river wave concept (Humphries et al. 2014) posited that most phenomena within at least the FRE aquatic domain can be viewed in a wave context. For example, river flow can be characterized as a wave that varies in frequency, length, and shape, and travels lengthwise and laterally through the channel. Wave position determines or regulates production and transport of organic material, with allochthonous input occurring primarily in troughs and ascending limb of the wave, and with autochthonous production occurring on the crests and declining limbs of the wave.

Muehlbauer et al. (2014) defined the biological stream width as the distance of travel of resource subsidies from the FRE aquatic domain into the surrounding upland terrain. They used meta-analysis to model the spatial extent of this “stream signature,” reporting that the 50 percent stream signature (the point at which subsidy resources are half the aquatic domain maximum) lay only 1.5 m from the stream edge, but that 10 percent of the signature can extend more than 0.5 km into the adjacent uplands. Thus, the biological stream width often is much larger than that defined hydrogeomorphologically.

While expansive in scope, the RCC is based on orderly, gradual downstream connectivity within a perennial alluvial channel network, and it does not well describe ephemeral and intermittent streams-riparian ecosystems or groundwater-surface water interactions (Stanford 1998). Ephemeral FREs are colloquially known as dry washes, arroyos, wadis, and other names throughout the world, and comprise more than half of the global stream channel network (Datry et al. 2014). Such stream ecosystems are becoming increasingly abundant as rivers are dewatered by human activities and subjected to a drying climate. A well-documented example was the conversion of the Santa Cruz River in Tucson, Arizona from a perennial to an ephemeral stream through groundwater pumping (Webb et al. 2014).

Flooding releases CO₂ sequestered by burial of organic matter and invertebrates, such as clams (Butman et al. in review; Smith et al. 2016), and that process is interrupted in ephemeral streams. Benthic invertebrates that shred, graze, or collect organic debris often are absent or rare in ephemeral streams, reducing decomposition rates, and their roles are often replaced by microbes and physical molar action when the streams flood.

Terrestrially, ephemeral versus intermittent riparian zones are bordered by distinctive suites of xeroriparian (dry riparian) to mesoriparian perennial plant species that provide cover and food resources (Johnson et al. 1984). Analysis of an ephemeral stream near Peshawar University in Pakistan revealed that deeply rooted woody perennial shrubs occurred in the wash, and weeds dominated the bed following winter rains, with drought resistant species occurring on terraces (Chaghtai and Khattak 1983). Aquatic productivity and trophic energetics of aridland ephemeral streams are reduced and interrupted during dry seasons (e.g., Jenkins and Boulton 2003), interrupting spatial and temporal “flow-through” RCC processes, but ephemeral channels commonly provide essential wildlife habitat connectivity. They perform as punctuated, rapidly functioning biogeochemical reactors (Larned et al. 2010). More study of ephemeral stream ecosystems continues to be warranted.

Biological Processes and Characteristics

Overview

Climatological, hydrogeological, and geomorphic physical processes generate the microscale-to-watershed template on which the microclimate and biological functions of FREs generate or develop nutrient dynamics, assemblage composition and structure, and trophic interactions (Merritt et al. 2010; Naiman et al. 1993, 1998, 2005). Here we describe and illustrate these processes and interrelationships through the figures presented below, with figure 11 as the template, figure 12 adding detail to figure 11, and subsequent figures to illuminate key ecological processes and interactions between linked aquatic and terrestrial domains. These biological processes and elements sometimes reciprocally influence physical factors, such as sedimentology, channel geometry, and microclimate (Merritt 2013; Montgomery et al. 2003; Pollen et al. 2004), as well as FRE characteristics, such as ecological resiliency. We discuss these biological processes and elements, placing additional emphasis on riparian vegetation formation and dynamics.

Nutrient and Organic Matter Production and Release

FREs export allochthonous (upland and upstream) and autochthonous fine to coarse woody debris, other organic matter, and nutrients downstream through ecological spirals (Newbold et al. 1981) (figs. 11, 12). Although the dominant direction of FRE matter transport is downslope and downstream, important returns of nutrients also can occur through upstream aerial or zoochorous transport of sediments, nutrients, and propagules (e.g., spawning salmon, wind-blown seeds, or adult forms of aquatic insects; review by Cederholm et al. 1999). N, P, and C are differentially stored in alluvial reaches but are generally exported from constrained reaches. Fluvial nutrient dynamics models are needed to relate nutrient fixation, storage, retention, transport, and recycling, but such models remain a largely overlooked dimension in FRE ecology (Bouwman et al. 2013).

Biodiversity

Elevated biodiversity in FREs is universally recognized. Nearly 7.5 percent of the nearly 1.5 million described species on Earth are aquatic and occur in freshwater habitats, and many more aquatic and riparian invertebrate species remain undescribed (Collon et al. 2014). In addition, many other species occur in adjacent wetland and riparian habitats. The high biodiversity and proportion of gamma diversity in FREs can be attributed to a suite of factors (Naiman et al. 1993). Gravity transports propagules downslope from the uplands and also downstream into different reaches and segments (Johansson et al. 1996; Stevens 2012). The dendritic network of a channel system provides a corridor for movement or range shifts for many species. As ecotones, FREs bring different suites of species together (Décamps and Tabacchi 1994; Gregory et al. 1991; Naiman and Décamps 1997). Also, rivers provide shifting mosaics of highly productive habitat, allowing different colonization opportunities over space and time (Naiman et al. 2005). Stevens and Ayers (2002) reported that nearly half of 1,400 vascular plant species in Grand Canyon occurred within 200 m of the Colorado River elevation, of which one-third were riparian and 10 percent were springs-dependent species. In addition, more than two-thirds of the regional fauna obligatorily or facultatively used riparian habitat. Thus, although the area of FRE habitat is trivial, it supports a vast proportion of regional biodiversity, particularly among aridland river basins (Jansson et al. 2007; Stevens 2012).

Nilsson et al. (1989) studied riparian plant species richness (S) along rivers in northwestern European rivers, reporting peak S at middle stream order. Substrate heterogeneity and fineness were the primary factors influencing total richness, with a unimodal peak in S at intermediate levels of substrate fineness. Renöfält et al. (2005) compared riparian-to-upland plant S in the Vindel River basin in northern Sweden, reporting that S was related to local, river-related processes and corridor-based dispersal. However, unlike Nilsson et al. (1989), they reported a monotonic decrease in S from the headwaters to the coast, and high floristic similarity between the uplands and the riparian zone. Differences between these studies highlight the roles of stream order and regional variation in upland plant diversity.

In an aridland comparison of riparian and upland vegetation, Bloss and Brotherson (1979) described plant assemblage composition in a Sonoran Desert valley near New River, Arizona. They reported that vegetation either intergraded or abruptly shifted from upland slopes into the river channel, based on the erosional structure of terraces. Leguminous shrubs and trees occurred differentially on middle portions of the moisture gradient. Although plant diversity was highest on upland slopes, diversity was positively related to soil moisture, and floodplain species exhibited the broadest niche widths. They concluded that disturbance as well as moisture availability influenced the transition from desert to riparian plant diversity.

Differences among the above and other studies highlight the need for comparative analyses of FRE plant diversity, composition, and structure across latitude and among humidity provinces.

Trophic Energetics and Structure

Sunlight is the primary source of terrestrial FRE energy, not only generating the hydrologic cycle, but also powering photosynthesis (e.g., Stevens 2012; Yard et al. 2005).

The proportional contribution of autochthonous versus allochthonous production and nutrients varies between aquatic and riparian domains in relation to the physical setting of the watershed, stream order, season, and reach-based channel geometry and connectivity (Fisher and Likens 1973), changing over time in a successional fashion if not disturbed by flooding (Fisher 1983; Fisher et al. 1982) (figs. 11, 12). High levels of intrinsic production may occur in clear headwater springs and low- to mid-order streams. Lower elevations in the basin may be warmer (or sometimes cooler if subsidence occurs) and often have longer growing seasons, but aquatic productivity may be reduced in higher order streams where organic and inorganic particles reduce PAR (e.g., Yard et al. 2005). Stevens (2012) also emphasized the PAR-limiting influences of cliff shading in large temperate river canyons.

FRE trophic structure varies among aquatic, riparian, and upland domains, and across the chemical and ecohydrological gradients occurring within them, as described above and illustrated in figures 11 and 12. Aquatic food-web structure is regulated by temperature (Glazier 2012), flow, sediment load, seasonality, shading, and many other factors. For example, Mustonen et al. (2016) used 12 experimental channels to examine the effects of flow and suspended sediment on primary producer, macroinvertebrate, and/or fungal production and decomposition. Flow and sediment impacts on the response variables were largely independent, but interaction effects were antagonistic (e.g., flow stimulated algal production, while sediment loading reduced production). While their results are largely intuitive, such studies help clarify and quantify the fundamental driving features of FRE ecology.

Gawne et al. (2007) tested predictions of the RCC, RPM, and FPC models on river metabolism through analysis of the ecological roles of microbial and macrophyte assemblages in three lowland tributaries of the Murray River in Australia. They concluded that all three models were supported to some extent, but the extent, causes, and consequences of aquatic primary production were varied, and no individual model fully explained the patterns observed. In contrast to the aquatic domain, riparian food-web dynamics are more diverse due to the more open nature of riparian-to-upland interactions and feedbacks. In a seminal paper, Carothers et al. (1974) reported that the highest diversity of breeding (primarily neotropical) birds in central Arizona occurred in cottonwood-willow riparian habitats bordered by agricultural field in central Arizona, with riparian vegetation structure affecting not only bird assemblage composition but also social organization. Although not yet studied to our knowledge, the noise levels generated by rivers in steep canyons also is likely to influence FRE avifaunal assemblages (e.g., McClure et al. 2013).

Trophic cascades are regularly observed in fish-dominated ecosystems and in some low-order fishless systems (e.g., Blinn 2008) but are limited in FREs by physical processes (e.g., hydrology, sediment transport, ice impacts), where average sheer stress/unit area appears to be negatively related to stream order (Magilligan, 1992). However, turbidity generally increases with stream order, reducing downstream PAR availability and primary through tertiary aquatic production (e.g., Yard et al. 2005). Complex trophic relationships also develop in riparian zones, directly and indirectly influencing primary producer structure and composition. For example, leaf beetles, grasshoppers, beaver, and ungulates all can strongly influence riparian vegetation composition, structure, and decomposition/soil formation (e.g., Bailey and Whitham 2006; Sacchi and Price 1988),

and such impacts can be modified by both secondary consumers (e.g., ants; Schweitzer et al. 2005) or top predators (e.g., wolves; Beschta and Ripple 2006, but see Marshall et al. 2012). In one example of complex riparian interactions, manna (honeydew) produced by the host-specific cicadellid tamarisk leafhoppers (*Opsiurus stactogalus*) stimulated soil fungal growth, which in turn killed germinating seedlings of both the host plant and other riparian plant species beneath *Tamarix* canopies (Simieon and Stevens 2015). Whether such multi-trophic-level interactions constitute an evolved process remains to be determined, but proximally it ensures *Tamarix* stand persistence through inhibitory (rather than facilitation or tolerance) successional mechanisms (*sensu* Connell and Slayter 1977). Just one of many complex riparian trophic interactions, this interaction is favored in relatively constant environmental conditions, and is most influential on the broad, low-gradient floodplains of higher order streams.

Trophic cascades also arise from interactions among other aquatic and terrestrial FRE taxa. For example, predatory aquatic invertebrates, such as hellgrammites (Megaloptera: Corydalidae), can function as top predators in clearwater streams, foraging actively at night when fish may be less able to detect prey. Amphibians can alter algal composition, algal production, and organic matter dynamics in small streams, and they can function as important aquatic and riparian predators (e.g., the giant aquatic salamander *Cryptobranchus alleganiensis*), thereby influencing aquatic-to-terrestrial ecosystem energy transfer (Whiles et al. 2006). The dual nature of amphibian life cycles may mean that the loss of an FRE amphibian species equates to the loss of two functional species, effects that may be greatest in neotropical stream ecosystems.

Finer-scale illustration of FRE trophic structure (fig. 12) depicts the complex food-web interactions among aquatic and terrestrial domains within reaches, which produce and receive ecosystem energy from autochthonous as well as from upslope, upstream (including tributary), and groundwater-derived allochthonous sources (e.g., Townsend et al. 2000). Four relatively discrete component triangles are illustrated in figure 12: autochthonous mainstream and riparian zone, and allochthonous tributary and upland plus tributary riparian triangles. These four triangles are depicted as being ecologically open and potentially interacting with each other (dashed lines). The most common inter-trophic interactions among the four components occur vertically (primary producers through tertiary consumers), but many other complex interactions exist among trophic levels among these four triangles. For example, across-triangle interactions include such food-web interactions as crocodilians feeding on riparian or upland ungulates and predators in tropical rivers.

Environmental variation within reaches and across spatial and temporal scales influences the relative contributions of the four FRE component triangles (fig. 12, inset A). For example, under a drying climate, decreased runoff may reduce or eliminate mainstream and riparian nutrient contributions. Conversely, increased wildfire frequency and severity may at least temporarily mask or inflate the influence of upland and tributary nutrient contributions to the watershed. Thus, relationships among component triangles are expected to vary over time and therefore are not expected to reach equilibrium.

FRE Biogeography

FRE biogeography involves colonization, recruitment, and population establishment overland by volant and other highly vagile species, as well as passive dispersal through

gravity, aerial drift, or zoochorous transport of propagules through both overland and dendritic stream corridors (fig. 11). Regardless of the pathway, FRE population persistence and assemblage resilience is predicated on the ability of a species to remain in or disperse-recover their position in the watershed. Therefore, persistence of all FRE species requires some form of upstream dispersal, with eviction or extirpation the inevitable consequence of failed *in situ* or headwater recruitment strategies.

FRE dispersal by riparian plants is achieved through hydrochory, anemochory, or zoochory. FRE propagules of seeds, rootstocks, eggs, or larvae drift downstream through hydrochory (Merritt and Wohl 2002). But propagules must be blown upstream or be transported by animals if that species is to persist in the FRE. Larval aquatic macroinvertebrates may drift downstream, while adult aquatic insects often fly or are blown upstream as aerial drift. Dragonflies, salmonids, and many other fish taxa migrate upstream to spawn, against the dominant flow direction, and some fish transport larval unionid mussel larvae upstream. Migratory western North American warblers and other passerine birds intensively use aridland riparian habitat as stop-over habitat during migration (Carlisle et al. 2009; Skagen et al. 2005; Stevens et al. 1977), a pattern not strongly evident in mesic eastern North America (Kelly and Hutto 2005).

However, western North American songbirds generally migrate northward along broad fronts, rather than using FREs as navigation corridors, although “specific populations are likely restricted to narrower migration routes,” such as riparian nesting species along FRE corridors (Carlisle et al. 2009; RRJ, unpublished research). Front-based bird migrations also occur among some western North American shorebirds, but many waterbird species appear to follow FRE corridors, particularly through complex landscapes (e.g., Stevens et al. 1997a). In addition, many non-volant vertebrate species follow river corridors as dendritic pathways, although terrestrial faunal movements can be thwarted by steep cliffs, perilous crossings, and anthropogenic landscape interruptions (Stevens 2012).

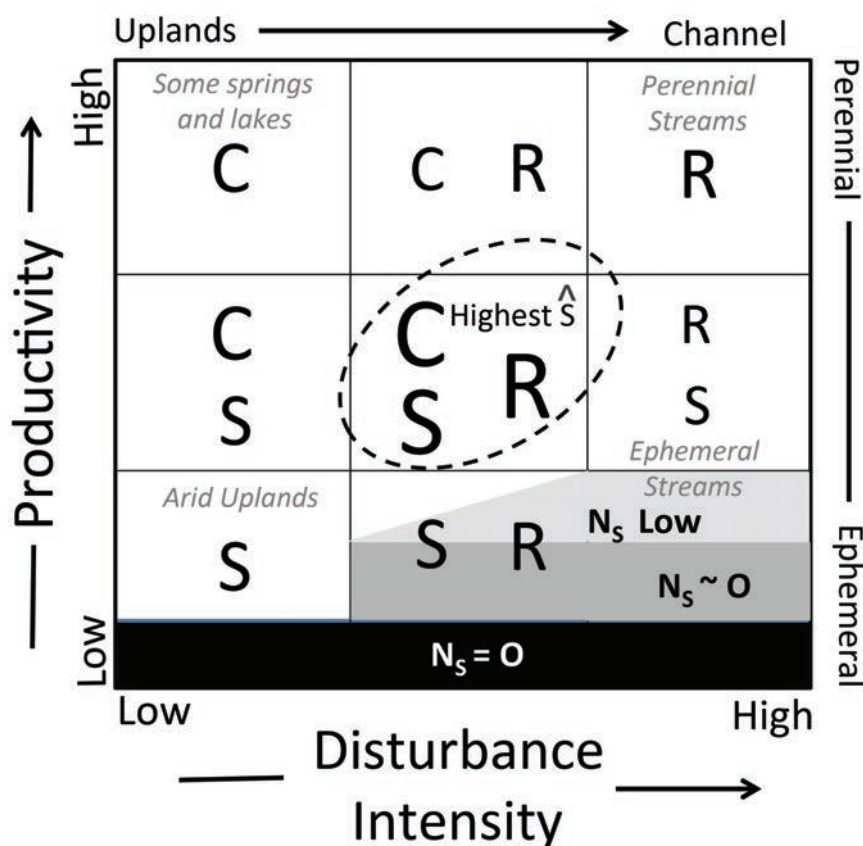
Colonization and extirpation frequencies vary by taxon and life history strategy and on the basis of physiological, life history, mobility, and reproductive strategies, which collectively influence species dominance in a given FRE reach. In relation to insular biogeographic theory (MacArthur and Wilson 1967), colonization probability in FREs is enhanced by productivity through habitat “hospitality” to colonizing taxa, while local extinction (extirpation) probability is more related to disturbance, particularly from scour (flooding, ice scour), low flows, and random or erratic events.

Disturbance

Ecological disturbance is defined as events that kill mature individuals within habitats. It exerts direct and indirect controls over sessile species richness, composition, and structure, as described in the dynamic equilibrium concept (DEC) (Huston 1979, 1994; Laliberté et al. 2013; Lehman and Tilman 2000) (figs. 11 and 13). Floods, channel inundation or desiccation, glacial movements, ice scour, slope failure, and other disturbances affect sessile riparian species richness by removal or killing of adult organisms and resetting of environmental conditions (Connell 1978; Sousa 1984).

Scour impacts arise from unit stream power, applied as sheer across the channel surface (Bendix 1992). Scour impacts vary in relation to latitude, lithology, and stream order in alluvial versus constrained reaches, and across stage, differentially affecting

Figure 13—Plant life history groups (Grime 1977) in relation to disturbance intensity and productivity gradients (Huston 1979, 1994). C—competitive species, R—ruderal species, S—stress tolerators. Black areas support no plant species ($N_s = 0$), gray areas have very low N_s , and white cells have some to high N_s . Highest “hat above S” [middle square]=maximum plant species richness.



lower terraces (Magilligan 1992). Due to shear stress and channel margin erosion, scour mortality of vegetation may differentially predominate lower terraces, while drowning mortality may be more likely in the latter. Stevens and Waring (1985) reported great variation in flood-related mortality among guilds of riparian plant species and across stage elevation in the Colorado River in Grand Canyon, Arizona. However, vegetation assemblage responses to flooding differ among terraces, reaches, and rivers. Pettit et al. (2001) reported reduced germination density, plant species richness, and riparian tree size in the intensively flood-scoured Blackwood River in southwestern Australia; however, they reported neutral germination responses and little reduction in species richness in response to flooding along the Ord River in northwestern Australia.

The impacts of ice formation and breakup on FREs are pronounced and are gaining attention in temperate and boreal rivers (Prowse and Culp 2003). At higher latitudes and elevations, ice formation and “shoving” routinely scour shorelines and bed surfaces and may dam channels, uplifting and redepositing fine to coarse substrata, including boulders and coarse woody debris. They may also alter channel geometry. In addition, processes such as melting black (benthic river) ice or surface ice breakup and scour can alter benthic and riparian composition complexity and structure (Scrimgeour et al. 1994).

Productivity

Riparian productivity is positively associated with biodiversity through intrinsic mechanisms, such as organism size distribution, niche specialization, assemblage history, as well as interaction with disturbance gradients (Fukami and Morin 2003; Hooper et al.

2005; Huston 1979, 1994; Marquard et al. 2009; Tilman et al. 2001) (figs. 11 and 13). Reach-based FRE productivity varies by stage (moisture and soil), aspect, and microclimate, as well as macro-scale climate, latitude, and elevation gradients. In lieu of a way to describe it, we refer to the colonization potential of a microhabitat as “ecological hospitability,” referring to the productivity and receptivity of a site to colonization. Low levels of productivity and high levels of disturbance reduce the richness of sessile species through resource limitation and reduced survival. Competition limits species richness at low levels of disturbance and high levels of productivity (Connell 1978; Huston 1979) (fig. 13).

Disturbance-Productivity Interactions

FRE riparian zones exhibit steep ecological gradients in disturbance and productivity, particularly in arid regions. However, riparian habitats have both the highest potential disturbance and productivity nearest the water’s edge. Gradients decrease with distance from, and elevation above, the shoreline (figs. 11 and 13). Stevens (1989) and Pollock et al. (1998) both reported support for the DEC (Huston 1979) for riparian plant species richness along western North American streams. However, Reice (1985) experimentally tested disturbance intensity on stream invertebrates, reporting no support for Connell’s (1978) intermediate disturbance hypothesis. Although high levels of disturbance limited diversity in his study, competitive exclusion did not appear to reduce species richness at low levels of disturbance.

The intermediate disturbance hypothesis (reviewed by Wilkinson 1999), as well as the insular biogeography model of MacArthur and Wilson (1967), were developed for sessile taxa (such as plants and corals) but not for vagile species, some individuals of which can actively avoid disturbance events (e.g., stream abandonment behavior by the giant water bug, *Abedus herberti*) (Lytle 1999). However, Townsend (2003) found support for the intermediate disturbance hypothesis for benthic macroinvertebrates among 54 streams with varying histories of flood disturbance, reporting that bed disturbance accounted for the most variation in both sessile and vagile taxon richness. Nonetheless, the role of disturbance and the explanatory power of these FRE biodiversity models vary among aquatic and riparian taxa.

Thus, while efforts have been made to distinguish the impacts of disturbance and productivity gradients in FREs, spatial autocorrelation prevents clear separation of the individual impacts of these two gradients on the structure of riparian vegetation or other sessile taxa (e.g., ant hives). Steady flow systems, such as zero order headwater hillslope springs or seeps that flow into highly disturbed channels, provide a more refined study context than do FREs in which to distinguish disturbance from productivity impacts. The impacts of other gradients (e.g., nutrient availability) on FRE biodiversity and ecological functions can also be more accurately assessed.

Life History Strategies

Life history strategies among aquatic and terrestrial plant and animal species display complex responses to the environmental gradients and gradient interactions in FREs. A central focus of FRE ecology has been classification of guilds—groups of species with similar life history traits, particularly recruitment habitats and interactions among riparian plants (e.g., Johnson et al. 1984)—and feeding or habitat niche use among animals. For

example, Hough-Snee et al. (2015) conducted an analysis of woody riparian plant life history traits in relation to environmental gradients and assemblage distributions in the Columbia and Missouri River basins in western North America. They identified five guilds of riparian plants based on rooting depth, canopy height, and resilience to flood disturbance, traits that may sort assemblages under a changing climate.

Grime (1977) identified three main plant life history strategies: short-lived, r-selected ruderal species; long-lived, K-selected competitors; and usually long-lived stress tolerators. Plant species characterized by these life history strategies vary spatially in relation to disturbance and productivity gradients, but disturbance-productivity interactions and competition for nutrients create conflicts within the Grime (1977) model (Craine 2005; Grace 1990; Huston 1979, 1994; Tilman 1988; Walker and Peet 1985). Plant species employ different strategies at different life history stages. For example, Salicaceae and *Tamarix* along southwestern United States streams have an exploitative, ruderal seedling establishment phase, but they also have more competitive and stress-tolerant mature phases (Stevens 1989). Nonetheless, Grime's (1977) three life history strategies may help explain some of Huston's (1979, 1994) dynamic equilibrium predictions: competitors are likely to dominate low disturbance environments, while ruderals are likely to dominate more highly disturbed habitats, and stress tolerators are likely to dominate in low-productivity settings (fig. 13). As a consequence, at least part of the reason that Huston's DEM predicts higher species richness at intermediate levels of both disturbance and productivity is that those gradient positions support all three of Grime's life history strategies.

Feeding guild and habitat use also have dominated classification and applied ecology of aquatic FRE macroinvertebrates. The RCC focused on the downstream transition of secondary production in relation to stream order (although with less emphasis on predators and drifting terrestrial invertebrates), stimulating a rigorous national effort to classify macroinvertebrates as bio-indicators of stream ecosystem health (e.g., Karr 1991; U.S. Environmental Protection Agency 2016; but see Heino et al. 2015 and Merritt et al. 2008). Water acceptable for human needs may support readily identifiable aquatic macroinvertebrate assemblages. However, U.S. water quality and quantity regulations fail to acknowledge that natural non-potable waters (like those commonly occurring in arid regions) support many common, important endemic and some endangered aquatic and wetland taxa and assemblages (e.g., Blinn 2008; Norment 2014).

While predatory invertebrates, amphibians, reptiles, birds, and mammals occasionally exert top-down trophic cascade influences on aquatic ecosystems, fish often are the most influential aquatic FRE species. Fish commonly affect lower trophic levels through both herbivory and trophic cascades. However, most conceptual modeling studies of river fish ecology involve applied species- and river-specific studies, usually directed toward flow regulation, pollution, harvest potential, and other anthropogenic impacts on socio-economically important fisheries. Continental-scale fluvial fish ecology studies (e.g., Dudgeon 2000) and global modeling across continents, river basins, and stream orders remain relatively rare. Ibañez et al. (2009) conducted a comparative study of river fish feeding guild structure in Africa, Europe, and North and South America, reporting general support for RCC-related hypotheses that overall species richness and the proportion of omnivorous species increased over stream order, while the proportion of invertebrate feeders declined. They also reported that piscivore and herbivore/detritivore taxa were

relatively depauperate in smaller North American and European streams.

In an effort similar to that of Grime (1977), Bennett (2015) and Mims et al. (2010) used multivariate statistics to reveal three fish life history strategies among North American freshwater fish species: (1) equilibrium fish species with low fecundity and high juvenile survivorship (corresponding to Grime's competitive species), (2) opportunistic species with early maturation and low juvenile survivorship (corresponding to Grime's ruderal species), and (3) periodic species with late maturation, high fecundity, and low juvenile survivorship (somewhat corresponding to Grime's stress-tolerant species). Such convergence of life history strategies among terrestrial primary producers and aquatic consumers suggests that similar biotic and abiotic constraints analogously shape FRE guilds within trophic levels in both aquatic and terrestrial domains.

An ecologically intriguing group of species occupy FRE torrent habitats. Torrent species include organisms as diverse as: aquatic mosses; various riparian plants (e.g., Asteraceae: *Brickellia longifolia*, Poaceae: *Phragmites australis*, and Tamaricaceae: *Tamarix pentandra*); various insect taxa (some plecopteran stone flies; hemipteran belostomatids (Lytle 1999); gerrid *Merobates* and *Trepobates* small water striders; some dipteran tipulid crane flies and simuliid buffalo gnats; some trichopteran web-spinning caddisflies); immature anguillid eels and many salmonid, cyprinid, and other fish taxa; and some bird species (e.g., South American torrent duck [*Merganetta armata*], New Zealand blue duck [*Hymenolaimus malacorhynchos*], and American Dipper [*Cinclus mexicanus*]). Such taxa are specifically adapted for life in high velocity aquatic settings, some even occupying madicolous habitats (shallow cascading flows of white water).

Riparian Vegetation

Overview

Plant species vary enormously in flood and drought tolerance physiology, as well as architecture, reproductive strategies, recruitment strategies, and distribution (Malanson 1993; Reichenbacher 1984). As with benthic invertebrates, the wide array of plant adaptive traits has stimulated many attempts to classify and subdivide upland and riparian assemblages into functional guilds (e.g., Cody 1991; Grime 1977; Hook 1984; Johnson et al. 1984) or mapping units. Such efforts may aid in modeling or management, but life-stage differences and the substantial residual noise in such models reveal the diversity of life history strategies required to cope with FRE spatio-temporal non-equilibrium environmental variability.

Global FRE Riparian Vegetation Distribution

The Holdridge (1947) diagram of global vegetation is based on upland gradients of potential evapotranspiration and annual precipitation across humidity provinces, and it is scaled to latitude and elevation (e.g., Lugo et al. 1999) (fig. 14). Riparian and wetland habitats are not considered in that model. They pose an ecologically and evolutionarily important contrast to upland vegetation: abundant moisture availability in riparian habitats greatly reduces the constraints imposed by evapotranspiration and precipitation, collapsing the two primary axes of the Holdridge diagram to differences among humidity provinces.

Figure 14—Simplified Holdridge (1947) global upland vegetation structure in relation to gradients of aridity, precipitation, evapotranspiration, latitude, and elevation.

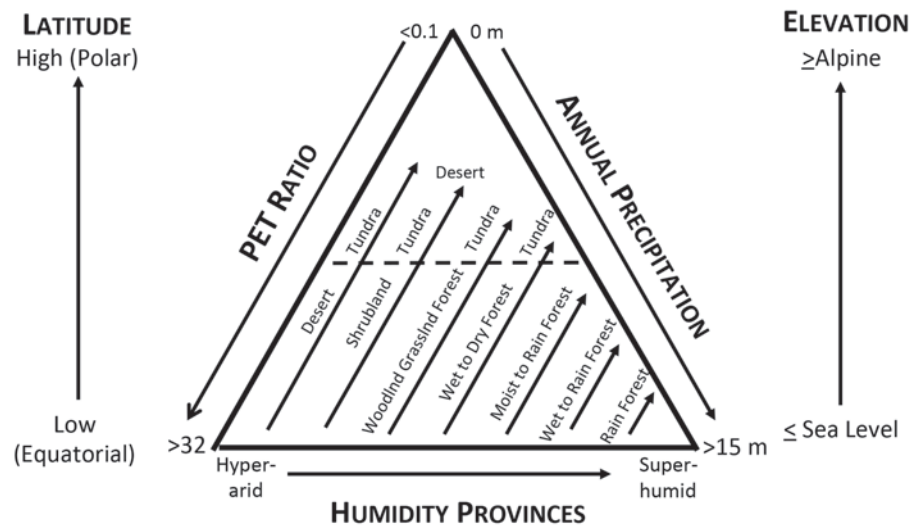
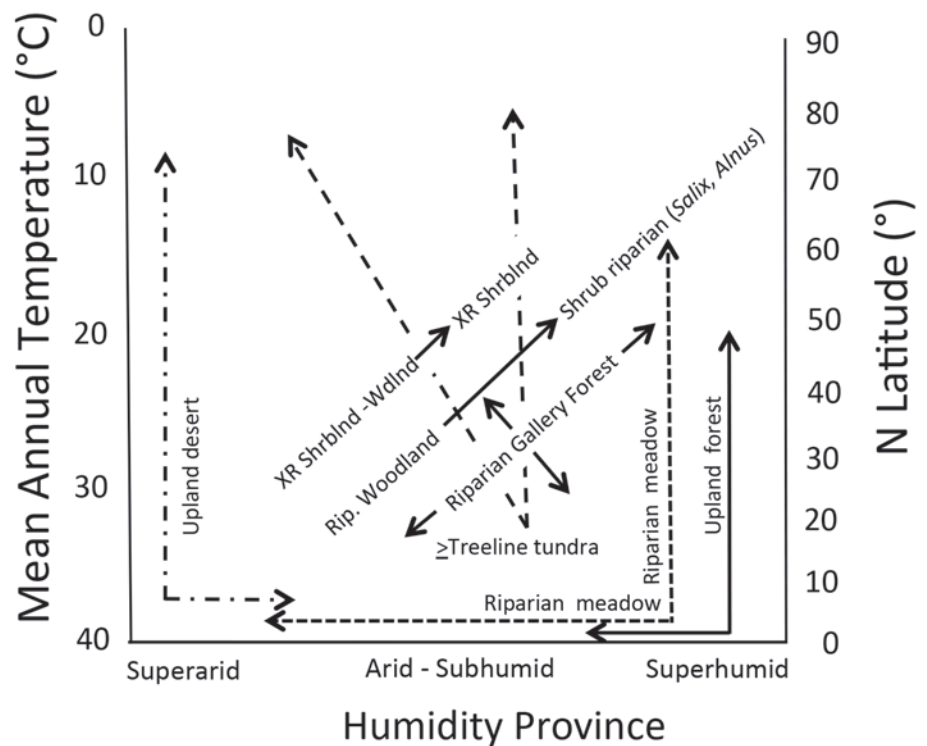


Figure 15—Modified Holdridge (1947) diagram describing the distribution and structure of riparian vegetation. Moisture availability limitations are reduced or eliminated by proximity to groundwater or surface water. Potential riparian vegetation structure is depicted in relation to humidity province, temperature regime, and latitude. Interactions among elevation, latitude, and stage are not depicted here.



Based on our observations across elevation throughout the New World, riparian vegetation appears to be predominately influenced by latitude, elevation, geomorphology, disturbance, groundwater and surface water sources, soil moisture, Holdridge humidity provinces. Riparian vegetation is also influenced to some extent by water quality (e.g., elevated aridity and soil-water salinity impose limits to vegetation at lowest elevations). Temperate regions, especially those in arid and semiarid regions in the New World Northern Hemisphere, often are dominated by galleries of usually deciduous forests (fig. 15). The spatial range of gallery riparian forests is remarkably broad, extending from 20-50° and across elevation at lower latitudes from 0.02-2.5 km. Riparian shrub and

woodland vegetation extend even more broadly across latitude and elevation. In humid to superhumid regions, adjacent upland forest vegetation often dominates riparian and ephemeral tributary habitats.

In arid to superarid regions, ephemeral channel xeroriparian habitats sustain temporally varying fluvial groundwater moisture availability, generating reduced but often compositionally diverse channel vegetation. Subsurface fluvial soil moisture availability also often extends across the floodplain, producing aridland riparian zonation and a transition of vegetation—potentially from gallery riparian forest through xeroriparian woodlands and shrublands, to facultatively riparian upland vegetation, to true upland vegetation. Riparian zonation is less apparent but nonetheless evident in mesic habitats (e.g., Hook 1984), with riparian dominance by bottomland tree species, such as *Taxodium distichum* (bald cypress), *Nyssa aquatica* (water tupelo), *Larix decidua* (larch), *Platanus* spp. (sycamores), and several Salicaceae species.

Water Uptake and Flood Tolerance Physiology

Osmotic control on water uptake capacity differs markedly between upland versus phreatophytic or wetland plant species, affecting stand development, composition, habitat structure, and zonation, particularly in arid regions (Carothers et al. 1979; Woodbury 1959). Upland species in arid lands often lack the ability to restrict water uptake, and consequently, they quickly become waterlogged and drown when inundated for even short periods. However, arid land phreatophyte species have the ability to regulate water uptake and many taxa can persist for extended periods of time when inundated (Kozlowski 1984; Stevens and Waring 1985; Warren and Turner 1975). While the evolutionary directionality of this physiological divergence apparently has yet to be explored, we hypothesize that selection has repeatedly and independently favored loss of osmotic control among xerophytic taxa as a derived trait. At any rate, the substantial physiological differences between these two groups of species strongly sort contemporary aridlands FRE plant assemblage composition across riparian terraces in relation to inundation and the depth to groundwater.

Concomitant with upland-riparian variation in water uptake strategies, the diel range of variation in xylem water potential (Ψ) from midnight to midday varies widely among riparian species, and it is based on soil moisture and riparian groundwater depth. Fluvial wetland species exhibit a high, narrow range of Ψ , while middle and upper riparian zone species have progressively lower and broader ranges of Ψ . These trends were abundantly evident among 18 common riparian zone species along the Colorado River in Grand Canyon, sampled at 13 sites with known stage-discharge relationships (fig. 16). This variation in species Ψ ranges is largely responsible for the stage-elevation zonation commonly observed in southwestern aridland riparian plant assemblages.

Zonation

In relation to the above physiological issues, aridland riparian vegetation, as well as lacustrine and lentic aquatic macrophytic vegetation, are characterized by zonation: bands of discrete plant assemblages situated co-parallel to the mainstream channel existing in well-defined stage zones (e.g., Bayley 1995; Brotherson 1987; Carothers et al. 1979; Friedman et al. 2006; Johnson 1991; Spence 1982; Stevens 1989; Woodbury et al. 1959) (fig. 17). For example, Friedman et al. (2006) examined the relationship between flow

and riparian vegetation along 58 km of the San Miguel River in southwestern Colorado. They found that riparian plant assemblages were arrayed along the hydrologic gradient, with species like coyote willow (*Salix exigua*) often occupying terraces with flood return frequencies of less than 2.2 years, and river birch (*Betula occidentalis*) occupying terraces just upslope. They also reported that proportional cover decreased upstream, where upland processes such as landslides dominated the channel.

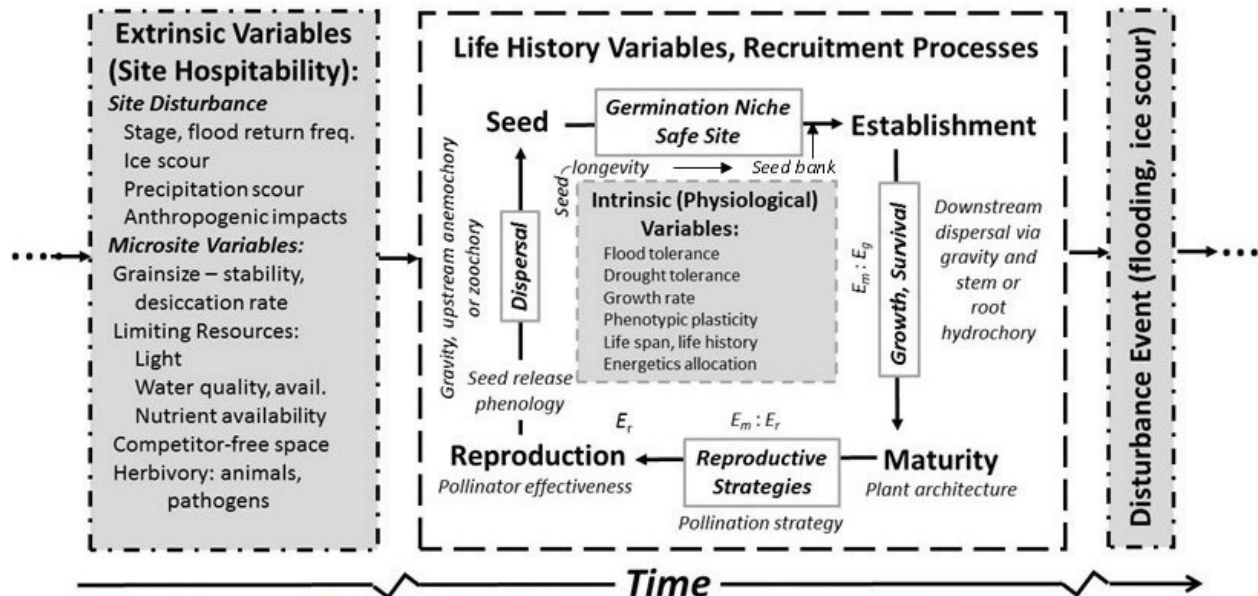
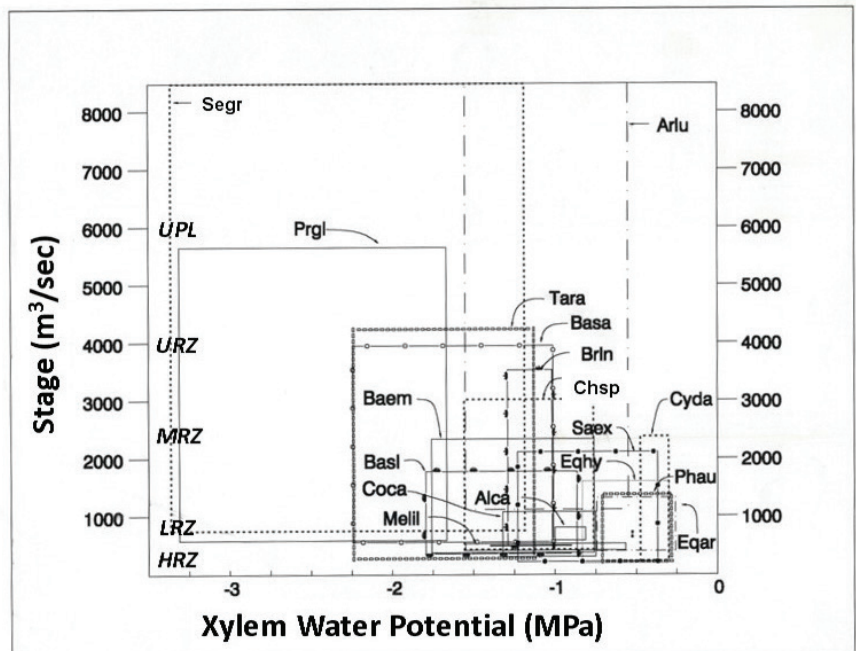


Figure 16—General conceptual model of individual riparian plant species colonization and stand replacement dynamics, with germination, establishment, growth, reproduction, and propagule dispersal occurring in relation to FRE hydrography. E_m , E_g , E_r , and ratios thereof are life history energetics (E) of plant growth (g), maintenance (m), and reproduction (r), respectively.

Figure 17—Range of stage elevations of 17 common obligate and facultative riparian plant species at 13 sites along the Colorado River in northern Arizona in relation to the full operating range of xylem water potential (MPa) for each species from midday (low) to night (high). HRZ—hydropriparian zone, LRZ—lower riparian zone, MRZ—middle riparian zone, UPL—upland zone, URZ—upper riparian zone. Plant species abbreviations: Alca—*Alhagi maurorum*, Arlu—*Artemesia ludoviciana*, Baem—*Baccharis emoryi*, Basa—*Baccharis sarothroides*, Basl—*Baccharis salicifolia*, Brln—*Brickellia longifolia*, Chsp—*Chlorocantha spinosa*, Coca—*Conyza canadensis*, Cyda—*Cynodon dactylon*, Eqar—*Equisetum arvense*, Eqhy—*Equisetum ferrissii*, Melil—*Melilotus* spp., Phau—*Phragmites australis*, Prgl—*Prosopis glandulosa*, Saex—*Salix exigua*, Segr—*Senegalia greggii*, Tara—*Tamarix* spp.



In addition to xylem water potential, riparian zonation also arises from variation in phenotypic plasticity of plant species in response to geomorphology and the disturbance regime, soil texture, and soil water and nutrient availability, as well as root architecture and rooting depth. Stevens (1989) grew 12-28 seedlings of 18 common southwestern riparian plant species for 1 month and measured the dry biomass of above-ground and root growth in fine, silty, nutrient-rich pre-dam Colorado River soil (the best naturally-available substratum) versus coarse, sandy, nutrient-poor post-dam soils (fig. 17). We used those data to calculate the phenotypic plasticity index (PPI_i) for each species i as the ratio of average dry post-dam belowground growth to average dry above-ground dry growth, as:

$$PPI_i = \frac{\frac{i_{post} = N_{i,post}}{\sum_{i_{post}=1} ((m_{i_{post_dbg}} / m_{i_{post_dag}}) \dots (m_{N_{i_{post_dbg}}} / m_{N_{i_{post_dag}}})) / N_{i_{post}}}}{\frac{i_{pre} = N_{i,pre}}{\sum_{i_{pre}=1} ((m_{i_{pre_dbg}} / m_{i_{pre_dag}}) \dots (m_{N_{i_{pre_dbg}}} / m_{N_{i_{pre_dag}}})) / N_{i_{pre}}}}$$

where $m_{i_{post_dbg}}$ and $m_{i_{post_dag}}$ are the average dry biomass of below- or above-ground growth of $N_{i_{post}}$ seedlings of species i grown in (suboptimal) post-dam fine-medium sand, compared to that average for seedlings of species i grown in optimal pre-dam fine silty sand.

For example, seedlings of *Baccharis salicifolia* seepwillow, a weedy LRZ shrub with high phenotypic plasticity, increased its relative allocation from aboveground leaf and stem growth by 5.5-fold to roots when grown in nutrient-poor post-dam sand.

We also report species-specific PPI responses to reproductive strategy, seed size, and seed longevity measured under field conditions. Ruderal *Baccharis salicifolia* and some nonnative species (e.g., *Tamarix* spp.) generally had higher PPI than did long-lived K-selected tree species, such as *Fraxinus pennsylvanica* (velvet ash), *Populus fremontii* (Fremont cottonwood), or *Salix gooddingii* (Goodding's willow). K-selected *Prosopis glandulosa* (honey mesquite), which can live more than 800 years in the URZ in Grand Canyon (R. Hereford, U.S. Geological Survey, personal communication), has a large, long-lived seed but also a moderately high phenotypic plasticity, conferring upon it an adaptive advantage in unpredictable habitats. Collectively, this analysis indicates that no single plant life history trait explains the success of any plant species in the riparian environment. It suggests that compensatory options exist within the suite of a plant species life history traits to permit survival in non-equilibrium riparian ecosystems.

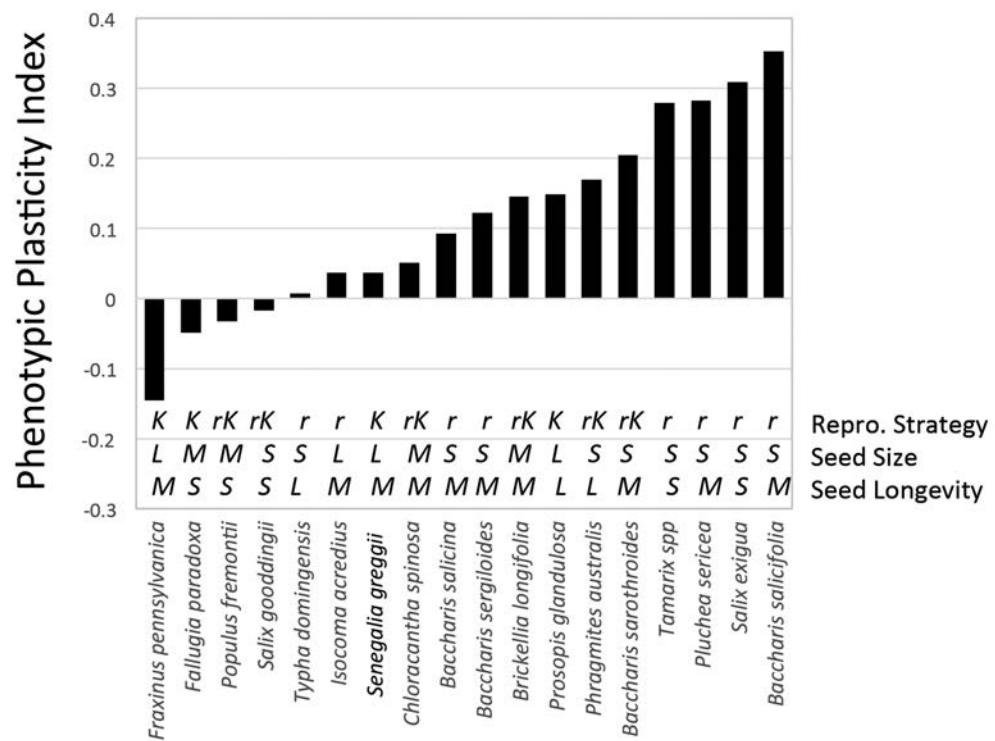
Riparian vegetation zonation also is common in mesic and humid-superhumid regions, but it is often less distinguishable than in arid regions. In humid environments, many upland species are tolerant of waterlogging and may have similar among-species variation in root architecture, plasticity, and Ψ range. For example, Dowe (2008) identified 263 plant species in three superhumid northern Australian watersheds, of which only 23 species (8.7 percent) were obligate riparian species. Orelana et al. (2012) reviewed and synthesized water use models for groundwater-dependent plant species, suggesting that more research was needed to clarify riparian water use, and to differentiate water use from saturated versus unsaturated zones.

Riparian Plant Recruitment and Stand Replacement

The niche-box model (NBM) (Merritt et al. 2010) classified guilds of riparian plants in relation to similarities among life history traits. The NBM incorporates and compares many autecological elements for each plant species to improve prediction of vegetation assemblage development in relation to hydrography and riparian conditions. While successfully grouping some species, the large amount of variation in the niche-box model multivariate plots reminds us about the tremendous variation in life history strategies among riparian plants, variance that is highly adaptive but which does not readily lend itself to simple classification.

We describe and illustrate the life cycle of an individual riparian plant species to clarify autoecological life history, energetic constraints, and stand replacement potential (fig. 18). HAZ-MRZ plant recruitment often takes place on the descending arm of the hydrograph after the most recent flood or ice scour (e.g., Fenner et al. 1984; Rood et al. 2007). Freshly scoured, moist, fine-grained substrata are exposed and serve as potential regeneration niche sites for germination and establishment (Grubb 1977; Harper 1977). The characteristics of such “safe germination site” vary by species and season and are the most critical phase of successful recruitment. Safe sites for seed-reproducing phreatophytes with small or short-lived seeds generally require open, moist, silt-rich sediment deposits, and those species typically have high seedling mortality and extensive self-thinning (Type III survivorship curve; Deevey 1947). Common phreatophytes (e.g., wetland herbs, such as *Carex*, *Juncus*, *Phragmites*, *Schoenoplectus*, *Typha*, and some clonal *Salix*) often disperse through hydrochory as rhizomes or rootable stems, and sometimes through zoochory (e.g., beaver dispersal of rootable stems). Plant species with larger seeds (greater maternal investment; e.g., *Prosopis*) may germinate in shady habitats and display either Type I or II survivorship, vigorous growth, and less ecotypically plastic architectural responses (Stevens 1989).

Figure 18—Phenotypic plasticity index of 18 common riparian plant species in the American Southwest (see text for calculation). Reproductive strategy: K selected, r selected, or rK intermediate. Seed size (relative): S small, L large, M medium. Seed longevity: L long-lived (> 2 years), M medium-lived (0.2-2 years), S short-lived (< 1 month).



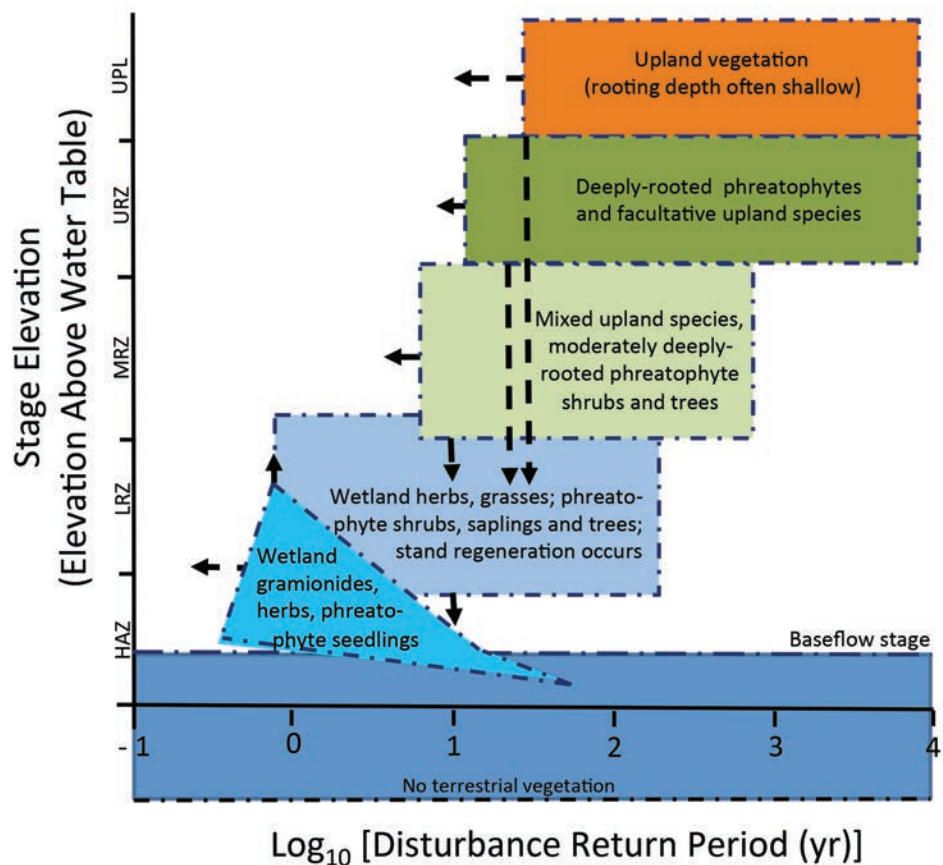
Following germination, establishment takes place as stems and roots grow at species- and microsite-specific rates (Stevens 1989) (fig. 18). Energy for growth (E_G) is that remaining after the individual expends energy on maintenance and respiration (E_M and E_R , respectively), which are relatively greater in more stressful habitats. Subsequent survival to recruitment age varies by species, location (i.e., stage elevation), and environmental conditions, including disturbance, nutrient availability, competition, herbivory, and other factors. Annual riparian species, living between flood spates, face a boom-or-bust fate. They maximize E_G , E_R , and the energy devoted to propagule production (E_S), perhaps by reducing emphasis on E_M or maximizing ecotypic plasticity. The persistence of annual riparian species within the reach requires relatively high levels of maternal investment in seed production, perhaps coupled with low seed longevity (i.e., < 1 year) and either continuous recolonization from upstream sources or *in situ* propagule retention, recruitment dynamics that have been little studied. In contrast, biennial and perennial plant species can adaptively balance E_G , E_M and E_R in relation to E_S . Individuals may defer E_S costs during periods of unusual stress (e.g., exceptional flow years), allowing those individuals to reallocate E_S energy to E_G and E_M and even defer reproduction if necessary.

Riparian Succession

Vegetation succession (predictable change over time) occurs through three modes: facilitation, inhibition, and tolerance (Connell and Slayter 1977). Riparian successional trajectories may differ between Holdridge humidity provinces and in relation to stream order, fluvial hydrodynamics (disturbance frequency), geomorphic setting, grainsize distribution, depth to water table, and biological effects—conditions that collectively create the mosaic template on which vegetation develops (Stanford et al. 2005). However, variation in successional trajectories has been little studied across stream order. At one extreme, zero and first order streams have insufficient stream power to prevent wetland (if open) or woody (if forested) vegetation from colonizing stream terraces. In such low-disturbance settings, riparian vegetation may entirely overwhelm the FRE, eliminating surface water (e.g., Kodrick-Brown and Brown 2007). However, at higher stream orders (larger, more highly disturbed riparian settings), the trunks of trees and driftwood piles may resist scour and affect channel geometry by stalling flow and depositing sediment, even to the extent of creating mid-channel islands (e.g., Tockner et al. 2003).

Geomorphic setting exerts dominant influences over riparian plant successional processes and modes within reaches, but its role often has been obscured in floodplain studies. Succession in middle- to higher-order unaltered rivers may be suspended in hydrologically active to middle riparian zones because annual-biennial flooding or ice scour resets the riparian zone to an unvegetated state (Campbell and Green 1968; Prowse and Culp 2003) (fig. 19). Lower riparian terraces are highly productive, but the frequency of scour favors species capable of sweepstakes colonization through germination, rapid exploitation of available space and resources, and intense competition before the next scouring event, and therefore favor r- (ruderal) over K- (competitive) selected species. Rapid growth of or colonization by woody phreatophytes may reciprocally force channel narrowing or alter meandering in some alluvial reaches (e.g. Johnson 1994; Hupp and Osterkamp 1996). However, flow events shape channel geometry in more constrained reaches, forcing riparian vegetation there to respond to, rather than reshaping, bar configuration (e.g., Birkeland 1996).

Figure 19—General model of temporal development or succession of aridland riparian plant zonation in relation to stage elevation and $\log_{10}$ (disturbance return period). Black lines show tendency of vegetation spatial and temporal distribution in mesic (humid) environments. HAZ—hydrologically active zone, LRZ—lower riparian zone, MRZ—middle riparian zone, UPL—upland zone, URZ—upper riparian zone.



Clonality in lower riparian zone species adds a further level of complexity to succession: Clonal *Phragmites* and *Arundo* grasses strongly resist scour and can deter sediment deposition during high flows, effectively armoring channels (e.g., cane breaks along the Lower Colorado, Rio Grande, and Mississippi Rivers). The root stocks of these and some woody phreatophytic clonal or rhizomatous species are highly flood tolerant and can persist belowground during scouring events, vigorously resprouting and growing out following disturbance, exploiting space and nutrients and quickly resuming dominance. Clonality also means that the genet (genetic individual) can move over time, as one portion of the root mass may be scoured away while another portion survives and regrows. Similar rapid colonization can occur on higher terraces after larger scouring events, but more time between disturbance events can allow other successional modes to occur.

Several recent studies have identified analogous successional patterns in riparian habitats. Naiman et al. (2005) identified four general stages of riparian succession: establishment, competitive stem exclusion, understory initiation, and maturity. Whether and how this progression occurs on all terraces remains unclear, as do the extent to which such patterns occur across latitude and humidity provinces. Egger et al. (2015) modeled terrace-based riparian succession in the Kootenai and Flathead Rivers in northwestern United States and southwestern Canada. They reported that individual species occupied similar hydraulic environments in different reaches, and that following impoundment (cessation of flood and ice scour), initial colonization and dominance by cottonwood (*Populus*) gave way over 60-150 year time scales to dominance by spruce (*Abies*). Although the mode was not identified, the latter transition likely occurred through

facilitation as the conifers establishing under deciduous canopy shade, coupled with tolerance as the conifers out-lived the co-occurring cottonwoods. In those temperate latitudes, the two taxa apparently share similar flood tolerance and root depth-to-groundwater relationships.

Geerling et al. (2006) and Metz et al. (2016) reported three alternative successional trajectories on floodplains of the lower Allier River in France over 60 years of analysis. These alternative trajectories included: (1) progression (successional transformation from water to exposed sediment to colonization, first by pioneer species, to transitional grasslands and shrublands to riparian forests); (2) retrogression (a reversed trajectory toward bare soils or open water); or (3) stable (unchanging and stand-replacing patch conditions). They did not relate those three Markovian alternative states to the species-based successional modes of Connell and Slayter (1977), but such an analysis would likely be integrative.

Surrounding upland assemblages strongly interact with upper riparian terrace vegetation. Hence, the mature (equilibrium or climax) vegetation stage in the above studies becomes a mixture of downslope-colonizing upland species on upper riparian terraces and, in arid regions, dominance by deeply rooted, long-lived phreatophytes that maintain root connections to the river water table (e.g., Woodbury 1959, Carothers et al. 1979).

Riparian plant succession also can be directed by biological processes. Mycorrhizal succession has been identified along Montana rivers, with arbuscular mycorrhizae succeeding to ectomycorrhizae at decadal or longer time scales (Piotrowski et al. 2008). The trajectory of riparian plant succession also can be altered by selective herbivory, particularly by ecosystem engineering rodents like beaver (Bailey and Whitham 2006), herbivorous insects (Simieon and Stevens 2015), plant diseases, and even some bird species (Stevens 1989). Overall, these studies indicate that reduction or elimination of flooding disturbance promotes as-yet-poorly-described stage-specific FRE succession.

FRE Evolutionary Ecology

FREs have been persistent habitats over evolutionary time, as demonstrated by the broad array of paleo-landforms and fossil deposits throughout the world (Behrensmeyer et al. 1992) and the enormous biodiversity and influence of rivers on upland biota. Evolutionary isolation and gene flow restriction can occur at microsite, reach- and among-basin scales, as well as between aquatic and riparian domains. Headwater elevation may influence along- and across-channel colonization (e.g., Vences et al. 2009). Stevens (2012) reported that the 32 km long, steep, canyon-bound Muav Gorge reach separated the Colorado River ecosystem in Grand Canyon into two basins: an isolated eastern basin that contains most of the river corridor's endemic plant and animal species, and the more open western basin dominated by Mohave Desert species and containing fewer endemic species.

Temporally, vicariance or large antecedent events, such as long-term drainage basin integration or natural or anthropogenic impoundment events, may contribute to isolation, restricting gene flow sufficiently to allow gene fixation. In addition, vegetation change in response to a drying climate across elevation in deep canyons may restrict across-basin colonization. An example is the well-known case of upland population isolation between

Kaibab and tassel-eared squirrels (*Sciurus aberti kaibabensis* versus *S. a. aberti*) on the North and South Rims of Grand Canyon, respectively, following repeated Pleistocene inter-glacial habitat separation events (Jones and Wettstein 1997).

At a finer scale, microhabitat isolation is particularly pronounced in large, deep canyons, resulting in isolation and formation of endemic species (Stevens 2012). Environmentally constant and harsh, in-canyon springs, caves, north- and south-facing slopes, and rim edges are settings in Grand Canyon that foster development of endemism. Aridland springs in particular are renowned as isolated hotspots of endemism due to their unique water quality and environmental constancy (Kreamer et al. 2015; Stevens and Meretsky 2008). FRE endemism in deep canyons may develop sequentially as microhabitats and associated species become increasingly isolated and rare during drying climate phases. Climate recovery can subsequently allow re-expansion of habitats and associated species—and in speciation events through adaptive radiation that increases biodiversity, as has occurred with hydrobiid springsnails (Hershler and Liu 2008) and cyprinodontid pupfish (Martin and Wainwright 2013).

Local genetic adaptation is likely an important characteristic of *r*- and intermediate *rK*-selected riparian species. For example, following flooding, LES monitored a 10 m² patch of Lower Colorado River riparian zone habitat that, after 1983 flood subsidence, supported germination of > 10⁴ seedlings of woody riparian species, including *Tamarix*, *Salix*, and *Populus*, but on which only a single individual *Tamarix* seedling survived to reproductive age. Such intensive selection results in highly individualistic, site-specific local adaptation. Subsequent reproductive mixing of those traits is likely to enhance species-level fitness by generating elevated genetic heterozygosity. Consequently, local-scale endemism tends to be relatively rare among North American riparian plant species, although this may not be the case in tropical rivers due to higher productivity (e.g., Dowe 2008; Harrison and Grace 2007).

FRE Ecology Research Recommendations and Conclusions

Fluvial-riparian ecosystems are hierarchically and dynamically influenced by physical and biotic processes that vary spatially over stream order and time within the watershed, approaching but rarely achieving equilibrium conditions in channel geometry, fluid and matter transport, ecosystem energy dynamics and structure, and ecological developmental state. A wide array of conceptual models has been used to describe aspects of FRE ecology and responses to natural and anthropogenic perturbations. Most models have focused on single or a reduced suite of variables at site-specific, within-reach, or other incomplete watershed scales, and most often of anthropogenically altered streams. In the WCM, we emphasize the importance of understanding temporal and spatial scaling across the entire basin.

Despite much progress, a wide array of important ecohydrological processes, questions, and issues remain to be addressed or more fully investigated and integrated into the WCM. Not presented in prioritized order, this list of additional research topics includes but is not limited to: (1) the roles of self-similarity across reach and stream order spatial and temporal scales; (2) groundwater-surface water interactions and connectivity; (3) the significance, extent, and roles of groundwater and headwater springs as zero order streams in FRE ecology (*sensu* Gomi et al. 2002; Lowe and Likens 2005); (4) interrelationships among lentic and lotic habitats; (5) the distribution,

importance and ecology of ephemeral streams and xeroriparian ecosystem ecology; (6) the interrelationships between interconnected ephemeral and xeroriparian riparian ecosystems; (7) the roles and importance of aspect, gradient, and photosynthetically active radiation in canyon-bound stream segments (e.g., Stevens 2012; Yard et al. 2005); (8) the ecological importance and roles of river microclimate; (9) the multi-dimensional roles of flooding, ice, and glacial effects, especially in boreal and high-elevation rivers; (10) multidirectional material and gene flow in dendritic pathways, which are dominated by downslope gravity and hydrochorous material, nutrient, and propagule transport, but that also have ecologically important upriver eolian and zoochorous transport mechanisms; (11) the role of plant physiology in riparian vegetation distribution; (12) the biogeographic significance of rivers as corridors, barriers/filters, and refugial systems (Stevens 2012); (13) stream order-driven and across-channel spatial impacts on biodiversity; (14) population and successional models among FRE biota and trophic levels; (15) FRE ecosystem genetics and evolutionary processes, including the development of endemism across latitude, longitude, and among tectonic landscapes; (16) climate change influences on FRE form and function; and (17) the role of noise on riparian songbird assemblage composition and structure.

Adequately incorporating the above research topics, and more fully constructing and testing the WCM, will require another generation of research, including collaborative discussion among hydrogeological, ecological, and socio-cultural disciplines (e.g., Fisher 1997). Such data and integration efforts are needed to improve understanding, modeling, and stewardship of FREs at local, regional, and global spatial and temporal scales.

River ecosystems are extraordinarily complex and vital to life on Earth. Informative and elegant as they are, the FRE models proposed to date remain incomplete. There also are many challenges associated with inadequacy of the physical and biological data required to calibrate and refine existing models and to develop new models. Here we attempted to summarize and illustrate the state of knowledge for FREs, and we point out additional elements that need further investigation and better integration. However, FREs cannot be readily, adequately, or usefully reduced to a suite of equations or simple illustrations. For example, some cultures commonly view rivers as living beings, supporting divine spirits. Integrating indigenous traditional ecological concepts and knowledge into improved stewardship has rarely been attempted. We suggest that improved comprehension of FREs may require consideration of other socio-cultural dimensions.

John Wesley Powell, whose quote opens this chapter, suggested that rivers can be understood as music. Rather than a Hutchinsonian stage on which the ecological play is enacted in the theater of evolution, a river ecosystem might better be considered as a time-transitive orchestral composition. Such a symphony might be composed of themes brought in by each major tributary and integrated in its watershed and geographic setting. In form, the symphony might be a fugue- like integration of variably self-similar subthemes amplified across stream order, with rhythms reflecting reach geomorphology, ecological character, and tempo. Each movement in the symphony might be a time-step in watershed development: the opening sonata describing the basin's geologic origination, the second movement portraying the FRE in its natural state, the third depicting the FRE under the terms of contemporary anthropogenic influences, and the final movement

recapitulating the river's ultimate stratigraphic and evolutionary contributions. Given the precepts of Morisawa's (1968) dynamic equilibrium model, we do not expect this fluvial symphony to be either particularly orderly or melodic.

Many rivers, large and small, have come and gone on Earth. Seen in cross section, 400-million-year-old Devonian river channels in upper Grand Canyon that intersect the modern Colorado River still serve as conduits for groundwater flow and perhaps direct the course of contemporary tributary incision (Stevens 2013). Thus, the spatial and temporal impacts of large paleo-FREs may last for hundreds of millions of years.

Would such a symphonic model help move river and watershed science forward? Each river's symphony can help remind us of our species' evolution and history, the limits of our capacity to understand multi-dimensional reality. Rivers inspire our core sense of wonder, our fear of, and our deep need for flowing and lentic freshwater, elements that have stimulated abundant fundamental, integrative, and applied FRE science. Composition of symphonies for major rivers would be a worthwhile artistic endeavor that might more broadly engage the public and the artistic community in environmental stewardship. But like all models, even the most elaborate river symphonies would fall short of fully representing these remarkable, important, and dynamic ecosystems.

A rich array of research topics and endeavors awaits future students of FRE ecology, and scientific research, artistry, and public involvement all continue to be urgently needed. Improved stewardship of the world's rivers to sustain vital ecological functions is essential to sustaining life and socio-economic well-being. This effort remains a critical challenge and responsibility for all of humanity. We welcome comments and suggestions on this synthesis, and we hope this chapter helps to stimulate the research, synthesis, and communications needed to reach this goal.

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References

- Akkemik, U.; D'Arrigo, R.; Cherubini, P.; Kose, N.; Jacoby, G.C. 2004. Tree-ring reconstructions of precipitation and streamflow for northwestern Turkey. *International Journal of Climatology*. 28:173–183.
- Alley, W.M.; Evenson, E.J.; Barber, N.L.; Bruce, B.W.; Dennehy, K.F.; Freeman, M.C.; Freeman, W.O.; Fischer, J.M.; Hughes, W.B.; Kennen, J.G.; Kiang, J.E.; Maloney, K.O.; Musgrove, M.L.; Ralston, B.E.; Tessler, S.; Verdin, J.P. 2013. Progress toward establishing a national assessment of water availability and use. U.S. Geological Survey Circular 1384. Washington, DC: U.S. Geological Survey. 34 p.
- Andrew, S.M.; Totland, Ø.; Moe, S.R.. 2014-15. Spatial variation in plant species richness and diversity along human disturbance and environmental gradients in a tropical wetland. *Wetlands Ecology and Management*. 23:395-404.

- Annear, T.; Chisholm, I.; Beecher, H.; Locke, A.; Aarrestad, P.; Coomer, C.; Estes, C.; Hunt, J.; Jacobson, R.; Jobsis, G.; Kauffman, J.; Marshall, J.; Mayes, K.; Smith, G.; Wentworth, R.; Stalnaker, C. 2004. Instream flows for riverine resource stewardship, revised ed. Cheyenne, WY: Instream Flow Council. 268 p.
- Annear, T, Lobb, C. Coomer, M. Woythal, C. Hendry, C. Estes, and K. Williams. 2009. International instream flow program initiative: A status report of state and provincial fish and wildlife agency instream flow activities and strategies for the future. Final report for Multi-State Conservation Grant Project WY M-7-T. Cheyenne, WY: Instream Flow Council. n.p.
- Bagstad, K.J.; Lite, S.J.; Stromberg, J.C. 2006. Vegetation, soils, and hydrogeomorphology of riparian patch types of a dryland river. *Western North American Naturalist*. 66: 23-44.
- Bailey, J.K.; Whitham, T.G. 2006. Interactions between cottonwood and beavers positively affect sawfly abundance. *Ecological Entomology*. 31: 294-297.
- Bayley, P.B. 1995. Understanding large river-floodplain ecosystems. *BioScience*. 45: 153-158.
- Behrensmeyer, A.K.; Damuth, J.A.; Dimichele, W.A.; Potts, R.; Sues, H-D.; Wing, S.L. [eds.]. 1992. *Terrestrial ecosystems through time: Evolutionary paleoecology of terrestrial plants and animals*. Chicago, IL: University of Chicago Press: 205-325.
- Bellmore, J.R.; Baxter, C.V. 2014. Effects of geomorphic process domains on river ecosystems: A comparison of floodplain and confined valley segments. *River Research and Applications*. 30: 617-630.
- Benda, L.; Andras, K.; Miller, D.; Bigelow, P. 2004a. Confluence effects in rivers: Interactions of basin scale, network geometry, and disturbance regimes. *Water Resources Research*. 40. W05402. DOI:10.1029/2003WR002583.
- Benda, L.; Poff, N.L.; Miller, D.; Dunne, T.; Reeves, G.; Pess, G.; Pollock, M.M. 2004b. The network dynamics hypothesis: How channel networks structure riverine habitats. *Bioscience*. 4:413-427.
- Bendix, J. 1992. Scale-related environmental influences on southern Californian riparian vegetation. Athens, GA: University of Georgia. Dissertation. 123 p.
- Benito, G.; O'Connor, J.E. 2003. Number and size of last-glacial Missoula floods in the Columbia River valley between the Pasco Basin, Washington, and Portland, Oregon. *Geological Society of America Bulletin*. 115: 624-638.
- Bennett, M.G. 2015. Effects of flow regime on fishes and fisheries: From life histories to ecosystem services. Carbondale, IL: Southern Illinois University. Dissertation. 210 p.
- Bennett, S.J.; Simon, A. 2013. Riparian vegetation and fluvial geomorphology. *American Geophysical Union Water Science and Application Series* 8. Washington, DC: American Geophysical Union. 282 p.
- Beschta, R.L.; Ripple, W.J. 2006. River channel dynamics following extirpation of wolves in northwestern Yellowstone National Park, USA. *Earth Surface Processes and Landforms*. 31: 1525-1539.
- Birkeland, G.H. 1996. Riparian vegetation and sandbar morphology along the lower Little Colorado River, Arizona. *Physical Geography*. 17:534-553.
- Blinn, D.W. 2008. The extreme environment, trophic structure, and ecosystem dynamics of a large, fishless desert spring. In: Stevens L.E.; Meretsky V.J., eds. *Aridland springs in North America: Ecology and conservation*. Tucson, AZ: University of Arizona Press: 98-126.
- Bloss, D.A.; Brotherson, J.D. 1979. Vegetation response to a moisture gradient on an ephemeral stream in central Arizona. *Great Basin Naturalist*. 39: 161-175.
- Bormann, F.H.; Likens, G.E. 1979. *Pattern and process in a forested ecosystem*. New York: Springer-Verlag. 253 p.

- Bouwman, A.F.; Giffioen, M.F.P.; Hefting, M.M.; Middelburg, J.J.; Middelkoop, H.; Slomp, C.P. 2013. Nutrient dynamics, transfer and retention along the aquatic continuum from land to ocean: toward integration of ecological and biogeochemical models. *Biogeosciences*. 10: 1–23.
- Bretz, J.H. 1923. The channeled scabland of the Columbia Plateau. *Journal of Geology*. 31: 617-649.
- Brotherson, J.D. 1987. Plant community zonation in response to soil gradients in a saline meadow near Utah Lake, Utah County, Utah. *Great Basin Naturalist*. 47: 322-333.
- Bruns, D.A.; Minshall, G.W.; Cushing C.E.; Cummins, K.W.; Brock J.T.; Vannote, R.L. 1984. Tributaries as modifiers of the river continuum concept: Analysis by polar ordination and regression models. *Archiv fur Hydrobiologie*. 99: 208-220.
- Buffington, J.M.; Montgomery, D.R. 2013. Geomorphic classification of rivers. In: Shroder, J.; Wohl, E.E., eds. *Treatise on geomorphology*. San Diego, CA: Academic Press: 730-767.
- Butman, B.; Twichell, DC; Rona, P.A.; Tucholke, B.E.; Middleton, T.J.; Robb, J.M. 2006. Sea floor topography and backscatter intensity of the Hudson Canyon region offshore of New York and New Jersey. U.S. Geological Survey Open-File Report 2004-1441, Version 2.0. Washington, DC: U.S. Geological Survey. Map.
- Butman D.; Wilson, H.F.; Barnes, R.T.; Xenopoulos, M.A.; Raymond, P.A. 2015. Disturbance mobilizes aged carbon to rivers. *Nature Geoscience*. 8: 112-116.
- Campbell, C.J.; Green, W. 1968. Perpetual succession of stream-channel vegetation in a semiarid region. *Journal of the Arizona Academy of Sciences*. 5: 86-98.
- Canals, M.; Danovaro, R.; Heussner, S.; Lykousis, V.; Puig, P.; Trincardi, F.; Calafat, A.M.; Durrieu de Madron, X.; Palanques, A.; Sánchez-Vidal, A. 2009. Cascades in Mediterranean submarine Grand Canyons. *Oceanography*. 22: 26–43.
- Cantonati, M.; Segadelli, S.; Ogata, K.; Tran, H.; Sanders, D.; Gerecke, R.; Rott, E.; Fillipini, M.; Gargini, A.; Celico, F. 2016. A global review on ambient limestone-precipitating springs (LPS): Hydrogeological setting, ecology, and conservation. *Science of the Total Environment*. 15: 568-624.
- Carlisle, J.D.; Skagen, S.K.; Kus, B.E.; Van Riper, C. III; Paxton, K.L.; Kelly, J.F. 2009. Landbird migration in the American West: Recent progress and future research directions. *The Condor*. 111: 211-225.
- Carothers, S.W.; Johnson, R.R.; Aitchison, S.W. 1974. Population structure and social organization in southwestern riparian birds. *American Zoologist*. 14: 97-108.
- Carothers, S.W.; Aitchison, S.W.; Johnson, R.R. 1979. Natural resources, white-water recreation and river management alternatives on the Colorado River, Grand Canyon National Park, Arizona. *Proceedings of the First Conference on Scientific Research in the National Parks*. 1: 253-260.
- Case, R.A.; MacDonald, G.M. 2003. Tree ring reconstructions of streamflow for three Canadian prairie rivers. *Journal of the American Water Resources Association*. 39: 703-716. <https://doi.org/10.1111/j.1752-1688.2003.tb03686.x>.
- Castleton, J.J.; Moore, J.R.; Aaron, J.; Christ, M.; Ivy-Ochs, S. 2016. Dynamics and legacy of 4.8 ka rock avalanche that dammed Zion Canyon, Utah, USA. *GSA Today*. 26: 4-9.
- Cederholm, C.J.; Kunze, M.D.; Murota, T.; Sibatani, A. 1999. Pacific salmon carcasses: Essential contributions of nutrients and energy for aquatic and terrestrial ecosystems. *Fisheries Habitat/Management*. 24: 6-15.
- Chaghtai, S.M.; Khattak, H-U-R. 1983. Ecology of a dry stream bed in Peshawar, Pakistan. *Pakistan Journal of Botany*. 15: 93-98.
- Clay, P.A.; Muehlbauer, J.D.; Doyle, M.W. 2015. Effect of tributary and braided confluences on aquatic macroinvertebrate communities and geomorphology in an alpine river watershed. *Freshwater Science*. 34: 845-856.

- Cody, M.L. 1991. Niche theory and plant growth form. *Vegetation*. 97: 39-55.
- Collen, B.; Whitton, F.; Dyer, E. E.; Baillie, J. E. M.; Cumberlidge, N.; Darwall, W. R. T.; Pollock, C.; Richman, N. I.; Soulsby, A.-M.; Böhm, M. 2014. Global patterns of freshwater species diversity, threat and endemism. *Global Ecology and Biogeography*. 23:40–51.
- Committee on Riparian Zone Functioning and Strategies for Management. 2002. *Riparian areas: Functions and strategies for management*. Washington, DC: National Academy Press Washington. 448 p.
- Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science*. 199: 1302–1310.
- Connell, J.H.; Slayter, R.O. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist*. 111: 1119-1144.
- Costa, J.E.; Schuster, R.L. 1987. The formation and failure of natural dams. U.S. Geological Survey Open-File Report 87-392. Washington, DC: U.S. Geological Survey. 39 p.
- Craine, J.M. 2005. Reconciling plant strategy theories of Grime and Tilman. *Journal of Ecology*. 93: 1041–1052.
- Crow, R.; K.E. Karlstrom; W. McIntosh; L. Peters; and N. Dunbar. 2008. History of Quaternary volcanism and lava dams in western Grand Canyon based on LIDAR analysis, (40)Ar/(39)Ar dating, and field studies: Implications for flow stratigraphy, timing of volcanic events, and lava dams. *Geosphere*. 4: 183-206.
- Cummins, K.W. 1976. The ecology of running water: theory and practice. In: Baker, D.B.; Jackson, W.B.; Prater, B.L., eds. *Proceedings of the Sandusky River Basin Symposium*, Tiffin, OH, USA, 2 May 1975. Washington, DC: U.S. Government Printing Office: 277-293.
- Dalrymple, G.B.; Hamblin, K.W. 1998. K-Ar ages of Pleistocene lava dams in the Grand Canyon in Arizona. *Proceedings of the National Academy of Sciences of the United States of America*. 95: 9744-9749.
- D'Arrigo, R.; Abram, N.; Ummenhofer, C.; Palmer, J.; Mudelsee, M. 2009. Reconstructed streamflow for Citarum River, Java, Indonesia: Linkages to tropical climate dynamics. *Climate Dynamics*. doi:10.1007/s00382–009–0717–2.
- Datry, T.; Larned, S.T.; Tocknerr, K. 2014. Intermittent rivers: A challenge for freshwater ecology. *BioScience*. doi: 10/1093/biosci/bit027.
- Day, R.T.; Keddy, R.A.; McNeill, J.; Carleton, T. 1988. Fertility and disturbance gradients: A summary model for riverine marsh vegetation. *Ecology*. 69: 1044-1054.
- Décamps, H.; and Tabacchi, E. 1994. Species richness along river margins. In: Hildrew, A.G.; Giller, P.S.; Raffaelli, D., eds. *Aquatic ecology: Scale, pattern and process*. Oxford, UK: Blackwell Scientific Publications: 1-20.
- Décamps, H.; Fortuné, M.; Gazelle, F.; Pautou, G. 1988. Historical influence of man in the riparian dynamics of a fluvial landscape. *Landscape Ecology*. 1: 163-173.
- Deevey, E.S. 1947. Life tables for natural populations of animals. *Quantitative Review of Biology*. 22: 283-314.
- Dowe, J.L. 2008. Distribution and ecological preferences of riparian vegetation in northern Australia. Report 4 in Lukacs, G.P.; Finlayson, G.P.; Finlayson, C.M. [eds.]. *A compendium of ecological information on Australia's northern tropical rivers*. Sub-project 1 of Australia's Tropical Rivers – an integrated data assessment and analysis (DET18). A report to Land & Water Australia. Townsville, Australia: National Centre for Tropical Wetland Research. n.p.
- Draught, A.E.; Rubin, D.M. 2006. Measurements of wind, aeolian sand transport, and precipitation in the Colorado River corridor, Grand Canyon, Arizona; January 2005 to January 2006. U.S. Geological Survey Open-File Report 2006-1188. Reston, VA: U.S. Geological Survey. 88 p.

- Dudgeon, D. 2000. The ecology of tropical Asian rivers and streams in relation to biodiversity conservation. *Annual Review of Ecology & Systematics*. 31: 239-263.
- Dye, A. 2010. Contribution of unregulated tributaries to the ecological functioning of the main channel of rivers. *Snowy River Recovery: Snowy Flow Response Monitoring and Modelling*. Sydney, Australia: New South Wales Office of Water. 16 p.
- Eamus, D.; Froend, R. 2006. Groundwater-dependent ecosystems: The where, what and why of GDEs. *Australian Journal of Botany*. 54: 91-96.
- Egger, G.E.; Politti, E.; Lautsch, E.; Benjankar, R.; Gill, K.M.; Rood, S.B. Floodplain forest succession reveals fluvial processes: A hydrogeomorphic model for temperate riparian woodlands. *Journal of Environmental Management*. 161: 72-82.
- Elston, D.P.; McKee, E.D.; Scott, G.R.; Gray, G.D. 1974. Miocene-Pliocene volcanism in the Hackberry Mountain area and evolution of the Verde Valley, north-central Arizona. In Karlstrom, T.N.V., Swann, G.A. Eastwood, R.L. eds. *Geology of northern Arizona, with notes on archaeology and paleoclimate, Part II – Area studies and field guide*. Flagstaff, AZ: Geological Society of America Rocky Mountain Section Meeting: 602-610.
- Ensign, S.H.; Doyle, M.W. 2006. Nutrient spiraling in streams and river networks. *Journal of Geophysical Research*. 111:G04009. doi:10.1029/2005JG000114.
- Famiglietti, J.S. 2014. The global groundwater crisis. *Nature Climate Change*. 4: 945-948.
- Fenner, P.; Brady, W.W.; Patten, D.R. 1984. Observations on seeds and seedlings of Fremont cottonwood. *Desert Plants*. 6:55-58.
- Fenton, C.R.; Poreda, R.J.; Nash, B.P.; Webb, R.H.; Cerling, T.E. 2004. Geochemical discrimination of five Pleistocene lava-dam outburst flood deposits, western Grand Canyon, Arizona. *Journal of Geology*. 112: 91-110.
- Fisher, S.G. 1997. Creativity, idea generation, and the functional morphology of streams. *Journal of the North American Benthological Society*. 16: 305-318.
- Fisher, S.G. 1983. Succession in streams. In Barnes, J.R.; Minshall, G.W. [eds.]. *Stream Ecology: Application and testing of general ecological theory*: 7-27.
- Fisher, S.G.; Likens, G.E. 1973. Energy flow in Bear Brook, New Hampshire: An integrative approach to stream ecosystem metabolism. *Ecological Monographs*. 43: 421-439.
- Fisher, S.G.; Gray, L.J.; Grimm, N.B.; Busch, D.E. 1982. Temporal succession in a desert stream ecosystem following flash flooding. *Ecological Monographs*. 52: 93-110.
- Fisher, S.G.; Grimm, N.B.; Marti, E.; Holmes, R.M.; Jones, J.B. 1998. Material spiraling in stream corridors: A telescoping ecosystem model. *Ecosystems*. 1:19-34.
- Foster, D.R.; Knight, D.H.; Franklin, J.F. 1998. Landscape patterns and legacies resulting from large, infrequent disturbances. *Ecosystems*. 1: 497-510.
- Friedman, J.M.; Auble, G.T.; Andrews, E.D.; Kittel, G.; Madole, R.F.; Griffin, E.R.; Allred, R.M. 2006. Transverse and longitudinal variation in woody riparian vegetation along a montane river. *Western North American Naturalist*. 66: 78-91.
- Frissell, C.A.; Liss, W.J.; Warren, C.E.; Hurley, M.C. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. *Environmental Management*. 10: 199-214.
- Fukami, T.; Morin, P.J. 2003. Productivity-biodiversity relationships depend on the history of community assembly. *Nature*. 424: 423-426.
- Gawne, B.; Merrick, C.; Williams, D.G.; Rees, G.; Oliver, R.; Bowen, P.M.; Treadwell, S.; Beattie, G.; Ellis, I.; Frankenberg, J.; Lorenz, Z. 2007. Patterns of primary and heterotrophic productivity in an arid lowland river. *River Research and Applications*. 23: 1070-1087.

- Geerling G.W.; Ragas, A.M.J.; Leuven, R.S.E.W.; van den Berg, J.H.; Breedveld, M.; Liefhebber, D.; Smits, A.J.M. 2006. Succession and rejuvenation in floodplains along the River Allier (France). *Hydrobiologia*. 565: 71–86.
- Giller, S.; Malmqvist, B. 1998. *The biology of streams and rivers*. Oxford, UK: Oxford University Press. 296 p.
- Glazier, D.S. 2012. Temperature affects food-chain length and macroinvertebrate species richness in spring ecosystems. *Freshwater Science*. 31: 575-585.
- Gomi, T.; Sidle, R.C.; Richardson, J.S. 2002. Understanding process and downstream linkages of headwater systems. *BioScience*. 52 :905-916.
- Grace, J.B. 1990. On the relationship between plant traits and competitive ability. In: Grace, J.B.; Tilman, D., eds. *Perspectives on plant competition*. San Diego, CA: Academic Press: 51-66.
- Gray, J.R.; Simões, F.J.M. 2008. Estimating sediment discharge. In: Garcia, M., ed. *Sedimentation engineering – processes, measurements, modeling, and practice*. Manual 110 (Appendix D). Reston, VA: American Society of Civil Engineers: 1065-1086.
- Gregory, S.V.; Swanson, F.J.; McKee, W.A.; Cummins, K.W. 1991. An ecosystem perspective of riparian zones. *BioScience*. 41: 540-551.
- Griffiths, R.E.; Anderson, D.E.; Springer, A.E. 2008. The morphology and hydrology of small spring-dominated channels. *Geomorphology*: doi:10/1016/j.geomorph.2008.05.038.
- Grime, J.P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist*. 111: 1169–1194.
- Grubb, P.J. 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biological Reviews*. 52: 107-145.
- Harper, J.L. 1977. *Population biology of plants*, 2nd edition. London: Academic Press. 922 p.
- Harrison, S.; Grace, J.B. 2007. Biogeographic affinity helps explain productivity-richness relationships at regional and local scales. *The American Naturalist*. 170: S5-S12.
- Harvey, J.; Gooseff, M. 2015. River corridor science: Hydrologic exchange and ecological consequences from bedforms to basins. *Water Resources Research*. 51: 6893-6922.
- Heino, J.; and 30 co-authors. 2015. A comparative analysis reveals weak relationships between ecological factors and beta diversity of stream insect metacommunities at two spatial scales. *Ecology and Evolution*. 5: 1235-1248.
- Hereford, R.; Jacoby, G.C.; McCord, V.A.S. 1995. Geomorphic history of the Virgin River in the Zion National Park area, southwest Utah. U.S. Geological Survey Open-File Report 95-515. Denver, CO: U.S. Geological Survey. 75 p.
- Hershler, R.; Liu, H-P. 2008. Ancient vicariance and recent dispersal of springsnails (Hydrobiidae: Pyrgulopsis) in the Death Valley system, California-Nevada. In: Reheis, M.C.; Hershler, R.; Miller, D.M., eds. *Late Cenozoic drainage history of the southwestern Great Basin and lower Colorado River region: Geologic and biologic perspectives*. Geological Society of America Special Paper 439: 91-101.
- Hey, R.D.; Bathurst, J.C.; Thorne, C.R. 1982. *Gravel-bed rivers: Fluvial processes, engineering, and management*. New York: John Wiley & Sons. 875 p.
- Hjulstrøm, F. 1939. Transportation of debris by moving water. In Trask, P.D., ed. *Recent marine sediments: A symposium*. Tulsa, OK: American Association of Petroleum Geologists: 5-31.
- Holbrook, J.; Schumm, S.A. 1999. Geomorphic and sedimentary response of rivers to tectonic deformation: a brief review and critique of a tool for recognizing subtle epeirogenic deformation in modern and ancient settings. *Tectonophysics*. 305: 287-306.

- Holdridge, L.R. 1947. Determination of world plant formations from simple climatic data. *Science*. 105: 367-368.
- Hook, D. 1984. Waterlogging tolerance of lowland tree species of the South. *Southern Journal of Applied Forestry*. 8: 136-149.
- Hooper, D.U.; Chapin, F.S.; Ewel, J.J.; Hector, A.; Inchausti, P.; Lavorel, S. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*. 75: 3–35.
- Horton, R.E. 1945. Erosional development of streams and their drainage basins: Hydrophysical Approach to quantitative morphology. *Bulletin of the Geological Society of America*. 56: 275-370.
- Hough-Snee, N.; Laub, B.G.; Merritt, D.M.; Long, A.L.; Nackley, L.L.; Roper, B.B.; Wheaton, J.M. 2015. Multi-scale environmental filters and niche partitioning govern the distributions of riparian vegetation guilds. *Ecosphere*. 6: 1-22. <http://dx.doi.org/10.1890/ES15-00064.1>.
- Humphries, P.; Keckeis, H.; Finlayson, B. 2014. The river wave concept: Integrating river ecosystem models. *BioScience*. doi: 10.1093/biosci/biu130.
- Hupp, C.R.; Osterkamp, W.R. 1985. Bottomland vegetation distribution along Passage Creek, Virginia, in relation to fluvial landforms. *Ecology*. 66: 670-681.
- Hupp, C.R.; Osterkamp, W.R. 1996. Riparian vegetation and fluvial geomorphic processes. *Geomorphology*. 14: 277–295.
- Huston M.A. 1979. A general hypothesis of species diversity. *American Naturalist*. 113: 81–101.
- Huston, M.A. 1994. Biological diversity: The coexistence of species on changing landscapes. Cambridge, UK: Cambridge University Press. 681 p.
- Hutchinson, G.E. 1967. A treatise on limnology. Volume II. Introduction to lake biology and the limnoplankton. New York: John Wiley & Sons. 1115 p.
- Hynes, H.B.N. 1970. The ecology of running waters. Toronto, Canada: University of Toronto Press. 555 p.
- Hynes, H.B.N. 1974. The ecology of polluted waters. Toronto, Canada: University of Toronto Press. 1245 p.
- Hynes, H.B.N. 1975. The stream and its valley. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*. 91: 1-15.
- Ibañez, C.; Belliard, J.; Hughes, R.M.; Irz, P.; Kamdem-Toham, A.; Lamouroux, N.; Tedesco, P.A.; Oberdorff, T. 2009. Convergence of temperate and tropical stream fish assemblages. *Ecography*. 32: 658–670.
- Jacobs, S.M.; Bechtold, J.S.; Biggs, H.C.; Grimm, N.B.; Lorentz, S.; McClain, M.R.; Naiman, R.J.; Perakis, S.S.; Pinay, G.; Scholes, M.C. 2007. Nutrient vectors and riparian processing: A review with special reference to African semiarid savanna ecosystems. *Ecosystems*: DOI: 10.1007/s10021-007-9092-1.
- Jansson, R.; Laudon, H.; Johansson, E.; Augspurger, C. 2007. The importance of groundwater discharge for plant species number in riparian zones. *Ecology*. 88: 131-139.
- Jenkins, K.M.; Boulton, A.J. 2003. Connectivity in a dryland river: Short-term aquatic microinvertebrate recruitment following floodplain inundation. *Ecology*. 84: 2708-2723.
- Johansson, M.E.; Nilsson, C.; Nilsson, E. 1996. Do rivers function as corridors for plant dispersal? *Journal of Vegetation Science*. 7: 593-598.
- Johnson, R.R. 1991. Historic changes in vegetation along the Colorado River in Grand Canyon. In: Colorado River ecology and dam management, Proceedings of a symposium, May 24-25, 1990, Santa Fe, New Mexico. Washington, DC: National Academy Press: 178-206.

- Johnson, W.C. 1994. Woodland expansion in the Platte River, Nebraska: Patterns and causes. *Ecological Monographs*. 64: 45-85.
- Johnson, R.R.; Jones, D.A. eds. 1977. Importance, preservation and management of riparian habitat: A symposium. Gen. Tech. Rep. RM-43. Fort Collins, CO; U.S. Department of Agriculture Forest Service Rocky Mountain Research Station. 217 p.
- Johnson, R.R.; Carothers, S.W.; Simpson, J.M. 1984. A riparian classification system. In: Warner, R.E.; Hendrix, K.M., eds. *California riparian systems*. Berkeley, CA: University of California Press: 375-382.
- Johnson, R.R.; Ziebell, C.D.; Patton, D.R.; Ffolliott, P.F.; Hamre, R.H., eds. 1985. Riparian ecosystems and their management: Reconciling conflicting uses. First North American Riparian Conference, Tucson, AZ. Gen. Tech. Rep. RM-GTR-120. Fort Collin, CO: U.S. Department of Agriculture, Forest Service Rocky Mountain Research Station. 523 p.
- Johnson, R.R.; Bennett, P.S.; Haight, L.T. 1989. Southwestern woody riparian vegetation and succession: An evolutionary approach. In: Abell, Dana L., Technical Coordinator. *Proceedings of the California Riparian Systems Conference: Protection, management, and restoration for the 1990s; 1988 September 22-24; Davis, CA*. Gen. Tech. Rep. PSW-GTR-110. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station: 135-139.
- Johnson, B.L.; Richardson, W.B.; Naimo, T.J. 1995. Past, present, and future concepts in large river ecology. *BioScience*. 45: 134-141.
- Jones, T.R.; Wettstein, P.J. 1997. Evolutionary genetics and phylogeography of tassel-eared squirrels (*Sciurus aberti*). *Journal of Mammalogy*. 78:115-133.
- Junghans, K. 2016. Sources of perennial stream flow in Arizona, USA. Flagstaff, AZ: Northern Arizona University. Thesis.
- Junghans, K.; Springer, A.E.; Stevens, L.E.; Ledbetter, J.D. 2016. Springs ecosystem distribution and density for improving stewardship. *Freshwater Science*. 35: 1330–1339.
- Junk, W.J.; Bayley, P.B.; Sparks, R.E. 1989. The flood pulse concept in river continuum systems. *Canadian Special Publication on Fisheries and Aquatic Sciences*. 106: 89-109.
- Kabede, S.; Travi, Y.; Alemayehu, T.; Ayenew, T. 2005. Groundwater recharge, circulation and geochemical evolution in the source region of the Blue Nile River, Ethiopia. *Applied Geochemistry*. 20: 1658-1676.
- Karr, J.R. 1991. Biological integrity: A long-neglected aspect of water resource management. *Ecological Applications*. 1: 66-84.
- Karr, J.R. 1999. Defining and measuring river health. *Freshwater Biology*. 41: 221-234.
- Karr, J. R.; Chu, E.W. 1999. *Restoring life in running waters: Better biological monitoring*. Washington, DC: Island Press.
- Kelly, J.F.; Hutto, R.L. 2005. An East-West comparison of migration in North American wood warblers. *The Condor*. 107: 197-211.
- Kennedy, T.A.; Muehlbauer, J.D.; Yackulic, C.B; Lytle, D.A.; Miller, S.W.; Dibble, K.L.; Korrtenhoven, E.W.; Metcalfe, A.N.; and Baxter, C.V. 2016. Flow management for hydropower extirpates aquatic insects, undermining river food webs. *BioScience*. DOI: 10.1093/biosci/biw059.
- Knighton, D. 1998. *Fluvial forms and processes*. New York: Oxford University Press. 218 p.
- Kodrick-Brown, A.; Brown, J.H. 2007. Native fishes, exotic mammals, and the conservation of desert springs. *Frontiers in Ecology and the Environment* 5: 549-553.
- Kozlowski, T.T. 1984. *Flooding and plant growth*. London: Academic Press. 356 p.

- Kreamer, D.K.; Stevens, L.E.; Ledbetter, J.D. 2015. Groundwater dependent ecosystems – Science, challenges, and policy. In Adelana, S.M., ed. Groundwater. Hauppauge, NY) Nova Science Publishers, Inc.: 205-230.
- Laliberté, E.; Lambers, H.; Norton, D.A.; Tylianakis, J.M.; Huston, M.A. 2013. A long-term experimental test of the dynamic equilibrium model of species diversity. *Oecologia*. 171: 439-448.
- Larned, S.T.; Datry, T.; Arscott, D.B.; Tockner, K. 2010. Emerging concepts in temporary-river ecology. *Freshwater Biology*. 55: 717-738.
- Lehman, C.L.; Tilman, D. 2000. Biodiversity, stability, and productivity in competitive communities. *American Naturalist*. 156: 534–552.
- Leopold, L.B.; Maddock, R. Jr. 1953. The hydraulic geometry of stream channels and some physiographic implications. Professional Paper 252. Washington, DC: U.S. Geological Survey. 57 p.
- Leopold, L.B.; Wolman, M.G.; Miller, J.P. 1964. Fluvial processes in geomorphology. San Francisco, CA: W.H. Freeman and Co. 544 p.
- Lewin, J. 1978. Floodplain geomorphology. *Progress in Physical Geography*. 2: 408-437.
- Li, R.; Simons, D.B.; Stevens, M.A. 1976. Morphology of cobble streams in small 720 watersheds. *Journal of the Hydraulic, Division American Society of Civil Engineers*. 102: 1101-1117.
- Lowe, W.H.; Likens, G.E. 2005. Moving headwater streams to the head of the class. *BioScience*. 55:196-197.
- Lubinski, K.S. 1993. A conceptual model of the upper Mississippi River system. U.S. Fish and Wildlife Service Environmental Management Technical Center Ecosystem Report 93-T001, Onalaska, WI: U.S. Fish and Wildlife Service Environmental Management Technical Center. 23 p.
- Lugo, A.E.; Brown, S.L.; Dodson, R.; Smith, T.S.; Shugart, H.H. 1999. The Holdridge life zones of the conterminous United States in relation to ecosystem mapping. *Journal of Biogeography*. 26: 1025-1038.
- Lukacs, G.P.; Finlayson, G.P.; Finlayson, C.M., eds. 2008. A compendium of ecological information on Australia's northern tropical rivers. Report to Land & Water Australia. Townsville, Australia: National Centre for Tropical Wetland Research. n.p.
- Lytle, D.A. 1999. Use of rainfall cues by *Abedus herberti* (Hemiptera: Belostomatidae): A mechanism for avoiding flash floods. *Journal of Insect Behavior*. 12:1-12.
- MacArthur, R.H.; Wilson, E.O. 1967. The theory of island biogeography. Princeton, NJ: Princeton University Press. 203 p.
- Mack, G.H.; Seager, W.R.; et al. 2006. Pliocene and Quaternary history of the Rio Grande, the axial river of the southern Rio Grande rift, New Mexico *Earth-Science Reviews*. 79:141–162.
- Magilligan, F.J. 1992. Thresholds and the spatial variability of flood power during extreme floods. *Geomorphology*. 5: 373-390.
- Malanson, G. P. 1993. Riparian landscapes. Cambridge, UK: Cambridge University Press. 296 p.
- Malard, F.; Tockner, K.; Dole-Oliver, M-J.; Ward, J.V. 2002. A landscape perspective of surface-subsurface hydrological exchanges in river corridors. *Freshwater Biology*. 47: 621-640.
- Malusa, J.; Overby, S.T.; Parnell, R.A. 2003. Potential for travertine formation: Fossil Creek, Arizona. *Applied Geochemistry*. 18: 1081-1093.
- Marquard, E.; A. Weigelt; C. Roscher; M. Gubsch; A. Lipowsky; and B. Schmid. 2009. Positive biodiversity-productivity relationship due to increased plant density. *Journal of Ecology*. 97: 696–704.

- Marshall, K.N.; Hobbs, N.T.; Cooper, D.J. 2012. Stream hydrology limits recovery of riparian ecosystems after wolf reintroduction. *Proceedings of the Royal Society B, Biological Sciences*. doi 10.1098/rspb.2012.2977.
- Martin, C.H.; Wainwright, P.C. 2013. Multiple fitness peaks on the adaptive landscape drive adaptive radiation in the wild. *Science*. 339: 208-211.
- McClure, C.J.W.; Ware, H.E.; Carlisle, J.; Kaltenecker, G.; Barber, J.R. 2013. An experimental investigation in the effects of traffic noise on distributions of birds: Avoiding the phantom road. *Proceedings of the Royal Society B*. doi 10.1098/rspb.2013.2290.
- Meehan, W.R.; Swanson, F.J.; Sedell, J.R. 1977. Influences of riparian vegetation on aquatic ecosystems with particular reference to salmonid fishes and their food supply. In: Johnson, R.R.; Jones, D.A. eds. 1977. Importance, preservation and management of riparian habitat: A symposium. Gen. Tech. Rep. RM-43. Fort Collins, CO; U.S. Department of Agriculture Forest Service Rocky Mountain Research Station: 137-145.
- Melo, D.M.; Woodhouse, C.A.; Morino, K. 2012. Dendrochronology and links to streamflow. *Journal of Hydrology*. 412-413:200-209.
- Merriam, G. 1984. Connectivity: A fundamental ecological characteristic of landscape pattern. In: Brandt, J.; Agger, P., eds. *Proceedings of the First International Seminar on Methodology in Landscape Ecology Research and Planning*. Roskilde Universitessforlag GeoRue, Roskilde. 1: 5-15.
- Merritt, D.M. 2013. Reciprocal relations between riparian vegetation, fluvial landforms, and channel processes. In: Shroder, J.F, ed. *Treatise on geomorphology*. New York: Elsevier: 219–243.
- Merritt, D.M.; Wohl, E. 2002. Processes governing hydrochory along rivers: hydraulics, hydrology, and dispersal phenology. *Ecological Applications*. 12: 1071–1087.
- Merritt, W.S.; Letcher, R.A.; Jakeman, A.J. 2003. A review of erosion and sediment transport models. *Environmental Modelling & Software*. 18: 761-799.
- Merritt, R.W.; Cummins, K.W.; Berg, M.B. 2008. *An introduction to the aquatic insects of North America*, 4th Edition. Dubuque, IA: Kendall-Hunt. 1158 p.
- Merritt, D.M.; Scott, M.L.; Poff, N.L.; Auble, G.T.; Lytle, D.A. 2010. Theory, methods, and tools for determining environmental flows for riparian vegetation: riparian vegetation-flow response guilds. *Freshwater Biology*. 55: 206-225.
- Metz, M.; Egger, G.; Díaz-Redondo, M.; Garófano-Gómez, V.; Hortobágyi, B.; Steiger, J.; Corenblit, D. 2016. Succession processes of a dynamic riparian ecosystem: The lower Allier River (France). 11th ISE 2016, Melbourne, Australia. Available online at: <https://publikationen.bibliothek.kit.edu/1000053744/3829702asEgger-25672-1.pdf>.
- Meybeck, M. 1982. Carbon, nitrogen and phosphorous transport by world rivers. *American Journal of Science*. 282: 401–450.
- Miller, M.P.; Buto, S.G.; Susong, D.D.; Rumsey, C.A. 2015. The importance of base flow in sustaining surface water flow in the upper Colorado River basin. *Water Resources Research*. 52: 3547-3562.
- Milliman, J.D.; Syvitski, J.P.M. 1992. Geomorphic/tectonic control of sediment discharge to the ocean: The importance of small mountainous rivers. *Journal of Geology*. 100: 525-544.
- Mims, M.C.; Olden, J.D.; Shattuck, Z.R.; Poff, N.L. 2010. Life history trait diversity of native freshwater fishes in North America. *Ecology of Freshwater Fish*. 19:390–400.
- Minshall, G.W. 1988. Stream ecosystem theory: a global perspective. *Journal of the North American Benthological Society*. 7: 263-288.
- Minshall, G.W.; Peterson, R.C.; Cummins, K.W.; Bott, T.L.; Sedell, J.R.; Cushing, C.E.; Vannote, R.L. 1983. Interbiome comparison of stream ecosystem dynamics. *Ecological Monographs*. 53:1-25.

- Minshall, G.W.; Cummins, K.W.; Petersen, R.C.; Cushing, C.E.; Bruns, D.A.; Sedell, J.R.; Vannote, R.L. 1985. Developments in stream ecosystem theory. *Canadian Journal of Fisheries and Aquatic Sciences*. 42:1045-1055.
- Montgomery, D.R. 1999. Process domains and the river continuum. *Journal of the American Water Resources Association*. 35: 397–410.
- Montgomery, D.R.; Collins, B.D.; Buffington, J.M.; Abbe, T.B. 2003. Geomorphic effects of wood in rivers. In: Gregory, S.; Boyer, K.; Gurnell, A.M. [eds.]. *The ecology and management of wood in world rivers*. Bethesda, MD: American Fisheries Society: 21-47.
- Morgan, L.A.; Shanks, W.C.III; Pierce, K.L.; Lovalvo, D.A.; Lee, G.K.; Webring, M.W.; Stephanson, W.J.; Johnson, S.Y.; Sarlan, S.S.; Schulze, B.; Finn, C.A. 2007. The floor of Yellowstone Lake is anything but quiet – new discoveries from high-resolution sonar imaging, seismic reflection profiling, and submersible studies. *U.S. Geological Survey Paper 1717*. Washington, DC: U.S. Geological Survey: 92-123.
- Morrison, R.R.; Stone, M.C.; Sada, D.W. 2013. Environmental response of a desert springbrook to incremental discharge reductions, Death Valley National Park, California, USA. *Journal of Arid Environments*. 99: 5-13.
- Morisawa, M. 1968. *Streams: Their dynamics and morphology*. New York: McGraw-Hill. 175 p.
- Muehlbauer, J.D.; Collins, S.F.; Doyle, M.W.; Tockner, K. 2014. How wide is a stream? Spatial extent of the potential “stream signature” in terrestrial food webs using meta-analysis. *Ecology*. 95: 44-55.
- Muehlbauer, J.D. The role of aspect and solar radiation on aquatic macroinvertebrate assemblage structure in the lower Little Colorado River, Arizona. *In press*.
- Muller-Schwarze, D. 2006. *Chemical ecology of vertebrates*. Cambridge, UK: Cambridge University Press. 563 p.
- Mustonen, K.-R.; Mykrä, H.; Louhi, P.; Markkola, A.; Tolkkinen, M.; Huusko, A.; Alioravainen, N.; Lehtinen, S.; Muotka, T. 2016. Sediments and flow have mainly independent effects on multitrophic stream communities and ecosystem functions. *Ecological Applications*. 26: 2116–2129.
- Naiman, R.J.; Bilby, R.E. [eds.]. 1998. *River ecology and management*. New York: Springer-Verlag. 705 p.
- Naiman, R. J.; Décamps, H. 1997. The ecology of interfaces: riparian zones. *Annual Review of Ecology and Systematics* 28: 621-658.
- Naiman, R.J.; Melillo, J.M.; Lock, M.A.; Ford, T.E.; Reice, S.R. 1987. Longitudinal patterns of ecosystem processes and community structure in a subarctic river continuum. *Ecology*. 68: 1139-1156.
- Naiman, R. J.; DéCamps, H.; and Pollock, M.M. 1993. The role of riparian corridors in maintaining regional biodiversity. *Ecological Applications*. 3: 209-212.
- Naiman, R.J.; DéCamps, H.; McClaim, M.E. 2005. *Riparia: Ecology, conservation, and management of streamside communities*. Boston, MA: Elsevier Academic. 430 p.
- National Research Council. 2002. *Riparian areas: Functions and strategies for management*. Washington, DC: National Academy Press. 448 p.
- Newbold, J.D.; Elwood, J.W.; O'Neill, R.V.; Winkle, W.V. 1981. Measuring nutrient spiralling in streams, *Canadian Journal of Fisheries and Aquatic Sciences*. 38: 860–863.
- Nilsson, C. 1983. Frequency distributions of vascular plants in the geolittoral vegetation along two rivers in northern Sweden. *Journal of Biogeography*. 10: 351–369.
- Nilsson, C. 1984. Effects of stream regulation on riparian vegetation. In Lilliehammer, A. and Saltveit, S.J. eds. *Regulated rivers*. New York: Oxford University Press: 93-106.

- Nilsson, C.; Svedmark, M. 2002. Basic principles and ecological consequences of changing water regimes: Riparian plant communities. *Environmental Management*. 30: 468-480.
- Nilsson, C.; Grelsson, G.; Johansson, M.E.; Sperens, U. 1989. Patterns of plant species richness along riverbanks. *Ecology*. 70: 77-84.
- Norment, C. 2014. Relicts of a beautiful sea: Survival, extinction, and conservation in a desert world. Chapel Hill, NC: University of North Carolina Press, Chapel Hill. 440 p.
- Odum, H. T. 1957. Trophic structure and productivity of Silver Springs, Florida. *Ecological Monographs*. 27: 55-112.
- Orelana, F.; Verma, P.; Loheide S.P. II; Daly, E. 2012. Monitoring and modeling water-vegetation interactions in groundwater-dependent ecosystems. *Reviews of Geophysics*. 50. DOI: 10.1019/2011RG000383.
- Palmer, M.A.; Bely, A.E.; Berg, K.E. 1992. Response of invertebrates to lotic disturbance: a test of the hyporheic refuge hypothesis. *Oecologia*. 89: 182-194.
- Parsons, M.; McLoughlin, C.A.; Kotschy, K.A.; Rogers, K.H.; Rountree, M.W. 2005. The effects of extreme floods on the biophysical heterogeneity of river landscapes. *Frontiers in Ecology and the Environment*. 3: 487-494.
- Pettit, N.E.; Froend, R.H.; Davies, P.M. 2001. Identifying the natural flow regime and the relationship with riparian vegetation for two contrasting western Australian rivers. *River Research and Application*. 17: 201-215.
- Petts, G.E.; Möller, H.; Roux, A.L., eds. 1989. Historical change in large alluvial rivers: Western Europe. Chichester, UK: John Wiley. 355 p.
- Piotrowski, J.S.; Lekberg, Y.; Harner, M.J.; Ramsey, P.W.; Rillig, M.C. 2008. Dynamics of mycorrhizae during development of riparian forests along an unregulated river. *Ecography*. 31: 245-253.
- Pollen, N.; Simon, A.; Collision, A.J.C. 2004. Advances in assessing the mechanical and hydrologic effects of riparian vegetation on streambank stability. In: Bennett, S.; and Simon, A., eds. *Riparian vegetation and fluvial geomorphology*. Washington, DC: American Geophysical Union, Water Science and Applications. 8: 125-139.
- Pollock, M.M.; Naiman, R.J.; Hanley, T.A. 1998. Plant species richness in riparian wetlands--A test of biodiversity theory. *Ecology*. 79: 94-105.
- Powell, J.W. 1895. The exploration of the Colorado River and its canyons. New York: Dover Publications. 409 p.
- Pringle, C.M.; Naiman, R.J.; Bretschko, G.; et al. 1988. Patch dynamics in lotic systems: the stream as a mosaic. *Journal of the North American Benthological Society*. 7: 503-524.
- Prowse, T.D.; Culp, J.M. 2003. Ice breakup: a neglected factor in river ecology. *Canadian Journal of Civil Engineering* 30: 128-144.
- Reeburgh, W.S.; Nebert, D.L. 1987. The birth and death of Russell Lake. Institute of Marine Science Article #832. Fairbanks, AK: University of Alaska. Available online at: <http://www2.gi.alaska.edu/ScienceForum/ASF8/832.html> (accessed 25 June 2016).
- Reice, S.R. 1985. Experimental disturbance and the maintenance of species diversity in a stream community. 67: 90-97.
- Reichenbacher, R.W. 1984. Ecology and evolution of south-western riparian plant communities. *Desert Plants*. 6: 1-62.
- Renöfält, B.M.; Nilsson, C.; Jansson, R. 2005. Spatial and temporal patterns of species richness in a riparian landscape. *Journal of Biogeography*. 32: 2025-2037.

- Rice, S.P.; Greenwood, M.T.; Joyce, C.G. 2001. Tributaries, sediment sources and the longitudinal organization of macroinvertebrate fauna along river systems. *Canadian Journal of Fisheries and Aquatic Science*. 58: 824-840.
- Rice, S.P.; Kiffney, P.; Greene, C.; Pess, G.R. 2008. The ecological importance of tributaries and confluences. In: Rice, S.P.; Roy, A.G.; Rhoads, B.L., eds. *River confluences, tributaries and the fluvial network*. Chichester, UK: John Wiley and Sons: 209-242.
- Rogers, J.D.; Pyles, M.R. 1980. Evidence of catastrophic erosional events in the Grand Canyon. *Proceedings of the 2nd Conference on Scientific Research in National Parks*. 5: 392-454.
- Rood, S.B.; Goater, L.A.; Mahoney, J.M.; Pearce, C.M.; Smith, D.G. 2007. Floods, fire, and ice: Disturbance ecology of riparian cottonwoods. *Botany*. 11: 1019-1032.
- Rosgen, D.L. 1996. *Applied river morphology*. Pagosa Springs, CO: Wildland Hydrology. v.p.
- Rosgen, D.L., 2008. Discussion of “Critical evaluation of how the Rosgen classification and associated “natural channel design” methods fail to integrate and quantify fluvial processes and channel responses”. *Journal of the American Water Resources Association*. 44: 782–792.
- Rueda, L.V.A. 2015. Turbulence, sediment transport, erosion, and sandbar beach failure processes in Grand Canyon. Tempe, AZ: Arizona State University. Dissertation. 158 p.
- Ruzo, A. 2016. *The boiling river: Adventure and discovery in the Amazon*. New York: Simon & Schuster Audio. Recorded book.
- Sabo, J.L.; Hagen, E.M. 2012. A network theory for resource exchange between rivers and their watersheds. *Water Resources Research*. 48 W04515, doi. 10.1029/2011 WR010703.
- Sacchi, C.F.; Price, P.W. 1988. Pollination of the arroyo willow, *Salix lasiolepis*: Role of insects and wind. *American Journal of Botany*. 75: 1387-1393.
- Schmidt, J.C.; Graf, J.B. 1990. Aggradation and degradation of alluvial sand deposits, 1965–1986, Colorado River, Grand Canyon National Park, Arizona. United States Geological Survey Professional Paper 1493:1-74. Washington, DC: U.S. Geological Survey. 74 p.
- Schumm, S.A., 1985. Patterns of alluvial rivers. *Annual Review of Earth and Planetary Sciences*. 13:5–27.
- Schweitzer, J.A.; Bailey, J.K.; Hart, S.C.; Wimp, G.M.; Chapman, S.K.; Whitham, T.G.; Setälä, H. 2005. The interaction of plant genotype and herbivory decelerate leaf litter decomposition and alter nutrient dynamics. *Oikos*. 110: 133-145.
- Scrimgeour, G.J.; Prowse, T.D.; Culp, J.M.; Chambers, P.A. 1994. Ecological effects of river ice breakup: A review and perspective. *Freshwater Biology*. 32: 261-275.
- Sedell, J.R.; Richey, J.E.; Swanson, R.J. 1989. The river continuum concept: A basis for the expected ecosystem behavior of very large rivers? *Canadian Special Publications in Fisheries and Aquatic Sciences*. 106: 49-55.
- Selwood, K.; Clark, R.H.; McGeoch, M.A.; MacNally, R. 2016. Green tongues into the arid zone: River floodplains extend the distribution of terrestrial bird species. *Ecosystems*. DOI 10.1007/s10021-016-0059-y.
- Shiklomanov, I. 1993. World fresh water resources. In Gleick, P.H., ed. *Water in crisis: A guide to the world's fresh water resources*. New York: Oxford University Press: 13-24.
- Simieon, G.; Stevens, L.E. 2015. *Tamarix* (Tamaricaceae), *Opsius stactogalus* (Cicidellidae), and litter fungi interactions limit riparian plant establishment. *Advances in Entomology*. 3: 65-81.
- Skagen, S.K.; Kelly, J.F.; Van Riper, C.III; Hutto, R.L.; Finch, D.M.; Krueper, D.J.; Melcher, C.P. 2005. Geography of spring landbird migration through riparian habitats in southwestern North America. *The Condor*. 107: 212-227.

- Smith J.A.; Auerbach, D.A.; Flessa, K.W.; Flecker, A.S.; Dietl, G.P. 2016. Fossil clam shells reveal unintended carbon cycling consequences of Colorado River management. *Royal Society Open Science*. 3: 160170.
- Sorey, M.L. 1991. Summary and conclusions. In: Sorey, M.L., ed. *Effects of potential geothermal development in the Corwin Springs Known Geothermal Resources Area, Montana, on the thermal features of Yellowstone National Park*. U.S. Geological Survey Water-Resources Investigations Report 91-4052. Denver, CO: U.S. Geological Survey: A1-17.
- Sousa, W.P. 1984. The role of disturbance in natural communities. *Annual Review of Ecology & Systematics*. 15: 353-391.
- Spence, D.H.N. 1982. The zonation of plants in freshwater lakes. *Advance in Ecological Research*. 12: 37-125.
- Springer, A.E. and L.E. Stevens. 2009. Spheres of discharge of springs. *Hydrogeology Journal* DOI 10.1007/s10040-008-0341-y.
- Springer, A.E.; Boldt, E.M.; Junghans, K.M. 2016. Local vs. regional groundwater flow delineation from stable isotopes at western North America springs. *Groundwater*. doi: 10.1111/gwat.12442.
- Stanford, J.A. 1998. Rivers in the landscape: Introduction to the special issue on riparian and groundwater ecology. *Freshwater Biology*. 40: 402-406.
- Stanford J.A.; Lorang M.S.; Hauer F.R. 2005. The shifting habitat mosaic of river ecosystems. *Internationale Vereinigung für Theoretische und Angewandte Limnologie Verhandlungen*. 29: 123-136.
- Stanitski-Martin, D. 1999. Seasonal energy balance relationships over the Colorado River and adjacent riparian habitat: Glen Canyon, Arizona. Tempe, AZ: Arizona State University. Dissertation. 106 p.
- Steiger, J.; Tabacchi, E.; Dufour, S.; Corenblit, D.; Peiry, J-L. 2005. Hydrogeomorphic processes affecting riparian habitat within alluvial channel-floodplain river systems: A review for the temperate zone. *River Research and Applications*. 21: 719-737.
- Stella, J.C.; Hayden, M.; Battles, J.J.; Fremier, A. 2011. The role of abandoned channels as refugia for sustaining pioneer riparian forest ecosystems. *Ecosystems*. 14: 776-790.
- Stevens, L.E. 1989. Mechanisms of riparian plant succession. Flagstaff, AZ: Northern Arizona University. Dissertation. 115 p.
- Stevens, L.E. 2012. The biogeographic significance of a large, deep canyon: Grand Canyon of the Colorado River, southwestern USA. In: Stevens, L.E., ed. *Global advances in biogeography*. Rijeka, Croatia: InTech Publications: 169-208.
- Stevens, L.E.; Ayers, T.J. 2002 The biodiversity and distribution of alien vascular plant and animals in the Grand Canyon region. In Tellman, B., ed. *Invasive exotic species in the Sonoran Region*. Tucson, AZ: University of Arizona Press: 241-265.
- Stevens, L.E.; Meretsky, V.J. 2008. *Aridland springs in North America: Ecology and management*. Tucson, AZ: University of Arizona Press. 406 p.
- Stevens, L.E.; Brown, B.T.; Simpson, J.M.; Johnson, R.R. 1977. The importance of riparian habitats to migrating birds. In: Johnson, R.R.; Jones, D., eds. *Proceedings of a symposium on the importance, preservation and management of riparian habitats*. Gen. Tech. Rep. RM-43. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 156-164.
- Stevens, L.E.; Buck, K.A.; Brown, B.T.; Kline, N. 1997a. Dam and geomorphic influences on Colorado River waterbird distribution, Grand Canyon, Arizona. *Regulated Rivers: Research & Management*. 13: 151-169.

- Stevens, L.E.; Schmidt, J.C.; Ayers, T.J.; Brown, B.T. 1995. Geomorphic influences on fluvial marsh development along the dam-regulated Colorado River in the Grand Canyon, Arizona. *Ecological Applications*. 5: 1035-1039.
- Stevens, L.E., J.P. Shannon and D.W. Blinn. 1997b. Benthic ecology of the Colorado River in Grand Canyon: Dam and geomorphic influences. *Regulated Rivers: Research & Management*. 13: 129-149.
- Stevens L.E.; Waring, G.L. 1985. Effects of prolonged flooding on riparian vegetation in Grand Canyon. In: Johnson, R.R. et al., eds. *Riparian ecosystems and their management*. Gen. Tech. Rep. RM-120. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 81-86.
- Stevens, V. 1997. The ecological role of coarse woody debris: An overview of the ecological importance of CWD in BC forests. British Columbia Ministry of Forests Research Program Work Paper 30/1997 Victoria, BC, Canada: British Columbia Ministry of Forests. 26 p.
- Strahler, A.N. 1957. Quantitative analysis of watershed geomorphology. *Transactions of the American Geophysical Union*. 38: 913-920.
- Stromberg, J.; Briggs, M.; Gourley, C.; Scott, M.; Shafroth, P.; Stevens, L. 2004. Human alterations of riparian ecosystems. In: Baker, M.B. Jr.; Ffolliott, P.F.; DeBano, L.; Neary, D.G., eds. *Riparian areas of the southwestern United States: Hydrology, ecology, and management*. Boca Raton, FL: Lewis Publishers: 99-126.
- Teears, T.D. 2016. The effect of water quality on the survival and fitness of brook trout (*Salvelinus fontinalis*) eggs, alevins and fry in aquaculture and deep springs along the South River in Waynesboro, VA. Harrisonburg, VA: James Madison University. Thesis 462. 71 p..
- Thedol, C.E. 1997. Hydrogeology of Lake Tahoe basin, California and Nevada, and results of a ground-water quality monitoring network, water years 1990-1992. U.S. Geological Survey Water-Resources Report 97-4072. Carson City, NV: U.S. Geological Survey. 53 p.
- Therrell, M.D.; Bialecki, M.B. 2015. A multi-century tree-ring record of spring flooding on the Mississippi River. *Journal of Hydrology*. 529: 490-498. doi.org/10.1016/j.jhydrol.2014.11.005.
- Thoms, M.C.; Parsons, M. 2002. Eco-geomorphology: An inter-disciplinary approach to river science. *International Association of Hydrological Science*. 276: 113-120.
- Thorp, J.H.; DeLong, M.D. 1994. The riverine productivity model: An heuristic view of carbon sources and organic processing in large river ecosystems. *Oikos*. 70: 305-308.
- Thorp, J.H.; Thoms, M.C.; DeLong, M.D. 2006. The riverine ecosystem synthesis: Biocomplexity in river networks across space and time. *River Research & Applications*. 22: 123-147.
- Thorp, J.H.; Thoms, M.C.; DeLong, M.D., eds. 2008. *The riverine ecosystem synthesis: Toward conceptual cohesiveness in river science*. London: Academic Press. 233 p.
- Tilman, D. 1988. *Plant strategies and the dynamics and function of plant communities*. Princeton, NJ: Princeton University Press. 360 p.
- Tilman, D.; Reibch, P.B.; Knops, j.; Wedin, D.; Mielke, T.; Lehman, C. 2001. Diversity and productivity in a long-term grassland experiment. *Science*. 294: 843-845.
- Timmons, J.M.; Karlstrom, K.E., eds. 2012. *Grand Canyon geology: Two billion years of Earth's history*. Geological Society of America Special Paper 489. Boulder, CO: Geological Society of America. 156 p.
- Tinkler, K.J.; Wohl, E.E. 1998. *Rivers over rock: Fluvial processes in bedrock channels*. American Geophysical Union Geophysical Monograph Series 107. Washington, DC: American Geophysical Union. 323 p.
- Tockner, K.; Malard, F.; Ward, J.V. 2000. An extension of the flood pulse concept. *Hydrological Processes*. 14: 2861-2883.

- Tockner, K.; Ward, J.V.; Edwards, P.J.; Kollmann, J.. 2002. Riverine landscapes: an introduction. *Freshwater Biology*. 47: 497-500.
- Tockner, K.; Ward, J.V.; Arscott, D.B.; Edwards, P.J.; Kollmann, J.; Gurnell, A.M.; Petts, G.E.; Maiolini, B. 2003. The Tagliamento River: A model ecosystem of European importance. *Aquatic Sciences*. 65: 239-253.
- Topping, D.J.; Schmidt, J.C.; Vierra, L.E. Jr. 2003. Computation and analysis of the instantaneous-discharge record for the Colorado River at Lees Ferry, Arizona – May 8, 1921, through September 30, 2000. U.S. Geological Survey Professional Paper Series 1677. Denver, CO: U.S. Geological Survey. 118 p.
- Topping, D.J.; Rubin, D.M.; Nelson, J.M., Kinzel, P.J. III.; Bennett, J.P. 2013. Linkage between grain-size evolution and sediment depletion during Colorado River floods. In Webb, R.H.; Schmidt, J.C.; Marzolf, G.R.; Valdez, R.A. *Geophysical Monograph Series*. 110. Washington, DC: American Geophysical Union: 71-98.
- Townsend, C.R. 1989. The patch dynamics concept of stream community ecology. *Journal of the North American Benthological Society*. 8: 36-50.
- Townsend, C.R. 2003. The intermediate disturbance hypothesis, refugia, and biodiversity in streams. *Limnology and Oceanography* 42. [Doi.org/10.4319/lo.1997.42.5.0938](https://doi.org/10.4319/lo.1997.42.5.0938).
- Townsend C.R.; Thompson, R.M.; McIntosh, A.R.; Kilroy, C.; Edwards, E.D.; Scarsbrook, M.R. 2000. Disturbance, resource supply and food-web architecture in streams. *Ecology Letters*. 1: 200–209.
- U.S. Army Corps of Engineers; U.S. Environmental Protection Agency. 2015. Clean Water rule: Definition of “Waters of the United States.” U.S. Federal Register. 80:37054-37127.
- U.S. Bureau of Reclamation. 2012. Colorado River basin water supply and demand study. Boulder City, NV: U.S. Bureau of Reclamation, Lower Colorado Region. 22 p.
- U.S. Environmental Protection Agency. 2016. National aquatic resource surveys. Accessible online at: <https://www.epa.gov/national-aquatic-resource-surveys> (accessed 5 November 2016).
- U.S. Natural Resources and Conservation Service. 2013. Part 629 - Glossary of landform and geologic terms; 1-135. www.nrcs.usda.gov/Internet/FSE_DOCUMENTS/nrcs142p2_052234.doc.
- Vannote, R. L.; Minshall, G.W.; Cummins, K.W.; Sedell, J.R.; Cushing, C.E. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences*. 37: 130–137.
- Vences M.; Wollenberg K.C.; Vieites, D.R.; Lees, D.C. 2009. Madagascar as a model region of species diversification. *Trends in Ecology & Evolution*. 24: 456–65.
- Vogel, S. 1981. *Life in moving fluids: The physical biology of flow*. Boston, MA: Willard Grant Press. 467 p.
- Walker, J.; Peet, R.K. 1985. Composition and species diversity of pine-wiregrass savannas of the Green Swamp, North Carolina. In Peet, R.K., ed. *Plant community ecology: Papers in honor of Robert H. Whittaker*. Dordrecht, The Netherlands: Dr. W. Junk Publishers: 303-320.
- Ward, J.V. 1989. The four-dimensional nature of lotic ecosystems. *Journal of the North American Benthological Society*. 8: 2-8.
- Ward, J.V. 1994. Ecology of alpine streams. *Freshwater Biology*. 32: 277–294.
- Ward, J.V.; Stanford, J.A. 1983. The serial discontinuity concept of river ecosystems. In: Fontaine, T.D.; Bartell, S.M., eds. *Dynamics of lotic ecosystems*. Ann Arbor, MI: Science Publications: 29-43.
- Ward, J.V.; Stanford, J.A. 1995. The serial discontinuity concept: extending the model to floodplain rivers. *Regulated Rivers: Research & Management*. 10: 159-168.
- Ward, J.V.; Bretschko, G.; Brunke, M.; Danielopol, D.; Gilbert, J.; Gonser, T.; Hildrew, A.G. 1998. The boundaries of river systems: The metazoan perspective. *Freshwater Biology*. 40: 531-569.

- Ward, J.V.; Tockner, K.; Arscott, D.B.; Claret, C. 2002. Riverine landscape diversity. *Freshwater Biology*. 47: 517-539.
- Ward, N.D.; Sawakuchi, H.O.; Richey, J.E. 2018. The Amazon River's ecosystem: Where land meets the sea. *Eos*. 99. <https://doi.org/10.1029/2018EO088573>.
- Warren, D.K.; Turner, R.M. 1975. Saltcedar (*Tamarix chinensis*) seed production, seedling establishment, and response to inundation. *Journal of the Arizona Academy of Sciences*. 10: 135-144.
- Webb R.H.; Betancourt, J.L.; Johnson, R.R.; Turner, R. M. 2014. Requiem for the Santa Cruz River: An environmental history of an Arizona river. Tucson, AZ: University of Arizona Press. 279 p.
- Whiles, M.R.; Lips, K.R.; Pringle, C.M.; Killham, S.S.; Bixby, R.J.; Brenes, R.; Connelly, S.; Colon-Gand, J.C.; Hunte-Brown, M.; Huryn, A.D.; Montgomery, C.; Peterson, S. 2006. The effects of amphibian population declines on the structure and function of neotropical stream ecosystems. *Frontiers in Ecology and the Environment*. 1: 27-34.
- White, P.S. 1979. Pattern, process, and natural disturbance in vegetation. *Botanical Reviews*. 45: 229-299.
- Whiteman, C.D. 1990. Observations of thermally developed wind systems in mountainous terrain. *Meteorological Monographs*. 45: 5-42.
- Wickert, A.D.; Mitrovica, J.X.; Williams, C.; Anderson, R.S. 2013. Gradual demise of a thin southern Laurentide ice sheet recorded by Mississippi drainage. *Nature*. 502: 668-671.
- Wilkinson, D.M. 1999. The disturbing history of intermediate disturbance. *Oikos*. 84:145-7.
- Winograd, I.J.; Thordarson, W. 1975. Hydrogeologic and hydrochemical framework, south-central Great Basin, Nevada-California, with special reference to the Nevada Test Site. U.S. Geological Survey Professional Paper 712-C. Washington, DC: U.S. Geological Survey. 126 p.
- Wohl, E. 2010. Mountain rivers revisited. American Geophysical Union GeoPress Water Resources Monograph 19. Washington, DC: American Geophysical Union. 583 p.
- Woodbury, A.M., ed. 1959. Ecological studies of flora and fauna in Glen Canyon. University of Utah Anthropological Paper, Glen Canyon Series Number 7. Salt Lake City, UT: University of Utah. 242 p.
- Woodward, J.C.; Macklin, M.G.; Krom, M.D.; Williams, M.A.J. 2007. The Nile: Evolution, Quaternary river environments and material fluxes. In: Gupta, A., ed. Large rivers: Geomorphology and management. London: John Wiley & Sons, Ltd: 261-292.
- Wurtsbaugh, W.A.; Heredia, N.A.; Laub, B.G.; Meredith, C.S.; Mohn, H.E.; Null, S.E.; Pluth, D.A.; Roper, B.B.; Saunders, W.C.; Stevens, D.K.; Walker, R.H.; Wheeler, K. 2015. Approaches for studying fish production: Do river and lake researchers have different perspectives? *Canadian Journal of Fisheries and Aquatic Sciences*. 72: 149-160. [dx.doi.org/10.1139/cjfas-2014-0210](https://doi.org/10.1139/cjfas-2014-0210).
- Yard, M.D.; Bennett, G.E.; Mietz, S.N.; Coggins, L.N. Jr.; Stevens, L.E.; Hueftle, S.; Blinn, D.W. 2005. Influence of topographic complexity on solar insolation estimates for the Colorado River, Grand Canyon, AZ. *Ecological Modeling*. 183: 157-172.