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River ecosystem conceptual models and non-perennial rivers: A critical review

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Abstract

Conceptual models underpin river ecosystem research. However, current models focus on continuously flowing rivers and few explicitly address characteristics such as flow cessation and drying. The applicability of existing conceptual models to nonperennial rivers that cease to flow (intermittent rivers and ephemeral streams, IRES) has not been evaluated. We reviewed 18 models, finding that they collectively describe main drivers of biogeochemical and ecological patterns and processes longitudinally (upstream-downstream), laterally (channel-riparian-floodplain), vertically (surface water-groundwater), and temporally across local and landscape scales. However, perennial rivers are longitudinally continuous while IRES are longitudinally discontinuous. Whereas perennial rivers have bidirectional lateral connections between aquatic and terrestrial ecosystems, in IRES, this connection is unidirectional for much of the time, from terrestrial-to-aquatic only. Vertical connectivity between surface and subsurface water occurs bidirectionally and is temporally consistent in perennial rivers. However, in IRES, this exchange is temporally variable, and can become unidirectional during drying or rewetting phases. Finally, drying adds

another dimension of flow variation to be considered across temporal and spatial scales in IRES, much as flooding is considered as a temporally and spatially dynamic process in perennial rivers. Here, we focus on ways in which existing models could be modified to accommodate drying as a fundamental process that can alter these patterns and processes across spatial and temporal dimensions in streams. This perspective is needed to support river science and management in our era of rapid global change, including increasing duration, frequency, and occurrence of drying.

Introduction

Conceptual models are fundamental to ecology. They identify ecological universalities across diverse taxonomies and geographies (Lawton, 1999). Such models have played a particularly important role in shaping how we understand and manage river ecosystems at different scales. Yet, most of these conceptual frameworks derive from research focused on continuously flowing ("perennial") rivers to advance our understanding of how hydrologic and geomorphologic processes structure river ecosystems. Intermittent rivers and ephemeral streams (hereafter, "IRES") do not continuously flow, and occur in all climates and biomes. They are extremely common in headwaters (Benstead & Leigh, 2012), in regions with lower runoff (Dodds, 1997), and comprise at least half of global river length (Datry, Larned, & Tockner, 2014). IRES are ecologically and hydrologically distinct from perennial rivers (Datry, Bonada, & Boulton, 2017). So, are our existing riverine conceptual models applicable to IRES?

Hydrological processes are foundational to river ecosystem conceptual models. Because hydrological processes in IRES are marked by flow-cessation, drying, and rewetting phases, conceptual models that embrace these processes would best represent IRES. A solid body of IRES research now exists (Datry et al., 2017), guided by conceptual work on IRES ecology (Datry et al., 2014; Stanley, Fisher, & Grimm, 1997) and hydrology (Costigan, Jaeger, Goss, Fritz, & Goebel, 2016; Godsey & Kirchner, 2014). Thus, we are positioned to critically review river ecosystem models and investigate how well they represent IRES in current river ecosystem conceptual models.

Our objective is critical. River ecosystem conceptual models often inform management practices. If our conceptual underpinnings do not accurately represent a substantial fraction of the river network, management and policy decisions may fail to achieve desired outcomes. Tools developed from existing conceptual models, such as biomonitoring approaches to assess ecosystem integrity, are often ineffective in IRES (Stubbington et al., 2018). Similarly, although the natural flow regime conceptual framework (Poff et al., 1997) promoted the implementation of environmental flows in river management (Richter & Thomas, 2007), its relevance to IRES is still uncertain (Acreman et al., 2014). Management mishaps are becoming increasingly common as extreme droughts and drying events increase (Tonkin et al., 2019), challenging water management strategies developed for perennial waterways (Shanafield et al., 2020). IRES provide essential ecosystem services to society (Datry, Boulton, et al., 2018; Koundouri, Boulton, Datry, & Souliotis, 2017), and therefore are in need of effective conservation and management. Finally, environmental policies are being redefined in the United States and elsewhere to specifically exclude many IRES as

waterways warranting legal protection (Marshall et al., 2018). As IRES will likely become more dominant in the Anthropocene (Datry et al., 2014), understanding whether they are accurately described by the conceptual models that underpin their management and legal protection is crucial.

Our paper critically evaluates existing river ecosystem conceptual models to advance the science and management of IRES. We reviewed 18 influential conceptual frameworks published between 1980 and 2016, classifying them into two broad categories. The first category focuses on local- or reach-scale processes along four major dimensions identified by Ward (1989): *longitudinal* (upstream-downstream), *lateral* (channel-floodplain), *vertical* (surface-subsurface), and *temporal* (variation over time). The second category considers river networks at landscape and larger spatial scales, concentrating on the spatial processes critical to the functioning of riverine ecosystems. We then assessed how well each of these frameworks applied to IRES, and how IRES might challenge central assumptions of each framework. Our findings lay the groundwork for a new perspective that includes river drying as a fundamental component of riverine conceptual models used to guide current and future research and management of river ecosystems.

River drying, flow cessation, and four-dimensional hydrologic continua at the reach scale

Longitudinal dimension.

Six river conceptual models explicitly address the longitudinal dimension of rivers (Table 1). As surface water flows downstream, it carries suspended organic matter (Vannote et al., 1980) and dissolved nutrients (Fisher et al., 1998) used by micro- and macro-organisms; most processed materials are exported downstream for further recycling. This material processing is posited to occur continuously along the length of a river. Moreover, riverine organisms can disperse among habitats along the upstream-downstream corridor.

Longitudinal dimension models focus explicitly on perennial rivers, but IRES challenge the central assumption of continuous upstream-downstream hydrological connectivity. Aquatic habitats in IRES are longitudinally discontinuous at the surface when they dry (Figure 1). During dry periods, many IRES become isolated pools of standing water, or surface-disconnected reaches that still flow (Figure 2). These disconnected pools and reaches are longitudinally isolated by dry reaches, preventing the downstream transport of materials in surface waters (Pringle, 2001). Alternating expansion and contraction of wet stream reaches over time drives nutrient and organic matter dynamics in IRES (von Schiller, Bernal, Dahm, & Martí, 2017) and controls population connectivity of riverine organisms (Allen et al., 2019). Moreover, longitudinal connectivity is the basis for the river continuum concept's predictions about how invertebrate functional feeding groups (shredders vs. collectors vs. filterers, etc.) should be distributed longitudinally based on changes in food supply from headwaters to the river mouth (Vannote et al., 1980). In IRES, however, life history or physiological traits that allow species to cope with the abiotic conditions associated with drying (e.g., rapid growth, multivoltinism, diapause, desiccation resistance) may be far more important than access to a specific food source (Aspin et al., 2019; Bogan, 2017).

Of the six longitudinal models, only the telescoping ecosystem model (Fisher et al., 1998) addresses longitudinal expansion and contraction in a manner directly relevant for IRES, probably because it draws heavily on research conducted in an intermittent stream (Sycamore Creek, Arizona, USA). The framework proposes that streams expand and contract longitudinally and laterally from the river channel like the concentric cylinders of a telescope, constituting a key physical process that controls nutrient dynamics in rivers (Fisher et al., 1998). This model has not yet been applied to other IRES beyond this system, and a more extensive testing across a range of systems would help in understanding its generality. Finally, we note that the river continuum concept has been modified to accommodate IRES by some researchers (e.g., grassland streams; Dodds, Gido, Whiles, Fritz, & Matthews, 2004).

Lateral dimension.

Six conceptual models emphasize lateral connectivity as a key factor structuring rivers ecosystems (Table 1). The expansion–contraction cycles of a river along its lateral dimension allow for bidirectional exchanges of organisms and materials between the main and side channels, floodplains, and riparian zones. Below bankfull conditions, lateral river expansion connects larger main channels with smaller side channels as flow increases (flow pulse concept; Tockner et al., 2000), which can both create river habitat (e.g., providing multiple flow paths through the river corridor) and homogenize it (e.g., water temperatures and nutrient concentrations). During overbank flows, lateral river expansion connects river channels with their floodplains (flood pulse concept; Junk et al., 1989). Mobile riverine organisms can then colonize inundated floodplains from the main channels, where they forage, spawn, and shelter from high water velocities of the main channel during a flood. The inundated floodplain becomes a source of nutrients for riverine biota that receive receding floodplain waters as flow returns to baseflow conditions.

This bidirectional exchange of organisms and materials along the lateral dimension does not always occur in IRES. When rivers are dry this exchange becomes primarily unidirectional because terrestrial organisms and material from riparian and floodplain habitats enter the channel, whereas transfer from channel to floodplains rarely occurs (Steward, Langhans, Corti, & Datry, 2017). The duration of the dry period affects these lateral connections, controlling the decomposition rates of leaf litter once the river rewets (Datry, Foulquier, et al., 2018). IRES that flow for only a few days after precipitation events may never produce sufficient adult aquatic insect emergence for riparian predators, and mobile aquatic organisms such as fish that may temporarily inhabit floodplains are rare in such rivers (Kerezsy, Gido, Magalhães, & Skelton, 2017). Unidirectional lateral connectivity may dominate IRES with short flow durations even when they have flow, except when heavy rainfall events generate overbank flow (Zimmer & McGlynn, 2017).

Despite IRES not conforming to our traditional understanding of the lateral dimension in rivers, aspects of these six models are indirectly relevant. For example, IRES retract more than perennial rivers along the lateral dimension, often to the point where no surface water remains. The flood pulse concept defines the floodplain as an “Aquatic-Terrestrial Transition Zone (ATTZ)”, where the expansion–contraction cycles depend on floods and the floodplain

has pronounced aquatic and terrestrial phases. Aquatic and terrestrial organisms may require anatomical, morphological, physiological, and/or behavioral adaptations to colonize and persist in the ATTZ (Junk et al., 1989). Thus, it is logical to extend the ATTZ from the floodplain to an intermittent river channel where aquatic biota have evolved physiological and behavioral adaptations that allow them to persist (Stubbington et al., 2017).

Vertical dimension.

Two river ecosystem conceptual models focus on the vertical dimension (Table 1). The vertical exchange of water, solutes, and organisms can occur via downwelling of surface water into the hyporheic zone (the saturated subsurface zone beneath the river channel) and upwelling of subsurface water into the river channel. The vertical dimension is crucial for riverine biogeochemical cycles and organisms that link hyporheic and benthic (riverbed) ecosystems. In most rivers, surface waters are mixed, oxygenated, and well-lit, whereas the hyporheic zone is transport-limited, oxygen-deficient, and light-limited. Hyporheic exchange of surface water- and groundwater-delivered material between these two physically and chemically distinct environments promotes spatial heterogeneity in biogeochemical transformations (Boano et al., 2014). Hyporheic exchange can also include invertebrates, particularly those that can tolerate low dissolved oxygen conditions and feed on carbon sources in the hyporheic zone (DelVecchia, Stanford, & Xu, 2016; Jones, Fisher, & Grimm, 1995).

The vertical dimension and surface-subsurface exchanges are important in IRES, but in a different way (Figure 1). In perennial rivers, hyporheic exchange is considered to occur consistently through time (Boano et al., 2014). By contrast, hyporheic exchange in IRES is not always continuous and may be unidirectional during drying (surface-to-subsurface only) and rewetting (subsurface-to-surface only) phases (Zimmer & McGlynn, 2017). Rewetting of some IRES is driven completely by influxes of groundwater, delivering groundwater-derived material and solutes into the river channel and causing rapid biogeochemical transformations (von Schiller et al., 2017). Vertical exchanges of gases can also be important, and rewetting events can initiate significant carbon dioxide effluxes from rivers to the atmosphere (Datry, Foulquier, et al., 2018). Drying rivers can be an important source of evaporative water vapor, and emissions from dry channels can be higher than emissions from upland soils (Gómez-Gener et al., 2016; Schiller et al., 2014). Additionally, the hyporheic zone can be an important refuge for benthic invertebrates during dry phases. Recolonization from the hyporheic zone can be more important than aerial oviposition or larval drift in structuring benthic community assembly after rewetting (Vander Vorste, Malard, & Datry, 2016), although hyporheic refuges can be less important in other systems when flow is reduced but surface water still remains (James, Dewson, & Death, 2008).

The hyporheic corridor concept (Stanford & Ward, 1993) is one of the few riverine conceptual models that mention IRES. Here, Stanford and Ward (1993) explicitly discuss “ephemeral springbrooks” that emerge during spring runoff periods, usually in abandoned meander channels. Flow in springbrooks decreases throughout the summer until surface water exists as pools connected by interstitial flow or the channels dry completely. Connectivity along the vertical dimension was posited to be critical in these dynamic

systems (Stanford & Ward, 1993), a prediction that has been supported in the subsequent decades of research on IRES (Stubbington et al., 2017; Vander Vorste et al., 2016; von Schiller et al., 2017).

Temporal dimension.

Rivers are temporally dynamic as flow can vary greatly over time. Five river conceptual models focus on the temporal dimension (Table 1), but each considers it differently. Ward (1989) focuses on how organisms respond to temporal flow disturbances, both behaviorally and evolutionarily. Poff et al. (1997) describe the flow regime as "the characteristic pattern of a river's flow quantity, timing, and variability" using a suite of flow regime characteristics, such as flow magnitude, frequency, duration, timing, and rate of change. Wohl et al. (2015) extend this perspective to incorporate sediment input, transport, and storage dynamics. The pulse shunt concept (Raymond et al., 2016) highlights how low-frequency, high-magnitude flow events are disproportionately important for dissolved organic matter dynamics throughout entire river networks. Finally, the river wave concept (Humphries et al., 2014) integrates multiple river ecosystem conceptual frameworks according to temporal variability in flow phase. This concept posits that the flood pulse concept (Junk et al., 1989) best explains river ecosystem dynamics during peak flows, the river continuum concept is most relevant during moderate flows (Vannote et al., 1980), and the riverine productivity model (Thorp & Delong, 1994) applies best during baseflows.

The temporal dimension and its associated variation in flow phase are highly relevant in IRES (Figures 2 and 3). However, previous conceptual frameworks consider only flow variation from baseflow at the lowest flow phase to overbank flood at the highest phase (Figure 3a–f). Flow phases between baseflow and complete drying occur in IRES (Figure 3e–g), but are not discussed in previous frameworks (Costigan et al., 2016). As baseflow recedes in IRES, surface flow stops and isolated pools may form. Surface water can disappear, but hyporheic water remains; as drying continues, both surface and hyporheic water are lost. Each of these flow phases is hydrologically and ecologically distinct, with different implications for hydrologic and sediment transport, biota, and biogeochemical cycles (Costigan et al., 2016; Stubbington et al., 2017; von Schiller et al., 2017). Importantly, variations in the duration, intensity, and frequency of these different phases over time, and spatially throughout a river network, have repercussions for biogeochemical and ecological processes. Therefore, we need to extend the range of possible flow phases when considering IRES.

The natural flow and sediment regimes (Poff et al., 1997; Wohl et al., 2015) are indirectly relevant to IRES. They center on temporal variability in flow and sediment dynamics in riverine corridors and how these regimes have been modified by human activities. The natural flow regime notes that temporal variation in flow within single rivers can produce habitats that range from free flowing, through standing to no water, and IRES are briefly mentioned when discussing low-flow conditions (Poff et al., 1997). Similarly, sediment regimes are the primary drivers of valley-floor processes in nonperennial and perennial rivers; however, some fundamental distinctions exist between them. In IRES, sediment flux and channel-bed grain size distributions from upstream to downstream can differ

substantially from those in perennial streams (Jaeger, Sutfin, Tooth, Michaelides, & Singer, 2017). Thus, IRES can fit into the natural flow and sediment regime frameworks with some further adjustments.

River drying and spatial processes and patterns

Nine river conceptual models focus on spatial processes and/or patterns, seeking to explain how river ecosystems vary across landscape and larger scales (Table 1). The river continuum concept (Vannote et al., 1980) and riverine productivity model (Thorp & Delong, 1994) both proposed that energy sources vary predictably according to river size and position within the broader river network. In contrast, the process domains concept (Montgomery, 1999), fluvial landscape ecology framework (Poole, 2002), network dynamics hypothesis (Benda et al., 2004) and the riverine ecosystem synthesis (Thorp et al., 2008) emphasize the patchy nature of the different stream habitat types that exist throughout a river network, as hydrologic processes vary across space due to differences in watershed size, topography, and geophysical characteristics. The multiple roles of water framework (Sponseller et al., 2013) describes water having three different ecological roles based on a river's position within the broader river network: (a) as a resource and habitat in smaller rivers, (b) as a vector for connectivity, and (c) as an agent of geomorphic change and disturbance in larger rivers. Finally, the stream biome gradient concept (Dodds et al., 2015) and the subsequent freshwater biome gradient framework (Dodds et al., 2019) present a framework for how river ecosystems should vary geographically, across continental and global scales and across climate gradients and biomes. These models specifically consider large geographic areas where intermittent or ephemeral flow should occur, with emphasis on the balance between potential and actual evapotranspiration.

River drying adds a temporal dimension to spatial variation in river ecosystem habitats. Drying is often a major driver of spatial heterogeneity in river networks (Figure 4). Flowing, nonflowing, and dry reaches can exist anywhere throughout the network, occurring in headwaters, tributaries, mainstems, and even river mouths. Moreover, Costigan et al. (2016) suggest that the typical locations of perennial and nonperennial sections in the river network may vary due to differences in climate. In arid areas, perennial rivers are either very large mainstems that drain wetter adjacent areas or small headwaters where perennial springs provide a constant source of water; nonperennial sections can be anywhere. Conversely, in humid areas nonperennial reaches are likely limited to headwaters, while downstream network reaches are usually perennial (Costigan et al., 2016). Thus, the consideration of local drying regimes as another hydrologic layer in the landscape would complement the spatial heterogeneity we typically consider within river networks and across biomes.

Two conceptual models focusing on spatial processes and patterns in streams are relevant for IRES. IRES are a focus of the multiple roles of water framework which discusses how variation in flow permanence generates three types of river habitat: a *pulse* domain where water may flow for minutes to weeks, a *seasonal* domain where water may flow for weeks to months, and a *perennial* domain where water continuously flows (Sponseller et al., 2013). In this framework, flood-associated disturbances and hydrologic exchange are key drivers of river ecosystem dynamics only when flow is perennial. Sponseller et al. (2013) also

discuss how IRES are more abundant in arid regions, echoing the discussion in the stream biome gradient concept (Dodds et al., 2015). Indeed, these are two of the most recent of the 18 conceptual models and were developed by authors working in regions where IRES are common.

The need for a new ecohydrological perspective for river ecosystems

Our review reveals that most current frameworks were designed for and derived from research on perennial rivers. Yet IRES are equally as abundant worldwide, and climate change and human water withdrawals are expanding IRES in space and time (Döll & Schmied, 2012; Grill et al., 2019). Accordingly, we call for a new perspective of river science: one that emphasizes drying as an important hydrological process that structures river ecosystems. As with existing river conceptual frameworks, such a perspective should be underpinned by science. It should also empower adaptive management of rivers in the Anthropocene, along with legislation and regulations regarding their environmental protection.

Below, we summarize the major points from our review that could form the basis of a new ecohydrological perspective, which could be used to modify existing conceptual models to account for IRES:

1. Upstream and downstream hydrological connections along the longitudinal dimension occur in all rivers, but are often episodic in IRES. During high-flow phases when the entire river network is flowing, the downstream transport of water, solutes, and organic matter predominates, and these materials are continually processed. During low-flow phases, downstream transport is primarily restricted to flowing reaches or subsurface flow. During zero-flow phases, isolated stagnant pools behave more like lentic (standing water) systems, and dry reaches become terrestrial and can be used by some organisms for migration (Bogan & Boersma, 2012; Sánchez-Montoya, Moleón, Sánchez-Zapata, & Tockner, 2016). These transitions between phases underscore the need for collaboration among lotic (running waters), lentic, and terrestrial ecologists to more fully understand processes governing IRES (Datry et al., 2014).

2. Reciprocal linkages along the lateral dimension are essential to river ecosystems, but this exchange may be more unidirectional in IRES. Although terrestrial-to-aquatic transfers of water, solutes, organic matter, and organisms are always important, the magnitude and potential importance of aquatic-to-terrestrial transfers decrease when the river is dry.

3. With the exception of bedrock rivers, connectivity along the vertical dimension is a fundamental riverine process, where water, solutes, and organisms are exchanged between the surface and the hyporheic zone. Again, this connectivity can become more unidirectional (surface-to-subsurface) as rivers dry, or limited if the riverbed is entirely bedrock. Subsurface-to-surface connections are also important in IRES, especially when hyporheic influxes to the surface are the

primary water delivery source during rewetting events. Often the hyporheic zone is a vital refuge for aquatic organisms during dry periods.

4. Flow variation along the temporal dimension is pivotal because all natural rivers are dynamic and vary in phase over time. However, IRES have been shown to have greater flow variation that includes zero flow, typically not included in river conceptual frameworks. The frequency, duration, and timing of these zero flows are critical in structuring riverine ecosystems, and must be considered in river research and management (Jaeger, Olden, & Pelland, 2014).

5. Hydrologic variability creates heterogeneity in abiotic conditions throughout a river network, which in turn creates variability in riverine biotic processes and a mosaic of aquatic and terrestrial habitats. As drying governs hydrologic heterogeneity in space and time in IRES, drying should be specifically incorporated into river science and management.

6. IRES are threatened ecosystems. They frequently serve as sites for dumping trash and dredging sediment, as conduits for waste water, and suffer severe hydrological alterations through artificial dewatering or augmented flows (Chiu, Leigh, Mazor, Cid, & Resh, 2017). They generally have less legal protection than perennial rivers due to the social undervaluation of their ecological attributes and ecosystem services (Marshall et al., 2018; Shanafield et al., 2020). Artificially intermittent rivers are likely to differ ecologically from natural IRES, and these differences are relevant to effective management of these systems.

River drying and the Anthropocene

Drying is a fundamental hydrological process that structures river ecosystems (Steffen, Grinevald, Crutzen, & McNeill, 2011); its magnitude and frequency is only increasing across the globe in response to climate change and greater human water extraction (Datry et al., 2014; Dhungel, Tarboton, Jin, & Hawkins, 2016). Dry river length has increased in different regions due to the combined effects of drought, surface water extraction, and groundwater pumping (Allen et al., 2019; Perkin et al., 2017). Temperatures will increase, leading to increased evapotranspiration and pushing systems closer or beyond the balance where water losses to the atmosphere exceed inputs. Some areas will become wetter and others drier under future climate scenarios, but increased climate variability is universally predicted to be widespread. The increased probability of dry periods (seasonal or multi-year droughts) elevates the probability of river drying.

Our review of 18 contemporary conceptual models of river ecosystems points to the fundamental importance of hydrology in structuring stream ecosystems, yet highlights that drying has rarely been explicitly considered. Given that IRES are ubiquitous and becoming more common in this era of rapid environmental change, we argue that an expanded ecohydrological perspective for rivers is urgently needed. As IRES comprise a significant component of the continuum of lotic waters, a more inclusive framework that explicitly incorporates such habitats would better represent the true range of natural and artificial river

ecosystems. This new framework will facilitate adaptive management and protection of all rivers rather than just those that continuously flow.

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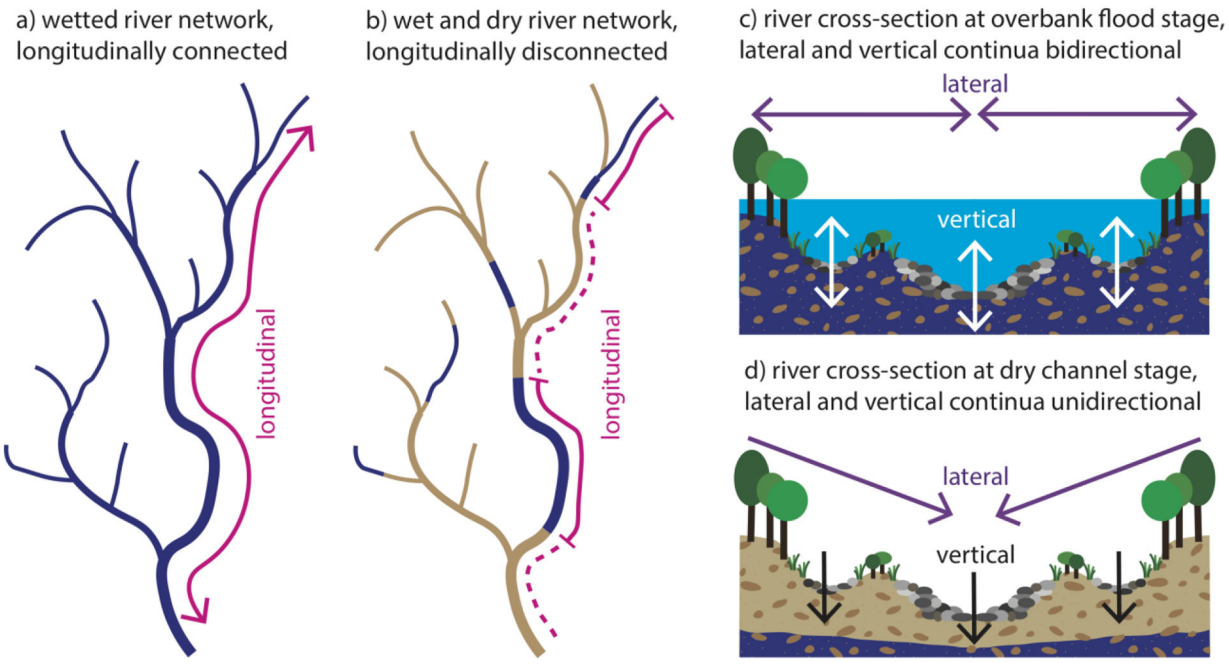

Figure 1.

Longitudinal, lateral, and vertical continua in rivers. River conceptual models have largely focused on flow phases when rivers are longitudinally connected (a), and when lateral and vertical continua are bidirectional (c). IRES have dry phases that lead to longitudinal disconnections (b) and unidirectional lateral and vertical continua (d). In b, surface water is present in blue reaches and absent in brown reaches (channel is dry). In c and d, blue vs. brown soil/sediments indicate saturated vs. unsaturated.

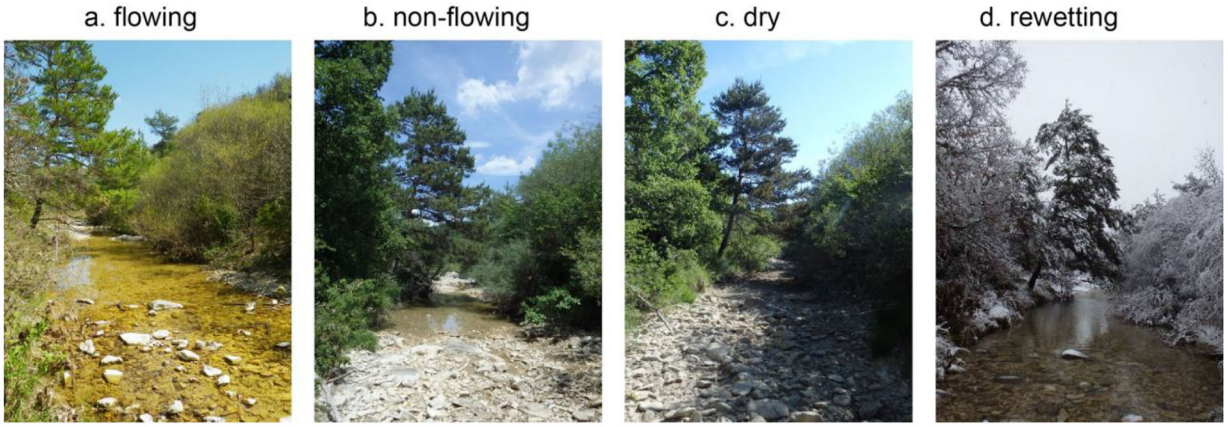

Figure 2.

Alternating flowing (a), non-flowing (b), dry (c), and rewetting phases (d) in an intermittent river (Calavon River, France). Photo credits: Bertrand Launay.

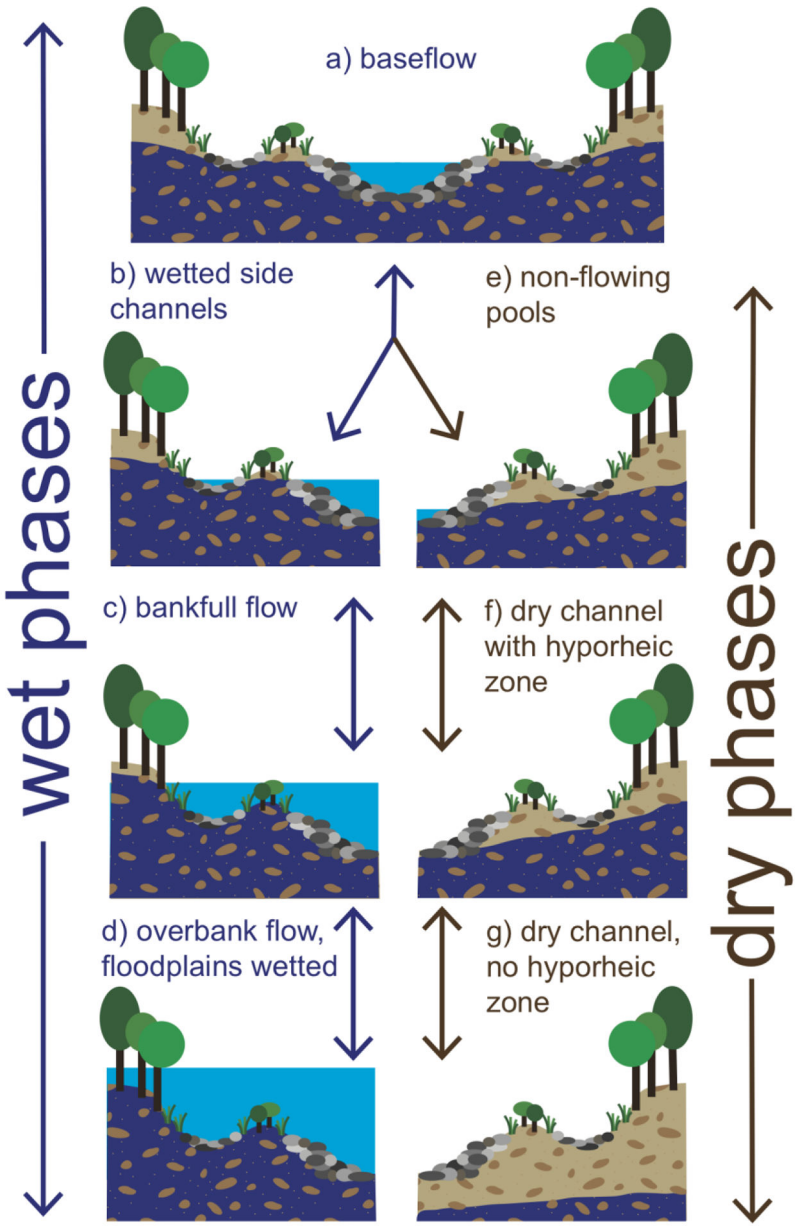

Figure 3.

Temporal variation in flow phases in rivers. River conceptual models have largely focused on the flowing “wet phases” between baseflow and overbank flows (panels a-f). IRES have non-flowing dry phases (panels e-g) that are also important in structuring river ecosystems. Blue vs. brown soil/sediments indicate saturated vs. unsaturated.

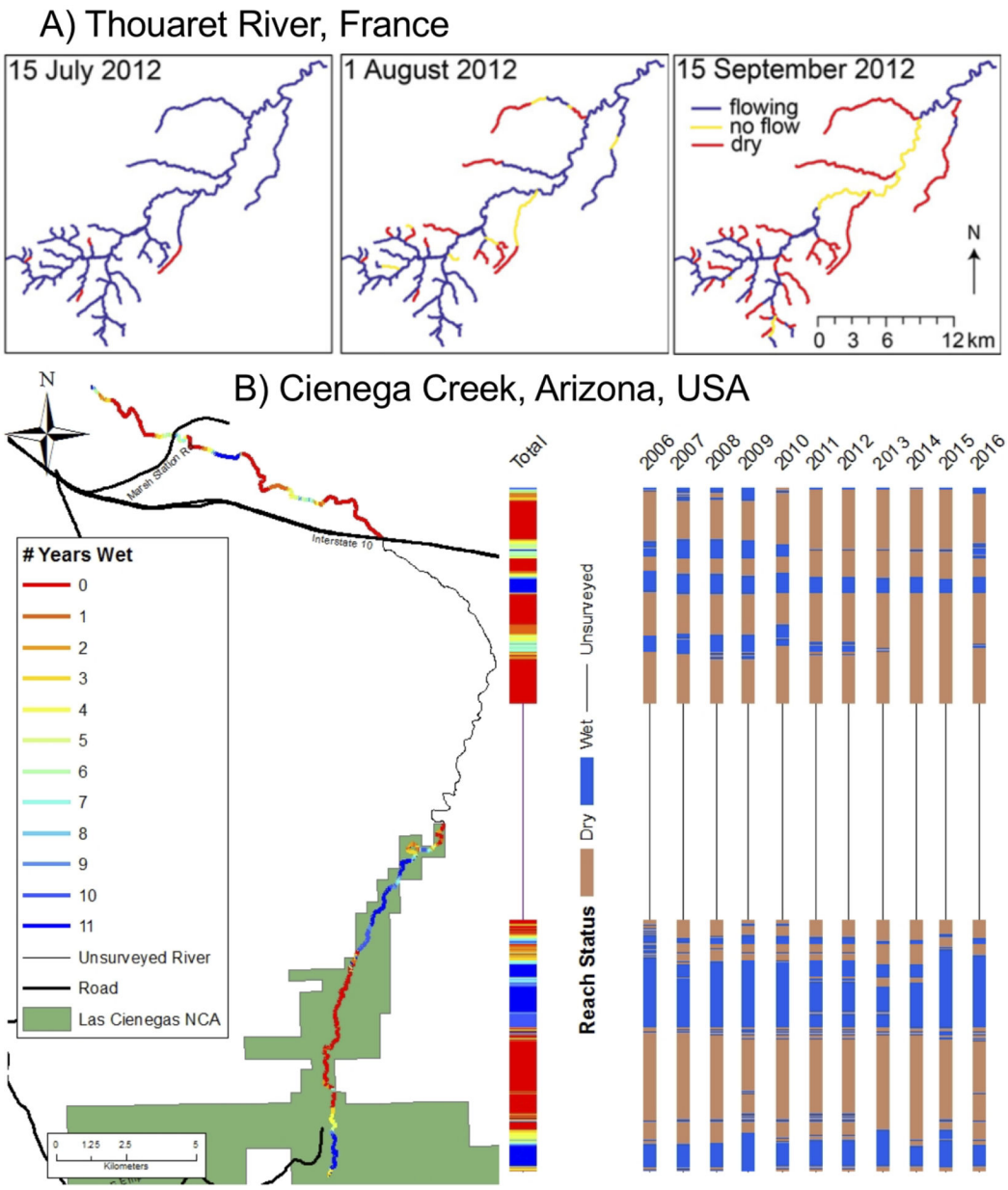

Figure 4.

Temporal dynamism in spatial drying patterns in IRES networks. A) Within-year variation in the Thouaret River, France, during the summer of 2012. Modified from (Datry *et al.* 2016). B) Between-year variation in Cienega Creek, Arizona, USA, measured annually during the dry season from 2006–2016. Modified from (Allen *et al.* 2019).

Table 1.

Summary table of the 18 river conceptual models that we reviewed. We classified models into categories by their focus on one or more of the 4-dimensional hydrologic continua (longitudinal, lateral, vertical, or temporal) or on spatial processes and patterns. We reviewed models for their relevance to IRES: only 3 were directly relevant, the remaining 15 were either indirectly relevant or were not relevant.

Name	Category	IRES Relevance	Citation
River Continuum Concept	Longitudinal, Lateral, Spatial	No	Vannote *et al.* (1980)
Serial Discontinuity Concept	Longitudinal	No	Stanford and Ward (1993)
Flood Pulse Concept	Lateral	Indirect	Junk *et al.* (1989)
4-D Nature of Lotic Ecosystems	Longitudinal, Lateral, Vertical, Temporal	No	Ward (1989)
Hyporheic Corridor Concept	Vertical	Yes	Stanford and Ward (1993)
Riverine Productivity Model	Spatial	No	Thorp and Delong (1994)
Natural Flow Regime	Temporal	Indirect	Poff *et al.* (1997)
Telescoping Ecosystem Model	Longitudinal, Lateral	Yes	Fisher *et al.* (1998)
Process Domains	Spatial	No	Montgomery (1999)
Flow Pulse Concept	Lateral	Indirect	Tockner *et al.* (2000)
Fluvial Landscape Ecology	Spatial	No	Poole (2002)
Network Dynamics Hypothesis	Spatial	No	Benda *et al.* (2004)
Riverine Ecosystem Synthesis	Spatial	No	Thorp *et al.* (2008)
Multiple Roles of Water	Spatial	Yes	Sponseller *et al.* (2013)
River Wave Concept	Longitudinal, Lateral, Temporal	No	Humphries *et al.* (2014)
Natural Sediment Regime	Temporal	Indirect	Wohl *et al.* (2015)
Stream Biome Gradient Concept/ Freshwater Biome Gradient Framework	Spatial	Indirect	Dodds *et al.* (2015, 2019)
Pulse Shunt Concept	Longitudinal, Temporal, Spatial	No	Raymond *et al.* (2016)