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

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Running head. River ecosystem models and non-perennial rivers

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Abstract

Commentato [U1]: My suggested changes still keep the words <250

Conceptual models underpin river ecosystem research. However, current models focus on perennially flowing rivers~~, those that always flow~~, and few explicitly address characteristics such as flow cessation and drying. The applicability of existing conceptual models to non-perennial rivers that cease to flow and/or dry (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 ~~often~~ unidirectional for much of the time, from terrestrial-to-aquatic only. Vertical connectivity between surface and sub-surface water occurs bidirectionally and is temporally consistent in perennial rivers. However,~~, but~~ 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.

Commentato [U2]: Needed? If so, surely when a river dries, it ceases to flow…

MAIN TEXT.

Introduction

Conceptual models are ~~the foundation of~~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 et al., 2014). IRES are ecologically and hydrologically distinct from perennial rivers (Datry et al., 2017). So, are our existing riverine conceptual models applicable to IRES?

Commentato [U3]: This amendment removes the insistence of a single foundation of ecology and doesn't jar with the start of the next para

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 ~~foundation~~ body of IRES ~~ecology~~ research now exists (Datry et al., 2017), guided by conceptual work on IRES ecology (Datry et al., 2014; Stanley et al., 1997) and hydrology (Costigan et al., 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.

River ecosystem conceptual models often guide river ecosystem management. If they do not accurately depict a substantial fraction of the river network, then management and policy decisions could irreversibly harm rivers. Tools developed from existing conceptual models, such as biomonitoring approaches to assess ecosystem integrity, are often ineffective in IRES

(Stubbington et al., 2017~~8~~). Similarly, while the Natural Flow Regime conceptual framework (Poff et al., 1997) promoted the implementation of environmental flows in river management (Richter & Thomas, 2007), its applicability in IRES is still uncertain (Acreman et al., 2014). River mismanagement examples 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 et al., 2018; Koundouri et al., 2017), and therefore are crucial waterbodies in need of effective conservation and management. Finally, environmental policies are being redefined in the US and elsewhere to specifically exclude many IRES as waterways warranting legal protection (Marshall et al. 2018) ~~(Thibault Datry et al., 2018; Koundouri et al., 2017)~~. 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.

Commentato [U4]: Check my changes here but I think that some of the cited references were unsuitable for their associated statements

Our paper reviews existing river ecosystem conceptual models to critically evaluate their application 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 applies~~d~~ 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 ~~that~~ used to guide current and future research and ~~underpin present-day~~ management of river ecosystems.

River drying, flow cessation, and the four dimensions of rivers 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 ~~or ponds~~ of standing water, or surface-disconnected reaches that still flow (Figure 2). These disconnected pools and reaches are longitudinally isolated by dry reaches~~ upstream and/or downstream~~, 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 et al., 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 ~~(shredders vs. collectors vs. filterers, etc.;~~ (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, des~~s~~iccation resistance) may be far more important than ~~being able to leverage~~access to a specific food source (Aspin et al., 2019; Bogan, 2017).

Commentato [U5]: OK?

Of these six 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 IRES (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 et al., 2004).

Lateral dimension. Six conceptual models emphasize lateral connectivity as a key factor ~~that~~ structuring river~~s~~ 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 ~~movement~~ transfer from channel to floodplains rarely occurs (Steward et al., 2017). The duration of the dry period affects these lateral connections, controlling the

Commentato [U6]: I think this word may be more precise here but it's just a minor style comment decomposition rates of leaf litter once the river rewets (Datry 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 et al., 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 ~~that may be available~~ in the hyporheic zone (DelVecchia et al., 2016; Jones et al., 1995).

Commentato [U7]: Seems redundant

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 et al., 2018). Drying rivers can be an important source of evaporative water vapor, and emissions from dry channels can be higher than emissions through upland soils (Scanlon et al., 2006). 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 et al., 2016), although hyporheic refuges can be less important in other systems when flow is reduced but surface water still remains (James et al., 2008).

The Hyporheic Corridor Concept (Stanford & Ward, 1993) is one of the few riverine conceptual models that mention IRES. Here, Stanford & 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~~e~~ 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 & 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 ~~stagnant,~~ 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 non-perennial 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 et al., 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 propose 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: 1) as a resource and habitat in smaller rivers, 2) as a vector for connectivity, and 3) as an agent of geomorphic change and disturbance in larger rivers. Finally, the Stream Biome Gradient Concept (Dodds et al., 2015) and the ~~following~~ 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, non-flowing, 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 non-perennial 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; non-perennial sections can be anywhere. Conversely, in humid areas non-perennial 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 ~~then ~~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 of these 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, there is an imperative 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 usually 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 processed continuously as they move downstream. During low-flow phases, downstream transport is primarily restricted to flowing reaches or

subsurface flows. During zero-flow phases, isolated stagnant pools behave more like lentic systems, and dry reaches become terrestrial and can be used by some organisms for migration (Bogan & Boersma, 2012; Sánchez- Montoya et al., 2016). These transitions between phases underscore the need for collaboration among lotic, lentic, and terrestrial ecologists to more fully understand processes governing IRES (Datry et al., 2014).

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

5. Spatial patterns in hydrologic processes create heterogeneity in abiotic conditions throughout a river network, in turn creating variability in riverine biotic processes. As drying governs hydrologic heterogeneity in space and time in IRES, drying should be specifically considered in river science and management.

6. IRES are threatened. 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). They frequently serve as sites for ~~trash~~ dumping trash and dredging sediment ~~dredging~~, as conduits for waste water, and suffer severe hydrological alterations through artificial dewatering or augmented flows (Chiu et al., 2017). 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 in this era of rapid environmental change (Steffen et al., 2011). River drying is increasing across the globe through climate change and increased human water extraction (Datry et al., 2014). 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 predicted to be widespread. The increased probability of dry periods (seasonal or multi-year droughts) increases the probability of river drying. 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). Moreover, IRES are among the types of freshwater systems most likely to experience hydrological changes due to climate change (Dhungel et al., 2016).

Our review of 18 contemporary conceptual models of river ecosystems shows that hydrological processes are fundamental in structuring stream ecosystems, but that drying has rarely been considered. Given that IRES are already ubiquitous and becoming more common due to global change, we argue that an expanded ecohydrological perspective for rivers is urgently needed to guide current and future river research and management. As IRES comprise a significant component of the continuum of lotic waters, ~~and~~ a 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, and will acknowledge flow cessation and drying as ~~a~~ crucial aspects of most flow regimes.

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References

Commentato [U10]: Need to follow journal style in whether article titles are in lower case (e.g. as in Acreman et al.) or whether upper case is used for many words (e.g. as in Benda et al.).

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Tables

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 four dimensions of rivers (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 & 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 & Ward (1993)
Riverine Productivity Model	Spatial	No	Thorp & 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)

Figures

Figure 1. Longitudinal, lateral, and vertical dimensions in rivers. River conceptual models have largely focused on flow phases when rivers are longitudinally connected (a), and when lateral and vertical dimensions are bidirectional (c). IRES have dry phases that lead to longitudinal disconnections (b) and unidirectional lateral and vertical dimensions (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, (in the ~~Natinoal~~ National Conservation Area, NCA, and downstream) measured annually during the dry season from 2006-2016. Modified from ~~(~~Allen et al.~~,~~ (2019).