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River ecosystem conceptual models and non-perennial rivers: A critical review 1

Daniel C Allen, T. Datry, Kate Boersma, Michael T Bogan, Andrew J. Boulton, Daniel Bruno, Michelle H Busch, Katie H Costigan, Walter K. Dodds, Ken M Fritz, et al.

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1 **Title.** River ecosystem conceptual models and non-perennial rivers: A critical review

2 **Running head.** River ecosystem models and non-perennial rivers

3 **Lead authors** (in alphabetical order, both lead authors contributed equally to the conceptual
4 development of the manuscript, the review of the conceptual models, and co-wrote the initial
5 drafts of the manuscript):

6 Daniel C. Allen, Department of Biology, University of Oklahoma, Norman, OK, 73019,

7 dcallen@ou.edu, Orcid: 0000-0002-0451-0564

8 Thibault Datry, INRAE, UR-RIVERLY, Centre de Lyon-Villeurbanne, 69626 Villeurbanne

9 CEDEX, France, thibault.datry@inrae.fr ORCID: 0000-0003-1390-6736

10

11 **Co-authors** (in alphabetical order, all co-authors contributed to the review of the conceptual
12 models and provided edits/comments to the manuscript):

13 *Kate S. Boersma, Department of Biology, University of San Diego, San Diego, CA 92110 USA,*
14 *kateboersma@sandiego.edu, Orcid: 0000-0002-0707-3283*

15

16 *Michael T. Bogan, School of Natural Resources and the Environment, University of Arizona,*
17 *Tucson, AZ 85716, USA, mbogan@email.arizona.edu, Orcid: 0000-0002-8150-8476*

18

19 *Andrew J. Boulton, School of Environmental and Rural Science, University of New England,*
20 *Armidale, NSW 2350, Australia, aboulton@une.edu.au. Orcid: 0000-0001-7393-2800*

21

22 *Daniel Bruno, Department of Biodiversity and Restoration, Pyrenean Institute of Ecology (IPE-*
23 *CSIC), Zaragoza, Spain, dbruno@ipe.csic.es, Orcid: 0000-0003-3976-9354*

24

25 *Michelle H. Busch, Department of Biology, University of Oklahoma, Norman, OK 73072 USA,*
26 *buschmh@ou.edu, Orcid: 0000-0003-4536-3000*

27

28 *Katie H. Costigan, School of Geosciences, University of Louisiana, Lafayette, LA 70503 USA,*
29 *costigan@louisiana.edu, Orcid: 0000-0002-5706-7439*

30

31 *Walter K. Dodds, Division of Biology, Kansas State University, Manhattan, KS 66502 USA,*
32 *wkdodds@ksu.edu, Orcid 0000-0002-6666-8930*

33

34 *Ken M. Fritz, Office of Research and Development, U.S. Environmental Protection Agency,*
35 *Cincinnati, OH 45268 USA, fritz.ken@epa.gov, Orcid 0000-0002-3831-2531*

36

37 Sarah E. Godsey, Department of Geosciences, Idaho State University, Pocatello, ID 83209
38 USA, godsey@isu.edu, Orcid: 0000-0001-6529-7886
39
40 Jeremy B. Jones, Institute of Arctic Biology and Department of Biology and Wildlife, University
41 of Alaska Fairbanks, Fairbanks, AK 99775 USA. jay.jones@alaska.edu, Orcid: 0000-0003-3540-
42 1392
43
44 Tatiana Kaletova, Department of Water Resources and Environmental Engineering, Slovak
45 University of Agriculture in Nitra, 94976 Nitra, Slovakia. tatiana.kaletova@uniag.sk, Orcid: 0000-
46 0003-2695-1448
47
48 Stephanie K. Kampf, Department of Ecosystem Science and Sustainability, Colorado State
49 University, Fort Collins, CO 80523-1476 USA. stephanie.kampf@colostate.edu, Orcid: 0000-
50 0001-8991-2679
51
52 Meryl C. Mims, Department of Biological Sciences, Virginia Tech, Blacksburg, VA 24060 USA.
53 mims@vt.edu, Orcid: 0000-0003-0570-988X
54
55 Thomas M. Neeson, Department of Geography and Environmental Sustainability, University of
56 Oklahoma, Norman OK 73019 USA. neeson@ou.edu Orcid: 0000-0001-6758-0511
57
58 Julian D. Olden, School of Aquatic and Fishery Sciences, University of Washington, Seattle,
59 WA, 98105, USA, olden@uw.edu Orcid: 0000-0003-2143-1187
60
61 Amandine V. Pastor, CE3C, Centre for Ecology, Evolution and Environmental Changes,
62 Faculdade de Ciências da Universidade de Lisboa, 1749-016 Lisboa, Portugal,
63 avpastor@fc.ul.pt, Orcid: 0000-0003-4526-7705
64
65 N. LeRoy Poff, Department of Biology, Colorado State University, Fort Collins, CO 80523, USA,
66 and Institute for Applied Ecology, University of Canberra, Canberra ACT 2617, Australia,
67 poff@lamar.colostate.edu, Orcid: 0000-0002-1390-8742
68
69 Benjamin L. Ruddell, School of Informatics Computing and Cyber Systems, Northern Arizona
70 University, Flagstaff, AZ 86004, USA, benjamin.ruddell@nau.edu Orcid: 0000-0003-2967-9339
71
72 Albert Ruhi, Department of Environmental Science, Policy, and Management, University of
73 California, Berkeley, Berkeley, CA 94720, USA, albert.ruhi@berkeley.edu
74
75 Gabriel Singer, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany,
76 gabriel.singer@igb-berlin.de, Orcid: 0000-0002-7389-9788
77
78 Paolo Veza, Department of Environment, Land and Infrastructure Engineering, Politecnico di
79 Torino, Italy, paolo.veza@polito.it, Orcid: 0000-0002-6784-8036
80
81 Adam S. Ward, O'Neill School of Public and Environmental Affairs, Indiana University,
82 Bloomington, IN, 47405, USA, adamward@indiana.edu Orcid: 0000-0002-6376-0061

83
84
85
86

Margaret Zimmer, Earth and Planetary Sciences, University of California, Santa Cruz, CA, 95064, USA, margaret.zimmer@ucsc.edu Orcid: 0000-0001-8287-1923

87 **Abstract**

88 Conceptual models underpin river ecosystem research. However, current models focus
89 on perennial rivers, those that always flow. Few explicitly address characteristics such as flow
90 cessation and drying, which are becoming more prevalent in the Anthropocene. The applicability
91 existing conceptual models to non-perennial rivers that cease to flow and/or dry (intermittent
92 rivers and ephemeral streams, IRES) has not been evaluated. We reviewed 18 models, finding
93 that they collectively describe main drivers of biogeochemical and ecological patterns and
94 processes longitudinally (upstream-downstream), laterally (channel-riparian-floodplain),
95 vertically (surface water-groundwater), and temporally across local and landscape scales.
96 However, we also found that most of these models do not account for how different these
97 patterns and processes are for IRES. We suggest ways in which existing models could be
98 modified to accommodate drying as a fundamental process that can alter these patterns and
99 processes across spatial and temporal dimensions in streams. This perspective is needed to
100 support river science and management in our era of rapid global change, including increasing
101 duration, frequency, and occurrence of drying.

102

103 **MAIN TEXT.**

104 **Introduction**

105 Conceptual models underpin ecology. They identify ecological universalities across
106 diverse taxonomies and geographies (Lawton, 1999). River ecosystem conceptual models have
107 historically focused on research from continuously flowing (“perennial”) rivers to advance our
108 understanding of how hydrologic and geomorphologic processes structure river ecosystems.
109 Intermittent rivers and ephemeral streams (hereafter, “IRES”) do not continuously flow, and
110 occur in all climates and biomes. They are extremely common in headwaters (Benstead &

111 Leigh, 2012), in regions with lower runoff (Dodds, 1997), and comprise at least half of global
112 river length (Datry et al., 2014). Moreover, rivers that freeze show some ecological and
113 hydrological parallels to IRES (Tolonen et al., 2019). IRES are ecologically and hydrologically
114 distinct from perennial rivers (Datry et al., 2017). So, are our existing riverine conceptual models
115 applicable to IRES?

116 Hydrological processes are foundational to river ecosystem conceptual models. Because
117 hydrological processes in IRES are marked by flow-cessation, drying, and rewetting phases,
118 conceptual models that embrace these processes would best represent IRES. A solid
119 foundation of IRES ecology research now exists (Datry et al., 2017), guided by conceptual work
120 on IRES ecology (Datry et al., 2014; Stanley et al., 1997) and hydrology (Costigan et al., 2016;
121 Godsey & Kirchner, 2014). Thus, we are now well positioned to critically review river ecosystem
122 models and investigate how well IRES are represented in current river ecosystem conceptual
123 models.

124 River ecosystem conceptual models often guide river ecosystem management. If they
125 do not accurately depict a substantial fraction of the river network, management and policy
126 decisions could irreversibly harm rivers. River mismanagement examples are becoming
127 increasingly common as extreme droughts and drying events increase (Tonkin et al., 2019),
128 challenging water management strategies developed for perennial waterways (Shanafield et al.,
129 2020). Tools developed from existing conceptual models, such as biomonitoring approaches to
130 assess ecosystem integrity, are often ineffective in IRES (Stubbington et al., 2018). Similarly,
131 while the Natural Flow Regime conceptual framework (Poff et al., 1997) promoted the
132 implementation of environmental flows in river management (Richter & Thomas, 2007), its
133 applicability in IRES is still uncertain (Acreman et al., 2014). Finally, environmental policies are
134 being redefined in the US and elsewhere to specifically exclude many IRES as waterways
135 warranting legal protection (Marshall et al., 2018). As IRES will likely become more dominant in

136 the Anthropocene (Datry et al., 2014), understanding whether they are accurately described by
137 the conceptual models that underpin their management and legal protection is crucial.

138 Our paper reviews existing river ecosystem conceptual models to critically evaluate their
139 application to advance the science and management of IRES. We reviewed 18 influential
140 conceptual frameworks published between 1980 and 2016, classifying them into two broad
141 categories. The first category focuses on local- or reach-scale processes along the four major
142 hydrologic continua identified by the “Four-Dimensional Nature of Lotic Ecosystems” conceptual
143 framework by (Ward, 1989): *longitudinal* (upstream-downstream), *lateral* (channel-floodplain),
144 *vertical* (surface-subsurface), and *temporal* (variation over time). The second category
145 considers river networks at landscape and larger spatial scales, concentrating on the spatial
146 processes critical to the functioning of riverine ecosystems. We then assessed how well each of
147 these frameworks applied to IRES, and how IRES might challenge central assumptions of each
148 framework. Our findings lay the groundwork for a new perspective that includes river drying as a
149 fundamental component of riverine conceptual models that underpin present-day management
150 of river ecosystems.

151

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

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

159 Longitudinal continuum models focus explicitly on perennial rivers, but IRES challenge
160 the central assumption of continuous upstream-downstream connectivity. IRES are
161 longitudinally discontinuous at the surface when they dry (Figure 1). During dry periods, many

162 IRES become isolated pools or ponds of standing water, or surface-disconnected reaches that
163 still flow (Figure 2). These disconnected pools and reaches are longitudinally isolated by dry
164 reaches upstream and/or downstream, preventing the downstream transport of materials in
165 surface waters (Pringle, 2001). Alternating expansion and contraction of wet stream reaches
166 over time drives nutrient and organic matter dynamics in IRES (von Schiller et al., 2017) and
167 controls population connectivity of riverine organisms (Allen et al., 2019).

168 Of these six models, only the Telescoping Ecosystem Model (Fisher et al., 1998)
169 addresses longitudinal expansion and contraction in a manner directly relevant for IRES,
170 probably because it draws heavily on research conducted in an IRES (Sycamore Creek,
171 Arizona, USA). The framework proposes that streams expand and contract longitudinally and
172 laterally from the river channel like the concentric cylinders of a telescope, constituting a key
173 physical process that controls nutrient dynamics in rivers (Fisher et al., 1998). This model has
174 not yet been applied to other IRES beyond this system, and a more extensive testing across a
175 range of systems would help in understanding its generality. Finally, we note that the River
176 Continuum Concept has been modified to accommodate IRES by some researchers (e.g.
177 grassland streams, (Dodds et al., 2004).

178 *Lateral continuum.* Six conceptual models emphasize lateral connectivity as a key factor
179 that structuring rivers ecosystems (Table 1). The expansion-contraction cycles of a river along
180 its lateral continua allow for bidirectional exchanges of organisms and materials between the
181 main and side channels, floodplains, and riparian zones. Below bankfull conditions, lateral river
182 expansion connects larger main channels with smaller side channels as flow increases (Flow
183 Pulse Concept, (Junk et al., 1989), which can both create river habitat (e.g. providing multiple
184 flow-paths through the river corridor) and homogenize it (e.g. water temperatures and nutrient
185 concentrations). During overbank flows, lateral river expansion connects river channels with
186 their floodplains (Flood Pulse Concept, (Tockner et al., 2000). Mobile riverine organisms can
187 then colonize inundated floodplains from the main channels, where they forage, spawn, and

188 shelter from high water velocities of the main channel during a flood. The inundated floodplain
189 becomes a source of nutrients for riverine biota that receive receding floodplain waters as flow
190 returns to baseflow conditions.

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

202 Despite IRES not conforming to our traditional understanding of the lateral continuum in
203 rivers, aspects of these six models are indirectly relevant. For example, IRES retract more than
204 perennial rivers along the lateral continuum, often to the point where no surface water remains.
205 The Flood Pulse Concept defines the floodplain as an “Aquatic-Terrestrial Transition Zone
206 (ATTZ)”, where the expansion-contraction cycles depend on floods and the floodplain has
207 pronounced aquatic and terrestrial phases. Aquatic and terrestrial organisms may require
208 anatomical, morphological, physiological, and/or behavioral adaptations to colonize and persist
209 in the ATTZ (Junk et al., 1989). Thus, it is logical to extend the ATTZ from the floodplain to an
210 intermittent river channel where aquatic biota have evolved physiological and behavioral
211 adaptations that allow them to persist (Stubbington et al., 2017).

212 *Vertical continuum.* Two river ecosystem conceptual models focus on the vertical
213 continuum (Table 1). The vertical exchange of water, solutes, and organisms, can occur via

214 downwelling of surface water into the hyporheic zone (the saturated subsurface zone beneath
215 the river channel) and upwelling of subsurface water into the river channel. The vertical
216 continuum is crucial for riverine biogeochemical cycles and organisms that link hyporheic and
217 benthic (riverbed) ecosystems. In most rivers, surface waters are mixed, oxygenated, and well-
218 lit, whereas the hyporheic zone is transport-limited, oxygen-deficient, and light-limited.

219 Hyporheic exchange of surface water- and groundwater-delivered material between these two
220 physically and chemically distinct environments promotes spatial heterogeneity in
221 biogeochemical transformations (Boano et al., 2014). Hyporheic exchange can also include
222 invertebrates, particularly those that can tolerate low dissolved oxygen conditions and feed on
223 ancient and methane-derived carbon sources in the hyporheic zone (DeIvecchia et al., 2016).

224 Vertical continua and surface-subsurface exchanges are important in IRES, but in a
225 different way (Figure 1). In perennial rivers, hyporheic exchange is considered to occur
226 consistently through time (Boano et al., 2014). By contrast, hyporheic exchange in IRES is not
227 always continuous and may be unidirectional during drying (surface-to-subsurface only) and
228 rewetting (subsurface-to-surface only) phases (Zimmer & McGlynn, 2017). Rewetting of some
229 IRES is driven completely by influxes of groundwater, delivering groundwater-derived material
230 and solutes into the river channel and causing rapid biogeochemical transformations (von
231 Schiller et al., 2017). Vertical exchanges of gases can also be important, and rewetting events
232 can initiate significant carbon dioxide effluxes from rivers to the atmosphere (Datry et al., 2018).
233 Drying rivers can be an important source of evaporative water vapor, and emissions from dry
234 channels can be higher than emissions through upland soils (Scanlon et al., 2006). Additionally,
235 the hyporheic zone can be an important refuge for benthic invertebrates during dry phases.
236 Recolonization from the hyporheic zone can be more important than aerial oviposition or larval
237 drift in structuring benthic community assembly after rewetting (Vander Vorste et al., 2016),
238 though hyporheic refuges can be less important in other systems when flow is reduced but
239 surface water still remains (James et al., 2008).

240 The Hyporheic Corridor Concept is one of the few riverine conceptual models that
241 mention IRES. (Stanford & Ward, 1993) discuss “ephemeral springbrooks” that emerge during
242 spring runoff periods, usually in abandoned meander channels. Flow in springbrooks decreases
243 throughout the summer until surface water exists as pools connected by interstitial flow or the
244 channels dry completely. Connectivity along the vertical continuum was posited to be critical in
245 these dynamic systems (Stanford & Ward, 1993), a prediction that has been supported in the
246 subsequent decades of research on IRES (Stubbington et al., 2017; Vander Vorste et al., 2016;
247 von Schiller et al., 2017).

248 *Temporal continuum.* Rivers are temporally dynamic as flow can vary greatly over time.
249 Five river conceptual models focus on the temporal continuum (Table 1), but each considers it
250 in a differently. (Ward, 1989) focuses on how organisms respond to temporal flow disturbances,
251 both behaviorally and evolutionarily. (Poff et al., 1997) describe the flow regime as “the
252 characteristic pattern of a river’s flow quantity, timing, and variability” using a suite of flow
253 regime characteristics, such as flow magnitude, frequency, duration, timing, and rate of change.
254 (Wohl et al., 2015) extends this perspective to incorporate sediment input, transport, and
255 storage dynamics. The Pulse Shunt Concept (Raymond et al., 2016) highlights how low-
256 frequency, high-magnitude flow events are disproportionately important for dissolved organic
257 matter dynamics throughout entire river networks. The River Wave Concept (Humphries et al.,
258 2014) integrates multiple river ecosystem conceptual frameworks according to temporal
259 variability in flow phase. It posits that the Flood-Pulse Concept (Junk et al., 1989) best explains
260 river ecosystem dynamics during peak flows, the River Continuum Concept is most relevant
261 during moderate flows (Vannote et al., 1980), and the Riverine Productivity Model (Thorp &
262 Delong, 1994) applies best during baseflows.

263 The temporal continuum and its associated variation in flow phase are highly relevant in
264 IRES (Figures 2 & 3). However, previous conceptual frameworks consider only flow variation
265 from baseflow at the lowest flow phase to overbank flood at the highest phase (Figure 3A-F).

266 Flow phases between baseflow and complete drying occur in IRES (Figure 3E-G), but are not
267 discussed in previous frameworks (Costigan et al., 2016). As baseflow recedes in IRES, surface
268 flow stops, and stagnant, isolated pools may form. Surface water can disappear, but hyporheic
269 water remains; as drying continues, both surface and hyporheic water are lost. Each of these
270 flow phases is hydrologically and ecologically distinct, with different implications for hydrologic
271 and sediment transport, biota, and biogeochemical cycles (Costigan et al., 2016; Stubbington et
272 al., 2017; von Schiller et al., 2017). Importantly, variation in the duration, intensity, and
273 frequency of these different phases over time, and spatially throughout a river network, have
274 repercussions for biogeochemical and ecological processes. Therefore, we need to extend the
275 range of possible flow phases when considering IRES.

276 The Natural Flow and Sediment Regimes (Poff et al., 1997; Wohl et al., 2015) are
277 indirectly relevant to IRES. They center on temporal variability in flow and sediment dynamics in
278 riverine corridors and how these regimes have been modified by human activities. The Natural
279 Flow Regime notes that temporal variation in flow within single rivers can produce habitats that
280 range from free-flowing, through standing to no water, and IRES are briefly mentioned when
281 discussing low-flow conditions (Poff et al., 1997). Similarly, sediment regimes are the primary
282 drivers of valley-floor processes in non-perennial and perennial rivers; however, some
283 fundamental distinctions exist between them. In IRES, sediment flux and channel-bed grain size
284 distributions from upstream to downstream can differ substantially from those in perennial
285 streams (Jaeger et al., 2017). Thus, IRES can fit into the Natural Flow and Sediment Regime
286 frameworks with some further adjustments.

287

288 **River drying and spatial processes and patterns**

289 Nine river conceptual models focus on spatial processes and/or patterns, seeking to
290 explain how river ecosystems vary across landscape and larger scales (Table 1). The River
291 Continuum Concept (Vannote et al., 1980) and Riverine Productivity Model (Thorp & Delong,

292 1994) both propose that energy sources vary predictably according to river size and position
293 within the broader river network. In contrast, the Process Domains concept (Montgomery,
294 1999), Fluvial Landscape Ecology framework (Poole, 2002), Network Dynamics Hypothesis
295 (Benda et al., 2004) and the Riverine Ecosystem Synthesis (Thorp et al., 2008) emphasize the
296 patchy nature of the different stream habitat types that exist throughout a river network, as
297 hydrologic processes vary across space due to differences in watershed size, topography, and
298 geophysical characteristics. The Multiple Roles of Water framework (Sponseller et al., 2013)
299 describes water having three different ecological roles based on a river's position within the
300 broader river network: 1) as a resource and habitat in smaller rivers, 2) as a vector for
301 connectivity, and 3) as an agent of geomorphic change and disturbance in larger rivers. Finally,
302 the Stream Biome Gradient Concept (Dodds et al., 2015) and the following Freshwater Biome
303 Gradient framework (Dodds et al., 2019) present a framework for how river ecosystems should
304 vary geographically, across continental and global scales and across climate gradients and
305 biomes. These models specifically consider large geographic areas where intermittent or
306 ephemeral flow should occur with emphasis on the balance between potential and actual
307 evapotranspiration.

308 River drying adds a temporal dimension to spatial variation in river ecosystem habitats.
309 Drying is often a major driver of spatial heterogeneity in river networks (Figure 4). Flowing, non-
310 flowing, and dry reaches can exist anywhere throughout the network, occurring in headwaters,
311 tributaries, mainstems, and even river mouths. Moreover, (Costigan et al., 2016) suggest that
312 the typical locations of perennial and non-perennial sections in the river network may vary due
313 to differences in climate. In arid areas, perennial rivers are either very large mainstems that
314 drain wetter adjacent areas or small headwaters where perennial springs provide a constant
315 source of water; non-perennial sections can be anywhere. Conversely, in humid areas non-
316 perennial reaches are likely limited to headwaters, while downstream network reaches are
317 usually perennial (Costigan et al., 2016). Thus, the consideration of local drying regimes as

318 another hydrologic layer in the landscape would complement the spatial heterogeneity we
319 typically consider within river networks and across biomes.

320 Two conceptual models focusing on spatial processes and patterns in streams are
321 relevant for IRES. IRES are a focus of the Multiple Roles of Water framework which discusses
322 how variation in flow permanence generates three types of river habitat: a *pulse* domain where
323 water may flow for minutes to weeks, a *seasonal* domain where water may flow for weeks to
324 months, and then a *perennial* domain where water continuously flows (Sponseller et al., 2013).
325 In this framework, flood-associated disturbances and hydrologic exchange are key drivers of
326 river ecosystem dynamics only when flow is perennial. (Sponseller et al., 2013) also discuss
327 how IRES are more abundant in arid regions, echoing the discussion in the Stream Biome
328 Gradient Concept (Dodds et al., 2015). Indeed, these are two of the most recent of the 18
329 conceptual models, and were developed by authors where IRES are common.

330

331 **The need for a new ecohydrological perspective for river ecosystems**

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

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

- 343 1. Upstream and downstream hydrological connections along the longitudinal
344 continuum occur in all rivers, but are usually episodic in IRES. During high-flow
345 phases when the entire river network is flowing, the downstream transport of
346 water, solutes, and organic matter predominates, and these materials are
347 processed continuously as they move downstream. During low-flow phases,
348 downstream transport is primarily restricted to flowing reaches or subsurface
349 flows. During zero-flow phases, isolated stagnant pools behave more like lentic
350 systems, and dry reaches become terrestrial and can be used by some
351 organisms for migration (Bogan & Boersma, 2012; Sánchez-Montoya et al.,
352 2016). These transitions between phases underscore the need for collaboration
353 among lotic, lentic, and terrestrial ecologists to more fully understand processes
354 governing IRES (Datry *et al.* 2014).
- 355 2. Reciprocal linkages along the lateral continuum are essential to river
356 ecosystems, but this exchange may be more unidirectional in intermittent rivers.
357 While terrestrial-to-aquatic transfer of water, solutes, organic matter, and
358 organisms are always important, the magnitude and potential importance of
359 aquatic-to-terrestrial transfers decreases when the river is dry.
- 360 3. Except in bedrock rivers, connectivity along the vertical continuum is a
361 fundamental riverine process, where water, solutes, and organisms are
362 exchanged between the surface and the hyporheic zone. Again, this connectivity
363 can become unidirectional (surface-to-subsurface) as rivers dry, or limited if the
364 riverbed is entirely bedrock. Subsurface-to-surface connections are also
365 important in IRES, especially when hyporheic influxes to the surface are the
366 primary water delivery source during rewetting events. Often the hyporheic zone
367 is a vital refuge for aquatic organisms during dry periods.

- 368 4. Flow variation along the temporal continuum is pivotal because all natural rivers
369 are dynamic and vary in phase over time. However, IRES have greater flow
370 variation that includes zero flow, typically not included in river conceptual
371 frameworks. The frequency, duration, and timing of these zero flows are critical in
372 structuring riverine ecosystems, and must be considered in river research and
373 management.
- 374 5. Spatial patterns in hydrologic processes create heterogeneity in abiotic
375 conditions throughout a river network, in turn creating variability in riverine biotic
376 processes. As drying governs hydrologic heterogeneity in space and time in
377 IRES, drying should be specifically considered in river science and management.
- 378 6. IRES are threatened. They generally have less legal protection than perennial
379 rivers due to the social undervaluation of their ecological attributes and
380 ecosystem services (Marshall et al., 2018; Shanafield et al., 2020). They
381 frequently serve as sites for trash dumping and sediment dredging, as conduits
382 for waste water, and suffer severe hydrological alterations through artificial
383 dewatering or augmented flows (Chiu et al., 2017). Artificially intermittent rivers
384 are likely to differ ecologically from natural IRES, and these differences are
385 relevant to effective management of these systems.

386

387 **River drying and the Anthropocene**

388 Drying is a fundamental hydrological process that structures river ecosystems in this era
389 of rapid environmental change (Steffen et al., 2011). River drying is increasing across the globe
390 through climate change and increased human water extraction (Datry et al., 2014).

391 Temperatures will increase, leading to increased evapotranspiration and pushing systems
392 closer or beyond the balance where water losses to the atmosphere exceed inputs. Some areas
393 will become wetter and others drier under future climate scenarios, but increased climate

394 variability is predicted to be widespread. The increased probability of dry periods (seasonal or
395 multi-year droughts) increases the probability of river drying. Dry river length has increased in
396 different regions due to the combined effects of drought, surface water extraction, and
397 groundwater pumping (Allen et al., 2019; Perkin et al., 2017). And as mentioned previously
398 freezing has some ecohydrological parallels to drying, and we know that river freezing regimes
399 are being altered due to climate change as well (Tolonen et al., 2019; Yang et al., 2020).
400 Moreover, IRES are among the types of freshwater systems most likely to experience
401 hydrological changes due to climate change (Dhungel et al., 2016).

402 Our review of 18 contemporary conceptual models of river ecosystems shows that
403 hydrological processes are fundamental in structuring stream ecosystems, but that drying has
404 rarely been considered. Given that IRES are already ubiquitous and becoming more common
405 due to global change, we argue that an expanded ecohydrological perspective for rivers is
406 urgently needed to guide current and future river research and management. IRES comprise a
407 significant component of the continuum of lotic waters, and a framework that explicitly
408 incorporates such habitats would better represent the true range of natural and artificial river
409 ecosystems. This new framework will facilitate adaptive management and protection of all rivers
410 rather than just those that continuously flow, and acknowledge flow cessation drying as a crucial
411 aspect of most flow regimes.

412

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423

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616

617 **Tables**

618 Table 1. Summary table of the 18 river conceptual models that we reviewed. We classified
 619 models into categories by their focus on one or more of the 4-dimensional hydrologic continua
 620 (longitudinal, lateral, vertical, or temporal) or on spatial processes and patterns. We reviewed
 621 models for their relevance to IRES: only 3 were directly relevant, the remaining 15 were either
 622 indirectly relevant or were not relevant.

623

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

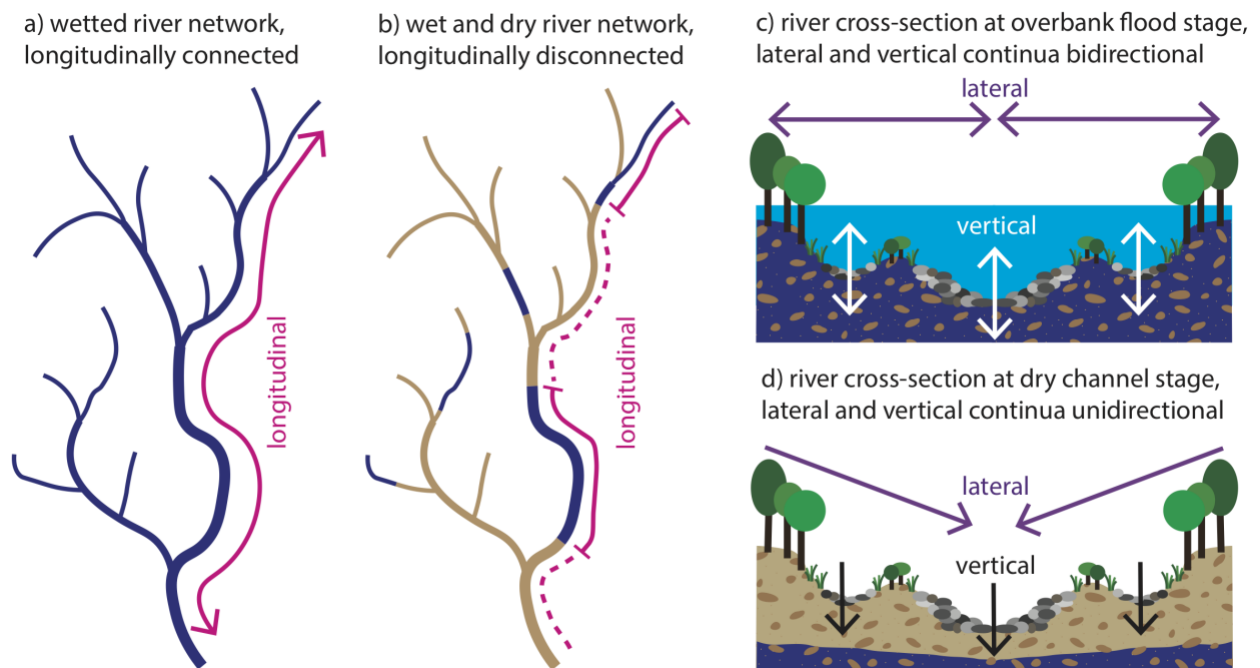
River Wave Concept	Longitudinal, Lateral, Temporal	No	Humphries et al., 2014
Natural Sediment Regime	Temporal	Indirect	Wohl et al., 2015
Stream Biome Gradient Concept/ Freshwater Biome Gradient Framework	Spatial	Indirect	Dodds et al., 2015, 2019
Pulse Shunt Concept	Longitudinal, Temporal, Spatial	No	Raymond et al., 2016

624

625

626 **Figures**

627 Figure 1. Longitudinal, lateral, and vertical continua in rivers. River conceptual models have
628 largely focused on flow phases when rivers are longitudinally connected (a), and when lateral
629 and vertical continua are bidirectional (c). IRES have dry phases that lead to longitudinal
630 disconnections (b) and unidirectional lateral and vertical continua (d). In b, surface water is
631 present in blue reaches and absent in brown reaches (channel is dry). In c and d, blue vs.
632 brown soil/sediments indicate saturated vs. unsaturated.



633

634

635

636 Figure 2. Alternating flowing (a), non-flowing (b), dry (c), and rewetting phases (d) in an
637 intermittent river (Calavon River, France). Photo credits: Bertrand Launay.

a. flowing



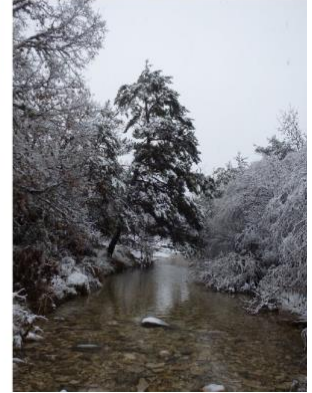
b. non-flowing



c. dry

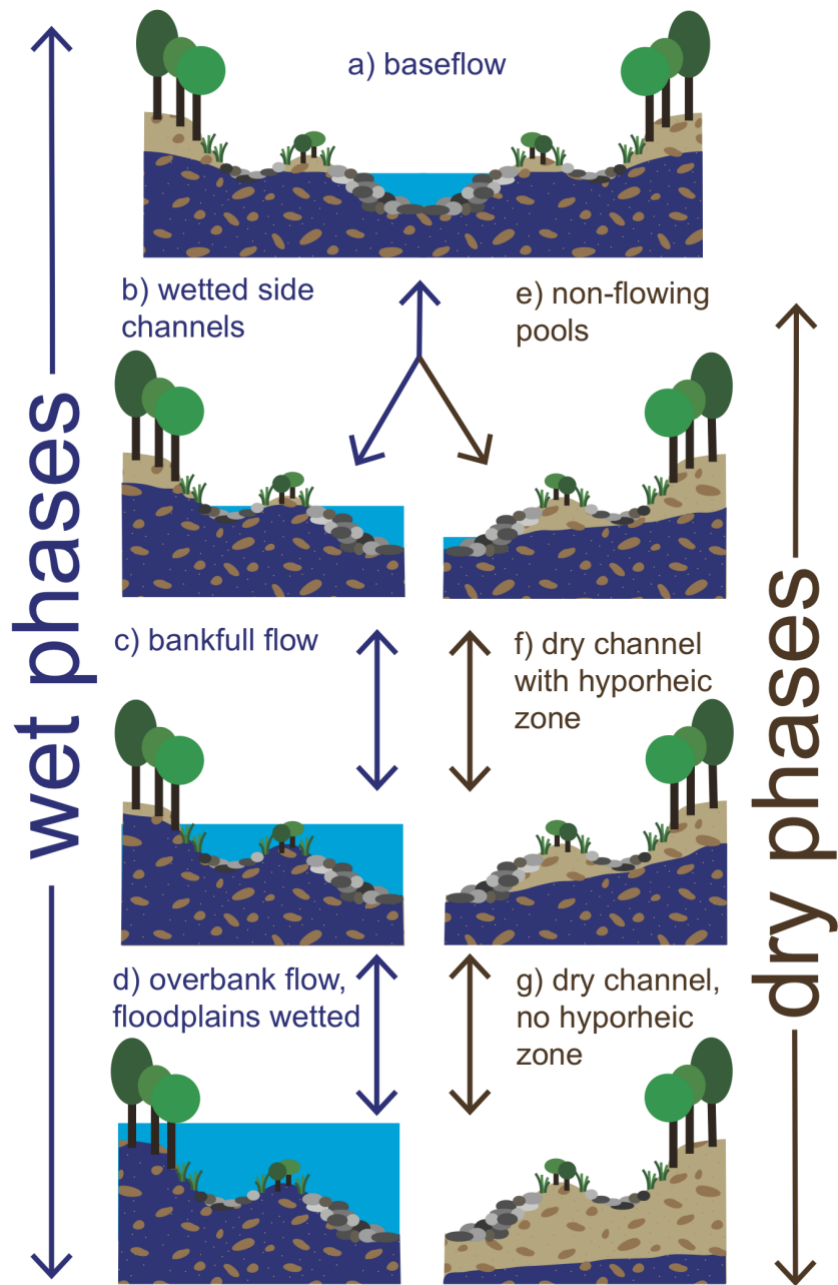


d. rewetting



638

639 Figure 3. Temporal variation in flow phases in rivers. River conceptual models have largely
 640 focused on the flowing “wet phases” between baseflow and overbank flows (panels a-f). IRES
 641 have non-flowing dry phases (panels e-g) that are also important in structuring river
 642 ecosystems. Blue vs. brown soil/sediments indicate saturated vs. unsaturated.

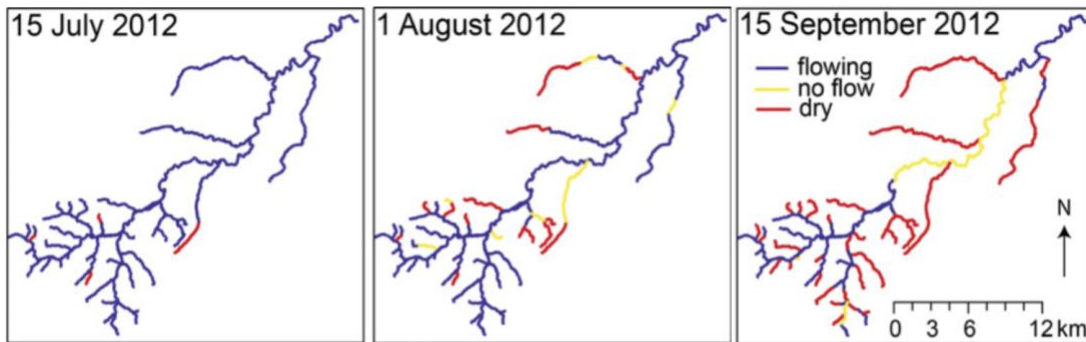


643

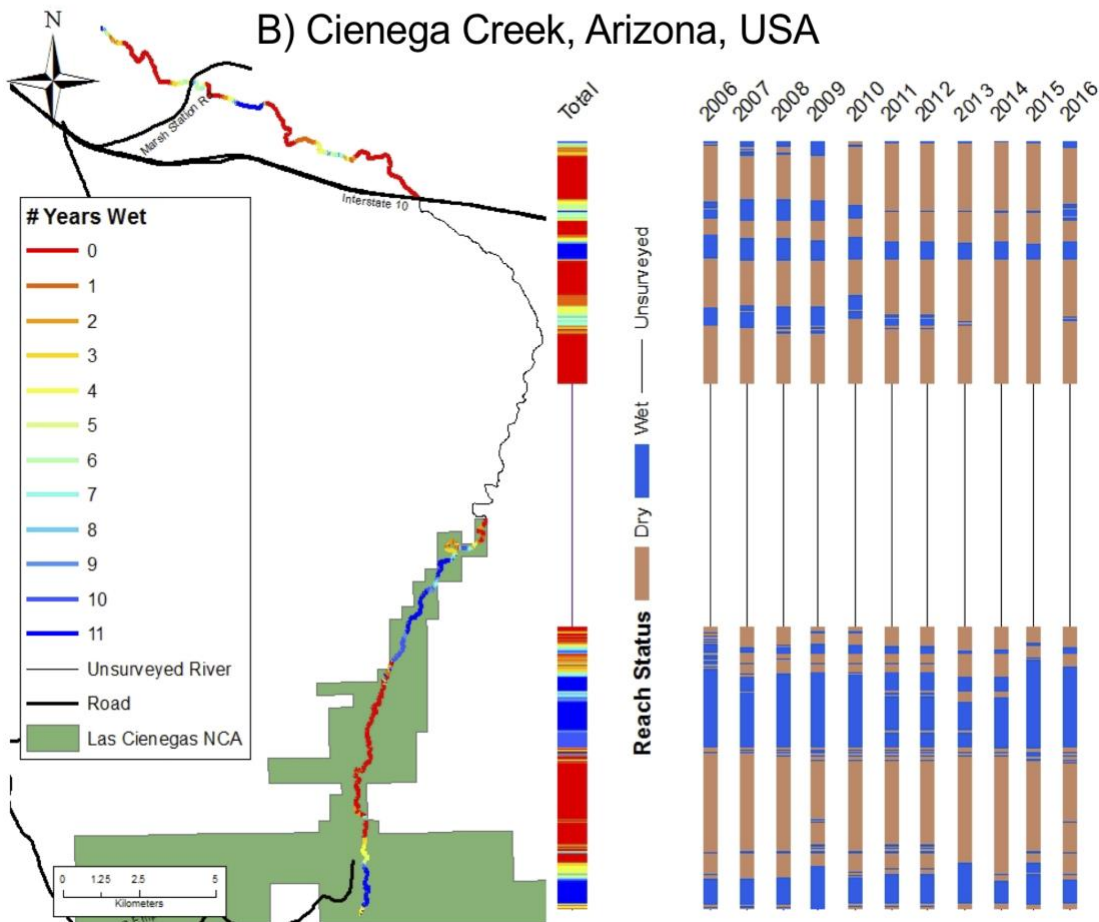
644

645 Figure 4. Temporal dynamism in spatial drying patterns in IRES networks. A) Within-year
 646 variation in the Thouaret River, France, during the summer of 2012. Modified from (Datry *et al.*
 647 2016). B) Between-year variation in Cienega Creek, Arizona, USA, (in the Natinoal
 648 Conservation Area, NCA, and downstream) measured annually during the dry season from
 649 2006-2016. Modified from (Allen *et al.* 2019).

A) Thouaret River, France



B) Cienega Creek, Arizona, USA



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