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Abstract

Conceptual models underpin river ecosystem research. However, current models focus on perennial rivers, those that always flow. Few explicitly address characteristics such as flow cessation and drying, which are becoming more prevalent in the Anthropocene. The applicability 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, we also found that most of these models do not account for how different these patterns and processes are for IRES. We suggest 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.

MAIN TEXT.

Introduction

Conceptual models underpin ecology. They identify ecological universalities across diverse taxonomies and geographies (Lawton, 1999). River ecosystem conceptual models have historically focused on research from 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 &

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 they 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 (Kerezsy 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 (DelVecchia 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, occuring 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

420 those of the researchers, and not necessarily the funding agencies. Although this work was

421 reviewed by the US Environmental Protection Agency and approved for publication, it might not

422 necessarily reflect official Agency policy.

423

424 **References**

425 Acreman, M., Arthington, A. H., Colloff, M. J., Couch, C., Crossman, N. D., Dyer, F., Overton, I.,

426   Pollino, C. A., Stewardson, M. J., & Young, W. (2014). Environmental flows for natural,

427   hybrid, and novel riverine ecosystems in a changing world. *Frontiers in Ecology and the*

428   *Environment*, *12*(8), 466–473. https://doi.org/10.1890/130134

429 Allen, D. C., Kopp, D. A., Costigan, K. H., Datry, T., Hugueny, B., Turner, D. S., Bodner, G. S.,

430   & Flood, T. J. (2019). Citizen scientists document long-term streamflow declines in

431   intermittent rivers of the desert southwest, USA. *Freshwater Science*, *38*(2), 244–256.

432   https://doi.org/10.1086/701483

433 Benda, L., Poff, N. L., Miller, D., Dunne, T., Reeves, G., Pess, G., & Pollock, M. (2004). The

434   Network Dynamics Hypothesis: How Channel Networks Structure Riverine Habitats.

435   *BioScience*, *54*(5), 413–427. https://doi.org/10.1641/0006-

436   3568(2004)054[0413:TNDHHC]2.0.CO;2

437 Benstead, J. P., & Leigh, D. S. (2012). An expanded role for river networks. *Nature Geoscience*,

438   *5*, 678–679. https://doi.org/10.1038/ngeo1593

439 Boano, F., Harvey, J. W., Marion, A., Packman, A. I., Revelli, R., Ridolfi, L., & Wörman, A.

440   (2014). Hyporheic flow and transport processes: Mechanisms, models, and

441   biogeochemical implications. *Reviews of Geophysics*, *52*(4), 603–679.

442   https://doi.org/10.1002/2012RG000417

443 Bogan, M. T., & Boersma, K. S. (2012). Aerial dispersal of aquatic invertebrates along and away

444   from arid-land streams. *Freshwater Science*, *31*(4), 1131–1144.

445   https://doi.org/10.1899/12-066.1

446 Chiu, M.-C., Leigh, C., Mazor, R., Cid, N., & Resh, V. (2017). Anthropogenic Threats to

447   Intermittent Rivers and Ephemeral Streams. In *Intermittent Rivers and Ephemeral*

448   *Streams* (pp. 433–454). Elsevier. https://doi.org/10.1016/B978-0-12-803835-2.00017-6

449 Costigan, K. H., Jaeger, K. L., Goss, C. W., Fritz, K. M., & Goebel, P. C. (2016). Understanding

450   controls on flow permanence in intermittent rivers to aid ecological research: Integrating

451   meteorology, geology and land cover. *Ecohydrology*, *9*(7), 1141–1153.

452   https://doi.org/10.1002/eco.1712

453 Datry, T., Foulquier, A., Corti, R., Schiller, D. von, Tockner, K., Mendoza-Lera, C., Clément, J.

454   C., Gessner, M. O., Moleón, M., Stubbington, R., Gücker, B., Albariño, R., Allen, D. C.,

455   Altermatt, F., Arce, M. I., Arnon, S., Banas, D., Banegas-Medina, A., Beller, E., …

456   Zoppini, A. (2018). A global analysis of terrestrial plant litter dynamics in non-perennial

457   waterways. *Nature Geoscience*, *11*(7), 497–503. https://doi.org/10.1038/s41561-018-

458   0134-4

459 Datry, T., Bonada, N., & Boulton, A. (Eds.). (2017). *Intermittent Rivers and Ephemeral Streams:*

460   *Ecology and Management*. Elsevier. https://doi.org/10.1016/C2015-0-00459-2

461 Datry, T., Larned, S., & Tockner, K. (2014). Intermittent Rivers: A Challenge for Freshwater

462   Ecology. *BioScience*, *64*(3), 229–235. https://doi.org/10.1093/biosci/bit027

463 DelVecchia, A. G., Stanford, J. A., & Xu, X. (2016). Ancient and methane-derived carbon

464   subsidizes contemporary food webs. *Nature Communications*, *7*, 13163.

465   https://doi.org/10.1038/ncomms13163

466 Dhungel, S., Tarboton, D. G., Jin, J., & Hawkins, C. P. (2016). Potential Effects of Climate

467   Change on Ecologically Relevant Streamflow Regimes. *River Research and*

468   *Applications*, *32*(9), 1827–1840. https://doi.org/10.1002/rra.3029

469 Dodds, W. K. (1997). Distribution of Runoff and Rivers Related to Vegetative Characteristics,

470   Latitude, and Slope: A Global Perspective. *Journal of the North American Benthological*

471   *Society*, *16*(1), 162–168. https://doi.org/10.2307/1468248

472   Dodds, W. K., Bruckerhoff, L., Batzer, D., Schechner, A., Pennock, C., Renner, E., Tromboni,

473   F., Bigham, K., & Grieger, S. (2019). The freshwater biome gradient framework:

474   Predicting macroscale properties based on latitude, altitude, and precipitation.

475   *Ecosphere*, *10*(7), e02786. https://doi.org/10.1002/ecs2.2786

476   Dodds, W. K., Gido, K., Whiles, M. R., Daniels, M. D., & Grudzinski, B. P. (2015). The Stream

477   Biome Gradient Concept: Factors controlling lotic systems across broad biogeographic

478   scales. *Freshwater Science*, *34*(1), 1–19. https://doi.org/10.1086/679756

479   Dodds, W. K., Gido, K., Whiles, M. R., Fritz, K. M., & Matthews, W. J. (2004). Life on the Edge:

480   The Ecology of Great Plains Prairie Streams. *BioScience*, *54*(3), 205–216.

481   https://doi.org/10.1641/0006-3568(2004)054[0205:LOTETE]2.0.CO;2

482   Döll, P., & Schmied, H. M. (2012). How is the impact of climate change on river flow regimes

483   related to the impact on mean annual runoff? A global-scale analysis. *Environmental*

484   *Research Letters*, *7*(1), 014037. https://doi.org/10.1088/1748-9326/7/1/014037

485   Fisher, S. G., Grimm, N. B., Martí, E., Holmes, R. M., & Jones, Jr., Jeremy B. (1998). Material

486   Spiraling in Stream Corridors: A Telescoping Ecosystem Model. *Ecosystems*, *1*(1), 19–

487   34. https://doi.org/10.1007/s100219900003

488   Godsey, S. E., & Kirchner, J. W. (2014). Dynamic, discontinuous stream networks:

489   Hydrologically driven variations in active drainage density, flowing channels and stream

490   order. *Hydrological Processes*, *28*(23), 5791–5803. https://doi.org/10.1002/hyp.10310

491   Grill, G., Lehner, B., Thieme, M., Geenen, B., Tickner, D., Antonelli, F., Babu, S., Borrelli, P.,

492   Cheng, L., Crochetiere, H., Macedo, H. E., Filgueiras, R., Goichot, M., Higgins, J.,

493   Hogan, Z., Lip, B., McClain, M. E., Meng, J., Mulligan, M., … Zarfl, C. (2019). Mapping

494   the world's free-flowing rivers. *Nature*, *569*(7755), 215–221.

495   https://doi.org/10.1038/s41586-019-1111-9

496   Humphries, P., Keckeis, H., & Finlayson, B. (2014). The River Wave Concept: Integrating River

497   Ecosystem Models. *BioScience*, *64*(10), 870–882. https://doi.org/10.1093/biosci/biu130

498   Jaeger, K. L., Sutfin, N. A., Tooth, S., Michaelides, K., & Singer, M. (2017). Geomorphology and

499   Sediment Regimes of Intermittent Rivers and Ephemeral Streams. In *Intermittent Rivers*

500   *and Ephemeral Streams: Ecology and Management. Datry, T, Bonada, N, Boulton, J*

501   *(eds).* (pp. 21–49). Elsevier. https://doi.org/10.1016/B978-0-12-803835-2.00002-4

502   James, A. B. W., Dewson, Z. S., & Death, R. G. (2008). Do stream macroinvertebrates use

503   instream refugia in response to severe short-term flow reduction in New Zealand

504   streams? *Freshwater Biology*, *53*(7), 1316–1334. https://doi.org/10.1111/j.1365-

505   2427.2008.01969.x

506   Junk, W., Bayley, P. B., & Sparks, R. E. (1989). The Flood Pulse Concept in River-Floodplain

507   Systems. In *Proceedings of the International Large River Symposium. Canadian Special*

508   *Publication of Fisheries and Aquatic Sciences 106. Dodge, DP (ed.).* (pp. 110–127).

509   Candian Government Publishing Centre.

510   Kerezsy, A., Gido, K., Magalhães, M. F., & Skelton, P. H. (2017). The Biota of Intermittent

511   Rivers and Ephemeral Streams: Fishes. In *Intermittent Rivers and Ephemeral Streams:*

512   *Ecology and Management. Datry, T, Bonada, N, Boulton, J (eds).* (pp. 273–298).

513   Elsevier. https://doi.org/10.1016/B978-0-12-803835-2.00010-3

514   Lawton, J. H. (1999). Are There General Laws in Ecology? *Oikos*, *84*(2), 177–192. JSTOR.

515   https://doi.org/10.2307/3546712

516   Marshall, J. C., Acuña, V., Allen, D. C., Bonada, N., Boulton, A. J., Carlson, S. M., Dahm, C. N.,

517   Datry, T., Leigh, C., Negus, P., Richardson, J. S., Sabater, S., Stevenson, R. J.,

518   Steward, A. L., Stubbington, R., Tockner, K., & Vorste, R. V. (2018). Protecting U.S.

519   temporary waterways. *Science*, *361*(6405), 856–857.

520   https://doi.org/10.1126/science.aav0839

521   Montgomery, D. R. (1999). Process Domains and the River Continuum. *JAWRA Journal of the*

522   *American Water Resources Association*, *35*(2), 397–410. https://doi.org/10.1111/j.1752-

523   1688.1999.tb03598.x

524   Perkin, J. S., Gido, K. B., Falke, J. A., Fausch, K. D., Crockett, H., Johnson, E. R., & Sanderson,

525   J. (2017). Groundwater declines are linked to changes in Great Plains stream fish

526   assemblages. *Proceedings of the National Academy of Sciences*, *114*(28), 7373–7378.

527   https://doi.org/10.1073/pnas.1618936114

528   Poff, N. L., Allan, J. D., Bain, M. B., Karr, J. R., Prestegaard, K. L., Richter, B. D., Sparks, R. E.,

529   & Stromberg, J. C. (1997). The Natural Flow Regime. *BioScience, 47*(11), 769–784.

530   https://doi.org/10.2307/1313099

531   Poole, G. C. (2002). Fluvial landscape ecology: Addressing uniqueness within the river

532   discontinuum. *Freshwater Biology*, *47*(4), 641–660. https://doi.org/10.1046/j.1365-

533   2427.2002.00922.x

534   Pringle, C. M. (2001). Hydrologic Connectivity and the Management of Biological Reserves: A

535   Global Perspective. *Ecological Applications*, *11*(4), 981–998.

536   https://doi.org/10.1890/1051-0761(2001)011[0981:HCATMO]2.0.CO;2

537   Raymond, P. A., Saiers, J. E., & Sobczak, W. V. (2016). Hydrological and biogeochemical

538   controls on watershed dissolved organic matter transport: Pulse-shunt concept. *Ecology*,

539   *97*(1), 5–16. https://doi.org/10.1890/14-1684.1

540   Richter, B., & Thomas, G. (2007). Restoring Environmental Flows by Modifying Dam

541   Operations. *Ecology and Society*, *12*(1). https://doi.org/10.5751/ES-02014-120112

542   Sánchez-Montoya, M. M., Moleón, M., Sánchez-Zapata, J. A., & Tockner, K. (2016). Dry

543   riverbeds: Corridors for terrestrial vertebrates. *Ecosphere*, *7*(10), e01508.

544   https://doi.org/10.1002/ecs2.1508

545   Scanlon, B. R., Keese, K. E., Flint, A. L., Flint, L. E., Gaye, C. B., Edmunds, W. M., & Simmers,

546   I. (2006). Global synthesis of groundwater recharge in semiarid and arid regions.

547   *Hydrological Processes*, *20*(15), 3335–3370. https://doi.org/10.1002/hyp.6335

548   Shanafield, M., Godsey, S., Datry, T., Hale, R., Zipper, S. C., Costigan, K. H., Krabbenhoft, C.

549   A., Dodds, W. K., Zimmer, M. A., Bogan, M., Kaiser, K. E., Burrows, R. M., Hammond, J.

550   C., Busch, M., Kampf, S., Mims, M. C., Burgin, A., & Olden, J. D. (2020). Science Gets

551   Up to Speed on Dry Rivers. *Eos*, *101*, https://doi.org/10.1029/2020EO139902.

552   Sponseller, R. A., Heffernan, J. B., & Fisher, S. G. (2013). On the multiple ecological roles of

553   water in river networks. *Ecosphere*, *4*(2), art17. https://doi.org/10.1890/ES12-00225.1

554   Stanford, J. A., & Ward, J. V. (1993). An Ecosystem Perspective of Alluvial Rivers: Connectivity

555   and the Hyporheic Corridor. *Journal of the North American Benthological Society*, *12*(1),

556   48–60. https://doi.org/10.2307/1467685

557   Stanley, E. H., Fisher, S. G., & Grimm, N. B. (1997). Ecosystem Expansion and Contraction in

558   Streams. *BioScience*, *47*(7), 427–435. https://doi.org/10.2307/1313058

559   Steffen, W., Grinevald, J., Crutzen, P., & McNeill, J. (2011). The Anthropocene: Conceptual and

560   historical perspectives. *Philosophical Transactions of the Royal Society A: Mathematical,*

561   *Physical and Engineering Sciences*, *369*(1938), 842–867.

562   https://doi.org/10.1098/rsta.2010.0327

563   Steward, A. L., Langhans, S. D., Corti, R., & Datry, T. (2017). The Biota of Intermittent Rivers

564   and Ephemeral Streams: Terrestrial AND Semiaquatic Invertebrates. In *Intermittent*

565   *Rivers and Ephemeral Streams: Ecology and Management. Datry, T, Bonada, N,*

566   *Boulton, J (eds).* (pp. 245–271). Elsevier. https://doi.org/10.1016/B978-0-12-803835-

567   2.00008-5

568   Stubbington, R., Bogan, M. T., Bonada, N., Boulton, A. J., Datry, T., Leigh, C., & Vander Vorste,

569   R. (2017). The Biota of Intermittent Rivers and Ephemeral Streams: Aquatic

570   Invertebrates. In *Intermittent Rivers and Ephemeral Streams: Ecology and Management.*

571   *Datry, T, Bonada, N, Boulton, J (eds).* (pp. 217–243). Elsevier.

572   https://doi.org/10.1016/B978-0-12-803835-2.00007-3

573   Stubbington, R., Chadd, R., Cid, N., Csabai, Z., Miliša, M., Morais, M., Munné, A., Pařil, P.,

574   Pešić, V., Tziortzis, I., Verdonschot, R. C. M., & Datry, T. (2018). Biomonitoring of

575   intermittent rivers and ephemeral streams in Europe: Current practice and priorities to

576   enhance ecological status assessments. *Science of The Total Environment*, *618*, 1096–

577   1113. https://doi.org/10.1016/j.scitotenv.2017.09.137

578   Thorp, J. H., & Delong, M. D. (1994). The Riverine Productivity Model: An Heuristic View of

579   Carbon Sources and Organic Processing in Large River Ecosystems. *Oikos*, *70*(2), 305–

580   308. JSTOR. https://doi.org/10.2307/3545642

581   Thorp, J. H., Thoms, M. C., & Delong, M. D. (2008). *The riverine ecosystem synthesis: Toward*

582   *conceptual cohesiveness in river science / James H. Thorp, Martin C. Thoms and*

583   *Michael D. Delong.* (1st ed..). Academic Press/Elsevier.

584   Tockner, K., Malard, F., & Ward, J. V. (2000). An extension of the flood pulse concept.

585   *Hydrological Processes*, *14*(16–17), 2861–2883. https://doi.org/10.1002/1099-

586   1085(200011/12)14:16/17<2861::AID-HYP124>3.0.CO;2-F

587   Tolonen, K. E., Picazo, F., Vilmi, A., Datry, T., Stubbington, R., Pařil, P., Perez Rocha, M., &

588   Heino, J. (2019). Parallels and contrasts between intermittently freezing and drying

589   streams: From individual adaptations to biodiversity variation. *Freshwater Biology*,

590   *64*(10), 1679–1691. https://doi.org/10.1111/fwb.13373

591   Tonkin, J. D., Poff, N. L., Bond, N. R., Horne, A., Merritt, D. M., Reynolds, L. V., Olden, J. D.,

592   Ruhi, A., & Lytle, D. A. (2019). Prepare river ecosystems for an uncertain future. *Nature*,

593   *570*(7761), 301–303. https://doi.org/10.1038/d41586-019-01877-1

594   Vander Vorste, R., Malard, F., & Datry, T. (2016). Is drift the primary process promoting the

595   resilience of river invertebrate communities? A manipulative field experiment in an

596   intermittent alluvial river. *Freshwater Biology*, *61*(8), 1276–1292.

597   https://doi.org/10.1111/fwb.12658

598   Vannote, R. L., Minshall, G. W., Cummins, K. W., Sedell, J. R., & Cushing, C. E. (1980). The

599   River Continuum Concept. *Canadian Journal of Fisheries and Aquatic Sciences*, *37*(1),

600   130–137. https://doi.org/10.1139/f80-017

601   von Schiller, D., Bernal, S., Dahm, C. N., & Martí, E. (2017). Nutrient and Organic Matter

602   Dynamics in Intermittent Rivers and Ephemeral Streams. In *Intermittent Rivers and*

603   *Ephemeral Streams: Ecology and Management. Datry, T, Bonada, N, Boulton, J (eds).*

604   (pp. 135–160). Elsevier. https://doi.org/10.1016/B978-0-12-803835-2.00006-1

605   Ward, J. V. (1989). The Four-Dimensional Nature of Lotic Ecosystems. *Journal of the North*

606   *American Benthological Society*, *8*(1), 2–8. https://doi.org/10.2307/1467397

607   Wohl, E., Bledsoe, B. P., Jacobson, R. B., Poff, N. L., Rathburn, S. L., Walters, D. M., & Wilcox,

608   A. C. (2015). The Natural Sediment Regime in Rivers: Broadening the Foundation for

609   Ecosystem Management. *BioScience*, *65*(4), 358–371.

610   https://doi.org/10.1093/biosci/biv002

611   Yang, X., Pavelsky, T. M., & Allen, G. H. (2020). The past and future of global river ice. *Nature*,

612   *577*(7788), 69–73. https://doi.org/10.1038/s41586-019-1848-1

613   Zimmer, M. A., & McGlynn, B. L. (2017). Ephemeral and intermittent runoff generation

614   processes in a low relief, highly weathered catchment. *Water Resources Research*,

615   *53*(8), 7055–7077. https://doi.org/10.1002/2016WR019742

616

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

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.
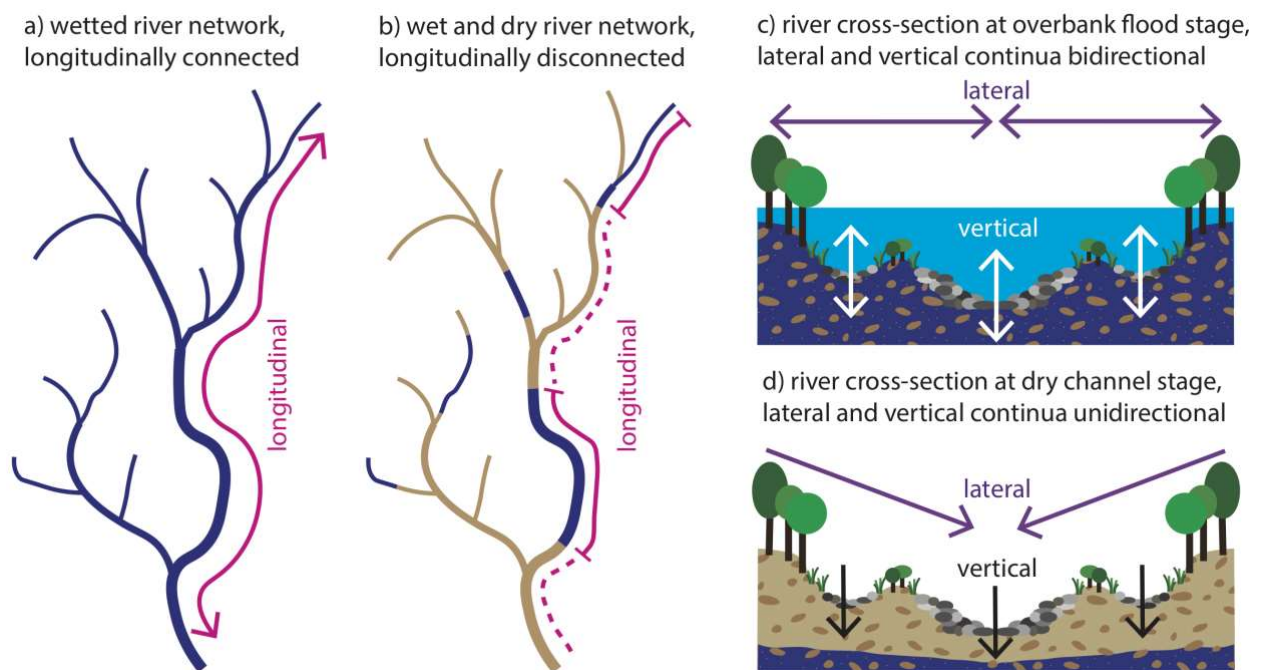
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635

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.
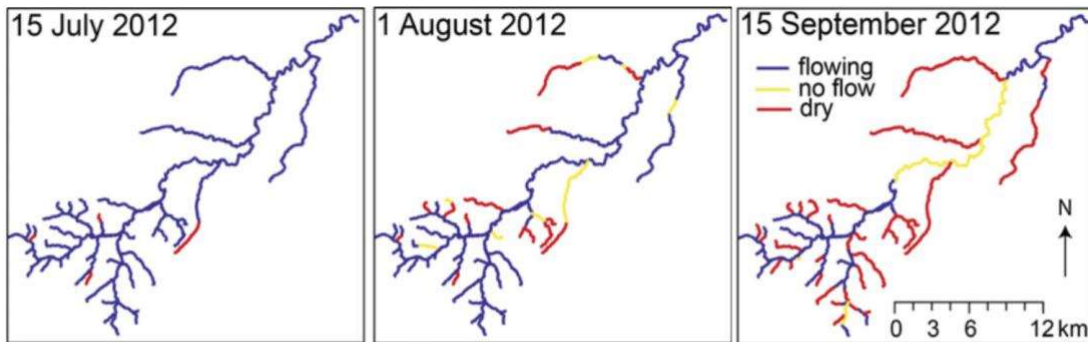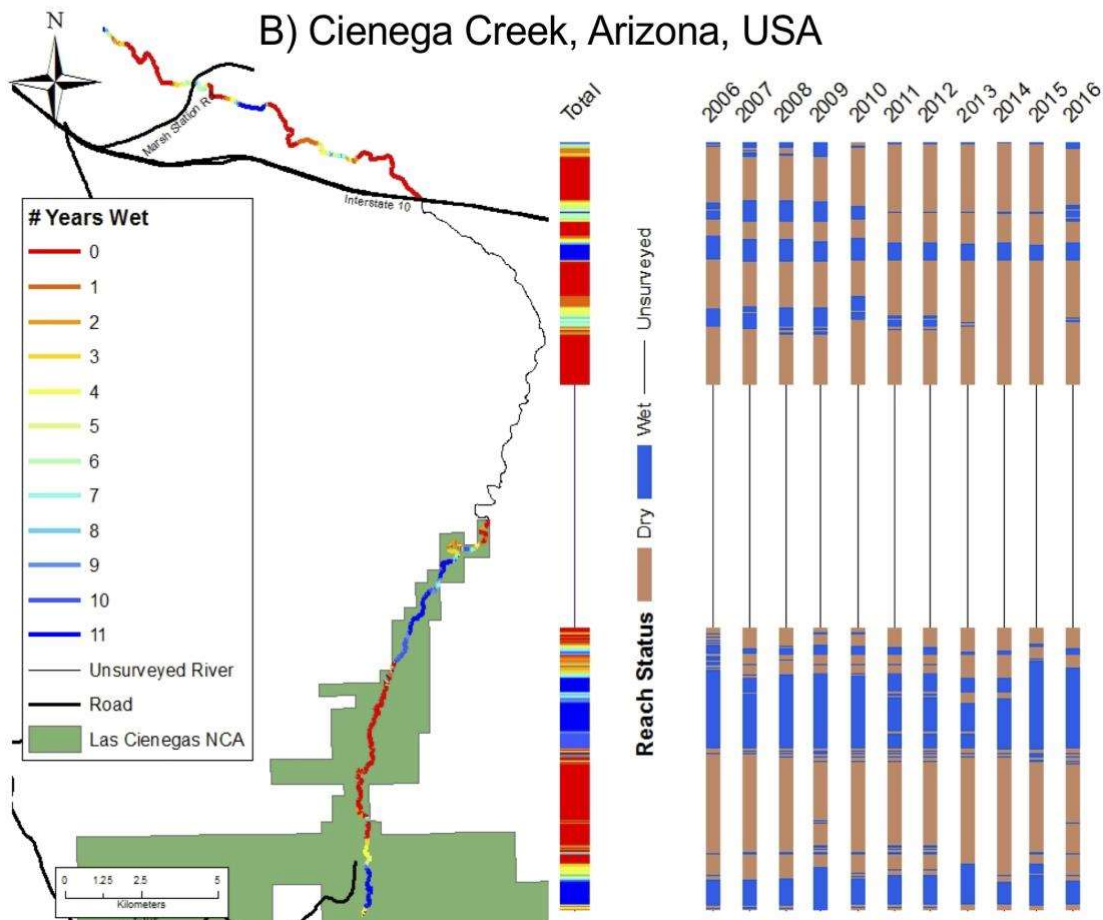

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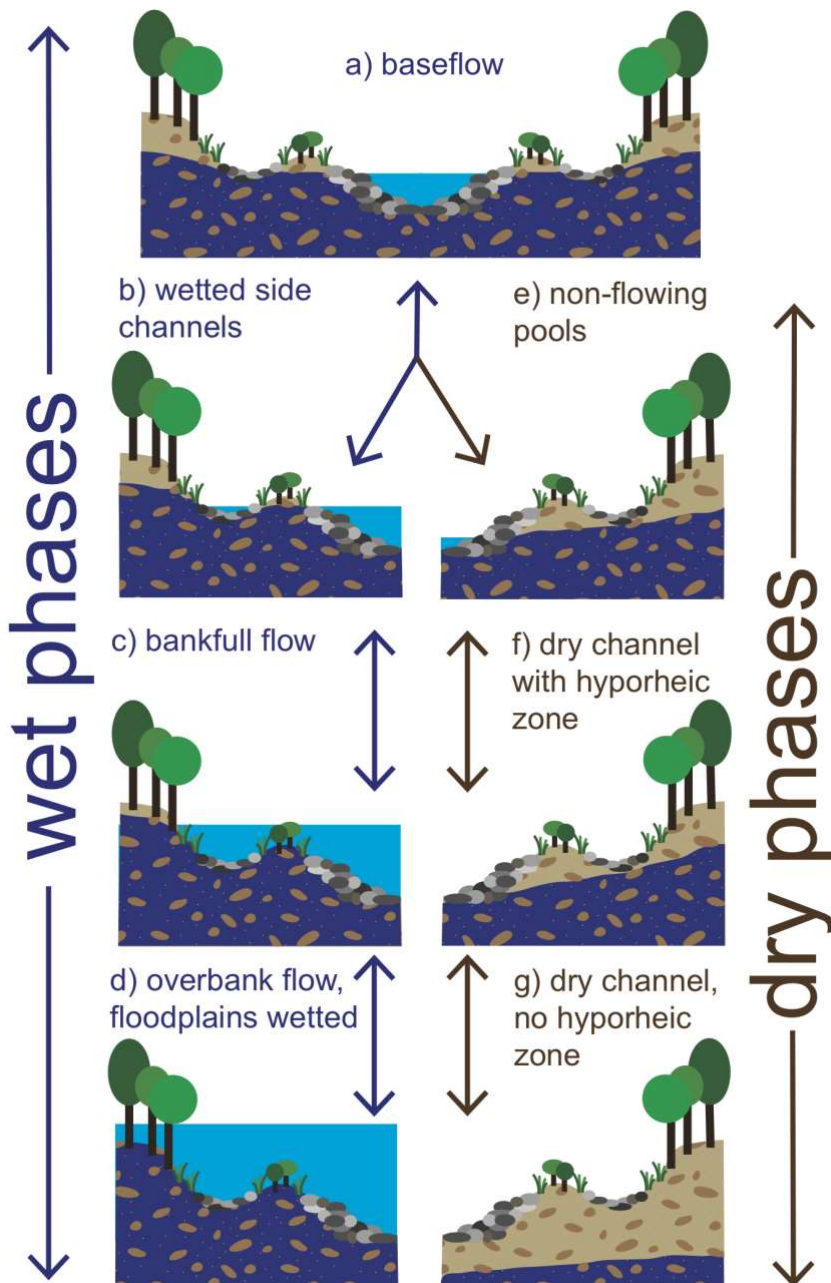
Figure 4. Temporal dynamism in spatial drying patterns in IRES networks. A) Within-year

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

Conservation Area, NCA, and downstream) measured annually during the dry season from

2006-2016. Modified from (Allen *et al.* 2019).