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1 **Drought in intermittent river and ephemeral stream networks**

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12

13 **Abstract**

14 Intermittent rivers and ephemeral streams (IRES), those watercourses that periodically cease
15 to flow or dry, are the world's most widespread type of river ecosystem. Our understanding
16 of the natural hydrology and ecology of IRES has greatly improved, but their responses to
17 extreme events such as drought remains a research frontier. In this review, we present the
18 state of the art, knowledge gaps, and research directions on droughts in IRES from an
19 ecohydrological perspective. We clarify the definition of droughts in IRES, giving
20 recommendations to promote transferability in how ecohydrological studies characterize
21 droughts in non-perennial stream networks. Based on a systematic search of the literature, we
22 also identify common patterns and sources of variation in the ecological responses of IRES to
23 droughts and provide a roadmap for further research to enable improved understanding and
24 management of IRES during those extreme hydrological events. Confusion in the
25 terminology and the lack of tools to assess the hydrological responses of IRES to drought
26 may have hindered the development of drought research in IRES. We found that 44% of
27 studies confused the term drought with seasonal drying and that those that measure droughts

28 in a transferable way are a minority. Studies on ecological responses to drought in IRES
29 networks are still rare and limited to a few climatic zones, organisms and mainly explored in
30 perennial sections. Our review highlights the need for additional research on this topic to
31 inform IRES management and conservation.

32 **Keywords:** fragmentation, extreme events, non-perennial rivers, population,
33 communities, hydrology

34 **Significance Statement**

35 Drought severity and frequency is increasing due to climate change, affecting river
36 ecosystems around the world. Here, we review the current understanding, knowledge gaps,
37 and research directions for investigating ecohydrological responses to droughts in intermittent
38 rivers and ephemeral streams, i.e., those streams that naturally cease to flow at some point in
39 time. Studies assessing the effects of droughts in IRES networks are still limited to a few
40 climatic zones, countries and organisms, most probably because disentangling ecological
41 responses from natural flow intermittence to those from drought remains a challenge.

42

43 **1. Introduction**

44 Intermittent rivers and ephemeral streams (IRES), those watercourses that periodically cease
45 to flow or dry, are the world's most widespread type of river ecosystem (Thibault Datry,
46 Bonada, & Boulton, 2017; Messenger et al., 2021). IRES comprise 51-60% of the global river
47 and stream network by length (Thibault. Datry, Larned, & Tockner, 2014; Messenger et al.,
48 2021), and range from ephemeral streams that occasionally flow for a few days after heavy
49 rain to intermittent rivers that may recede to isolated pools or dry out completely. While most
50 prevalent in arid and semi-arid regions, IRES naturally occur in all climates, biomes, and
51 continents, including in the humid tropics and polar regions (Thibault Datry et al., 2017;
52 Messenger et al., 2021; Stubbington, England, Wood, & Sefton, 2017).

53 Anthropogenic global change has affected the hydrology of IRES (Hammond et al., 2021;
54 Sauquet et al., 2021; Trambly, Llasat, Randin, & Coppola, 2020). The duration, frequency,
55 timing, and spatial extent of flow cessation is changing in many IRES globally due to climate
56 change, water abstraction and land-use changes (de Graaf, Gleeson, van Beek, Sutanudjaja, &
57 Bierkens, 2019; Larned, Datry, Arscott, & Tockner, 2010). While climate-driven shifts from
58 perennial to intermittent flow are predicted to increase in the next decades for streams and
59 rivers across global regions (Döll & Schmied, 2012), naturally intermittent watercourses have
60 also become perennial due to flow regulation and effluent recharge (Halaburka et al., 2013;
61 Hamdhani, Eppehimer, & Bogan, 2020). Our understanding of the natural hydrology and
62 ecology of IRES has greatly improved in the past decade, but their responses to extreme
63 events such as drought and to climate change remains a research frontier.

64 Contrasting with the predictable cycles of flow cessation and resumption that are typical of
65 most IRES, hydrological droughts are unpredictable and severe events characterized by long-
66 lasting and spatially extended deficit in surface water (Tallaksen & Van Lanen, 2004).

67 During droughts, water discharge decreases and aquatic habitats contract beyond their long-
68 term seasonal averages (Boulton, 2003). Droughts can cause drying conditions to extend
69 temporally and spatially within IRES networks (Jaeger, Olden, & Pelland, 2014). During
70 such events, perennial or near-perennial reaches may dry out partially or completely and
71 intermittent reaches may experience longer and more severe dry periods (Lake, 2011).

72 Hydrological droughts lead to a cascade of abiotic changes that alter the ecological and
73 biogeochemical functioning of IRES networks. For instance, increasing drying extent can

74 increase river network fragmentation, which decreases dispersal capacities and thus
75 compromises the resilience and survival of aquatic organisms (Jaeger et al., 2014). The biotic
76 communities of IRES are typically hypothesized to be more resistant and resilient to droughts
77 than perennial communities based on the assumption that species adaptations to regular
78 drying provide advantages under drought conditions (Hill et al., 2019). However, there is
79 limited evidence to date for such subdued responses to drought in IRES (Bogan & Lytle,
80 2011), as unpredictable and severe drying events may overcome any seasonal adaptations.

81 Until recently, the ecohydrology of droughts in IRES has received little attention (Hill et al.,
82 2019; Lake, 2011). Most research on IRES has focused on understanding how seasonal
83 drying influences ecological processes and patterns in river networks (Thibault Datry et al.,
84 2017; Leigh & Datry, 2017; Vander Vorste, Sarremejane, & Datry, 2020). While Lake (2011)
85 provided an extensive overview of the ecological literature of droughts in IRES, little
86 distinction was made between studies that focus on regular flow intermittence from those on
87 anomalous drying. Since then, a growing body of literature has documented ecological
88 responses to droughts at individual sites or for individual ecosystem components, yet a global
89 overview of the ecohydrology of droughts in IRES is still lacking.

90 Here, we review the current understanding, knowledge gaps, and research directions for
91 investigating droughts in intermittent rivers and ephemeral streams from an ecohydrological
92 perspective. Based on a systematic search of the literature, we first identify trends and gaps in
93 the ecohydrology of IRES during droughts. Second, we define droughts in IRES and give
94 recommendations to promote transferability in how ecohydrological studies characterize
95 droughts in non-perennial stream networks. Third, we summarize knowledge on the
96 ecohydrology of IRES, focusing on how physical, biological and ecological processes are
97 naturally and seasonally affected by varying spatial and temporal drying patterns. Fourth, we
98 review the ecological consequences of droughts on riverine biotic communities as well as the
99 impact of anthropogenic stressors on ecosystem responses to droughts in IRES. Last, we
100 provide a roadmap for further research to enable improved understanding and management of
101 IRES during droughts. Our review highlights the need for additional research on this topic to
102 inform conservation of IRES in the Anthropocene given the ongoing increase in frequency
103 and severity of droughts (Cook et al., 2020; Lehner et al., 2017; Pokhrel et al., 2021; Spinoni,
104 Vogt, Naumann, Barbosa, & Dosio, 2018) .

105 We performed a systematic search on Web of Science to identify literature on
106 ecohydrological responses in IRES during droughts (see Appendix 1 for the search terms).
107 This search combined a term related to intermittence (e.g. temporary, intermittent), a
108 descriptor of a lotic waterbody (e.g. river, stream) and the word drought. Our word list was
109 limited to the most specific terms used to refer to IRES to avoid collecting unspecific
110 literature (but see Bush et al. 2020 for a more exhaustive list of terms). Whereas we obtained
111 12206 hits when searching for a waterbody term and drought, we only received 904 hits (i.e.,
112 7.4% of the former) when searching for literature specifically addressing IRES and drought
113 (Appendix 1). Of these 904 articles, 109 addressed ecohydrological responses to drought in
114 IRES, of which 43% (n=46) used the term “drought” to refer to seasonal drying and were
115 thus excluded from further analysis. Of the 63 remaining studies, 3 were reviews, 4 were
116 experiments and the rest were field studies that looked at community (73%), population
117 (23%), and/or hydro-biogeochemical processes and ecosystem function (9%) responses to
118 drought in IRES (some studies investigated multiple types of responses, organisms, and
119 climates). Most experiments and field studies looked at macroinvertebrate (57%) or fish
120 (32%) responses, and 85% of studies focused on Mediterranean and semi-arid to arid climates
121 even though 53% of IRES, by length, occur outside of those climates (**Figure 1**; see
122 **Appendix 1, Fig. S1** for a map of climate zones). Knowledge on the ecohydrology of IRES
123 during drought is thus limited. In this review, we summarize available evidence when
124 possible but present hypotheses for those processes and scales for which little information
125 exists.

126

127 **2. Defining and describing droughts in IRES**

128

129 **2.1. Common definitions of drought**

130 A drought can be most concisely defined as “a deficit of water relative to normal conditions”
131 (Sheffield & Wood, 2011). Droughts are classified into four major types based on the
132 impacted system of interest (Wilhite & Glantz, 1985): (1) a meteorological drought (also
133 called climatological drought) is a deficiency in precipitation, sometimes together with
134 increased potential evapotranspiration, that is long-lasting and spans a large area; (2) an
135 agricultural drought (also called soil moisture drought) is a deficit in plant-available water,
136 usually impacting crops; (3) a hydrological drought is a deficit in surface or subsurface water
137 levels or flows (see Van Loon, 2015 for a recent review); and (4) a socio-economic drought

138 expresses a failure of water resources systems to meet water demands by society, often
139 combining the three other types of droughts (Mishra & Singh, 2010). A fifth kind of drought
140 has long been subsumed under the socio-economic category but is increasingly recognized as
141 a distinct category: ecological drought (Crausbay et al., 2017; Tallaksen & Van Lanen, 2004).
142 An ecological drought is “an episodic deficit in water availability that drives ecosystems
143 beyond thresholds of vulnerability, impacts ecosystem services, and triggers feedbacks in
144 natural and/or human systems” (Crausbay et al., 2017).

145

146 The reason for such specificity in defining droughts is that management actions and policies
147 are influenced by which type of drought is defined and how (Lloyd-Hughes, 2014). Drought
148 response strategies vary according to the severity and extent of water deficit, and must be
149 adapted to the differences in temporal and spatial characteristics among drought types (e.g.,
150 hydrological droughts are spatially more heterogeneous than meteorological droughts;
151 (Changnon, 1987; Eltahir & Yeh, 1999; Van Loon, 2015). Defining drought is also needed to
152 avoid conflation between meteorological droughts and climatic aridity (Wilhite, 1992). A
153 meteorological drought is a finite event, an anomalous precipitation deficit, whereas aridity is
154 a climate normal expressing a continual negative water balance due to evapotranspiration
155 exceeding precipitation. As such, these two phenomena require distinct policies and water
156 resource management actions. In this section, our aim is first to assess the usage of the term
157 drought in IRES research, thus focusing mostly on meteorological and hydrological droughts,
158 and second, to better define hydrological droughts in IRES.

159

160 **2.2. Limitations of current definitions of droughts in IRES**

161 The term drought is loosely handled in freshwater ecology. Few studies in this field define
162 their use of the term or quantitatively describe the drought at hand (Humphries & Baldwin,
163 2003; Lake, 2011). Those studies that mention a type of drought usually do so by
164 distinguishing between seasonal and supra-seasonal types of hydrological droughts (Lake
165 2003; Kovach et al., 2019). Seasonal droughts are seen as predictable, periodic and of limited
166 severity, while supra-seasonal droughts are unpredictable, aseasonal or extending beyond one
167 season, with greater magnitude and severity (Boulton, 2003; Humphries & Baldwin, 2003;
168 Lake, 2003). Lake (2003) differentiated seasonal droughts as “press” disturbances (i.e.,
169 arising sharply, and rapidly reaching a level that is maintained constant over time; (Lake,

170 2000) from supra-seasonal droughts that he conceptualized as “ramp” disturbances (i.e.,
171 progressively and steadily increasing over time; Lake, 2000).

172

173 Here we contend that the use of the term “seasonal drought” is not beneficial to the
174 scholarship of freshwater ecology, particularly as it relates to IRES. Just as meteorological
175 droughts must be distinguished from aridity, hydrological droughts must be distinguished
176 from natural flow intermittence in IRES. Flow cessation by itself is not an anomaly in IRES.
177 On the contrary, water flows for only a few weeks or days every year in many non-perennial
178 rivers (Vidal-Abarca et al., 2020). Dryland stream catchments typically exhibit great intra-
179 and inter-annual variability in rainfall (Tooth, 2000), so flow does not necessarily follow
180 regular seasonal patterns in non-perennial rivers — further invalidating the relevance of the
181 term seasonal drought. Whether seasonal drought is a legitimate term is not a new debate in
182 hydrology and meteorology (e.g., McBryde, 1982; Steila, 1981), yet we believe that its usage
183 is particularly counter-productive to the study and conservation of IRES. Of the 109 studies
184 returned by our initial literature search (Appendix 1), nearly half used the term drought
185 synonymously with flow intermittence or called it only ‘drought’ rather than ‘seasonal
186 drought’. Its usage muddles the literature on droughts in IRES (as exemplified in this review),
187 but also harms public perception of IRES by perpetuating negative connotations associated
188 with flow intermittence (Leigh, Boersma, Galatowitsch, Milner, & Stubbington, 2019;
189 Rodríguez-Lozano, Woelfle-Erskine, Bogan, & Carlson, 2020).

190

191 Beyond definitions, we found that few studies characterized the droughts that they
192 investigated in hydrological terms. Of the 55 articles we reviewed that examined a specific
193 drought in IRES, 5 omitted to describe it altogether, 20 only provided a description of the
194 associated meteorological drought, 22 only described the drought hydrologically, and 8
195 provided both meteorological and hydrological descriptors of the drought. Describing the
196 flow conditions of a system under drought is an important first step. However, transferable
197 measures of the attributes of droughts are also needed to enable comparison across studies,
198 time periods, regions and watersheds — such attributes include the severity (or intensity),
199 timing, duration, and spatial extent of the drought. In **Table 1**, we provide definitions of
200 common flow regime and drought attributes (and see the following Section 2.3 on
201 quantitative indices used in deriving these attributes). Of those studies that described the
202 drought meteorologically, 64% relied on established, transferable indices (e.g., Standardized
203 Precipitation Index, Palmer Drought Severity Index). By contrast, only 4 studies in total

204 provided an established, transferable measure of the hydrological drought under study (e.g.,
205 hydrological return period of annual flow, Palmer Hydrological Drought Index). This lack of
206 description of droughts by ecological studies is a long-standing issue which limits the
207 generalizability of their findings and impedes comparative analyses (Lake, 2011). And while
208 reporting the characteristics of the meteorological drought associated with the hydrological
209 drought under study provides valuable information, it does not enable a standardized
210 comparison across localities because identical meteorological droughts can result in
211 significantly different hydrological conditions across regions and watersheds.

212

213 How meteorological anomalies translate to hydrological droughts is a complex phenomenon
214 that depends on climate, each river's flow regime, catchment characteristics, streambed
215 substrate, reach geomorphology, antecedent conditions, and human responses to droughts
216 (Van Loon, 2015; **Figure 2**). Hydrological droughts tend to be spatially much patchier than
217 meteorological droughts, which are driven by large-scale atmospheric processes (Tallaksen,
218 Hisdal, & Lanen, 2009). Woelfle-Erskine, Larsen, & Carlson (2017) documented
219 considerable variability in flow intermittence between stream sections less than one kilometre
220 apart on Fay Creek, California in response to the drought of 2011-2017; these observed
221 differences had population-level consequences on the viability of salmon habitat. Flow
222 intermittence in IRES is also strongly linked to groundwater dynamics, whose response to
223 droughts is mediated by additional local characteristics, so that these watercourses exhibit
224 even greater variability in their responses to precipitation deficits (Fennell, Geris, Wilkinson,
225 Daalmans, & Soulsby, 2020; Lovill, Hahm, & Dietrich, 2018; Shanafield, Bourke, Zimmer,
226 & Costigan, 2021). As such, the recovery of normal baseflow is not only slow but also
227 notoriously difficult to predict; discharge often returns to pre-drought levels years after
228 precipitation resumes following supra-seasonal droughts (Deitch, van Docto, Obedzinski,
229 Nossaman, & Bartshire, 2018). In about one third of unregulated watersheds across south-
230 eastern Australia, runoff had not returned to pre-drought levels seven years after the end of
231 the Millennium Drought, indicating a shift to an alternative stable state (Peterson, Saft, Peel,
232 & John, 2021). In human-impacted systems, reactive over-withdrawal for irrigation and
233 domestic uses can aggravate the effects of a mild meteorological drought into a severe
234 hydrological drought (Van Loon et al., 2016). Given that meteorological drought attributes
235 cannot be consistently translated to hydrological terms, descriptions of the hydrological
236 character of droughts in case studies are needed to promote a broader understanding of the
237 ecohydrology of droughts in IRES.

238

239 **2.3. Quantitative hydrological drought indices for IRES**

240 Hydrological anomalies are rarely quantified in IRES studies partly because existing drought
241 indices are ill-fitted to intermittent flow regimes. More than 150 indices have been developed
242 to describe the magnitude, duration, intensity, severity, frequency, and geographic extent of
243 droughts (Haile, Tang, Li, Liu, & Zhang, 2020; Van Loon, 2015; Zargar, Sadiq, Naser, &
244 Khan, 2011). These metrics can be broadly categorized between threshold level methods and
245 standardized indices (Van Loon, 2015).

246

247 Threshold level methods rely on the establishment of a specific value for a
248 hydrometeorological variable below which the system is considered to be in a drought
249 (Zelenhasić & Salvai, 1987; Hisdal et al. 2004). Flow duration curves displaying the
250 relationship between any discharge value and the percentage of time (frequency) that this
251 discharge is equalled or exceeded form the basis of threshold indices (Smakhtin, 2001;
252 Yevjevich, 1967). Based on this curve, a threshold discharge is picked below which a drought
253 is deemed to occur. The threshold frequency usually ranges between Q70 and Q95 (the
254 discharges that are exceeded 70% and 95% of the time respectively) for perennial rivers
255 (Smakhtin, 2001; Van Loon, 2015). Additional refinements exist, including the use of
256 temporally varying thresholds (Hisdal et al. 2004). Threshold indices enable the calculation
257 of drought duration, severity, and frequency, and do not require that a parametric distribution
258 be fit to the data. However, drought statistics cannot easily be transferred across geographies
259 because there is no standard threshold in use (Van Loon 2015).

260

261 Standardized drought indices represent anomalies from a normal situation in a standardized
262 way, thus enabling comparison across regions (Mishra & Singh, 2010). The most widely used
263 meteorological drought index is the Standardized Precipitation Index (SPI). SPI fits long-term
264 precipitation records to a probability distribution that is subsequently transformed to a normal
265 distribution with zero mean and unit standard deviation (Mckee, Doesken, & Kleist, 1993).
266 SPI can be computed over different time periods (e.g., 1, 6, 24 months), but its interpretation
267 remains invariant to temporal and spatial scales, geographic regions, and climates. For
268 instance, SPI12 month < -2 reflects a deficit in precipitation over 12 months that is more than
269 two standard deviations below the long-term mean. Such a drought should theoretically occur
270 only a handful of times every 100 years ($< 5\%$ of the time) and is usually labelled as

271 “extremely dry” (Hayes, Svoboda, Wihite, & Vanyarkho, 1999). The hydrological
272 equivalent to SPI is the Standardized Streamflow Index (SSI), calculated from observed or
273 simulated long-term discharge records (Vicente-Serrano et al., 2012).

274

275 Common drought indices, whether standardized or threshold-based, imperfectly quantify the
276 hydrological disturbances that drive ecological responses to drought in IRES (**Figure 3**).

277 Threshold-based methods as currently implemented are even less relevant than standardized
278 drought indices for studying IRES because thresholds between Q70 and Q95 would result in
279 considering any zero-flow event as a drought (**Figure 3a**, Lake, 2011; Van Loon, 2015).

280 Higher thresholds have been proposed, between Q5 and Q20, to describe droughts in IRES
281 (Gustard & Demuth 2008; Ko & Tarhule, 1994; Tate & Freeman, 2000), but their relevance
282 to ecohydrological studies is questionable. In terms of standardized indices, the SPI only
283 characterizes meteorological droughts, and the SSI cannot fully characterize the fundamental
284 shift that occurs when a watercourse falls dry for abnormally long periods of time (**Figure**
285 **3b**). Due to this shortcoming, several global drought studies have altogether excluded arid
286 regions from their analysis (e.g., Prudhomme et al., 2014; Wanders & Wada, 2015). While
287 adaptations to standardized indices exist (Stagge, Tallaksen, Gudmundsson, Van Loon, &
288 Stahl, 2015), a single index, to our knowledge, adequately characterizes hydrological
289 droughts in IRES. Developed by Van Huijgevoort, Hazenberg, Van Lanen, & Uijlenhoet
290 (2012), this approach combines i) a temporally variable threshold-level method, with ii)
291 thresholding based on consecutive zero-flow days, to identify droughts that span across
292 periods of zero and non-zero discharge, and exceed natural flow intermittence (**Figure 3**).

293

294 We propose that a new set of indices be used to improve our understanding of the linkages
295 between hydrological disturbance and ecological responses during droughts in IRES. We
296 briefly present three possible indices: the threshold-level method developed by (Van
297 Huijgevoort et al., 2012), a standardized index, and a spatially-explicit index. The first two
298 methods require long-term streamflow records while the last one is more appropriate for
299 intensively monitored catchments. These indices could complement existing composite
300 hydrological drought indices (Hayes, Svoboda, Wall, & Widhalm, 2011) to improve our
301 accounting of the effect of droughts on IRES.

302

303 The threshold-level method by Van Huijgevoort et al. (2012) yields a continuous time series
304 of estimated percentiles for both flowing and non-flowing conditions. Periods with percentile

305 values below or equal to a defined threshold (e.g., 10th or 20th percentile) are then considered
306 to be droughts, from which start- and end-dates can be computed as well as the magnitude,
307 severity, and duration of the drought. See Appendix 1 for details on how to calculate this
308 index.

309

310 A standardized drought index for IRES only requires adapting the SSI by using flow
311 intermittence (i.e., the number of zero-flow days) instead of mean discharge over the period
312 of interest (see calculation in Appendix 1). The resulting time series could complement the
313 SPI or SSI with, for example, values under -1.5 being considered severe droughts. Compared
314 to the threshold-level method by (Van Huijgevoort et al., 2012), this approach is more
315 comparable across regions and enables analysis at multiple time scales. However, it is likely
316 sensitive to the choice of probability distribution and fitting method, similarly to SSI
317 (Tijdeman, Stahl, & Tallaksen, 2020; Vicente-Serrano et al., 2012), and does not account for
318 depressed peak and average flow. The same procedure could also be applied to describe
319 hydrological droughts in terms of aquatic phases beyond flow cessation by instead using the
320 proportion of days with flowing water, non-flowing water and connected pools, disconnected
321 pools, or a dry channel (when this information is available, e.g., Sefton, Parry, England, &
322 Angell, 2019).

323

324 Considering the importance of the spatial dynamics of wetting and rewetting in IRES
325 networks, droughts should ideally also be described with spatially explicit indices at the
326 catchment scale. Similarly to indices based on discharge or flow intermittence, spatial
327 drought indices for IRES can rely on the probability of exceedance of landscape metrics
328 computed at regular intervals. An example landscape metric is the Dendritic Connectivity
329 Index (DCI). DCI is a network-wide indicator of longitudinal connectivity based on the
330 expected probability of an organism being able to move freely between two random points in
331 the network (Cote, Kehler, Bourne, & Wiersma, 2009). Reaches are considered to be
332 disconnected from the rest of the network when pools become disconnected or dry, or
333 because of physical barriers (e.g., waterfalls, weirs, dams). DCI was used by Jaeger et al.,
334 (2014) to quantify watershed-scale changes in connectivity resulting from increased flow
335 intermittence under climate change in the Verde River Basin, United States. Aside from DCI,
336 ecologically-scaled landscape indices tailored to IRES, like the average patch carrying
337 capacity and connectivity, can also be employed to express the potential effect of droughts on
338 network structure for a specific group of species of interest (Cid et al., 2020; Thibault Datry,

339 Bonada, & Heino, 2016; Vos, Verboom, Opdam, & Ter Braak, 2001). Monitoring data on the
340 aquatic state of all reaches within an IRES network can be acquired from sensor arrays (e.g.,
341 electrical resistance sensors; Jaeger & Olden, 2012), field observations by the general public
342 and scientists (Allen et al., 2019; Gallart et al., 2017; Sefton et al., 2019; van Meerveld,
343 Kirchner, Vis, Assendelft, & Seibert, 2019), or remote sensing (for larger streams and
344 watercourses with limited riparian vegetation, e.g., Bishop-Taylor, Tulbure, & Broich, 2018),
345 all of which can be complemented by spatiotemporal infilling procedures (Eastman, Parry,
346 Sefton, Park, & England, 2021).

347

348 Long-term data are essential for all drought indices to determine what constitutes normal
349 versus anomalous water levels (Van Loon, 2015). However, streamflow gauging data for
350 IRES are scarce and their interpretation is error-prone (van Meerveld et al., 2020; Zimmer et
351 al., 2020). IRES in semi-arid and arid zones are difficult to gauge, while in wetter climates,
352 flow intermittence occurs mostly in under-monitored low-order streams (Zimmer et al.,
353 2020). Although IRES comprise more than half of the global river network (Messenger et al.,
354 2021), less than a fifth of gauging stations monitor flow in IRES (based on the Global
355 Streamflow Indices and Metadata archive; Do, Gudmundsson, Leonard, & Westra, 2018;
356 Gudmundsson, Do, Leonard, & Westra, 2018). The average record length for IRES gauging
357 stations is also 7 years shorter than for stations on perennial water courses globally (25 and
358 32 years for IRES and perennial stations, respectively). In comparison, drought indices
359 usually require a minimum of 30 years of continuous data (Jain, Jain, & Pandey, 2014; Link,
360 Wild, Snyder, Hejazi, & Vernon, 2020). Synthetic time series of historical flow intermittence
361 can be generated (e.g., Jaeger et al., 2019; Yu, Bond, Bunn, Xu, & Kennard, 2018) but come
362 with significant uncertainty, especially given the intrinsically anomalous nature of droughts.
363 Further improvements in hydrometric monitoring, remote sensing, and hydrological
364 monitoring will thus be key to improve our ability to monitor droughts in IRES.

365 **3. The 'typical' ecohydrology of IRES**

366 **3.1. Temporal patterns of flow intermittence and ecological responses.**

367 During a typical drying-rewetting cycle, IRES shift from flowing conditions to pool and dry
368 riverbed phases. Whereas some IRES remain under a non-flowing pool phase throughout the
369 flow cessation event (e.g. Anna, Yorgos, Konstantinos, & Maria, 2009), others shift directly
370 from flowing to dry phases (e.g. Datry, 2012). During dry phases, some IRES maintain an

371 active underlying hyporheic zone (Boulton & Lake, 1992), while in others, the water level of
372 the hyporheic zone decreases quickly and becomes dry as well (Thibault Datry, 2012). Flow
373 resumption can happen as a sudden rewetting event with an advancing wetted front driven by
374 high discharge following rainfall (Cohen & Laronne, 2005; Corti & Datry, 2012), instigating
375 a rapid reversal of the sequence from dry to flowing phases. But rewetting can also occur
376 more steadily, when rainfall is localised to headwaters or when rewetting is driven by rising
377 groundwater levels (Stanley, Fisher, & Grimm, 1997; Tockner, Malard, & Ward, 2000).

378 During these temporal sequences of phases, strong environmental constraints occur on
379 aquatic organisms with typical steps (Thibault Datry et al., 2017). When flow recedes in
380 flowing channels, lateral aquatic habitats with fringing vegetation in the riparian zone
381 become isolated, which removes key habitats for animals that feed, shelter, spawn or emerge
382 in these areas (**Figure 4**). When drying continues, riffles are the first in-stream habitats to
383 disappear as pools become isolated in the channel. This represents an important step because
384 it virtually eliminates most rheophilic fish and invertebrates from local communities (Anna et
385 al., 2009). When a channel shifts from lotic to lentic conditions, biological communities also
386 change abruptly towards pond-like communities (Anna et al., 2009; Bonada et al., 2020; Hill
387 & Milner, 2018). However, if pools remain disconnected, many can become unviable for
388 most organisms due to high temperatures, low dissolved oxygen and concentrated nutrients
389 (Thibault Datry, 2017; Woelfle-Erskine et al., 2017). In some cases, active hyporheic inflow
390 can replenish pools with cool and oxygenated water (Anna et al., 2009; Bonada et al., 2020).
391 When drying continues, pools dry up and the complete disappearance of surface water is
392 clearly the most critical stage for most aquatic organisms, from microbes to fish (**Figure 4**).
393 Many organisms die, providing considerable pulses of food for terrestrial scavengers and
394 predators (Corti, Larned, & Datry, 2013; Steward, von Schiller, Tockner, Marshall, & Bunn,
395 2012). A subset of species have developed physiological adaptation to cope with desiccation
396 and can form a “seedbank” in the moist sediments, awaiting flow resumption to become
397 active again (Stubbington & Datry, 2013). Last, some organisms can seek refuge in the
398 underlying hyporheic zone (Stubbington, 2012; Vander Vorste, Malard, & Datry, 2016).
399 However, this is true only for hyporheic zones which do not desiccate completely as the dry
400 period persists (Pařil, Polářek, et al., 2019).

401 Hydrological signatures of flow cessation in IRES are strong and universal determinants of
402 aquatic biodiversity (Arscott, Larned, Scarsbrook, & Lambert, 2010; Bonada, Rieradevall, &

403 Prat, 2007; Leigh & Datry, 2017). This is particularly the case for flow intermittence, defined
404 as the proportion of the year without surface water flow. Flow intermittence has been shown
405 to be the main driver of invertebrate taxonomic richness in rivers and streams across different
406 continents and climate zones (Thibault. Datry, Larned, Fritz, et al., 2014). More generally,
407 the taxonomic richness of many aquatic phyla linearly decreases with increasing flow
408 intermittence (Thibault. Datry, Larned, & Tockner, 2014). At a given site, the duration of
409 drying events controls the survival of stranded aquatic organisms during dry phases (Pařil,
410 Polářek, et al., 2019) and the ability of the invertebrate seedbank to contribute to the
411 resilience of aquatic communities upon rewetting (Stubbington & Datry, 2013).

412 **3.2. Spatial patterns of flow intermittence and ecological responses.**

413 The spatial organisation of habitats has critical roles for biodiversity dynamics in IRES
414 networks. Notably, the co-occurrence at the network scale of flowing, non-flowing and dry
415 reaches leads to the simultaneous presence of lotic, lentic, and terrestrial communities in the
416 landscape (Thibault. Datry, Larned, & Tockner, 2014). The spatial arrangement, temporal
417 turnover, and connectivity of these three habitat conditions constantly vary with surface water
418 discharge and groundwater level fluctuations, in turn generating multiple colonisation and
419 extinction events in the landscape (Crabot, Heino, Launay, & Datry, 2020). Theoretical work
420 indicates that the distance between adjacent flowing sections within a river network is a
421 pivotal determinant of the distribution of aquatic organisms with low dispersal abilities
422 (Thibault Datry, Pella, Leigh, Bonada, & Hugueny, 2016). Recent empirical studies further
423 demonstrated that network fragmentation by drying influences invertebrate community
424 diversity and composition (Gauthier et al., 2020; Sarremejane et al., 2020). For example,
425 Gauthier et al. 2020 showed that physical distances among habitat patches that accounted for
426 drying better explained metacommunity dynamics in a set of ten intermittent river networks
427 than environmental distances.

428 More recently, research has explored the influence of the longitudinal configuration and
429 extent of drying on the aquatic biodiversity of river networks (Crabot et al., 2020;
430 Sarremejane et al., 2020; Sarremejane, Stubbington, et al., 2021). The dynamics of aquatic
431 invertebrate communities in river networks where drying occurs in headwaters, for example,
432 is very different from those in rivers in which drying occurs in downstream sections (Crabot
433 et al., 2020). Higher connectivity and refuge availability in downstream river sections may
434 promote a higher local richness, but lower beta diversity, in river networks where drying

435 occurs primarily in downstream sections compared to those where drying is predominantly
436 constrained to headwaters (Crabot et al., 2020). This is because connectivity to colonisation
437 sources such as refuges is higher in mainstems than in isolated headwaters (Brown and Swan
438 2010). Passive downstream drift from upstream habitats is more likely if drying occurs in the
439 downstream sections of a river network (Vander Vorste, Malard, et al., 2016). In contrast,
440 drying headwaters may only be recolonized through active upstream dispersal, which is rare
441 and ineffective for most aquatic taxa. Insect species with strong aerial dispersal capacities can
442 however overcome dispersal limitations among isolated headwaters (Sarremejane, Mykrä,
443 Bonada, Aroviita, & Muotka, 2017) and their assembly may not be impacted by the
444 configuration of drying (Cañedo-Argüelles et al., 2015). The presence of refuges such as
445 pools and hyporheic zones also tends to increase downstream, due to increased
446 geomorphological complexity (Jaeger, Sutfin, Tooth, Michaelides, & Singer, 2017),
447 increased mean annual discharge (Messenger et al., 2021) and enhanced surface water-
448 groundwater interactions (Malard, Tockner, Dole-Olivier, & Ward, 2002).

449 **4. Ecohydrological interactions in IRES during droughts**

450 **4.1. Abiotic implications of hydrological droughts**

451 The effects of droughts on river ecosystems, including flow cessation and riverbed drying can
452 be comparable to those occurring seasonally in intermittent rivers (Bogan, Boersma, & Lytle,
453 2015; Boulton, 2003). However, droughts increase the severity, duration, and spatial extent of
454 drying beyond usual seasonal drying conditions in IRES (Lake, 2011). During droughts,
455 rivers that typically stop to flow in scattered reaches for a few weeks per year may shrink to
456 disconnected pools or dry across their entire length for months (**Figures 5 & 6**; e.g., Hill et
457 al., 2019); reaches that normally recede into isolated pools from mid-summer until early
458 autumn may fully dry by early summer, rewetting only in winter; and ephemeral streams may
459 not flow for multiple years (e.g., 620 days; De Soyza, Killingbeck, & Whitford, 2004).
460 During a drought, the proportion of pools that dry and the distance between pools increase
461 compared to normal years, the size of remaining pools decreases (Vander et al., 2020),
462 sediment and litter desiccate further and deeper, and perennial springs may dry out as the
463 groundwater table falls.

464 The ecological response to drying during drought follows a ‘stepped’ pattern (Boulton, 2003)
465 whereby periods of gradual change are punctuated by rapid transitions as each shift of state
466 leads to the abrupt loss or fragmentation of a habitat (Boulton, 2003). During droughts, IRES

467 may reach new states in which ecosystems are pushed past additional steps, potentially
468 crossing irreversible thresholds.

469 Between shifts in aquatic states, the degradation of water quality is the primary driver of
470 ecological responses (Lake, 2011). Prolonged water deficit during a drought induces a suite
471 of physicochemical changes (Gómez, Arce, Baldwin, & Dahm, 2017) that occur faster and
472 are more severe than during regular flow cessation events, thus exposing the biota to extreme
473 conditions compared to normal years. For example, during a drought, temperature rose from
474 14 to 25°C and dissolved oxygen decreased from 12 to 4 mg L⁻¹ in 2 weeks in three pools of
475 the Albarine river in France (Datry, 2017), exceeding physiological thresholds for many
476 aquatic species (Vander Vorste, Mermillod-Blondin, Hervant, Mons, & Datry, 2016a).
477 Typically, dissolved oxygen, sediment size, and pool volume quickly decrease once riffle
478 become disconnected while temperature and conductivity increase, with salinity sometimes
479 reaching exceptionally high levels (Bae & Park, 2019; Golladay, Gagnon, Kearns, Battle, &
480 Hicks, 2004; Lind, Robson, & Mitchell, 2006; Obedzinski, Nossaman Pierce, Horton, &
481 Deitch, 2018; Woelfle-Erskine et al., 2017). As a supra-seasonal drought progressed in the
482 Wimmera River (Australia), for example, electrical conductivity in downstream reaches
483 increased from 4 x 10³ µS cm⁻¹ during the summer of the first year to 35 x 10³ µS cm⁻¹ the
484 third year (Lind et al. 2006; typical sea water conductivity: ~50 x 10³ µS cm⁻¹). Dissolved
485 oxygen may initially increase due to higher light penetration conditions (e.g., Kalogianni,
486 Vourka, Karaouzas, Vardakas, & Skoulikidis, 2017), but rising water temperature,
487 stratification, and the accumulation of organic matter and nutrients in stagnant pools
488 eventually lead to hypoxic events beyond the tolerance of species adapted to shorter flow
489 cessation events (Larimore, Childers, & Heckrotte, 1959; Woelfle-Erskine et al., 2017). In
490 Fay Creek in California, pools remained disconnected nearly twice as long during the third
491 year of the drought (2014) compared to the first year, pushing minimum dissolved oxygen in
492 several pools below 2 ppm, the lethal limit for resident salmonids (Woelfle-Erskine et al.,
493 2017). Animal-mediated nutrient cycling changes over time, P and N excretion steeply
494 declining owing to large reductions in biomass and shifts in assemblage structure of
495 macroconsumers (Hopper, Gido, Pennock, Hedden, Guinnip, et al., 2020). The concentration
496 of organic pollutants and toxicants increases (Boulton, 2003). Pools can also become filled
497 with exceptional amounts of terrestrial leaf litter during longer periods of flow disconnection
498 lasting into Autumn or if riparian plants become water stressed, further lowering oxygen
499 levels and causing ‘blackwater’ conditions when the water turns a deep brown colour from

500 leached dissolved organic carbon (Larimore et al., 1959; McMaster & Bond, 2008). Under
501 drought conditions, habitat availability, dissolved oxygen levels, temperature, groundwater
502 depth, and salinity may cross lethal thresholds for an increasing number of animal and plant
503 species (Aspin, Hart, et al., 2019; Garssen, Verhoeven, & Soons, 2014; Gough, Landis, &
504 Stoeckel, 2012; Hopper, Gido, Pennock, Hedden, Frenette, et al., 2020; Woelfle-Erskine et
505 al., 2017).

506 As a drought continues and pools shrink to abnormally low levels, the distribution and
507 physicochemical properties of groundwater sources increasingly drive abiotic conditions
508 (Larsen & Woelfle-Erskine, 2018; Schlief & Mutz, 2011). Pool temperature can remain
509 stable throughout the drought, or may even decrease as cold groundwater inflow becomes a
510 dominant source (Larsen & Woelfle-Erskine, 2018; Schlief & Mutz, 2011). Most critical for
511 the survival of resident organisms, however, is the contribution of groundwater to dissolved
512 oxygen levels. Groundwater typically contributes low-oxygen water to watercourses (Hansen,
513 1975; Malard & Hervant, 1999). In a German lowland IRES under drought, Schlief & Mutz
514 (2011) attributed severe reductions in oxygen concentrations following pool disconnection to
515 the inflow of deoxygenated groundwater. However, temperature, oxygen, and conductivity
516 are highly variable across groundwater sources. For instance, inflows of young groundwater
517 (with $DO > 5 \text{ mg L}^{-1}$) maintained relatively high dissolved oxygen in pools and promoted
518 water movement in salmon-bearing IRES during the great California drought (2011-2017),
519 potentially enhancing gas exchange across the air-water interface and preventing stratification
520 (Larsen & Woelfle-Erskine, 2018). Groundwater seeps have also been shown to provide the
521 only available habitat for rheophilic taxa after flow cessation (Bogan, Leidy, Neuhaus,
522 Hernandez, & Carlson, 2019). Groundwater sources that maintain tolerable habitat conditions
523 during regular flow cessation events and in the early stages of a drought may, however,
524 disappear as a drought slowly propagates from surface water to groundwater (Van Loon,
525 2015).

526 Once pools have dried, and without flow resumption, sediment moisture decreases and
527 temperature increases as drought condition persist. Gough, Landis, & Stoeckel (2012)
528 recorded daily peaks in dry streambed temperature of 45°C to 50°C in Opintlocco Creek,
529 Alabama (U.S.). Deeper sediment is characterized by lower temperatures and greater thermal
530 inertia, buffering organisms from large diel variations in temperature (Gough et al., 2012).

531 Eventually, however, even deeper sediment, litter, and cavities that usually provide perennial
532 refuge during regular flow intermittence become fully dry.

533 Abiotic conditions generally follow typical trajectories after flow cessation in normal years,
534 but during droughts, contrasting responses can be observed from year to year, between
535 neighbouring catchments, among reaches within a catchment, and even from pool to pool. In
536 constrained river reaches with impervious substrate, overhanging vegetation, and upstream
537 influx of groundwater, pools may subsist for much longer, while other sections may fully dry
538 out (Obedzinski et al., 2018). As a drought progresses, heterogeneity in abiotic conditions
539 first increases among habitat patches when flow ceases and pools become disconnected. Each
540 pool follows a different trajectory that is contingent on microhabitats (e.g., pool geometry,
541 shading, groundwater influx) and community assemblage (Hopper, Gido, Pennock, Hedden,
542 Guinnip, et al., 2020). Woelfle-Erskine et al. (2017) documented lethal dissolved oxygen
543 levels together with high conductivity in most pools, yet some pools maintained relatively
544 high dissolved oxygen despite high conductivity. The bottom of pools may be microsites of
545 high dissolved oxygen (Woelfle-Erskine et al., 2017) or completely anoxic and stratified
546 (Schlief & Mutz, 2011). Owing to this heterogeneity in site responses, reaches and pools
547 whose usual trajectory in abiotic conditions makes them refuges during periods of seasonal
548 flow intermittence may become ecological traps during droughts (Vander et al., 2020).

549

550 **4.2. Ecological resistance and local processes**

551

552 As drought progresses, discharge, water level and aquatic habitat size and connectivity
553 decrease, leading to successions of habitat losses that may lead to changes in community
554 composition in both perennial and intermittent reaches of a river network (Chadd et al., 2017;
555 Herbst, Cooper, Medhurst, Wiseman, & Hunsaker, 2019). The responses of IRES-inhabiting
556 organisms to droughts depend on their traits and ability to withstand or avoid severe drying
557 conditions (Robson, Chester, & Austin, 2011). Traits promoting resistance to predictable
558 drying events may include strategies such as aerial respiration, low-oxygen and high-
559 temperature tolerances, desiccation-resistances, and short life-cycle (Bonada et al., 2007;
560 Matthews & Marsh-Matthews, 2003; Richards, 2010). Typically, these traits have been found
561 in greater abundances in communities exposed to drought (Aspin, Khamis, et al., 2019;
562 Bêche & Resh, 2007; Herbst et al., 2019) and in greater proportion in IRES than perennial
563 communities (Leigh et al., 2016; Timoner, Colls, Acuña, & Sabater, 2019). Therefore, IRES
564 communities are sometimes thought to be more resistant and/or resilient to drought than

565 perennial communities because adaptations to drying could confer advantages during
566 droughts (Hill et al., 2019; Sarremejane et al., 2020). However, aquatic communities in IRES
567 are assembled depending on species capacity to persist during, or recolonize between, drying
568 phases of given characteristics, including severity, duration, timing and frequency. Droughts,
569 by modifying intermittent phase characteristics, could strongly alter IRES communities
570 adapted to such a predictable drying regime (Bogan & Lytle, 2011; Jaeger et al., 2014).

571
572 In IRES, the duration of the dry phase is a key driver of organism persistence (Colls,
573 Timoner, Font, & Sabater, 2020; Pařil, Polářek, et al., 2019; Pernecker, Mauchart, & Csabai,
574 2020; Vadher, Millett, Stubbington, & Wood, 2018). How much a drought extends this phase
575 therefore strongly determines organism survival and post-drying community composition in
576 IRES. Desiccation-resistance strategies can allow organism persistence during dry phases of
577 several months to years. These strategies include dormancy at different life stage for insects
578 (e.g. Stoneflies: Bogan, 2017; fishflies: Cover, Seo, & Resh, 2015, caddisflies: Salavert,
579 Zamora-Muñoz, Ruiz-Rodríguez, Fernández-Cortés, & Soler, 2008) or fish (African
580 lungfish; Fishman, Pack, Delaney, & Galante, 1986) or protective pigment and cell structures
581 in algal and bacterial biofilms (Colls et al., 2019; Gionchetta, Oliva, Menéndez, Lopez, &
582 Anna, 2019; Robson, 2000). For example, Jenkins & Boulton (2007) showed that
583 microorganisms such as Rotifers and Cladoceran could be found in sediments rewetted after a
584 20-yr dry phase, but Cladoceran abundances decreased drastically between their 6-yr and 20-
585 yr dry phase treatments. These strategies, conceptualized as temporal dispersal (Buoro &
586 Carlson, 2014), allow organisms to persist locally and recolonize quickly at rewetting, but
587 strongly depend on the duration of the dry period. Some organisms with no specific
588 dormancy forms such as fishes (Kawanishi, Inoue, Dohi, Fujii, & Miyake, 2013; Rodríguez-
589 Lozano, Leidy, & Carlson, 2019) and invertebrates (Golladay et al., 2004; Gough et al., 2012;
590 Pařil, Polářek, et al., 2019; Pernecker et al., 2020; Stubbington, Gunn, Little, Worrall, &
591 Wood, 2016; Stubbington, Sarremejane, & Datry, 2019) may find refuge in the humid
592 subsurface sediment where they can subsist for a few days to months. For example, Pařil et
593 al., (2019) showed that 80% of the invertebrate species of an intermittent river community
594 could persist in dry sediments but richness decreased exponentially with the duration of the
595 dry phase and half of the species died within the first 60 days of drying. Similarly, small
596 benthic fishes of the genus *Cobitis* sp. can survive up to 40 days in dry sediments (Kawanishi
597 et al., 2013) and *Uniomorus tetralasmus* mussels up to 30 weeks in moist sediment (Gough et
598 al., 2012). If the dry phase extends beyond these thresholds, mass mortality events are likely.

599 Droughts could thus induce important community and population changes in IRES if drying
600 exceeds the duration or intensity that organisms experience seasonally and have developed
601 adaptation for (Figure 7, Aspin, Hart, et al., 2019; Aspin, Khamis, et al., 2019). Crossing
602 these critical thresholds could lead to long-term and irreversible changes in population
603 dynamics and community composition, particularly if negative responses are synchronized
604 within the river network (Sarremejane, Stubbington, et al., 2021). Such changes can be
605 sudden, and few instances have been documented. Identifying thresholds after which
606 communities or population dynamics shift is therefore a pressing research need.

607

608 Survival during a drought also depends on the severity of drying, which usually increases
609 with drought duration. Remnant pools serve as refuge for many invertebrates (Burk &
610 Kennedy, 2013), fishes (Vander et al., 2020) and amphibians (Zylstra, Swann, & Steidl,
611 2019), whose populations rely on the persistence of these habitats to survive as the river
612 network contracts. During severe droughts, pools may fully dry, after which the only *in situ*
613 refugia left for aquatic animals are damp sediment and litter, crayfish burrows, and the
614 hyporheic zone (Chester & Robson, 2011). Sediment moisture can be an important factor
615 determining organism persistence in the substrate during a dry phase for biofilms (Gionchetta
616 et al., 2019), invertebrates (Stubbington & Datry, 2013) and fishes (Coleman, Raadik,
617 Pettigrove, & Hoffmann, 2017). During droughts the water table may recede below the
618 hyporheic zone, leading to increased mortality of invertebrates that typically find refuge in
619 the subsurface (Pernecker et al., 2020; Vadher et al., 2018; Vander Vorste, Mermillod-
620 Blondin, et al., 2016b). For example, Vander Vorste, Mermillod-Blondin, et al. (2016)
621 showed in a mesocosm experiment that the survival of Gammarids decreased by 39% as the
622 water table decreased below 30 cm. Riparian vegetation also plays a key role in preserving
623 streambed moisture through shading, which promotes invertebrate (Lymbery et al., 2021) and
624 biofilm (Colls et al., 2019) survival during dry periods. Intense droughts can lead to earlier
625 riparian tree defoliation and mortality, which increase streambed solar exposition and drying
626 severity, causing higher mortalities of the stream biota. As groundwater levels decrease
627 beyond the reach of roots during severe drought, the mortality of riparian trees may increase
628 (Zhou et al., 2020).

629

630 The success of desiccation-resistance strategies may also depend on the timing of a drying
631 event. Life cycles of IRES-inhabiting organisms are often synchronized with a predictable
632 drying phase (Williams, 1996). The earlier onsets of drying during drought could hence affect

633 species with specific phenology, leading for example to earlier insect emergence and
634 shortened aquatic life cycles (Leberfinger, Bohman, & Herrmann, 2010). In the
635 Mediterranean climate, where dry phases are considered highly seasonal and predictable
636 (Tonkin, Bogan, Bonada, Rios-Touma, & Lytle, 2017), caddisflies of the genus *Mesophylax*
637 sp. emerge before the onset of the drying phase, aestivate as adults in karstic caves and then
638 recolonize intermittent streams at rewetting in autumn (Salavert et al., 2008). The success of
639 such strategies could be compromised if drought induces earlier drying events, not allowing
640 species to complete their aquatic larval stages. Similarly, *Demosgnathus fuscus* salamander
641 larvae (North Carolina, U.S.A.) are strictly aquatic from the time they hatch (August to
642 October) until metamorphosis the following spring, such that free-flowing water is critical for
643 larval survival during this period of the year (Price, Browne, & Dorcas, 2012). Finally, by
644 altering river network connectivity earlier in the year, droughts can also prevent longitudinal
645 migration, stopping fish from reaching in-stream refugia and resulting in reproductive failure
646 (e.g., anadromous *Oncorhynchus kisutch* coho salmon, Woelfle-Erskine et al., 2017;
647 potamodromous *Chasmistes cujus* Cui-ui, Scopettone et al., 2015).

648

649 The indirect role of biotic interactions like predation and competition in shaping the
650 ecological impacts of drought in IRES is poorly studied (Bond, Lake, & Arthington, 2008;
651 Boulton, 2003). While the relative role of local and regional processes in shaping community
652 assembly is increasingly well-studied in IRES (Cañedo-Argüelles et al., 2020; Rolls, Heino,
653 & Chessman, 2016), the relative strength of environmental filters versus biotic interactions in
654 determining population and community responses to drying has received comparatively little
655 attention. As habitats shrink, animal densities increase in remnant pools and refugia, leading
656 to crowding, increased predation and competition (Matthews & Marsh-Matthews 2003).
657 Competition and predation may even prevent species from accessing refuges (Magoulick &
658 Kobza, 2003). For instance, competitive exclusion of steelhead salmon (*Oncorhynchus*
659 *mykiss*) from deeper pools by coho salmon may drive differences in response to drought
660 among these two species in intermittent streams of California (Woelfle-Erskine et al. 2017).
661 This phenomenon is also evidenced by shifts in dominance between native and non-native
662 species after droughts (see Section 4.5). As the ratio of aquatic to terrestrial habitat decreases
663 in the channel, aquatic organisms become increasingly vulnerable to terrestrial predation as
664 well (Magoulick & Kobza, 2003). Terrestrial predation of smaller freshwater mussels was an
665 important driver of mortality in *Westralunio carteri* after emersion and may explain size-
666 based differences in burrowing behavior observed during a drought in south-western

667 Australia (Lymbery et al., 2021). We expect that shifts in biotic interactions observed during
668 seasonal drying are amplified by more intense and prolonged drying, yet the potential
669 crossing of tipping points during droughts (e.g., local extirpation of a predator or competitor)
670 may lead to a deeper reshuffling of interspecific relationships.

671

672 **4.3. Ecological resilience and regional processes**

673

674 Droughts are spatially extended events that impact entire river networks, inducing extended
675 changes in aquatic habitat configurations and increased fragmentation (**Figure 6**, Allen et al.,
676 2019; Jaeger et al., 2014; Sefton et al., 2019). Such extended changes hinder organism
677 resilience — i.e., their capacity to recolonize and re-establish viable populations post-drought
678 (Chester & Robson, 2011) — by affecting survival in refuges and connectivity to potential
679 recolonization sources. Organism resilience depends on functional attributes like dispersal
680 capacity, life-cycles and reproductive strategies (Robson et al., 2011). For example,
681 multivoltine organisms with strong dispersal capacity and/or high number of propagules may
682 be able to recover from drought more quickly than long-lived organisms with weak dispersal
683 capacity (Bogan et al., 2017; Robson et al., 2011). Algae and bacteria constituting biofilms
684 can recover within a few days/weeks of water resumption from dormant forms and through
685 drift (Romaní & Sabater, 1997). Aquatic invertebrate community recovery from drought in
686 IRES typically takes from six months to a few years, longer than recovery from regular flow
687 intermittence (Hill et al., 2019; Pařil, Polářek, et al., 2019). Recolonization by invertebrates
688 may occur through drift, active aquatic migration (Eveleens, McIntosh, & Warburton, 2019;
689 Pařil, Leigh, et al., 2019), and/or overland aerial dispersal (Bogan & Boersma, 2012; Cañedo-
690 Argüelles et al., 2015). Fish mainly recolonize from downstream or perennial pool refuges
691 (Davey & Kelly, 2007), usually within a few days to months (Magalhães, Beja, Schlosser, &
692 Collares-Pereira, 2007; Magoulick & Kobza, 2003). However, biological resilience to
693 drought in IRES also depends on local resistance (see previous section), connectivity to and
694 distance from regional refuges, and time between drought events (Jaeger et al., 2014;
695 Sarremejane, Stubbington, et al., 2021).

696 Increasing drying extent may reduce recovery potential by increasing the proportion of
697 populations impacted by low flow and drying conditions across the river network and thus
698 limiting rescue effects post-disturbance (Crabot et al., 2020; Sarremejane, Stubbington, et al.,
699 2021; Zelnik, Arnoldi, & Loreau, 2018). Sarremejane et al. (2021) showed that increasing

700 drying extent during drought could lead to synchronous declines in invertebrate populations
701 across an intermittent river network, particularly for species with low resistance and/or
702 resilience capacity. Such decline drastically increased population extinction risks after three
703 drought years with 50% of the network fragmented by drying. Drought may particularly
704 impede community and population recovery if perennial refuges become intermittent and
705 disconnected (Bogan & Lytle, 2011; Hopper, Gido, Pennock, Hedden, Frenette, et al., 2020;
706 Vander et al., 2020). Many mobile organisms such as amphibians, fish and insects may find
707 refuge in specific perennial pools or perennial river sections, sometimes with strong fidelity,
708 and recolonize intermittent sections post rewetting (Bogan et al., 2019; Chester & Robson,
709 2011; Davey & Kelly, 2007). Thus, the contraction and loss of those habitats may have long
710 term impacts on community and population structures at local and regional scales (Bêche,
711 Connors, Resh, & Merenlender, 2009; Bogan et al., 2015; Bogan & Lytle, 2011; Sponseller,
712 Grimm, Boulton, & Sabo, 2010).

713 The connectivity and distance of a community to perennial refuge is an important driver of
714 post-drying community composition (Bogan & Boersma, 2012; Bogan et al., 2015;
715 Sarremejane et al., 2020; White et al., 2018). Community recovery from drying and drought
716 therefore vary among sites within a network depending on their connectivity (Gauthier, Le
717 Goff, Launay, Douady, & Datry, 2021; Sarremejane, Truchy, et al., 2021). Isolated
718 headwaters, for instance, are likely to take longer to recover from disturbance than more
719 connected downstream sections (Tornwall, Swan, & Brown, 2017). Whether a drought
720 predominantly affects headwaters or downstream reaches may thus have contrasting
721 outcomes on the composition of communities, their spatial variability (i.e. β diversity; Crabot
722 et al., 2020) and resilience. Therefore, increasing drying extent during drought could affect
723 regional processes, leading to important changes in metacommunities and metapopulation
724 dynamics, particularly if refuges are lost or if drought is too extended or frequent to allow
725 resilience.

726

727 The frequency of drying and rewetting events can alter population and community
728 persistence, by affecting the time between drying events and thus resilience capacity (Crabot
729 et al., 2020; Leigh & Datry, 2017). If the frequency of drying events is high, many species
730 may not have time to recover during short flowing phases, hence, diversity typically declines
731 with increasing drying frequency (Leigh & Datry, 2017). The proportion of multivoltine
732 organism abundances typically increases or remain constant compared to semivoltine insects

733 during droughts (Aspin, Khamis, et al., 2019; Herbst et al., 2019), indicating that organism
734 with shorter and multiple cycles per year could be better able to cope with droughts, as they
735 can recolonize and develop quickly between drying events. Short rewetting events during
736 droughts often caused by precipitation could also allow the invertebrate seedbank
737 (Stubbington & Datry, 2013) and biofilms (Gionchetta et al., 2019) to persist by maintaining
738 moisture within the sediment (**Figure 7**). More frequent droughts may however lead to long
739 term changes in community compositions within IRES networks if the time between drought
740 events is too short to allow long-lived organism populations to recover between drought
741 events.

742

743 **4.4. Community responses across flow intermittence regimes**

744

745 Comparisons of stream community responses to drought across reaches with different
746 intermittence regimes have yielded mixed evidence (Bêche et al., 2009; Cañedo-Argüelles et
747 al., 2020; Herbst et al., 2019; Hill et al., 2019; Rolls et al., 2016; Sarremejane et al., 2020;
748 Sarremejane, Stubbington, et al., 2021; Westwood, England, Johns, & Stubbington, 2020).
749 Several studies found congruent drought-induced changes in community composition across
750 streams with different permanence regimes (Bêche et al., 2009; Herbst et al., 2019). For
751 example, Bêche et al. (2009) showed that invertebrate community composition of perennial,
752 intermittent and ephemeral streams in semi-arid California all shifted during a drought and
753 had not returned to an initial (pre-drought) state even 8 years after the end of the drought. In
754 the same study, fish populations were equally affected by drought across intermittence
755 regimes but recovery differed; whereas fish populations recovered within 2 years in perennial
756 sections, they took 5 years in ephemeral streams and did not recover in intermittent sites,
757 likely due to differences in connectivity to refuges among sites. Elsewhere, responses to
758 drought have been shown to vary across permanence regimes. Hill et al. (2019) and
759 Sarremejane et al. (2019) observed that the responses of invertebrate communities to drought
760 in English streams with different permanence regimes differed, and that near-perennial
761 communities (i.e., experiencing drying only during drought events) took longer or did not
762 completely recover by the end of their study compared to communities in more intermittent
763 sites (which also showed variable recovery trajectories). These studies therefore suggest that
764 intermittent river communities can, in some instances, be more resilient to droughts than
765 those of perennial rivers. What drives these contrasts in long-term responses to drought
766 among locations remains unresolved — community resilience may depend on the studied

767 organism (e.g., fish vs. macroinvertebrate; Bêche et al., 2009) and their traits, the influence of
768 additional stressors, or on the severity of the drought compared to that experienced over
769 evolutionary times. Further research is needed to determine under which biotic and abiotic
770 conditions community response to drought may differ along a gradient of intermittence.

771

772 From a metacommunity perspective, variable responses among reaches of distinct
773 permanence regimes across a river network may enhance recovery because asynchronous
774 responses between communities promote rescue effects post-disturbance (Sarremejane,
775 Stubbington, et al., 2021). Increasing variability among communities (i.e., beta diversity) may
776 occur at the network scale during drought if habitat conditions become more heterogeneous
777 and connectivity decreases (Rolls et al., 2016). Alternatively, extreme droughts may also
778 induce declines in beta diversity if communities become spatially homogeneous due to the
779 selection of a resistant subset of taxa from the regional species pool (γ diversity; Chase,
780 2007).

781

782 Most research on community response to drought in IRES networks have focussed on
783 responses of perennial sections and refuges (Bogan & Lytle, 2011; Sponseller et al., 2010).
784 For example, Bogan & Lytle (2011) showed that the drying of permanent pools in a formerly
785 perennial river network during a supra-seasonal drought caused drastic shifts in invertebrate
786 communities. Following the drought, community composition did not recover and instead
787 reached a new stable state: large-bodied top predators present before the drought were
788 replaced by more abundant and smaller meso-predators. Permanent shifts in the flow regime
789 of river sections from perennial to intermittent following a drought are likely to have long-
790 term impacts on aquatic communities in IRES networks, particularly if perennial refuges run
791 dry (**Figure 7**). Rapidly improving our understanding of these shifts from perennial to
792 intermittent regimes is key as they become more common with climate change and increasing
793 water demands.

794

795 **4.5. Droughts in interaction with anthropogenic stressors**

796 Droughts in IRES often co-occur with anthropogenic stressors (Thibault, Datry, Larned, &
797 Tockner, 2014). These stressors include climate change, fragmentation by dams, biological
798 invasions, water abstraction and pollution, and land-use alterations. The impacts of droughts
799 on IRES are likely to accentuate — or be accentuated by — the effect of other anthropogenic

800 stressors as multiple interacting stressors may lead to synergistic impacts on the ecosystems
801 (but see Jackson, Loewen, Vinebrooke, & Chimimba, 2016). However, while the multi-
802 stressor environments framework has bloomed in the past decade, particularly in freshwater
803 ecosystems (Ormerod, Dobson, Hildrew, & Townsend, 2010), its application in IRES is still
804 in its infancy (Marshall & Negus, 2018), so that there is a dearth of evidence on how drought
805 interacts with other stressors in these ecosystems.

806

807 As the climate is changing, droughts may not only become more frequent and severe, but also
808 be more frequently associated with other extreme events, including floods and heatwaves
809 (Derouin, 2021). For example, drought and floods are two extremes with contrasting
810 characteristics, and traits conferring resistance to drought may differ from those conferring
811 resistance to floods (Eveleens et al. 2019). The combined occurrence or succession of these
812 contrasting extreme events may thus strongly impact freshwater ecosystems (Woodward,
813 Bonada, Feeley, & Giller, 2015). Heatwaves may also accentuate the effect of droughts by
814 leading to faster drying of — and increased temperatures in — aquatic habitats remaining
815 after flow cessation (e.g., disconnected pools). Such warming may induce increased and
816 premature organism mortality, as well as changes in microbial (Arias Font, Khamis, Milner,
817 Smith, & Ledger, 2021) and fish activity (Mameri, Branco, Ferreira, & Santos, 2020).
818 Drought can also trigger wildfires (Littell, Peterson, Riley, Liu, & Luce, 2016), which in turn
819 can have deleterious effects on amphibians (Zylstra et al., 2019), fishes (Turner, Osborne,
820 McPhee, & Kruse, 2015) and invertebrates (Robson, Chester, Matthews, & Johnston, 2018;
821 Verkaik et al., 2015) populations and communities. For example, Zilsta et al. (2019) showed
822 that Leopard frog populations declined during drought years and downstream of sites exposed
823 to wildfires due to increased post-fire erosion. Robson et al. (2018) also found that fires and
824 droughts could have antagonistic effects on the invertebrate communities of Australian
825 streams. For example, the abundance of filter-feeder invertebrates increased with fire, which
826 counterbalanced the negative effect of drought on this trophic guild.

827

828 Combined alterations in flow and thermal regimes caused by drought can also favour
829 establishment and dominance of non-native species of riparian plants (Glenn & Nagler, 2005;
830 Scott, Reynolds, Shafroth, & Spence, 2018), fish (Bêche et al., 2009; Bernardo, Ilhéu,
831 Matono, & Costa, 2003; Hopper, Gido, Pennock, Hedden, Frenette, et al., 2020; Jaeger et al.,
832 2014; Rogosch et al., 2019; Whiterod, Hammer, & Vilizzi, 2015) and invertebrates (Kouba et
833 al., 2016; Larson, Magoulick, Turner, & Laycock, 2009) in IRES. Such invasions are

834 facilitated if invasive species are more resilient and resistant to drought than native species.
835 For example, Kouba et al. (2016) found that non-native crayfish were able to survive longer
836 than native European species during drought because of their capacity to burrow deeper into
837 the sediment. Drought can also benefit non-native predators at the expense of small-bodied
838 native species (Propst, Gido, & Stefferud, 2008), presumably owing to habitat contraction
839 and increased biotic interactions (Magoulick & Kobza, 2003). Conversely, drought can limit
840 the progression of invasive species by increasing their mortality or decreasing their dispersal
841 through increasing fragmentation, the same way natural intermittence may prevent the
842 establishment of non-native species (Bogan et al., 2019; Coleman et al., 2017). However,
843 evidence of drought-induced stalling of non-native species establishment in IRES is lacking.
844 Anecdotal observation of Asian clam (*Corbicula fluminea*) mortality due to hypoxia in
845 drought-stricken stream reaches of southwestern Georgia (U.S.; Golladay et al., 2004), range
846 expansion limitations of Brown trout (*Salmo trutta*) in the upper reaches of the Lerderberg
847 River (Australia; Closs & Lake, 1996) and the extirpation of exotic common carp (*Cyprinus*
848 *carpio* L.) populations from Granite Creeks in Victoria (Australia; Lake, 2003) are the only
849 examples in IRES known to the authors. Therefore, it is likely that recurrent drought tends to
850 accelerate rather than slow the progression of invasive species within IRES networks.

851
852 Anthropogenic activities in IRES catchments, including agriculture or wastewater treatment,
853 can induce increased concentrations of water pollutants or eutrophication, whose effects on
854 IRES can be amplified when combined with drought. For example, as water recedes during
855 drought, anoxia and the concentration of chemical compounds may increase to unsafe levels
856 for aquatic biota taking refuge in pools (Palma et al., 2020). Overall, however, we know little
857 about the interactions between droughts and human induced pollution, particularly in IRES.

858
859 Finally, fragmentation caused by dams and weirs is likely to compound the effect of droughts
860 by limiting recolonization capacity post-drought. Under non-drought conditions, biodiversity
861 dynamics in an IRES networks were shown to be overwhelmingly driven by permanent
862 fragmentation, including weirs and small retention ponds, rather than by temporary
863 fragmentation from drying (Gauthier et al. 2021), suggesting that anthropogenic barriers can
864 be a strong determinant of diversity patterns in drying river networks. Recently, Marshall,
865 Lobegeiger & Starkey (2020) showed that instream barriers such as weirs reduced fish
866 movement opportunities by more than 70% during and following a two-year drought in south
867 Australia, compromising fish access to refuges and post-disturbance recovery.

868 **5. Conclusion and perspectives**

869 Although a rich body of literature exists on the effects of droughts on flowing waters,
870 research on their impacts on IRES ecosystems remains limited. Confusion in terminology and
871 the lack of tools and data to assess the hydrological responses of IRES to drought may have
872 hindered development of drought research in IRES. We found that 43% of studies confused
873 the term drought with seasonal drying and that a minority of studies measure droughts in a
874 transferable way. Studies on ecological responses to drought in IRES networks are still rare
875 and limited to a few climatic zones, countries, organisms, and mainly explored in perennial
876 sections, most probably because disentangling responses between natural flow intermittence
877 and drought remains a challenge. By accentuating the severity, duration, and extent of drying
878 across IRES networks, droughts may cause irreversible ecohydrological changes if tipping
879 points are crossed and resilience is compromised. Network-scale perspectives encompassing
880 a gradient of flow intermittence are needed to explore the drivers of ecological responses to
881 droughts in IRES.

882 We identified interdisciplinary research directions (Table 2) whose pursuit should improve
883 our understanding of the hydrological, ecological and socio-economical responses of IRES to
884 drought. These research directions are non-exhaustive but represent gaps that should be
885 addressed as priorities to develop further drought-research in IRES. In this review, we strictly
886 focused on ecological responses to drought at the scale of populations and communities yet
887 we also lack a synthesis of the effects of droughts on the biogeochemistry and ecosystem
888 services of IRES (Arce et al., 2019; Datry et al., 2018; Table 2). As droughts are
889 unpredictable and their legacy on hydrological and ecological processes may last for years,
890 additional long-term monitoring of IRES networks is needed to capture the effects of extreme
891 events on these ecosystems and measure their resilience (Kovach et al., 2019; Table 2).
892 Research involving ecologists and hydrologists could help develop metrics for identifying
893 tipping points beyond which the hydro-ecological resilience capacity of IRES is
894 compromised (Table 2). More generally, increased collaboration between hydrologists,
895 ecologists, social scientists and managers is needed to explore the impacts of droughts on
896 IRES and the adverse effects of shifts from perennial to intermittent regimes from a socio-
897 ecological perspective (Table 2). Such interdisciplinary research could help designing nature-
898 based solutions (Maes & Jacobs, 2017) to ensure the resilience of IRES hydro-ecosystems
899 and dependent socio-economical systems in a changing and uncertain climatic future.

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912 **Data availability statement**

913 The data used in this review will be deposited on an open repository such as figshare.

914

915

916 **References**

917 Allen, D. C., Kopp, D. A., Costigan, K. H., Datry, T., Hugueny, B., Turner, D. S., ... Flood,
918 T. J. (2019). Citizen scientists document long-term stream flow declines in intermittent
919 rivers of the desert southwest. *Freshwater Science*, 38(2).

920 <https://doi.org/10.1086/701483>.

921 Anna, A., Yorgos, C., Konstantinos, P., & Maria, L. (2009). Do intermittent and ephemeral
922 mediterranean rivers belong to the same river type? *Aquatic Ecology*, 43(2), 465–476.

923 <https://doi.org/10.1007/s10452-008-9176-9>

924 Arce, M. I., Mendoza-Lera, C., Almagro, M., Catalán, N., Romaní, A. M., Martí, E., ... von
925 Schiller, D. (2019). A conceptual framework for understanding the biogeochemistry of
926 dry riverbeds through the lens of soil science. *Earth-Science Reviews*, 188, 441–453.

927 <https://doi.org/10.1016/J.EARSCIREV.2018.12.001>

- 928 Arias Font, R., Khamis, K., Milner, A. M., Smith, G. H. S., & Ledger, M. E. (2021). Low
929 flow and heatwaves alter ecosystem functioning in a stream mesocosm experiment.
930 *Science of the Total Environment*, 777, 146067.
931 <https://doi.org/10.1016/j.scitotenv.2021.146067>
- 932 Arscott, D. B., Larned, S., Scarsbrook, M. R., & Lambert, P. (2010). Aquatic invertebrate
933 community structure along an intermittence gradient: Selwyn River, New Zealand.
934 *Journal of the North American Benthological Society*, 29(2), 530–545.
935 <https://doi.org/10.1899/08-124.1>
- 936 Aspin, T. W. H., Hart, K., Khamis, K., Milner, A. M., O’Callaghan, M. J., Trimmer, M., ...
937 Ledger, M. E. (2019). Drought intensification alters the composition, body size, and
938 trophic structure of invertebrate assemblages in a stream mesocosm experiment.
939 *Freshwater Biology*, 64(4), 750-760. <https://doi.org/10.1111/fwb.13259>
- 940 Aspin, T. W. H., Khamis, K., Matthews, T. J., Milner, A. M., O’Callaghan, M. J., Trimmer,
941 M., ... Ledger, M. E. (2019). Extreme drought pushes stream invertebrate communities
942 over functional thresholds. *Global Change Biology*, 25(1), 230–244.
943 <https://doi.org/10.1111/gcb.14495>
- 944 Bae, M. J., & Park, Y. S. (2019). Evaluation of precipitation impacts on benthic
945 macroinvertebrate communities at three different stream types. *Ecological Indicators*,
946 102(September 2018), 446–456. <https://doi.org/10.1016/j.ecolind.2019.02.060>
- 947 Bêche, L. A., Connors, P. G., Resh, V. H., & Merenlender, A. M. (2009). Resilience of fishes
948 and invertebrates to prolonged drought in two California streams. *Ecography*, 32(1),
949 778–788. <https://doi.org/10.1111/j.1600-0587.2009.05612.x>
- 950 Bêche, L. A., & Resh, V. H. (2007). Biological traits of benthic macroinvertebrates in
951 California mediterranean-climate streams: Long-term annual variability and trait
952 diversity patterns. *Fundamental and Applied Limnology*, 169(1), 1–23.
953 <https://doi.org/10.1127/1863-9135/2007/0169-0001>
- 954 Bernardo, J. M., Ilhéu, M., Matono, P., & Costa, A. M. (2003). Interannual variation of fish
955 assemblage structure in a Mediterranean river: Implications of streamflow on the
956 dominance of native or exotic species. *River Research and Applications*, 19(5–6), 521–

- 957 532. <https://doi.org/10.1002/rra.726>
- 958 Bishop-Taylor, R., Tumbure, M. G., & Broich, M. (2018). Evaluating static and dynamic
959 landscape connectivity modelling using a 25-year remote sensing time series. *Landscape*
960 *Ecology*, *33*(4), 625–640. <https://doi.org/10.1007/s10980-018-0624-1>
- 961 Bogan, M. T. (2017). Hurry up and wait: Life cycle and distribution of an intermittent stream
962 specialist (*Mesocapnia arizonensis*). *Freshwater Science*, *36*(4), 805–815.
963 <https://doi.org/10.1086/694746>
- 964 Bogan, M. T., & Boersma, K. S. (2012). Aerial dispersal of aquatic invertebrates along and
965 away from arid-land streams. *Freshwater Science*, *31*(4), 1131–1144.
966 <https://doi.org/10.1899/12-066.1>
- 967 Bogan, M. T., Boersma, K. S., & Lytle, D. A. (2015). Resistance and resilience of
968 invertebrate communities to seasonal and suprasedasonal drought in arid-land headwater
969 streams. *Freshwater Biology*, *60*(12), 2547–2558. <https://doi.org/10.1111/fwb.12522>
- 970 Bogan, M. T., Chester, E. T., Datry, T., Murphy, A. L., Robson, B. J., Ruhi, A., ... Whitney,
971 J. E. (2017). Resistance, resilience, and community recovery in intermittent rivers and
972 ephemeral streams. In Thibault Datry, N. Bonada, & A. J. Boulton (Eds.), *Intermittent*
973 *rivers and ephemeral streams: ecology and management* (pp. 349–376). Elsevier Inc.
974 <https://doi.org/10.1016/B978-0-12-803835-2.00013-9>
- 975 Bogan, M. T., Leidy, R. A., Neuhaus, L., Hernandez, C. J., & Carlson, S. M. (2019).
976 Biodiversity value of remnant pools in an intermittent stream during the great California
977 drought. *Aquatic Conservation*, *29*(6), 976–989. <https://doi.org/10.1002/aqc.3109>
- 978 Bogan, M. T., & Lytle, D. A. (2011). Severe drought drives novel community trajectories in
979 desert stream pools. *Freshwater Biology*, *56*(10), 2070–2081.
980 <https://doi.org/10.1111/j.1365-2427.2011.02638.x>
- 981 Bonada, N., Cañedo-Argüelles, M., Gallart, F., von Schiller, D., Fortuño, P., Latron, J., ...
982 Cid, N. (2020). Conservation and management of isolated pools in temporary rivers.
983 *Water*, *12*(10), 2870. <https://doi.org/10.3390/w12102870>
- 984 Bonada, N., Rieradevall, M., & Prat, N. (2007). Macroinvertebrate community structure and

- 985 biological traits related to flow permanence in a Mediterranean river network.
986 *Hydrobiologia*, 589(1), 91–106. <https://doi.org/10.1007/s10750-007-0723-5>
- 987 Bond, N. R., Lake, P. S., & Arthington, A. H. (2008). The impacts of drought on freshwater
988 ecosystems: an Australian perspective. *Hydrobiologia* 2008 600:1, 600(1), 3–16.
989 <https://doi.org/10.1007/S10750-008-9326-Z>
- 990 Boulton, A. J. (2003). Parallels and contrasts in the effects of drought on stream
991 macroinvertebrate assemblages. *Freshwater Biology*, 48(7), 1173–1185.
992 <https://doi.org/10.1046/j.1365-2427.2003.01084.x>
- 993 Boulton, A. J., & Lake, P. S. (1992). The ecology of two intermittent streams in Victoria,
994 Australia. *Freshwater Biology*, 27(1), 123–138. <https://doi.org/10.1111/j.1365-2427.1992.tb00528.x>
- 996 Buoro, M., & Carlson, S. M. (2014). Life-history syndromes: Integrating dispersal through
997 space and time. *Ecology Letters*, 17(6), 756–767. <https://doi.org/10.1111/ele.12275>
- 998 Burk, R. A., & Kennedy, J. H. (2013). Invertebrate communities of groundwater-dependent
999 refugia with varying hydrology and riparian cover during a suprasedasonal drought.
1000 *Journal of Freshwater Ecology*, 28(2), 251–270.
1001 <https://doi.org/10.1080/02705060.2012.753121>
- 1002 Busch, M.H., Costigan, K.H., Fritz, K.M., Datry, T., Krabbenhoft, C.A., Hammond, J.C., ...
1003 Allen, D.C. (2020) What's in a Name? Patterns, Trends, and Suggestions for Defining
1004 Non-Perennial Rivers and Streams. *Water*, 12, 1980. <https://doi.org/10.3390/w12071980>
- 1005 Cañedo-Argüelles, M., Boersma, K. S., Bogan, M. T., Olden, J. D., Phillipsen, I. C.,
1006 Schriever, T. A., & Lytle, D. A. (2015). Dispersal strength determines meta-community
1007 structure in a dendritic riverine network. *Journal of Biogeography*, 42(4), 778–790.
1008 <https://doi.org/10.1111/jbi.12457>
- 1009 Cañedo-Argüelles, M., Gutiérrez-Cánovas, C., Acosta, R., Cid, N., Castro-López, D.,
1010 Fortuño, P., ... Bonada, N. (2020). As time goes by : 20 years of changes in the aquatic
1011 macroinvertebrate metacommunity of Mediterranean river networks. *Journal of*
1012 *Biogeography*, 47(9), 1861–1874. <https://doi.org/10.1111/jbi.13913>

- 1013 Chadd, R. P., England, J. A., Constable, D., Dunbar, M. J., Extence, C. A., Leeming, D. J., ...
1014 Wood, P. J. (2017). An index to track the ecological effects of drought development and
1015 recovery on riverine invertebrate communities. *Ecological Indicators*, 82, 344–356.
1016 <https://doi.org/10.1016/j.ecolind.2017.06.058>
- 1017 Changnon, S. A. (1987). Detecting drought conditions in Illinois. *Circular No. 169*.
- 1018 Chase, J. M. (2007). Drought mediates the importance of stochastic community assembly.
1019 *Proceedings of the National Academy of Sciences*, 104(44), 17430–17434.
1020 <https://doi.org/10.1073/pnas.0704350104>
- 1021 Chester, E. T., & Robson, B. J. (2011). Drought refuges, spatial scale and recolonisation by
1022 invertebrates in non-perennial streams. *Freshwater Biology*, 56(10), 2094–2104.
1023 <https://doi.org/10.1111/j.1365-2427.2011.02644.x>
- 1024 Cid, N., Bonada, N., Heino, J., Cañedo-Argüelles, M., Crabot, J., Sarremejane, R., ... Datry,
1025 T. (2020). A Metacommunity Approach to Improve Biological Assessments in Highly
1026 Dynamic Freshwater Ecosystems. *BioScience*, 70(5), 427–438.
1027 <https://doi.org/10.1093/biosci/biaa033>
- 1028 Closs, G. P., & Lake, P. S. (1996). Drought, differential mortality and the coexistence of a
1029 native and an introduced fish species in a south east Australian intermittent stream.
1030 *Environmental Biology of Fishes*, 47(1), 17–26. <https://doi.org/10.1007/BF00002376>
- 1031 Cohen, H., & Laronne, J. B. (2005). High rates of sediment transport by flashfloods in the
1032 Southern Judean Desert, Israel. *Hydrological Processes*, 19(8), 1687–1702.
1033 <https://doi.org/10.1002/hyp.5630>
- 1034 Coleman, R. A., Raadik, T. A., Pettigrove, V., & Hoffmann, A. A. (2017). Taking advantage
1035 of adaptations when managing threatened species within variable environments: The
1036 case of the dwarf galaxias, *Galaxiella pusilla* (Teleostei, Galaxiidae). *Marine and*
1037 *Freshwater Research*, 68(1), 175–186. <https://doi.org/10.1071/MF15332>
- 1038 Colls, M., Timoner, X., Font, C., & Sabater, S. (2019). Effects of duration , frequency , and
1039 severity of the non-flow period on stream biofilm metabolism. *Ecosystems*, 22, 1393–
1040 1405. <https://doi.org/10.1007/s10021-019-00345-1>

- 1041 Cook, B. I., Mankin, J. S., Marvel, K., Williams, A. P., Smerdon, J. E., & Anchukaitis, K. J.
1042 (2020). Twenty-First Century Drought Projections in the CMIP6 Forcing Scenarios.
1043 *Earth's Future*, 8(6), e2019EF001461. <https://doi.org/10.1029/2019EF001461>
- 1044 Corti, R., & Datry, T. (2012). Invertebrates and sestonic matter in an advancing wetted front
1045 travelling down a dry river bed (Albarine, France). *Freshwater Science*, 31(4), 1187–
1046 1201. <https://doi.org/10.1899/12-017.1>
- 1047 Corti, R., Larned, S. T., & Datry, T. (2013). A comparison of pitfall-trap and quadrat
1048 methods for sampling ground-dwelling invertebrates in dry riverbeds. *Hydrobiologia*,
1049 717(1), 13–26. <https://doi.org/10.1007/s10750-013-1563-0>
- 1050 Cote, D., Kehler, D. G., Bourne, C., & Wiersma, Y. F. (2009). A new measure of longitudinal
1051 connectivity for stream networks. *Landscape Ecology*, 24(1), 101–113.
1052 <https://doi.org/10.1007/s10980-008-9283-y>
- 1053 Cover, M. R., Seo, J. H., & Resh, V. H. (2015). Life History, Burrowing behavior, and
1054 distribution of *Neohermes filicornis* (Megaloptera: Corydalidae), a long-lived aquatic
1055 insect in intermittent streams. *Western North American Naturalist*, 75(4), 474–490.
1056 <https://doi.org/10.3398/064.075.0405>
- 1057 Crabot, J., Heino, J., Launay, B., & Datry, T. (2020). Drying determines the temporal
1058 dynamics of stream invertebrate structural and functional beta diversity. *Ecography*,
1059 43(4), 620–635. <https://doi.org/10.1111/ecog.04835>
- 1060 Crausbay, S. D., Ramirez, A. R., Carter, S. L., Cross, M. S., Hall, K. R., Bathke, D. J., ...
1061 Sanford, T. (2017). Defining ecological drought for the twenty-first century. *Bulletin of*
1062 *the American Meteorological Society*, 98(12), 2543–2550.
1063 <https://doi.org/10.1175/BAMS-D-16-0292.1>
- 1064 Datry, T., Boulton, A. J., Bonada, N., Fritz, K., Leigh, C., Sauquet, E., ... Dahm, C. N.
1065 (2018). Flow intermittence and ecosystem services in rivers of the Anthropocene.
1066 *Journal of Applied Ecology*, 55(1), 353–364. <https://doi.org/10.1111/1365-2664.12941>
- 1067 Datry, T., Larned, S. T., Fritz, K. M., Bogan, M. T., Wood, P. J., Meyer, E. I., & Santos, a.
1068 N. (2014). Broad-scale patterns of invertebrate richness and community composition in
1069 temporary rivers: effects of flow intermittence. *Ecography*, 37(1), 94–104.

- 1070 <https://doi.org/10.1111/j.1600-0587.2013.00287.x>
- 1071 Datry, T., Larned, S. T., & Tockner, K. (2014). Intermittent Rivers: A Challenge for
1072 Freshwater Ecology. *BioScience*, 64(3), 229–235. <https://doi.org/10.1093/biosci/bit027>
- 1073 Datry, T. (2012). Benthic and hyporheic invertebrate assemblages along a flow intermittence
1074 gradient: effects of duration of dry events. *Freshwater Biology*, 57(3), 563–574.
1075 <https://doi.org/10.1111/j.1365-2427.2011.02725.x>
- 1076 Datry, T. (2017). Ecological Effects of Flow Intermittence in Gravel-Bed Rivers. *Gravel-Bed
1077 Rivers: Process and Disasters*, 261–297. <https://doi.org/10.1002/9781118971437.CH10>
- 1078 Datry, T., Bonada, N., & Boulton, A. J. (2017). *Intermittent rivers and ephemeral streams :
1079 ecology and management*. Amsterdam, Netherlands: Academic Press.
- 1080 Datry, T., Bonada, N., & Heino, J. (2016). Towards understanding the organisation of
1081 metacommunities in highly dynamic ecological systems. *Oikos*, 125(125), 149–159.
1082 <https://doi.org/10.1111/oik.02922>
- 1083 Datry, T., Pella, H., Leigh, C., Bonada, N., & Hugueny, B. (2016). A landscape approach to
1084 advance intermittent river ecology. *Freshwater Biology*, 61(8), 1200-1213.
1085 <https://doi.org/10.1111/fwb.12645>
- 1086 Davey, A. J. H., & Kelly, D. J. (2007). Fish community responses to drying disturbances in
1087 an intermittent stream: A landscape perspective. *Freshwater Biology*, 52(9), 1719–1733.
1088 <https://doi.org/10.1111/j.1365-2427.2007.01800.x>
- 1089 de Graaf, I. E. M., Gleeson, T., van Beek, L. P. H., Sutanudjaja, E. H., & Bierkens, M. F. P.
1090 (2019). Environmental flow limits to global groundwater pumping. *Nature*, 574(7776),
1091 90–94. <https://doi.org/10.1038/s41586-019-1594-4>
- 1092 De Soyza, A. G., Killingbeck, K. T., & Whitford, W. G. (2004). Plant water relations and
1093 photosynthesis during and after drought in a Chihuahuan desert arroyo, 59, 27–39.
1094 <https://doi.org/10.1016/j.jaridenv.2004.01.011>
- 1095 Deitch, M. J., van Docto, M., Obedzinski, M., Nossaman, S. P., & Bartshire, A. (2018).
1096 Impact of multi-annual drought on streamflow and habitat in coastal California salmonid
1097 streams. *Hydrological Sciences Journal*, 63(8), 1219–1235.

- 1098 <https://doi.org/10.1080/02626667.2018.1492722>
- 1099 Derouin, S. (2021). Simultaneous Drought and Heat Wave Events Are Becoming More
1100 Common. *Eos*, *102*. <https://doi.org/10.1029/2021eo154034>
- 1101 Do, H. X., Gudmundsson, L., Leonard, M., & Westra, S. (2018). The Global Streamflow
1102 Indices and Metadata Archive (GSIM)-Part 1: The production of a daily streamflow
1103 archive and metadata. *Earth System Science Data*, *10*(2), 765–785.
1104 <https://doi.org/10.5194/essd-10-765-2018>
- 1105 Döll, P., & Schmied, H. M. (2012). How is the impact of climate change on river flow
1106 regimes related to the impact on mean annual runoff? A global-scale analysis.
1107 *Environmental Research Letters*, *7*(1), 014037. <https://doi.org/10.1088/1748->
1108 [9326/7/1/014037](https://doi.org/10.1088/1748-9326/7/1/014037)
- 1109 Eastman, M., Parry, S., Sefton, C., Park, J., & England, J. (2021). Reconstructing
1110 spatiotemporal dynamics in hydrological state along intermittent rivers. *Water*, *13*(4),
1111 493. <https://doi.org/10.3390/w13040493>
- 1112 Eltahir, E. A. B., & Yeh, P. J. F. (1999). On the asymmetric response of aquifer water level to
1113 floods and droughts in Illinois. *Water Resources Research*, *35*(4), 1199–1217.
1114 <https://doi.org/10.1029/1998WR900071>
- 1115 Eveleens, R. A., McIntosh, A. R., & Warburton, H. J. (2019). Interactive community
1116 responses to disturbance in streams: disturbance history moderates the influence of
1117 disturbance types. *Oikos*, *128*(8), 1170–1181. <https://doi.org/10.1111/oik.05868>
- 1118 Fennell, J., Geris, J., Wilkinson, M. E., Daalmans, R., & Soulsby, C. (2020). Lessons from
1119 the 2018 drought for management of local water supplies in upland areas: A tracer-based
1120 assessment. *Hydrological Processes*. <https://doi.org/10.1002/hyp.13867>
- 1121 Fishman, A. P., Pack, A. I., Delaney, R. G., & Galante, R. J. (1986). Estivation in
1122 Protopterus. *Journal of Morphology*, *190*(1 S), 237–248.
1123 <https://doi.org/10.1002/jmor.1051900416>
- 1124 Gallart, F., Cid, N., Latron, J., Llorens, P., Bonada, N., Jeuffroy, J., ... Prat, N. (2017).
1125 TREHS: An open-access software tool for investigating and evaluating temporary river

- 1126 regimes as a first step for their ecological status assessment. *Science of The Total*
1127 *Environment*, 607–608, 519–540. <https://doi.org/10.1016/J.SCITOTENV.2017.06.209>
- 1128 Garssen, A. G., Verhoeven, J. T. A., & Soons, M. B. (2014). Effects of climate-induced
1129 increases in summer drought on riparian plant species: A meta-analysis. *Freshwater*
1130 *Biology*, 59(5), 1052–1063. <https://doi.org/10.1111/fwb.12328>
- 1131 Gauthier, M., Launay, B., Le Goff, G., Pella, H., Douady, C. J., & Datry, T. (2020).
1132 Fragmentation promotes the role of dispersal in determining 10 intermittent headwater
1133 stream metacommunities. *Freshwater Biology*, 65(12), 2169–2185.
1134 <https://doi.org/10.1111/fwb.13611>
- 1135 Gauthier, M., Le Goff, G., Launay, B., Douady, C. J., & Datry, T. (2021). Dispersal
1136 limitation by structures is more important than intermittent drying effects for
1137 metacommunity dynamics in a highly fragmented river network. *Freshwater Science*,
1138 40(2), 302–315. <https://doi.org/10.1086/714376>
- 1139 Gionchetta, G., Oliva, F., Menéndez, M., Lopez, P., & Anna, L. (2019). Key role of
1140 streambed moisture and flash storms for microbial resistance and resilience to long- -
1141 term drought. *Freshwater Biology*, 64(2), 306–322. <https://doi.org/10.1111/fwb.13218>
- 1142 Glenn, E. P., & Nagler, P. L. (2005). Comparative ecophysiology of *Tamarix ramosissima*
1143 and native trees in western U.S. riparian zones. *Journal of Arid Environments*, 61(3),
1144 419–446. <https://doi.org/10.1016/j.jaridenv.2004.09.025>
- 1145 Golladay, S. W., Gagnon, P., Kearns, M., Battle, J. M., & Hicks, D. W. (2004). Response of
1146 freshwater mussel assemblages (Bivalvia : Unionidae) to a record drought in the Gulf
1147 Coastal Plain of southwestern Georgia. *Journal of the North American Benthological*
1148 *Society*, 23(3), 494–506.
- 1149 Gómez, R., Arce, M. I., Baldwin, D. S., & Dahm, C. N. (2017). Water Physicochemistry in
1150 Intermittent Rivers and Ephemeral Streams. In *Intermittent Rivers and Ephemeral*
1151 *Streams: Ecology and Management* (pp. 109–134). Elsevier Inc.
1152 <https://doi.org/10.1016/B978-0-12-803835-2.00005-X>
- 1153 Gough, H. M., Landis, A. M. G., & Stoeckel, J. A. (2012). Behaviour and physiology are
1154 linked in the responses of freshwater mussels to drought. *Freshwater Biology*, 57, 2356–

- 1155 2366. <https://doi.org/10.1111/fwb.12015>
- 1156 Gudmundsson, L., Do, H. X., Leonard, M., & Westra, S. (2018). The Global Streamflow
 1157 Indices and Metadata Archive (GSIM)-Part 2: Quality control, time-series indices and
 1158 homogeneity assessment. *Earth System Science Data*, *10*(2), 787–804.
 1159 <https://doi.org/10.5194/essd-10-787-2018>
- 1160 Gustard, A., & Demuth, S. (2008). *Manual on low-flow estimation and prediction*.
 1161 *Operational Hydrology Report No. 50*. World Meteorological Organization (WMO).
- 1162 Haile, G. G., Tang, Q., Li, W., Liu, X., & Zhang, X. (2020). Drought: Progress in broadening
 1163 its understanding. *WIREs Water*, *7*(2), e1407–e1407. <https://doi.org/10.1002/wat2.1407>
- 1164 Halaburka, B. J., Lawrence, J. E., Bischel, H. N., Hsiao, J., Plumlee, M. H., Resh, V. H., &
 1165 Luthy, R. G. (2013). Economic and ecological costs and benefits of streamflow
 1166 augmentation using recycled water in a california coastal stream. *Environmental Science*
 1167 *and Technology*, *47*(19), 10735–10743. <https://doi.org/10.1021/es305011z>
- 1168 Hamdhani, H., Eppehimer, D. E., & Bogan, M. T. (2020, September 1). Release of treated
 1169 effluent into streams: A global review of ecological impacts with a consideration of its
 1170 potential use for environmental flows. *Freshwater Biology*. Blackwell Publishing Ltd.
 1171 <https://doi.org/10.1111/fwb.13519>
- 1172 Hammond, J. C., Zimmer, M., Shanafield, M., Kaiser, K., Godsey, S. E., Mims, M. C., ...
 1173 Allen, D. C. (2021, January 28). Spatial Patterns and Drivers of Nonperennial Flow
 1174 Regimes in the Contiguous United States. *Geophysical Research Letters*. Blackwell
 1175 Publishing Ltd. <https://doi.org/10.1029/2020GL090794>
- 1176 Hansen, E. A. (1975). Some Effects of Groundwater on Brown Trout Redds. *Transactions of*
 1177 *the American Fisheries Society*, *104*(1), 100–110. Retrieved from
 1178 [https://afspubs.onlinelibrary.wiley.com/doi/10.1577/1548-](https://afspubs.onlinelibrary.wiley.com/doi/10.1577/1548-8659%281975%29104%3C100%3ASEO%3E2.0.CO%3B2)
 1179 [8659%281975%29104%3C100%3ASEO%3E2.0.CO%3B2](https://afspubs.onlinelibrary.wiley.com/doi/10.1577/1548-8659%281975%29104%3C100%3ASEO%3E2.0.CO%3B2)
- 1180 Hayes, M. J., Svoboda, M. D., Wihite, D. A., & Vanyarkho, O. V. (1999). Monitoring the
 1181 1996 drought using the standardized precipitation index. *Bulletin of the American*
 1182 *Meteorological So*, 429–438. Retrieved from
 1183 <https://journals.ametsoc.org/view/journals/bams/80/3/1520->

- 1184 0477_1999_080_0429_mtduts_2_0_co_2.xml
- 1185 Hayes, M., Svoboda, M., Wall, N., & Widhalm, M. (2011). The Lincoln declaration on
1186 drought indices: universal meteorological drought index recommended. *Bulletin of the*
1187 *American Meteorological Society*, 92(4), 485–488. Retrieved from
1188 <http://www.jstor.org/stable/26226865>
- 1189 Herbst, D. B., Cooper, S. D., Medhurst, R. B., Wiseman, S. W., & Hunsaker, C. T. (2019).
1190 Drought ecohydrology alters the structure and function of benthic invertebrate
1191 communities in mountain streams. *Freshwater Biology*, 64(5), 886–902.
1192 <https://doi.org/10.1111/fwb.13270>
- 1193 Hill, M. J., Mathers, K. L., Little, S., Worrall, T., Gunn, J., & Wood, P. J. (2019). Ecological
1194 effects of a supra-seasonal drought on macroinvertebrate communities differ between
1195 near-perennial and ephemeral river reaches. *Aquatic Sciences*, 81(4), 62.
1196 <https://doi.org/10.1007/s00027-019-0659-7>
- 1197 Hill, M. J., & Milner, V. S. (2018). Ponding in intermittent streams : A refuge for lotic taxa
1198 and a habitat for newly colonising taxa ? *Science of the Total Environment*, 628–629(7),
1199 1308–1316. <https://doi.org/10.1016/j.scitotenv.2018.02.162>
- 1200 Hisdal, H., Tallaksen, L. M., Clausen, B., Peters, E., Gustard, A., & VanLauen, H. (2004).
1201 Hydrological drought characteristics. *Developments in water science*, 48(5), 139-198.
- 1202 Hopper, G. W., Gido, K. B., Pennock, C. A., Hedden, S. C., Frenette, B. D., Barts, N., ...
1203 Bruckerhoff, L. A. (2020). Nowhere to swim : interspecific responses of prairie stream
1204 fishes in isolated pools during severe drought. *Aquatic Sciences*.
1205 <https://doi.org/10.1007/s00027-020-0716-2>
- 1206 Hopper, G. W., Gido, K. B., Pennock, C. A., Hedden, S. C., Guinnip, J. P., Fisher, M. A., ...
1207 Bruckerhoff, L. A. (2020). Biomass loss and change in species dominance shift stream
1208 community excretion stoichiometry during severe drought. *Freshwater Biology*, 65(3),
1209 403–416. <https://doi.org/10.1111/fwb.13433>
- 1210 Humphries, P., & Baldwin, D. S. (2003). Drought and aquatic ecosystems: An introduction.
1211 *Freshwater Biology*. John Wiley & Sons, Ltd. [https://doi.org/10.1046/j.1365-](https://doi.org/10.1046/j.1365-2427.2003.01092.x)
1212 [2427.2003.01092.x](https://doi.org/10.1046/j.1365-2427.2003.01092.x)

- 1213 Jackson, M. C., Loewen, C. J. G., Vinebrooke, R. D., & Chimimba, C. T. (2016, January 1).
1214 Net effects of multiple stressors in freshwater ecosystems: A meta-analysis. *Global*
1215 *Change Biology*. Blackwell Publishing Ltd. <https://doi.org/10.1111/gcb.13028>
- 1216 Jaeger, K. L., & Olden, J. D. (2012). Electrical resistance sensor arrays as a means to quantify
1217 longitudinal connectivity of rivers. *River Research and Applications*, 28(10), 1843–
1218 1852. <https://doi.org/10.1002/rra.1554>
- 1219 Jaeger, K. L., Olden, J. D., & Pelland, N. A. (2014). Climate change poised to threaten
1220 hydrologic connectivity and endemic fishes in dryland streams. *Proceedings of the*
1221 *National Academy of Sciences of the United States of America*, 111(38), 13894–13899.
1222 <https://doi.org/10.1073/pnas.1320890111>
- 1223 Jaeger, K. L., Sando, R., McShane, R. R., Dunham, J. B., Hockman-Wert, D. P., Kaiser, K.
1224 E., ... Blasch, K. W. (2019). Probability of Streamflow Permanence Model
1225 (PROSPER): A spatially continuous model of annual streamflow permanence
1226 throughout the Pacific Northwest. *Journal of Hydrology X*, 2, 100005.
1227 <https://doi.org/10.1016/J.HYDROA.2018.100005>
- 1228 Jaeger, K. L., Sutfin, N. A., Tooth, S., Michaelides, K., & Singer, M. (2017). Geomorphology
1229 and Sediment Regimes of Intermittent Rivers and Ephemeral Streams. In *Intermittent*
1230 *Rivers and Ephemeral Streams: Ecology and Management* (pp. 21–49). Elsevier Inc.
1231 <https://doi.org/10.1016/B978-0-12-803835-2.00002-4>
- 1232 Jain, V. K., Jain, M. K., & Pandey, R. P. (2014). Effect of the Length of the Streamflow
1233 Record on Truncation Level for Assessment of Streamflow Drought Characteristics.
1234 *Journal of Hydrologic Engineering*, 19(7), 1361–1373.
1235 [https://doi.org/10.1061/\(asce\)he.1943-5584.0000922](https://doi.org/10.1061/(asce)he.1943-5584.0000922)
- 1236 Jenkins, K. M., & Boulton, A. J. (2007). Detecting impacts and setting restoration targets in
1237 arid-zone rivers : aquatic micro-invertebrate responses to reduced floodplain inundation.
1238 *Journal of Applied Ecology*, 44(4), 823–832. <https://doi.org/10.1111/j.1365->
1239 [2664.2007.01298.x](https://doi.org/10.1111/j.1365-2664.2007.01298.x)
- 1240 Kalogianni, E., Vourka, A., Karaouzas, I., Vardakas, L., & Skoulikidis, N. T. (2017).
1241 Combined effects of water stress and pollution on macroinvertebrate and fish

- 1242 assemblages in a Mediterranean intermittent river. *Science of the Total Environment*,
1243 604, 639–650. <https://doi.org/10.1016/j.scitotenv.2017.06.078>
- 1244 Kawanishi, R., Inoue, M., Dohi, R., Fujii, A., & Miyake, Y. (2013). The role of the hyporheic
1245 zone for a benthic fish in an intermittent river: A refuge, not a graveyard. *Aquatic*
1246 *Sciences*, 75(3), 425–431. <https://doi.org/10.1007/s00027-013-0289-4>
- 1247 Ko, M. K., & Tarhule, A. (1994). Streamflow droughts of northern nigerian rivers.
1248 *Hydrological Sciences Journal*, 39(1), 19–34.
1249 <https://doi.org/10.1080/02626669409492717>
- 1250 Kouba, A., Tikal, J., Císař, P., Veselý, L., Fořt, M., & Přiborský, J. (2016). The significance
1251 of droughts for hyporheic dwellers : evidence from freshwater crayfish. *Nature Scientific*
1252 *Reports* 6:26569. <https://doi.org/10.1038/srep26569>
- 1253 Kovach, R. P., Dunham, J. B., Al-Chokhachy, R., Snyder, C. D., Letcher, B. H., Young, J.,
1254 ... Muhlfeld, C. C. (2019). An integrated framework for ecological drought across
1255 riverscapes of North America. *BioScience* 69(6), 418–431.
1256 <https://doi.org/10.1093/biosci/biz040>
- 1257 Lake, P. S. (2000). Disturbance, patchiness, and diversity in streams. *Journal of the North*
1258 *American Benthological Society*, 19(4). <https://doi.org/10.2307/1468118>
- 1259 Lake, P. S. (2003). Ecological effects of perturbation by drought in flowing waters.
1260 *Freshwater Biology*, 48(7), 1161–1172. [https://doi.org/10.1046/j.1365-](https://doi.org/10.1046/j.1365-2427.2003.01086.x)
1261 [2427.2003.01086.x](https://doi.org/10.1046/j.1365-2427.2003.01086.x)
- 1262 Lake, P. S. (2011). *Drought and aquatic ecosystems: effects and responses*. John Wiley &
1263 Sons.
- 1264 Larimore, R. W., Childers, W. F., & Heckrotte, C. (1959). Destruction and re-establishment
1265 of stream fish and invertebrates affected by drought. *Transactions of the American*
1266 *Fisheries Society*, 88(4), 261–285. [https://doi.org/10.1577/1548-](https://doi.org/10.1577/1548-8659(1959)88[261:DAROSF]2.0.CO;2)
1267 [8659\(1959\)88\[261:DAROSF\]2.0.CO;2](https://doi.org/10.1577/1548-8659(1959)88[261:DAROSF]2.0.CO;2)
- 1268 Larned, S. T., Datry, T., Arscott, D. B., & Tockner, K. (2010). Emerging concepts in
1269 temporary-river ecology. *Freshwater Biology*, 55(4), 717–738.

- 1270 <https://doi.org/10.1111/j.1365-2427.2009.02322.x>
- 1271 Larsen, L. G., & Woelfle-Erskine, C. (2018). Groundwater is key to salmonid persistence and
1272 recruitment in intermittent Mediterranean-climate streams. *Water Resources Research*,
1273 54(11), 8909–8930. <https://doi.org/10.1029/2018WR023324>
- 1274 Larson, E. R., Magoulick, D. D., Turner, C., & Laycock, K. H. (2009). Disturbance and
1275 species displacement: Different tolerances to stream drying and desiccation in a native
1276 and an invasive crayfish. *Freshwater Biology*, 54(9), 1899–1908.
1277 <https://doi.org/10.1111/j.1365-2427.2009.02243.x>
- 1278 Leberfinger, K., Bohman, I., & Herrmann, J. (2010). Drought impact on stream detritivores :
1279 experimental effects on leaf litter breakdown and life cycles, 247–254.
1280 <https://doi.org/10.1007/s10750-010-0337-1>
- 1281 Lehner, F., Coats, S., Stocker, T. F., Pendergrass, A. G., Sanderson, B. M., Raible, C. C., &
1282 Smerdon, J. E. (2017). Projected drought risk in 1.5°C and 2°C warmer climates.
1283 *Geophysical Research Letters*, 44(14), 7419–7428.
1284 <https://doi.org/10.1002/2017GL074117>
- 1285 Leigh, C., Boersma, K. S., Galatowitsch, M. L., Milner, V. S., & Stubbington, R. (2019). Are
1286 all rivers equal? The role of education in attitudes towards temporary and perennial
1287 rivers. *People and Nature*, 1(2), 181–190. <https://doi.org/10.1002/pan3.22>
- 1288 Leigh, C., Bonada, N., Boulton, A. J., Hugueny, B., Larned, S. T., Vander Vorste, R., &
1289 Datry, T. (2016). Invertebrate assemblage responses and the dual roles of resistance and
1290 resilience to drying in intermittent rivers. *Aquatic Sciences*, 78(2), 291–301.
1291 <https://doi.org/10.1007/s00027-015-0427-2>
- 1292 Leigh, C., & Datry, T. (2017). Drying as a primary hydrological determinant of biodiversity
1293 in river systems: a broad-scale analysis. *Ecography*, 40(4), 487–499.
1294 <https://doi.org/10.1111/ecog.02230>
- 1295 Lind, P. R., Robson, B. J., & Mitchell, B. D. (2006). The influence of reduced flow during a
1296 drought on patterns of variation in macroinvertebrate assemblages across a spatial
1297 hierarchy in two lowland rivers, 2282–2295. [https://doi.org/10.1111/j.1365-](https://doi.org/10.1111/j.1365-2427.2006.01650.x)
1298 [2427.2006.01650.x](https://doi.org/10.1111/j.1365-2427.2006.01650.x)

- 1299 Link, R., Wild, T. B., Snyder, A. C., Hejazi, M. I., & Vernon, C. R. (2020). 100 years of data
1300 is not enough to establish reliable drought thresholds. *Journal of Hydrology X*, 7,
1301 100052. <https://doi.org/10.1016/j.hydroa.2020.100052>
- 1302 Littell, J. S., Peterson, D. L., Riley, K. L., Liu, Y., & Luce, C. H. (2016). A review of the
1303 relationships between drought and forest fire in the United States. *Global Change*
1304 *Biology*, 22(7), 2353–2369. <https://doi.org/10.1111/gcb.13275>
- 1305 Lloyd-Hughes, B. (2014). The impracticality of a universal drought definition. *Theoretical*
1306 *and Applied Climatology*, 117(3–4), 607–611. [https://doi.org/10.1007/s00704-013-1025-](https://doi.org/10.1007/s00704-013-1025-7)
1307 7
- 1308 Lovill, S. M., Hahm, W. J., & Dietrich, W. E. (2018). Drainage from the critical zone:
1309 lithologic controls on the persistence and spatial extent of wetted channels during the
1310 summer dry season. *Water Resources Research*, 54(8), 5702–5726.
1311 <https://doi.org/10.1029/2017WR021903>
- 1312 Lymbery, A. J., Ma, L., Lymbery, S. J., Klunzinger, M. W., Beatty, S. J., & Morgan, D. L.
1313 (2021). Burrowing behavior protects a threatened freshwater mussel in drying rivers.
1314 *Hydrobiologia*, 848, 3141–3152. <https://doi.org/10.1007/s10750-020-04268-0>
- 1315 Maes, J., & Jacobs, S. (2017). Nature-Based Solutions for Europe’s Sustainable
1316 Development. *Conservation Letters*, 10(1), 121–124.
1317 <https://doi.org/10.1111/CONL.12216>
- 1318 Magalhães, M. F., Beja, P., Schlosser, I. J., & Collares-Pereira, M. J. (2007). Effects of multi-
1319 year droughts on fish assemblages of seasonally drying Mediterranean streams.
1320 *Freshwater Biology*, 52(8), 1494–1510. [https://doi.org/10.1111/J.1365-](https://doi.org/10.1111/J.1365-2427.2007.01781.X)
1321 2427.2007.01781.X
- 1322 Magoulick, D. D., & Kobza, R. M. (2003). The role of refugia for fishes during drought: a
1323 review and synthesis. *Freshwater Biology*, 48(7), 1186–1198.
1324 <https://doi.org/10.1046/j.1365-2427.2003.01089.x>
- 1325 Malard, F., & Hervant, F. (1999). Oxygen supply and the adaptations of animals in
1326 groundwater. *Freshwater Biology*, 41(1), 1-30. [https://doi.org/10.1046/j.1365-](https://doi.org/10.1046/j.1365-2427.1999.00379.x)
1327 2427.1999.00379.x

- 1328 Malard, F., Tockner, K., Dole-Olivier, M. J., & Ward, J. V. (2002). A landscape perspective
1329 of surface-subsurface hydrological exchanges in river corridors. *Freshwater Biology*,
1330 47(4), 621–640. <https://doi.org/10.1046/j.1365-2427.2002.00906.x>
- 1331 Mameri, D., Branco, P., Ferreira, M. T., & Santos, J. M. (2020). Heatwave effects on the
1332 swimming behaviour of a Mediterranean freshwater fish, the Iberian barbel *Luciobarbus*
1333 *bocagei*. *Science of the Total Environment*, 730, 139152.
1334 <https://doi.org/10.1016/j.scitotenv.2020.139152>
- 1335 Marshall, J. C., Lobegeiger, J.S, & Starkey, A. (2021) Risks to fish populations in dryland
1336 rivers from the combined threats of drought and instream barriers. *Frontiers in*
1337 *Environmental Sciences*. <https://doi.org/10.3389/fenvs.2021.671556>
- 1338 Marshall, J. C., & Negus, P. M. (2018). Application of a multistressor risk framework to the
1339 monitoring, assessment, and diagnosis of river health. In *Multiple Stressors in River*
1340 *Ecosystems: Status, Impacts and Prospects for the Future* (pp. 255–280). Elsevier.
1341 <https://doi.org/10.1016/B978-0-12-811713-2.00015-7>
- 1342 Matthews, W. J., & Marsh-Matthews, E. (2003). Effects of drought on fish across axes of
1343 space, time and ecological complexity. *Freshwater Biology*, 48(7), 1232–1253.
1344 <https://doi.org/10.1046/j.1365-2427.2003.01087.x>
- 1345 McBryde, F. W. (1982). “Drought” as a Seasonal Phenomenon. *The Professional*
1346 *Geographer*, 34(3), 347.
- 1347 Mckee, T. B., Doesken, N. J., & Kleist, J. (1993). The relationship of drought frequency and
1348 duration to time scales. *Eighth Conference on Applied Climatology*, 17–22.
- 1349 McMaster, D., & Bond, N. (2008). A field and experimental study on the tolerances of fish to
1350 *Eucalyptus camaldulensis* leachate and low dissolved oxygen concentrations. *Marine*
1351 *and Freshwater Research*, 59(2), 177–185. <https://doi.org/10.1071/MF07140>
- 1352 Messenger, M. L., Lehner, B., Cockburn, C., Lamouroux, N., Pella, H., Snelder, T., ... Datry,
1353 T. (2021). Global prevalence of non-perennial rivers and streams. *Nature*, 594(7863),
1354 391–397. <https://doi.org/10.1038/s41586-021-03565-5>
- 1355 Mishra, A. K., & Singh, V. P. (2010). A review of drought concepts. *Journal of Hydrology*,

- 1356 391, 202-216. <https://doi.org/10.1016/j.jhydrol.2010.07.012>
- 1357 Obedzinski, M., Nossaman Pierce, S., Horton, G. E., & Deitch, M. J. (2018). Effects of flow-
1358 related variables on oversummer Survival of juvenile Coho salmon in intermittent
1359 streams. *Transactions of the American Fisheries Society*, 147, 588–605.
1360 <https://doi.org/10.1002/tafs.10057>
- 1361 Ormerod, S. J., Dobson, M., Hildrew, A. G., & Townsend, C. R. (2010). Multiple stressors in
1362 freshwater ecosystems. *Freshwater Biology*, 55(1), 1–4. <https://doi.org/10.1111/j.1365-2427.2009.02395.x>
1363
- 1364 Palma, P., Fialho, S., Lima, A., Novais, M. H., Costa, J. M., Montemurro, N., ... Lopez de
1365 Alda, M. (2020). Pharmaceuticals in a Mediterranean Basin : The influence of temporal
1366 and hydrological patterns in environmental risk assessment. *Science of the Total
1367 Environment*, 709, 136205. <https://doi.org/10.1016/j.scitotenv.2019.136205>
- 1368 Pařil, P., Leigh, C., Polářek, M., Sarremejane, R., Řezníčková, P., Dostálová, A., &
1369 Stubbington, R. (2019). Short-term streambed drying events alter amphipod population
1370 structure in a central European stream. *Fundamental and Applied Limnology*, 193(1).
1371 <https://doi.org/10.1127/fal/2019/1164>
- 1372 Pařil, P., Polářek, M., Loskotová, B., Straka, M., Crabot, J., & Datry, T. (2019). An
1373 unexpected source of invertebrate community recovery in intermittent streams from a
1374 humid continental climate, *Freshwater Biology*, 64(11), 1971–1983.
1375 <https://doi.org/10.1111/fwb.13386>
- 1376 Pernecker, B., Mauchart, P., & Csabai, Z. (2020). What to do if streams go dry? Behaviour of
1377 Balkan Goldenring (*Cordulegaster heros*, Odonata) larvae in a simulated drought
1378 experiment in SW Hungary. *Ecological Entomology*, 45(6), 1457–1465.
1379 <https://doi.org/10.1111/een.12931>
- 1380 Peterson, T. J., Saft, M., Peel, M. C., & John, A. (2021). Watersheds may not recover from
1381 drought. *Science*, 372(6543), 745–749. <https://doi.org/10.1126/science.abd5085>
- 1382 Pokhrel, Y., Felfelani, F., Satoh, Y., Boulange, J., Burek, P., Gädeke, A., ... Wada, Y.
1383 (2021). Global terrestrial water storage and drought severity under climate change.
1384 *Nature Climate Change*, 11(3), 226–233. <https://doi.org/10.1038/s41558-020-00972-w>

- 1385 Price, S. J., Browne, R. A., & Dorcas, M. E. (2012). Resistance and resilience of a stream
1386 salamander to suprasedasonal drought. *Herpetologica*, 68(3), 312–323.
- 1387 Propst, D. L., Gido, K. B., & Stefferud, J. A. (2008). Natural flow regimes, nonnative fishes,
1388 and native fish persistence in arid-land river systems. *Ecological Applications*, 18(5),
1389 1236–1252. <https://doi.org/10.1890/07-1489.1>
- 1390 Prudhomme, C., Giuntoli, I., Robinson, E. L., Clark, D. B., Arnell, N. W., Dankers, R., ...
1391 Wissler, D. (2014). Hydrological droughts in the 21st century, hotspots and uncertainties
1392 from a global multimodel ensemble experiment. *Proceedings of the National Academy
1393 of Sciences*, 111(9), 3262–3267. <https://doi.org/10.1073/pnas.1222473110>
- 1394 Richards, J. G. (2010). Metabolic rate suppression as a mechanism for surviving
1395 environmental challenge in fish. *Progress in Molecular and Subcellular Biology*.
1396 Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-642-02421-4_6
- 1397 Robson, B. J. (2000). Role of residual biofilm in the recolonization of rocky intermittent
1398 streams by benthic algae. *Marine and Freshwater Research*, 51(7), 725–732.
1399 <https://doi.org/10.1071/MF00012>
- 1400 Robson, B. J., Chester, E. ., Matthews, T. G., & Johnston, K. (2018). Post-wildfire recovery
1401 of invertebrate diversity in drought-affected headwater streams. *Aquatic Sciences*, 80,
1402 21. <https://doi.org/10.1007/s00027-018-0570-7>
- 1403 Robson, B. J., Chester, E. T. B., & Austin, C. M. C. (2011). Why life history information
1404 matters : drought refuges and macroinvertebrate persistence in non-perennial streams
1405 subject to a drier climate. *Marine and Freshwater Research*, 62, 801–810.
- 1406 Rodríguez-Lozano, P., Leidy, R. A., & Carlson, S. M. (2019). Brook lamprey survival in the
1407 dry riverbed of an intermittent stream. *Journal of Arid Environments*, 166, 83–85.
1408 <https://doi.org/10.1016/j.jaridenv.2019.04.016>
- 1409 Rodríguez-Lozano, P., Woelfle-Erskine, C., Bogan, M. T., & Carlson, S. M. (2020). Are non-
1410 perennial rivers considered as valuable and worthy of conservation as perennial rivers?
1411 *Sustainability*, 12(14), 5782. <https://doi.org/10.3390/su12145782>
- 1412 Rogosch, J., Tonkin, J. D., Lytle, D. A., Merritt, D. M., Reynolds, L. V., & Olden, J. D.

- 1413 (2019). Increasing drought favors nonnative fishes in a dryland river : evidence from a
1414 multispecies demographic model. *Ecosphere*, *10*(4), e02681.
1415 <https://doi.org/10.1002/ecs2.2681>
- 1416 Rolls, R. J., Heino, J., & Chessman, B. C. (2016). Unravelling the joint effects of flow
1417 regime, climatic variability and dispersal mode on beta diversity of riverine
1418 communities. *Freshwater Biology*, *61*(8), 1350–1364. <https://doi.org/10.1111/fwb.12793>
- 1419 Romaní, A. M., & Sabater, S. (1997). Metabolism recovery of a stromatolitic biofilm after
1420 drought in a Mediterranean stream. *Archiv Fur Hydrobiologie*, *140*(2), 261–271.
1421 <https://doi.org/10.1127/archiv-hydrobiol/140/1997/261>
- 1422 Salavert, V., Zamora-Muñoz, C., Ruiz-Rodríguez, M., Fernández-Cortés, A., & Soler, J. J.
1423 (2008). Climatic conditions, diapause and migration in a troglophile caddisfly.
1424 *Freshwater Biology*, *53*(8), 1606–1617. [https://doi.org/10.1111/j.1365-](https://doi.org/10.1111/j.1365-2427.2008.02000.x)
1425 [2427.2008.02000.x](https://doi.org/10.1111/j.1365-2427.2008.02000.x)
- 1426 Sarremejane, R., England, J., Sefton, C. E. M., Parry, S., Eastman, M., & Stubbington, R.
1427 (2020). Local and regional drivers influence how aquatic community diversity,
1428 resistance and resilience vary in response to drying. *Oikos*, *129*(12), 1877–1890.
1429 <https://doi.org/10.1111/oik.07645>
- 1430 Sarremejane, R., Mykrä, H., Bonada, N., Aroviita, J., & Muotka, T. (2017). Habitat
1431 connectivity and dispersal ability drive the assembly mechanisms of macroinvertebrate
1432 communities in river networks. *Freshwater Biology*, *62*(6), 1073–1082.
1433 <https://doi.org/10.1111/fwb.12926>
- 1434 Sarremejane, R., Stubbington, R., England, J., Sefton, C. E. M., Eastman, M., Parry, S., &
1435 Ruhi, A. (2021). Drought effects on invertebrate metapopulation dynamics and quasi-
1436 extinction risk in an intermittent river network. *Global Change Biology*, gcb.15720.
1437 <https://doi.org/10.1111/gcb.15720>
- 1438 Sarremejane, R., Truchy, A., McKie, B. G., Mykrä, H., Johnson, R. K., Huusko, A., ...
1439 Muotka, T. (2021). Stochastic processes and ecological connectivity drive stream
1440 invertebrate community responses to short-term drought. *Journal of Animal Ecology*,
1441 *90*(4), 886–898. <https://doi.org/10.1111/1365-2656.13417>

- 1442 Sauquet, E., Shanafield, M., Hammond, J. C., Sefton, C., Leigh, C., & Datry, T. (2021).
1443 Classification and trends in intermittent river flow regimes in Australia, northwestern
1444 Europe and USA: A global perspective. *Journal of Hydrology*, 597, 126170.
1445 <https://doi.org/10.1016/j.jhydrol.2021.126170>
- 1446 Schlief, J., & Mutz, M. (2011). Leaf decay processes during and after a supra-seasonal
1447 hydrological drought in a temperate lowland stream. *International Review of*
1448 *Hydrobiology*, 96(6), 633–655. <https://doi.org/10.1002/iroh.201111322>
- 1449 Scopettone, G. G., Rissler, P. H., Fabes, M. C., & Shea, S. P. (2015). Population dynamics
1450 of the cui-ui of pyramid lake , Nevada : a potamodromous catostomid subject to failed
1451 reproduction. *North American Journal of Fisheries Management*, 35(5), 853–864.
1452 <https://doi.org/10.1080/02755947.2015.1057350>
- 1453 Scott, M. L., Reynolds, L. V, Shafroth, P. B., & Spence, J. R. (2018). The role of a non -
1454 native tree in riparian vegetation expansion and channel narrowing along a dryland river,
1455 (October 2017), 1–17. <https://doi.org/10.1002/eco.1988>
- 1456 Sefton, C. E. M., Parry, S., England, J., & Angell, G. (2019). Visualising and quantifying the
1457 variability of hydrological state in intermittent rivers. *Fundamental and Applied*
1458 *Limnology*, 193(1), 21–38. <https://doi.org/10.1127/fal/2019/1149>
- 1459 Shanafield, M., Bourke, S. A., Zimmer, M. A., & Costigan, K. H. (2021, March 1). An
1460 overview of the hydrology of non-perennial rivers and streams. *Wiley Interdisciplinary*
1461 *Reviews: Water*. John Wiley and Sons Inc. <https://doi.org/10.1002/wat2.1504>
- 1462 Sheffield, J., & Wood, E. F. (2011). *Drought : past problems and future scenarios*. London
1463 and Washington DC: Earthscan. Retrieved from <http://site.ebrary.com/id/10617505>
- 1464 Smakhtin, V. U. (2001, January 10). Low flow hydrology: A review. *Journal of Hydrology*.
1465 Elsevier. [https://doi.org/10.1016/S0022-1694\(00\)00340-1](https://doi.org/10.1016/S0022-1694(00)00340-1)
- 1466 Spinoni, J., Vogt, J. V., Naumann, G., Barbosa, P., & Dosio, A. (2018). Will drought events
1467 become more frequent and severe in Europe? *International Journal of Climatology*,
1468 38(4), 1718–1736. <https://doi.org/10.1002/joc.5291>
- 1469 Sponseller, R. A., Grimm, N. B., Boulton, A. J., & Sabo, J. L. (2010). Responses of

- 1470 macroinvertebrate communities to long-term flow variability in a Sonoran Desert
1471 stream. *Global Change Biology*, 16(10), 2891–2900. <https://doi.org/10.1111/j.1365->
1472 2486.2010.02200.x
- 1473 Stagge, J. H., Tallaksen, L. M., Gudmundsson, L., Van Loon, A. F., & Stahl, K. (2015).
1474 Candidate Distributions for Climatological Drought Indices (SPI and SPEI).
1475 *International Journal of Climatology*, 35(13), 4027–4040.
1476 <https://doi.org/https://doi.org/10.1002/joc.4267>
- 1477 Stanley, E. H., Fisher, S. G., & Grimm, N. B. (1997). Ecosystem expansion and contraction
1478 in streams: Desert streams vary in both space and time and fluctuate dramatically in size.
1479 *BioScience*, 47(7), 427–435. <https://doi.org/10.2307/1313058>
- 1480 Steila, D. (1981). A Note On Climatic Terminology. *The Professional Geographer*, 33(3),
1481 373.
- 1482 Steward, A. L., von Schiller, D., Tockner, K., Marshall, J. C., & Bunn, S. E. (2012). When
1483 the river runs dry: human and ecological values of dry riverbeds. *Frontiers in Ecology*
1484 *and the Environment*, 10(4), 202–209. <https://doi.org/10.1890/110136>
- 1485 Stubbington, R. (2012). The hyporheic zone as an invertebrate refuge: a review of variability
1486 in space, time, taxa and behaviour. *Marine and Freshwater Research*, 63(4), 293.
1487 <https://doi.org/10.1071/MF11196>
- 1488 Stubbington, R., & Datry, T. (2013). The macroinvertebrate seedbank promotes community
1489 persistence in temporary rivers across climate zones. *Freshwater Biology*, 58(6), 1202–
1490 1220. <https://doi.org/10.1111/fwb.12121>
- 1491 Stubbington, R., England, J., Wood, P. J., & Sefton, C. E. M. (2017). Temporary streams in
1492 temperate zones: recognizing, monitoring and restoring transitional aquatic-terrestrial
1493 ecosystems. *WIREs Water*, 4(4), 1223. <https://doi.org/10.1002/wat2.1223>
- 1494 Stubbington, R., Gunn, J., Little, S., Worrall, T. P., & Wood, P. J. (2016). Macroinvertebrate
1495 seedbank composition in relation to antecedent duration of drying and multiple wet-dry
1496 cycles in a temporary stream. *Freshwater Biology*, 61(8), 1293–1307.
1497 <https://doi.org/10.1111/fwb.12770>

- 1498 Stubbington, R., Sarremejane, R., & Datry, T. (2019). Alpha and beta diversity of connected
1499 benthic–subsurface invertebrate communities respond to drying in dynamic river
1500 ecosystems. *Ecography*, 42, 2060–2073. <https://doi.org/10.1111/ecog.04592>
- 1501 Tallaksen, L. M., Hisdal, H., & Lanen, H. A. J. V. (2009). Space-time modelling of
1502 catchment scale drought characteristics. *Journal of Hydrology*, 375(3–4), 363–372.
1503 <https://doi.org/10.1016/j.jhydrol.2009.06.032>
- 1504 Tallaksen, L. M., & Van Lanen, H. A. J. (2004). *Hydrological drought : processes and*
1505 *estimation methods for streamflow and groundwater*. Amsterdam, Netherlands: Elsevier.
- 1506 Tate, E. L., & Freeman, S. N. (2000). Trois méthodes pour la modélisation des étiages
1507 saisonniers en Afrique Australe: L’utilisation de données inférieures à un seuil de
1508 détection. *Hydrological Sciences Journal*, 45(1), 27–42.
1509 <https://doi.org/10.1080/02626660009492304>
- 1510 Tjeldeman, E., Stahl, K., & Tallaksen, L. M. (2020). Drought characteristics derived based on
1511 the standardized streamflow index: a large sample comparison for parametric and
1512 nonparametric methods. *Water Resources Research*, 56(10), e2019WR026315-
1513 e2019WR026315. <https://doi.org/10.1029/2019WR026315>
- 1514 Timoner, X., Colls, M., Acuña, V., & Sabater, S. (2020). Does biofilm origin matter ?
1515 Biofilm responses to non-flow period in permanent and temporary streams. *Freshwater*
1516 *Biology*, 65(3), 514-523. <https://doi.org/10.1111/fwb.13447>
- 1517 Tockner, K., Malard, F., & Ward, J. V. (2000). An extension of the food pulse concept.
1518 *Hydrological Processes*, 14(16–17), 2861–2883. <https://doi.org/10.1002/1099-1085>
- 1519 Tonkin, J. D., Bogan, M. T., Bonada, N., Rios-Touma, B., & Lytle, D. A. (2017). Seasonality
1520 and predictability shape temporal species diversity. *Ecology*, 98(5), 1201–1216.
1521 <https://doi.org/10.1002/ecy.1761>
- 1522 Tooth, S. (2000). Process, form and change in dryland rivers: a review of recent research.
1523 *Earth-Science Reviews*, 51(1–4), 67–107. [https://doi.org/10.1016/S0012-](https://doi.org/10.1016/S0012-8252(00)00014-3)
1524 [8252\(00\)00014-3](https://doi.org/10.1016/S0012-8252(00)00014-3)
- 1525 Tornwall, B. M., Swan, C. M., & Brown, B. L. (2017). Manipulation of local environment

- 1526 produces different diversity outcomes depending on location within a river network.
1527 *Oecologia*, 184(3), 663–674. <https://doi.org/10.1007/s00442-017-3891-7>
- 1528 Tramblay, Y., Llasat, M. C., Randin, C., & Coppola, E. (2020, September 1). Climate change
1529 impacts on water resources in the Mediterranean. *Regional Environmental Change*.
1530 Springer. <https://doi.org/10.1007/s10113-020-01665-y>
- 1531 Turner, T. F., Osborne, M. J., McPhee, M. V., & Kruse, C. G. (2015). High and dry:
1532 intermittent watersheds provide a test case for genetic response of desert fishes to
1533 climate change. *Conservation Genetics*, 16(2), 399–410. [https://doi.org/10.1007/s10592-](https://doi.org/10.1007/s10592-014-0666-0)
1534 [014-0666-0](https://doi.org/10.1007/s10592-014-0666-0)
- 1535 Vadher, A. N., Millett, J., Stubbington, R., & Wood, P. J. (2018). Drying duration and stream
1536 characteristics influence macroinvertebrate survivorship within the sediments of a
1537 temporary channel and exposed gravel bars of a connected perennial stream.
1538 *Hydrobiologia*, 814(1), 121–132. <https://doi.org/10.1007/s10750-018-3544-9>
- 1539 Van Huijgevoort, M. H. J., Hazenberg, P., Van Lanen, H. A. J., & Uijlenhoet, R. (2012). A
1540 generic method for hydrological drought identification across different climate regions.
1541 *Hydrology and Earth System Sciences*, 16(8), 2437–2451. [https://doi.org/10.5194/hess-](https://doi.org/10.5194/hess-16-2437-2012)
1542 [16-2437-2012](https://doi.org/10.5194/hess-16-2437-2012)
- 1543 Van Loon, A. F. (2015). Hydrological drought explained. *Wiley Interdisciplinary Reviews:*
1544 *Water*, 2(4), 359–392. <https://doi.org/10.1002/wat2.1085>
- 1545 Van Loon, A. F., Gleeson, T., Clark, J., Van Dijk, A. I. J. M., Stahl, K., Hannaford, J., ...
1546 Van Lanen, H. A. J. (2016). Drought in the Anthropocene. *Nature Geoscience*, 9(2), 89–
1547 91. Nature Publishing Group. <https://doi.org/10.1038/ngeo2646>
- 1548 van Meerveld, H. J. I., Kirchner, J. W., Vis, M. J. P., Assendelft, R. S., & Seibert, J. (2019).
1549 Expansion and contraction of the flowing stream network alter hillslope flowpath
1550 lengths and the shape of the travel time distribution. *Hydrology and Earth System*
1551 *Sciences*, 23(11), 4825–4834. <https://doi.org/10.5194/hess-23-4825-2019>
- 1552 van Meerveld, H. J. I., Sauquet, E., Gallart, F., Sefton, C., Seibert, J., & Bishop, K. (2020).
1553 Aqua temporaria incognita. *Hydrological Processes*. John Wiley and Sons Ltd.
1554 <https://doi.org/10.1002/hyp.13979>

- 1555 Vander, R., Mariska, V., Sarah, O., Pierce, N., Carlson, S. M., & Grantham, T. E. (2020).
1556 Refuges and ecological traps : Extreme drought threatens persistence of an endangered
1557 fish in intermittent streams, (March), 3834–3845. <https://doi.org/10.1111/gcb.15116>
- 1558 Vander Vorste, R., Malard, F., & Datry, T. (2016). Is drift the primary process promoting the
1559 resilience of river invertebrate communities? A manipulative field experiment in an
1560 intermittent alluvial river. *Freshwater Biology*, 61(8), 1276–1292.
1561 <https://doi.org/10.1111/fwb.12658>
- 1562 Vander Vorste, R., Mermillod-Blondin, F., Hervant, F., Mons, R., & Datry, T. (2016a).
1563 *Gammarus pulex* (Crustacea: Amphipoda) avoids increasing water temperature and
1564 intraspecific competition through vertical migration into the hyporheic zone: a
1565 mesocosm experiment. *Aquatic Sciences*, 79(1), 45–55. [https://doi.org/10.1007/S00027-](https://doi.org/10.1007/S00027-016-0478-Z)
1566 [016-0478-Z](https://doi.org/10.1007/S00027-016-0478-Z)
- 1567 Vander Vorste, R., Mermillod-Blondin, F., Hervant, F., Mons, R., Forcellini, M., & Datry, T.
1568 (2016b). Increased depth to the water table during river drying decreases the resilience
1569 of *Gammarus pulex* and alters ecosystem function. *Ecohydrology*, 9(7), 1177–1186.
1570 <https://doi.org/10.1002/eco.1716>
- 1571 Vander Vorste, R., Sarremejane, R., & Datry, T. (2020). Intermittent rivers and ephemeral
1572 streams: a unique biome with important contributions to biodiversity and ecosystem
1573 services. In *Encyclopedia of the World's Biomes* (pp. 419–429). Elsevier.
1574 <https://doi.org/10.1016/b978-0-12-409548-9.12054-8>
- 1575 Verkaik, I., Vila-Escalé, M., Rieradevall, M., Baxter, C. V., Lake, P. S., Minshall, G. W., ...
1576 Prat, N. (2015). Stream macroinvertebrate community responses to fire: Are they the
1577 same in different fire-prone biogeographic regions? *Freshwater Science*, 34(4), 1527–
1578 1541. <https://doi.org/10.1086/683370>
- 1579 Vicente-Serrano, S. M., López-Moreno, J. I., Beguería, S., Lorenzo-Lacruz, J., Azorin-
1580 Molina, C., & Morán-Tejeda, E. (2012). Accurate Computation of a Streamflow
1581 Drought Index. *Journal of Hydrologic Engineering*, 17(2), 318–332.
1582 [https://doi.org/10.1061/\(asce\)he.1943-5584.0000433](https://doi.org/10.1061/(asce)he.1943-5584.0000433)
- 1583 Vidal-Abarca, M. R., Gómez, R., Sánchez-Montoya, M. M., Arce, M. I., Nicolás, N., &

- 1584 Suárez, M. L. (2020). Defining dry rivers as the most extreme type of non-perennial
1585 fluvial ecosystems. *Sustainability*, *12*(17), 7202. <https://doi.org/10.3390/su12177202>
- 1586 Vos, C. C., Verboom, J., Opdam, P. F. M., & Ter Braak, C. J. F. (2001). Toward ecologically
1587 scaled landscape indices. *American Naturalist*, *157*(1), 24–41.
1588 <https://doi.org/10.1086/317004>
- 1589 Wanders, N., & Wada, Y. (2015). Human and climate impacts on the 21st century
1590 hydrological drought. *Journal of Hydrology*, *526*, 208–220.
1591 <https://doi.org/10.1016/j.jhydrol.2014.10.047>
- 1592 Westwood, C. G., England, J., Johns, T., & Stubbington, R. (2020). A revised classification
1593 of temperate lowland groundwater-fed headwater streams based on their flora. *Water
1594 and Environment Journal*, *34*, 573–585. <https://doi.org/10.1111/wej.12561>
- 1595 White, J. C., House, A., PUNCHARD, N., Hannah, D. M., Wilding, N. A., & Wood, P. J. (2018).
1596 Macroinvertebrate community responses to hydrological controls and groundwater
1597 abstraction effects across intermittent and perennial headwater streams. *Science of the
1598 Total Environment*, *610–611*(2016), 1514–1526.
1599 <https://doi.org/10.1016/j.scitotenv.2017.06.081>
- 1600 Whiterod, N. S., Hammer, M. P., & Vilizzi, L. (2015). Spatial and temporal variability in fish
1601 community structure in Mediterranean climate temporary streams. *Fundamental and
1602 Applied Limnology*, *18*(November), 135–150. <https://doi.org/10.1127/fal/2015/0771>
- 1603 Wilhite, D. A. (1992). *Preparing for drought: A guidebook for developing countries*. Nairobi:
1604 United Nations Environment Programme.
- 1605 Wilhite, D. A., & Glantz, M. H. (1985). Understanding: the drought phenomenon: the role of
1606 definitions. *Water International*, *10*(3), 111–120.
- 1607 Williams, D. D. (1996). Environmental constraints in temporary fresh waters and their
1608 consequences for the insect fauna. *Journal of the North American Benthological Society*,
1609 *15*(4), 634–650. <https://doi.org/10.2307/1467813>
- 1610 Woelfle-Erskine, C., Larsen, L. G., & Carlson, S. M. (2017). Abiotic habitat thresholds for
1611 salmonid over-summer survival in intermittent streams. *Ecosphere*, *8*(2), e01645.

- 1612 <https://doi.org/10.1002/ecs2.1645>
- 1613 Woodward, G., Bonada, N., Feeley, H. B., & Giller, P. S. (2015). Resilience of a stream
1614 community to extreme climatic events and long-term recovery from a catastrophic flood.
1615 *Freshwater Biology*, 60(12), 2497–2510. <https://doi.org/10.1111/fwb.12592>
- 1616 Yevjevich, V. (1967). *An Objective Approach to Definitions and Investigations of*
1617 *Continental Hydrologic Droughts*. Fort Collins, Colorado: Colorado State University.
- 1618 Yu (于松延), S., Bond, N. R., Bunn, S. E., Xu, Z., & Kennard, M. J. (2018). Quantifying
1619 spatial and temporal patterns of flow intermittency using spatially contiguous runoff
1620 data. *Journal of Hydrology*, 559, 861–872.
1621 <https://doi.org/10.1016/J.JHYDROL.2018.03.009>
- 1622 Zargar, A., Sadiq, R., Naser, B., & Khan, F. I. (2011). A review of drought indices.
1623 *Environmental Reviews*. 19, 333-349. <https://doi.org/10.1139/a11-013>
- 1624 Zelenhasić, E., & Salvai, A. (1987). A method of streamflow drought analysis. *Water*
1625 *Resources Research*, 23(1), 156–168. <https://doi.org/10.1029/WR023i001p00156>
- 1626 Zelnik, Y. R., Arnoldi, J.-F., & Loreau, M. (2018). The impact of spatial and temporal
1627 dimensions of disturbances on ecosystem stability. *Frontiers in Ecology and Evolution*,
1628 6(9). <https://doi.org/10.3389/fevo.2018.00224>
- 1629 Zhou, H., Chen, Y., Zhu, C., Li, Z., Fang, G., & Li, Y. (2020). Climate change may
1630 accelerate the decline of desert riparian forest in the lower Tarim River , Northwestern
1631 China : Evidence from tree-rings of *Populus euphratica*. *Ecological Indicators*, 111,
1632 105997. <https://doi.org/10.1016/j.ecolind.2019.105997>
- 1633 Zimmer, M. A., Kaiser, K. E., Blaszcak, J. R., Zipper, S. C., Hammond, J. C., Fritz, K. M.,
1634 ... Allen, D. C. (2020). Zero or not? Causes and consequences of zero-flow stream gage
1635 readings. *Wiley Interdisciplinary Reviews: Water*. John Wiley and Sons Inc.
1636 <https://doi.org/10.1002/wat2.1436>
- 1637 Zylstra, E. R., Swann, D. E., & Steidl, R. J. (2019). water availability governs survival of an
1638 amphibian in arid mountain streams. *Freshwater Biology*, 64(6), 164–174.
1639 <https://doi.org/10.1111/fwb.13204>

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1644 **Tables**

1645 **Table 1:** Definition of the different attributes of flow regime and hydrological drought

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Phenomenon	Attribute	Definition
Flow regime (adapted from Poff et al. 1997 ¹)	Magnitude	The amount of water moving past a fixed location per unit of time (e.g. mean minimum monthly discharge)
	Frequency	How often a flow above a given magnitude recurs over some specified time interval (e.g., annual number of no-flow events)
	Duration	The period of time associated with a specific flow condition (e.g., mean monthly number of days having zero daily flow)
	Timing (or predictability)	The period and the regularity with which flows of defined magnitude occur (e.g., mean date of the first no-flow occurrence)
Hydrological drought (adapted from Dracup et al. 1980 ² and Mishra and Singh 2010 ³)	Rate of change	How quickly flow changes from one magnitude to another (e.g., dry-down duration, the number of days from a local streamflow peak to the first occurrence of no-flow)
	Timing	Initiation and termination dates of a streamflow deficit
	Duration	The number of consecutive time periods (e.g., months, years) for which the streamflow is below the long-term mean or another defined threshold reflecting a critical level
	Severity	The cumulative deficit of streamflow below the critical level for that duration
	Intensity (or magnitude)	The average deficit of streamflow for that duration (severity/duration)

Spatial extent

The areas, river sections, basins, or regions affected by streamflow deficit (e.g. the cumulative dry river length)

- 1647
1648 (1) Poff, N. L. R., Allan, J. D., Bain, M. B., Karr, J. R., Prestegard, K. L., Richter, B. D., Sparks, R. E., & Stromberg, J. C. (1997). The natural
1649 flow regime: A paradigm for river conservation and restoration. *BioScience*, 47(11), 769–784. <https://doi.org/10.2307/1313099>; (2) Dracup
1650 J.A., Lee K.S., Paulson E.G., (1980). On the definition of droughts. *Water Resource Research*, 16, 297–302; (3) Mishra, A. K., & Singh, V.
1651 P. (2010). A review of drought concepts. *Journal of Hydrology*, 391, 202-216. <https://doi.org/10.1016/j.jhydrol.2010.07.012>

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Table 2: Research questions and perspectives to improve our understanding of IRES responses to droughts.

Research question	Scientific breakthrough examples	Disciplines
What drives the propagation from meteorological drought to hydrological drought in IRES?	Identify river reaches whose hydrology is most severely affected by meteorological droughts.	Hydrology, hydrogeology, modelling
How do the delayed onset and recovery of groundwater drought affect IRES ecosystem resilience?	Understand the role of groundwater in mediating the short and long-term effects of hydrological drought.	Hydrology, hydrogeology, modelling
To which extent are drought impacts amplified by increased human withdrawals of water during droughts?	Understand how surface and groundwater abstraction dynamics interact during drought episodes in IRES.	Hydrology, hydrogeology, modelling
Where and under which conditions are IRES ecosystems, including organisms, populations and communities are most sensitive to drought?	Determine the tipping points in drying patterns after which the resilience of individual species and communities in IRES river networks is compromised.	Hydrology, ecology

What are the long-term hydrological and ecological trajectories in IRES after droughts?	Understand the legacy of droughts on IRES resilience.	Hydrology, hydrogeology, ecology
How do floods and droughts interact in IRES?	Quantify the relative roles of extreme hydrological events on IRES resilience.	Hydrology, hydrogeology, ecology
What is the impact of drought compared to seasonal intermittence on biotic interactions?	Disentangle the relative role of abiotic and biotic factors in determining community trajectories in IRES after droughts.	Ecology
How do droughts in IRES networks affect nearby terrestrial ecosystems?	Identify the ripple effects of droughts in terrestrial food webs during and after the event.	Ecology, biogeochemistry
What are the effects of drought on local to network-scale ecosystem processes (e.g., decomposition, CO ₂ emissions)?	Understand how droughts can disrupt ecosystem-wide processes.	Hydrology, ecology, biogeochemistry
How do IRES ecosystems respond to different suites of interacting stressors?	Quantify the interactive effects of multiple stressors in a context of flow intermittence.	Hydrology, ecology, ecotoxicology
What are the differences in ecological responses between natural and human-induced IRES?	Predict socio-ecological consequences of shifts from perennial to intermittent flow regimes and vice-versa.	Hydrology, hydrogeology, ecology, ecotoxicology, social sciences

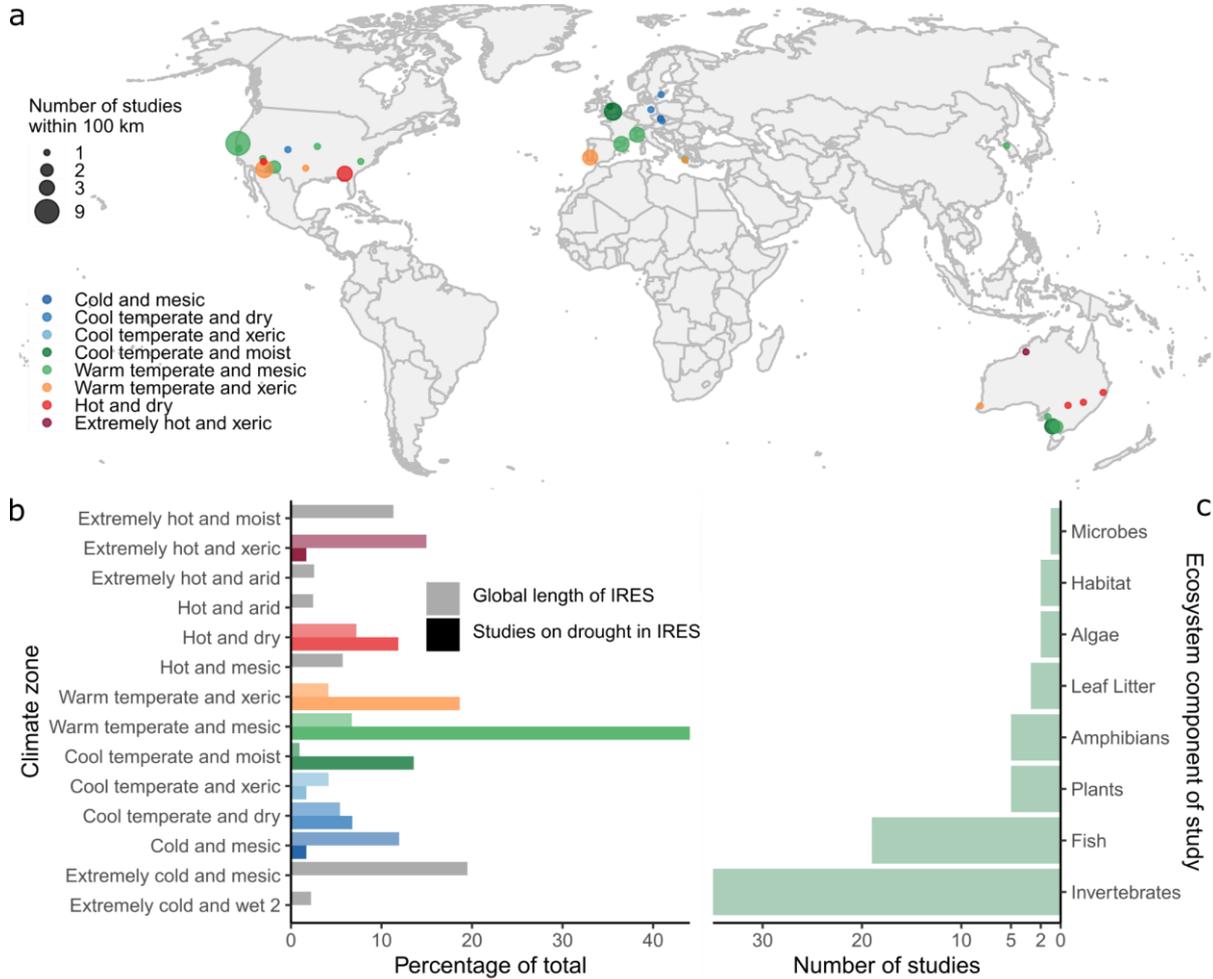
<p>How do droughts affect the provision of ecosystem services in IRES river networks?</p>	<p>Translate the changes in biophysical templates due to drying into socio-economical responses.</p>	<p>Hydrology, hydrogeology, ecology, social sciences, economy, modelling</p>
<p>How can societies mitigate and adapt to drought-induced changes in flow regimes?</p>	<p>Test and develop management strategies, including Nature-Based Solutions to mitigate the effects of droughts in IRES.</p>	<p>Hydrology, hydrogeology, ecology, social sciences, economy, modelling</p>

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1656 **Figures**

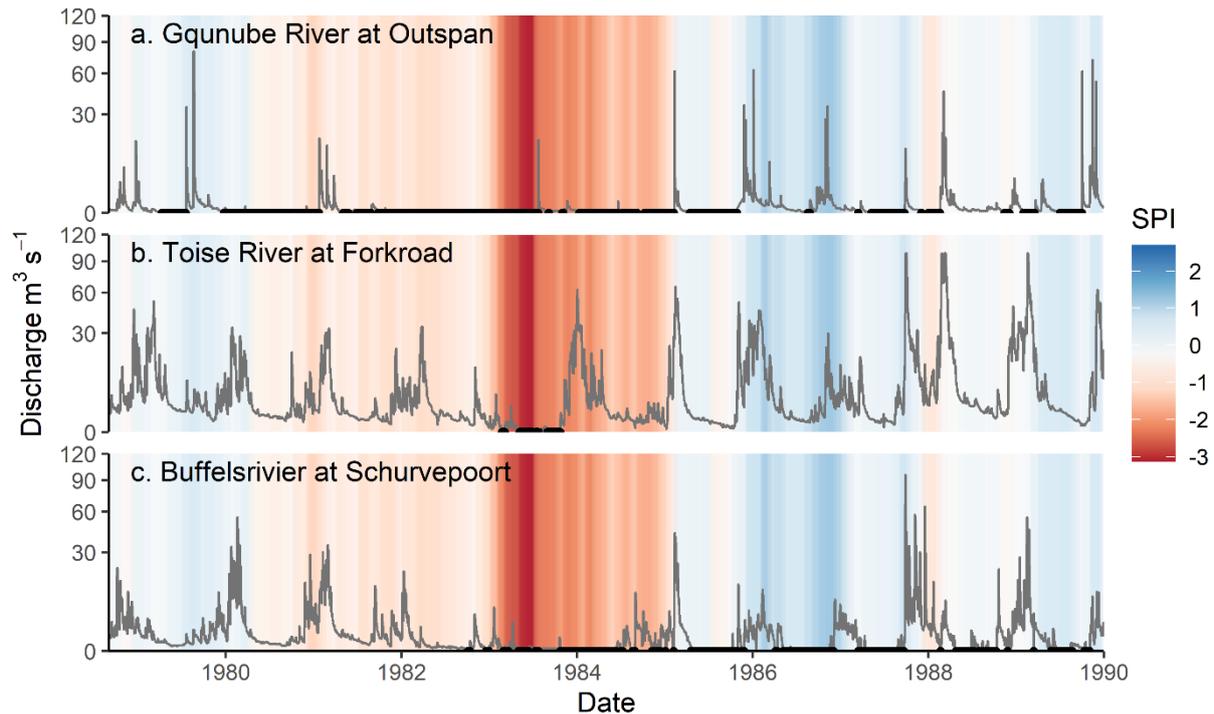
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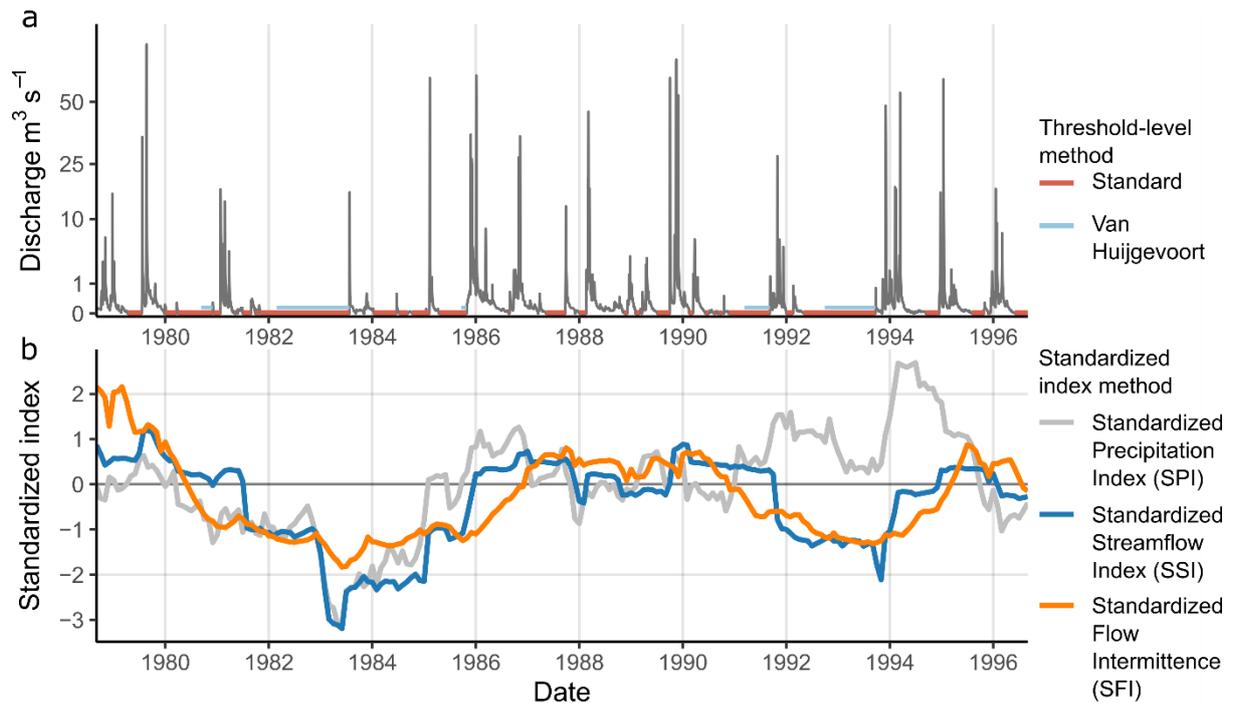
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1659 **Figure 1: Global distribution of studies on the ecohydrological responses of intermittent**
 1660 **rivers and ephemeral streams (IRES) to droughts.** Studies were clustered by geographic
 1661 location and climate (a), larger points show locations with more studies. Comparing the
 1662 distribution of studies (darker-colored bars) to that of IRES (lighter-colored bars; Messenger et
 1663 al. 2021) across climate zones (b) reveal climates for which there are currently no studies
 1664 (grey bars) and climates that are disproportionately studied (e.g., warm temperate and mesic,
 1665 cool temperate and moist). Most research on IRES responses to drought have focused on
 1666 invertebrates and fish (c). See Appendix 1, Figure S1 for the full distribution of climate zones
 1667 (Global Environmental Stratification; Metzger et al., 2013; zones that include less than 1% of
 1668 the world’s IRES length and were not studied are not included in panel B).

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 1671 **Figure 2: The hydrological consequences of meteorological droughts vary among rivers**
 1672 **with different flow regimes.** The responses of three rivers of eastern South Africa to a
 1673 drought in the early 1980s differ. In a naturally intermittent river (a), flow cessation is a
 1674 natural process, but droughts can result in more prolonged and severe drying; in naturally
 1675 perennial rivers (b-c), severe droughts can cause temporary flow cessation (b), and in
 1676 exceptional cases, permanently shift the flow regime of a river from perennial to non-
 1677 perennial (c). Thicker, black sections of the hydrograph line identify days of zero flow. The
 1678 shading reflects daily Standardized Precipitation Index (SPI) values calculated over the
 1679 previous 24 months (see Section 2.3 for more details on this index).
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Figure 3: Commonly-used drought indices imperfectly reflect hydrological droughts in the naturally intermittent Gqunube River at Outspan in South Africa.

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(a) a standard threshold-level drought index that flags every discharge value at or under Q90

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classifies all instances of flow cessation as drought days (red highlight). The drought index

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developed by Van Huijgevoort, by contrast, only flags abnormally long periods of zero

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discharge as drought events (blue highlight). Of the standardized drought indices (b), the

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Standardized Precipitation Index (SPI; grey line) is the most commonly used but only reflects

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the meteorological character of a drought. In this case, the SPI calculated based on a weather

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station near the Gqunube River (< 70 km) does not reflect a hydrological drought in 1993

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identified with the Standardized Streamflow Index (SSI; blue line) and Standardized Flow

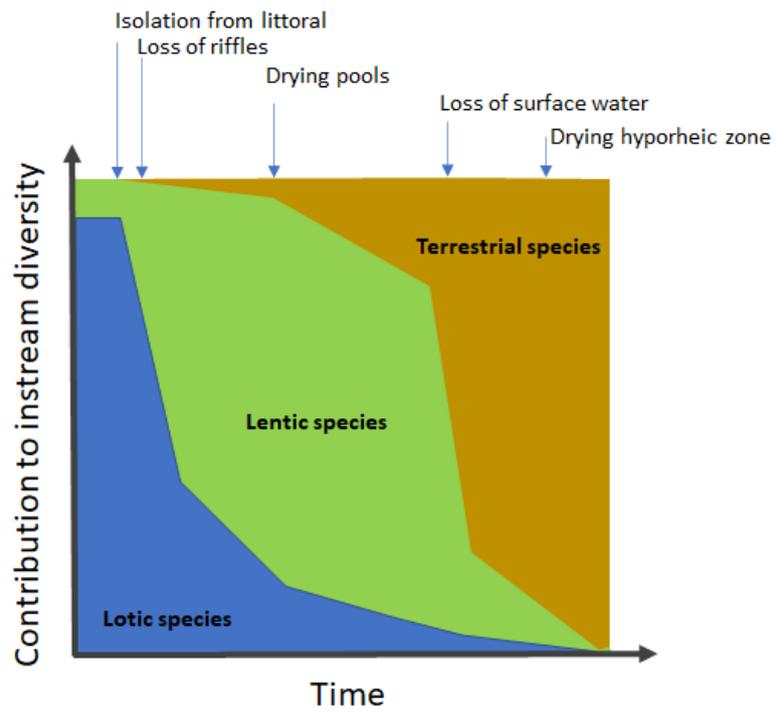
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Intermittence (SFI; orange line). All three standardized indices were computed at the monthly

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time scale based on records over the previous 24 months.

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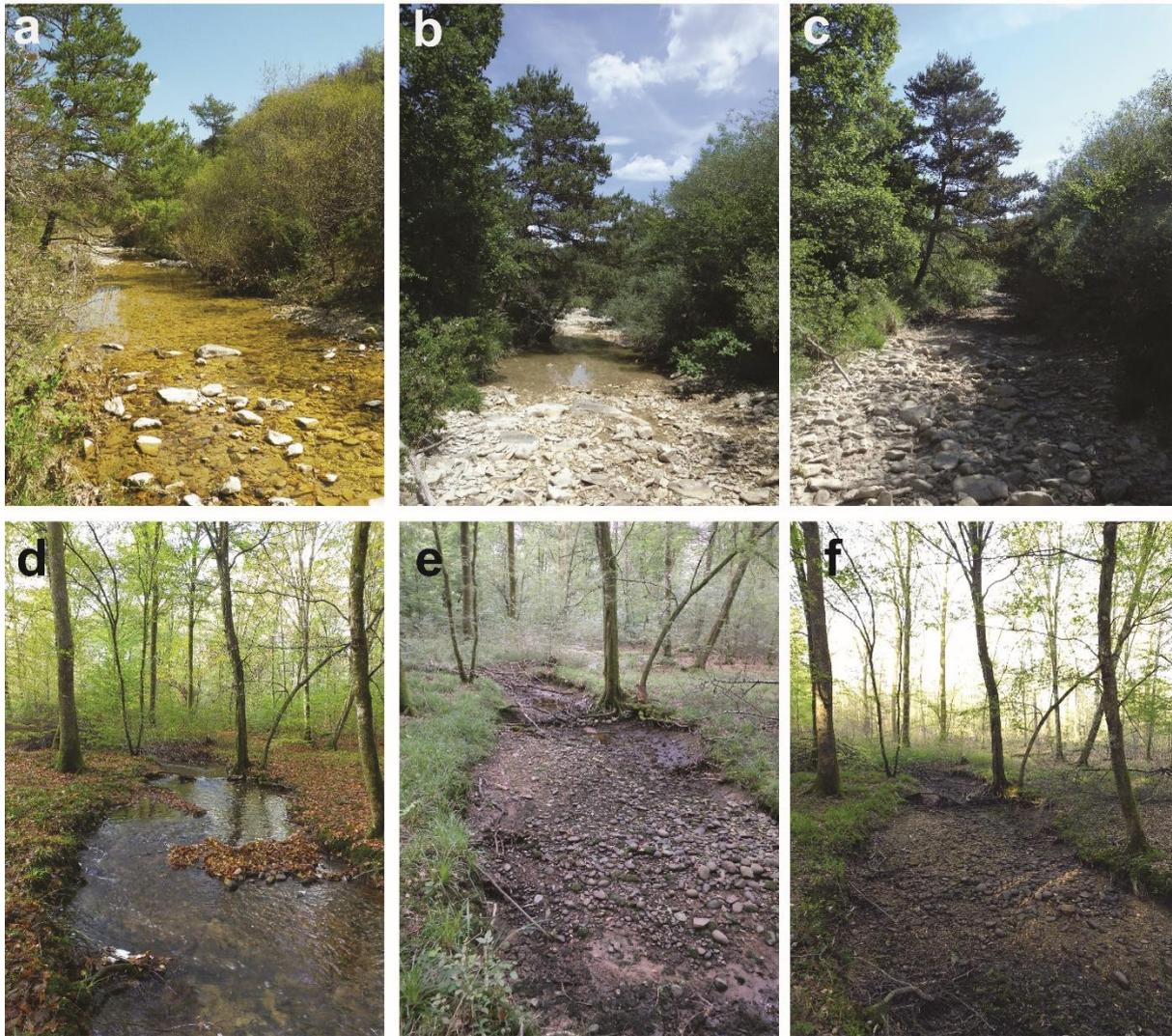
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1696 **Figure 4:** Stepped changes in instream community composition as drying progresses and
 1697 aquatic habitats are lost in IRES. Figure inspired by Boulton (2003).

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1702 **Figure 5: Two IRES in different hydrological stages, including one during a drought.**

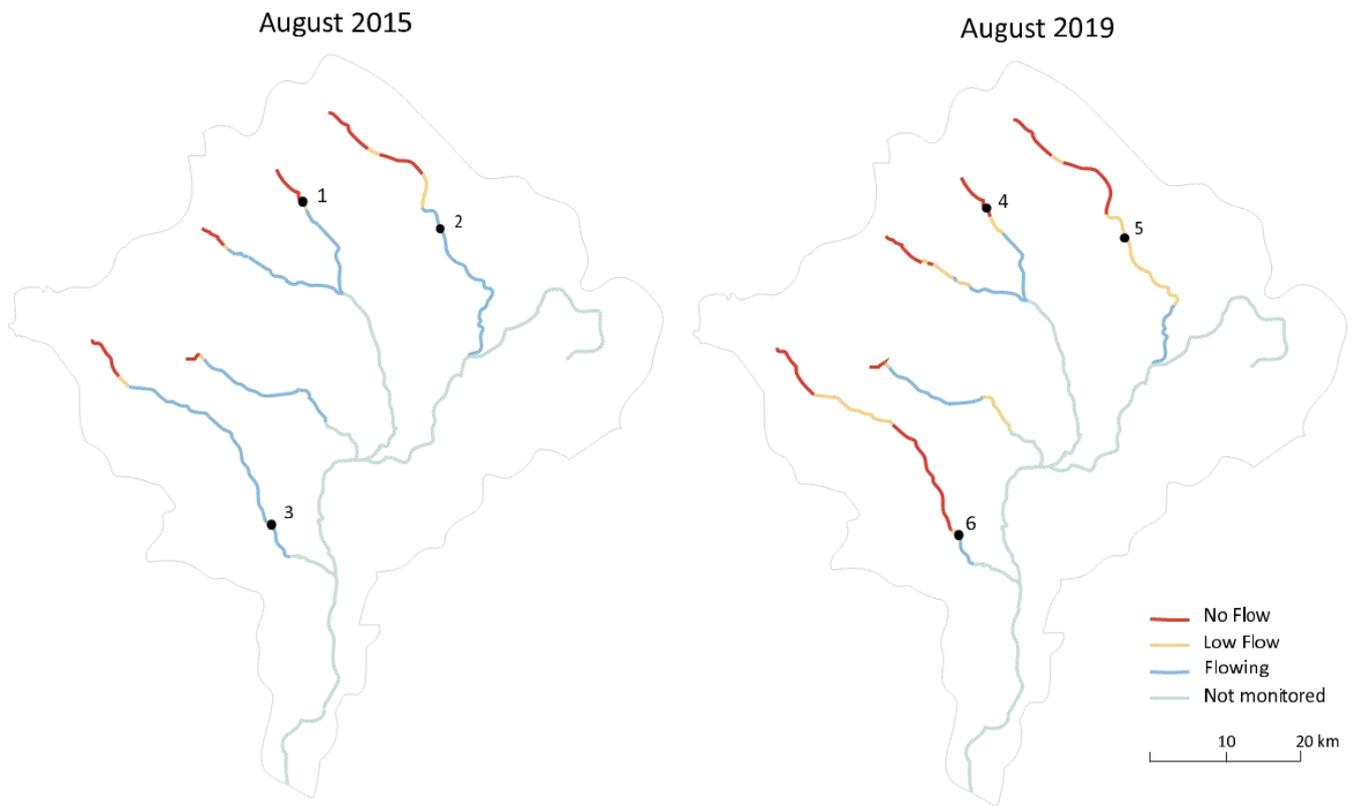
1703 The Calavon River, Southeastern France, during flowing (a), non-flowing (b) phases and with

1704 an extremely dry streambed during a drought in 2017 (c). The Clauge River, Eastern France,

1705 for the same hydrological phases: flowing (d), non-flowing (e) phases and during a drought in

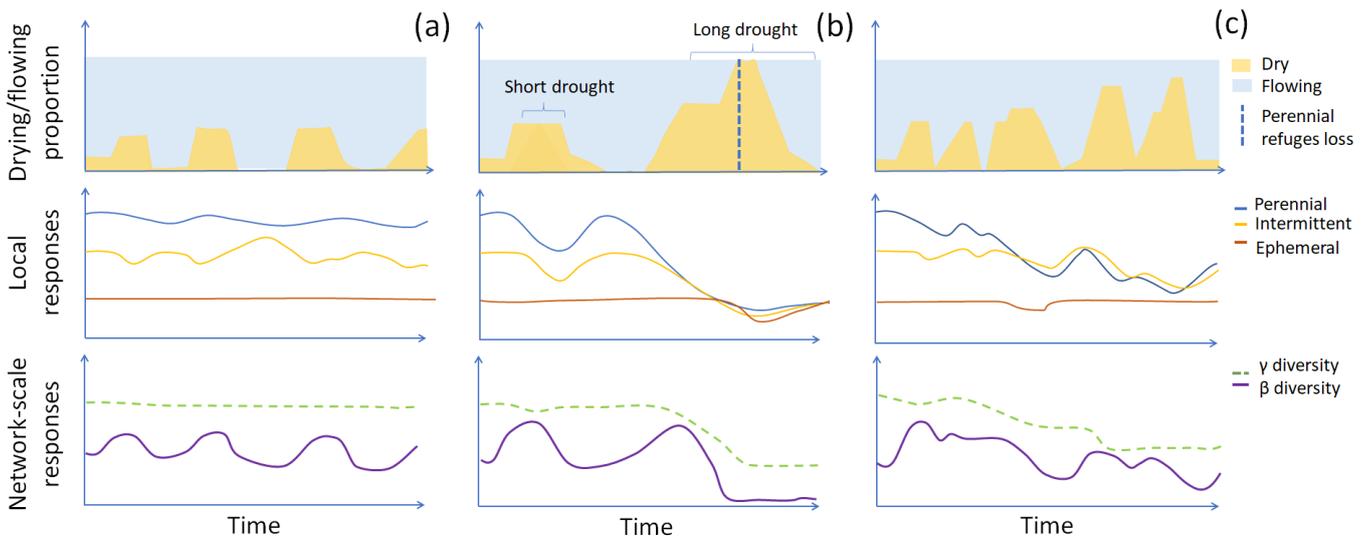
1706 2017 (f). Photos: Bertrand Launay.

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1708 **Figure 6: Changes in the configuration of flow conditions and habitat within an IRES**
 1709 **river network (The Colne river, England) between an average (1-3) and a drought (4-6)**
 1710 **year.**
 1711

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1714 **Figure 7: Effects of intermittent drying (a) and droughts duration (b) and frequency (c)**
 1715 **on the extent of drying reaches at the network scale (upper panel) and hypothesized**
 1716 **responses of local (i.e., diversity and abundances; middle panels) and regional (i.e. β and**
 1717 **γ diversity; lower panels) biodiversity.** In IRES where drying is cyclic and an inherent part
 1718 of the natural flow regime, local and regional diversity may fluctuate between the dry and wet
 1719 season. However, droughts can induce decreases in local diversity and population density
 1720 beyond those observed during seasonal drying, with likely stronger initial responses in
 1721 perennial and intermittent streams as habitats contract than in ephemeral streams mainly
 1722 composed of resistant taxa. Short droughts may induce increases in community variability if
 1723 network scale environmental conditions become more variable and if refuges prevent
 1724 regional extinctions. Spatially and temporally extended drought may however lead to
 1725 synchronous declines in diversity across streams with different permanence regimes as
 1726 resistance capacities of species are exceeded. Such events can lead to decrease in regional
 1727 diversity and a homogenization of communities at the regional scale if only a subset of
 1728 resistant species remain everywhere. Drought periods interrupted by short periods of rainfall
 1729 may allow the persistence of diversity by avoiding complete loss of refuges. However,
 1730 increases in drought frequencies may lead to a selection of a set of taxa with short life cycle
 1731 able to recover quickly between droughts, leading to a homogenization of the communities at
 1732 the network scale.

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