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## Challenges, developments and perspectives in intermittent river ecology

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1 **Challenges, developments and perspectives in intermittent river ecology**

2

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18 **Running head:** Intermittent river ecology

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26 **Summary**

- 27       **1.** Although more than half the world's river networks comprise channels that  
28           periodically cease to flow and dry (intermittent rivers [IRs]), river ecology was largely  
29           developed from and for perennial systems. Ecological knowledge of IRs is rapidly  
30           increasing, so there is a need to synthesize this knowledge and deepen ecological  
31           understanding.
- 32       **2.** In this Special Issue, we bring together 13 papers spanning observational case studies,  
33           field and laboratory experiments and reviews to guide research and management in  
34           this productive field of freshwater science. We summarize new developments in IR  
35           ecology, identify research gaps and needs, and address how the study of IRs as highly  
36           dynamic ecosystems informs ecological understanding more broadly.
- 37       **3.** This series of articles reveals that contemporary IR ecology is a multifaceted and  
38           maturing field of research at the interface between aquatic and terrestrial ecology. This  
39           research contributes to freshwater and general ecology by testing concepts across a  
40           range of topics, including disturbance ecology, metacommunity ecology and coupled  
41           aquatic-terrestrial ecosystems.
- 42       **4.** Drying affects flow continuity through time and flow connectivity across longitudinal,  
43           lateral and vertical dimensions of space, which aligns well with the recent emphasis of  
44           mainstream ecology on meta-system perspectives. Although most articles here focus  
45           on the wet phase, there is growing interest in dry phases, and in the terrestrial  
46           vegetation and invertebrate assemblages living in and along IR channels. We  
47           encourage interdisciplinary studies on IRs to further blur the demarcation between  
48           aquatic and terrestrial ecosystems and develop more integrated perspectives.
- 49       **5.** As a result of climate change and human modification of landscapes and waterways,  
50           flooding and drought are expected to become more extreme and widespread. Shifts in

51 streamflow regimes from perennial to intermittent may exacerbate the duration and  
52 frequency of dry phases in IRs with serious implications for river ecosystems and the  
53 quality and diversity of services they provide.

54

## 55 **Introduction**

56 River ecology initially developed from and for the study of perennial rivers and streams  
57 (Datry *et al.*, 2014a). Yet more than half the channels comprising river networks globally  
58 cease to flow or dry periodically (Acuña *et al.*, 2014; Datry *et al.*, 2014a), with the proportion  
59 exceeding 80% in some regions (Levick *et al.*, 2005; Sabater & Tockner, 2010). Moreover, the  
60 frequency and duration of flow cessation and drying are increasing in many rivers in response  
61 to climate change and growing demands for fresh water (McKerchar & Schmidt, 2007;  
62 Larned *et al.*, 2011; Jäeger, Olden & Pelland, 2014). Several large and once-perennial rivers  
63 no longer flow continuously to their deltas, including the Yellow (China), Colorado (U.S.A),  
64 Amu and Syr Darya (Central Asia) and Nile (Egypt) (Gleick, 2003; Postel & Richter, 2012),  
65 and the number of perennial systems becoming intermittent is expected to increase (Larned *et*  
66 *al.*, 2010; Döll & Schmied, 2012; Jaeger, Olden & Pelland, 2014). Rivers and streams without  
67 continuous flow have been named by a variety of terms, such as non-perennial, temporary,  
68 intermittent, ephemeral, seasonal and episodic (Uys & O'Keeffe, 1997; Williams, 2005;  
69 Arthington *et al.*, 2014). For sake of consistency, generality and simplicity, we refer to them  
70 here as intermittent rivers (IRs): any river or stream that ceases to flow or dries at any point in  
71 time and space (Acuña *et al.*, 2014; Datry *et al.*, 2014a), whether naturally or as a result of  
72 human activities.

73

74 After years of relative obscurity, the ecological study of IRs is trending upward. The interest  
75 from river scientists and managers in IRs has grown rapidly in the past decade (Datry, Arscott

76 & Sabater, 2011, Arthington, Bernardo & Ilhéu 2014) and the number of IR studies published  
77 in freshwater and ecology journals, including *Freshwater Biology*, has grown considerably  
78 (Fig. 1). According to the results of a Web of Science search conducted by Leigh et al. (2016  
79 a) in 2014, over 70% of IR literature published in these journals on the topics of fish and  
80 invertebrate ecology, biogeochemistry, and hydrological and ecological-condition assessment  
81 has appeared since the mid-2000s (Fig. 1). Ecological research on IRs now appears in high-  
82 rank (e.g. Raymond *et al.*, 2013; Jaeger *et al.*, 2014; Acuña *et al.* 2014) and general ecology  
83 journals (Boersma *et al.* 2014; Datry, Larned & Tockner, 2014a; Datry *et al.*, 2014b; Cañedo-  
84 Argüelles *et al.* 2015). Since 2008, almost every major freshwater conference has had a  
85 special session on IRs in its program, producing special issues of journals on the topic of IRs  
86 or related themes such as hydrological (dis)connectivity (e.g. Nadeau & Rains, 2007; Datry *et*  
87 *al.* 2011; Arthington *et al.*, 2014). Several international projects on IRs have been initiated,  
88 including the MIRAGE European project ([www.igb-berlin.de/mirage.html](http://www.igb-berlin.de/mirage.html), 2009-2011) and  
89 its continuation as a Life project ([www.lifetribers.eu](http://www.lifetribers.eu), 2014-2016), the international  
90 Intermittent River Biodiversity Analysis and Synthesis program ([www.irbas.fr](http://www.irbas.fr), 2013-2016),  
91 the 1000 Intermittent River Project ([http://1000\\_intermittent\\_rivers\\_project.irstea.fr](http://1000_intermittent_rivers_project.irstea.fr), 2015-)  
92 and a H2020 European COST Action (Science and Management of Intermittent Rivers and  
93 ephemeral streams ([http://www.cost.eu/COST\\_Actions/ca/CA15113](http://www.cost.eu/COST_Actions/ca/CA15113), 2016-2020). This  
94 growing interest in IRs from scientists and managers indicates the prevalence and specificities  
95 of IRs, but also the scientific contribution that the study of IRs can make to general ecology  
96 and the growing awareness of the social, cultural, economic and environmental values of  
97 these systems.

98

99 **From humble beginnings, the future of IR ecology is bright**

100 In this Special Issue, we specifically seek to examine how IR ecology is maturing and how  
101 some key questions in ecology can be addressed through the study of IRs as highly dynamic  
102 ecosystems. We bring together 13 papers, including this introduction, spanning observational  
103 case studies (Corti & Datry, 2016; Datry *et al.*, 2016 a, b; Marshall *et al.*, 2016; Rolls, Heino  
104 & Chessman, 2016; Siebers *et al.*, 2016; Stromberg & Merritt, 2016; Welter & Fisher, 2016;  
105 Whitney *et al.*, 2016), field (Vander Vorste, Malard & Datry, 2016) and laboratory  
106 (Stubbington *et al.*, 2016) experiments, and reviews (Leigh *et al.*, 2016 a).

107

108 Leigh *et al.* (2016 a) review the basic and applied ecological literature on IRs, document the  
109 genealogy of ideas and highlight major advances across several research themes. While IR  
110 studies were instrumental in the development of fluvial geomorphology theory (e.g., Schumm  
111 & Hadley, 1953; Leopold & Miller, 1956), research on temporary standing waters (e.g.,  
112 Wiggins, Mackay & Smith, 1980) and perennial systems (e.g., Harrel, Davis & Dorris, 1967)  
113 was influencing early work on IRs. Persistent research themes that have informed ecological  
114 theory and IR management include resistance and resilience to drying. Leigh *et al.* (2016 a)  
115 show through their review that the recent boom in IR publications coincides with the  
116 increasing need for science to inform policy concerning the legal status of IRs, and  
117 recognition that the number and length of IRs are likely to increase with climate change and  
118 growing human demands for fresh water. In aggregate, IR research has a strong future with  
119 growing interest around the world and across multiple research themes.

120

121 **IRs are highly dynamic ecological systems: landscape mosaics, biogeochemistry and**  
122 **biological organisation in IRs**

123 Landscapes change over time through physical and biological drivers that are patchily  
124 distributed, spatially and temporally (Bormann & Likens, 1979). Although terrestrial

125 landscapes and branching riverine networks differ in many respects, the terrestrially based  
126 concept of shifting habitat mosaics applies well to rivers because of their dynamic nature, the  
127 interrelationships between hydrology, fluvial geomorphology and the distribution of biota,  
128 and water as a vector linking patches (Ward, Malard & Tockner, 2002; Stanford, Lorang &  
129 Hauer, 2005; Altermatt, 2013). Datry *et al.* (2016 a) use hydrogeographic data collected by  
130 citizen scientists to describe the spatio-temporal dynamics of IR habitats within five river  
131 networks in west-central France, their hydrologic controls, and associated extinction risk and  
132 colonisation for hypothetical fish and aquatic insects. Whereas general configuration and  
133 compositional patterns of IR habitats were found among the networks studied, a high degree  
134 of complexity was seen in landscape-metric variability over relatively short time frames and  
135 among neighbouring catchments. Describing IRs with landscape metrics adds spatial  
136 dimensions that are typically missed by flow metrics alone and may be particularly applicable  
137 to internally coupled aquatic-terrestrial systems (i.e., dry, lentic and lotic conditions within  
138 and across reaches). Datry *et al.* (2016 a) propose that a landscape approach not only  
139 advances ecological understanding within IRs, but that this perspective will further advance  
140 IRs as models for studying network dynamics in general.

141

142 The spatio-temporal variability in flow and mosaic composition of IR landscapes (dry, lentic  
143 and lotic patches) poses particular challenges for determining the extent of material transport,  
144 transformation and retention across networks (Malard, Tockner & Ward, 1999; Larned *et al.*,  
145 2010; Sponseller, Heffernan & Fisher, 2013). Transport of nutrients and organic matter from  
146 terrestrial hillslopes into intermittent channels can generate hot spots of microbial activity, but  
147 this may depend on the spatial extent of the hydrologic flow paths generated by rainfall pulses  
148 and how long resources, including water, remain available. Welter & Fisher (2016) show how  
149 storm characteristics influence the extent of hydrologic connectivity along a terrestrial-aquatic



150 flowpath in the Sycamore Creek catchment of Arizona, U.S.A., and thereby affect  
151 denitrification and nitrogen retention. They show that the size, timing and intensity of storms  
152 control hydrologic connectivity in small streams and that riparian terrace and hillslope soils  
153 have the highest denitrification potential. Deep and moist channel sediments (i.e. the  
154 hyporheic zone) have low denitrification potential but contribute to nitrogen loss for a longer  
155 period of time overall. The study reveals important links between rainfall pulses, vertical and  
156 horizontal hydrologic connectivity and the magnitude of transport, storage and processing of  
157 nutrient and organic material in arid IR landscapes.

158

159 IRs in many regions are renowned for their high levels of flow variability (e.g. Puckridge *et*  
160 *al.*, 1998; Poff *et al.*, 2006, Bonada *et al.*, 2007), which can profoundly affect biogeochemical  
161 processes, creating ‘hot spots’ and ‘hot moments’ within IRs (Fisher *et al.*, 2001; Datry *et al.*,  
162 2014a). As surface flows become discontinuous and pools contract, particulate and dissolved  
163 organic matter (DOM) become concentrated and can subsequently change in composition  
164 through the drying phase. Siebers *et al.* (2016) investigate the flow-related causes of such  
165 changes in pools of dryland Australian IRs using a combination of  $\delta^{18}\text{O}$  and  $\delta^2\text{H}$  values of  
166 surface and alluvial ground waters and DOM fluorescence excitation–emission spectroscopy.  
167 Although the extent to which pools remain connected to alluvial ground water is strongly  
168 linked to changes in fluorescence, the findings suggest that high variability in groundwater-  
169 surface water mixing contributes to substantial variability in compositional patterns among  
170 pools. This study emphasizes that variation in biogeochemical processes and DOM  
171 characteristics within these systems cannot be attributed to the presence or absence of surface  
172 flow alone, highlighting the complexity of IR flow regimes and hydrological-(dis)connectivity  
173 dynamics.

174

175 Landscape characteristics and hydrological-(dis)connectivity dynamics can also interact with  
176 species traits to influence local extinction, connectivity and movement behaviour of biota  
177 (Fausch *et al.*, 2002; Datry *et al.*, 2015). In many dryland IRs, for example, fish can be  
178 confined to isolated waterholes for much of the year and are able to colonise the network only  
179 during brief flow events. The ways fish use waterholes over time and space to either re-  
180 establish populations following dry periods (resilience) or maintain populations during dry  
181 periods (resistance) are key determinants of population persistence (Jaeger *et al.*, 2014).  
182 Marshall *et al.* (2016) tagged 215 individuals of three common species of large-bodied fish  
183 and monitored their movements in and between waterholes of the Moonie River (Queensland,  
184 Australia) for 3 years. Although some individuals of all species moved during flow events  
185 without clear upstream or downstream preference, others remained within the same waterhole  
186 throughout the study. Timing of flow resumption, independent of its magnitude or duration,  
187 was a key trigger for fish movement, and many individuals returned to the same waterhole  
188 after flow ceased. Maintaining such behaviour in a highly variable environment may improve  
189 survival and management and conservation strategies should promote movement  
190 opportunities for fish at large spatial scales to preserve population resilience.

191

192 Predicting responses of terrestrial vegetation in the riparian zones of IRs (and other river  
193 types) to changes in hydrological (dis)connectivity and water availability is also vital for  
194 effective river management and conservation. Terrestrial plant diversity, composition and  
195 health not only are affected strongly by water availability but also can influence water  
196 availability via their effects on evapotranspiration and the terrestrial water cycle (Stromberg *et al.*  
197 *et al.*, 2007; Sterling, Ducharme & Polcher, 2013; Van Dijk *et al.*, 2013). Stromberg & Merritt  
198 (2016) use functional traits that capture the mechanisms underlying habitat preferences and  
199 tolerances of dryland riparian plants to classify guilds associated with ephemeral, intermittent

200 and perennial reaches of Arizonan rivers. The use of functional traits presents a transferable  
201 approach that goes beyond taxonomy and simple life-form or region-of-origin classification,  
202 and can be used to predict changes in plant guild and trait composition in response to shifts in  
203 flow intermittence and flood frequency. In particular, their findings emphasize the need to  
204 conserve ephemeral and intermittent reaches, not just the rare perennial reaches, within river  
205 networks of arid landscapes to maximize plant-guild diversity.

206

207 **Revival of disturbance ecology: community resistance and resilience in IRs at the**  
208 **aquatic-terrestrial interface**

209 Many mechanisms contribute to the well known resilience of aquatic invertebrate  
210 communities in IRs to periodic drying (Stanley *et al.*, 1994; Fritz & Dodds, 2004; Vander  
211 Vorste *et al.* 2015; Leigh *et al.*, 2016 a). Challenging the view that drift is the primary  
212 mechanism, Vander Vorste *et al.* (2016) suggest that other processes such as colonization from  
213 the hyporheic zone may be equally important. By manipulating both flow and drift, and  
214 creating artificial dry spells in channels of a braided alluvial IR, they show that community  
215 resilience is not significantly altered by the absence of drift. The results instead point to the  
216 hyporheic zone as the main source of colonists. The importance of the hyporheic zone as a  
217 vertical refuge from drying in IRs depends on multiple factors, including physical habitat  
218 characteristics (e.g. sediment porosity) and biotic features (e.g. invertebrate behaviour and  
219 morphology; Stubbington, 2012). Vander Vorste *et al.* (2016) emphasize the need to consider  
220 all potential sources of colonists as contributors to community resilience across the entire  
221 spectrum of IRs and invertebrate inhabitants.

222

223 Resistance as well as resilience is important in promoting biological persistence in IRs.

224 Stubbington *et al.* (2016) investigate one such resistance mechanism by examining and

225 rehydrating the ‘seedbank’ of IRs, which comprises the life stages of aquatic invertebrates  
226 that remain viable in bed sediments during dry phases. Their results provide some support for  
227 the hypothesis that longer dry phases decrease the abundance and richness of the seedbank but  
228 also highlight the complexity of wet-dry cycling, seasonality and invertebrate life-cycle  
229 relationships. Their study adds to the scant knowledge of IR seedbank ecology (e.g. Storey &  
230 Quinn, 2013; Stubbington & Datry, 2013) and, we hope, will inspire researchers to devise  
231 experiments to disentangle effects of environmental variables that influence biotic responses  
232 to drying and survival in dry riverbeds.

233

234 Indeed, evidence indicates that dry riverbeds are not ecologically dead (e.g. Steward *et al.*,  
235 2012; Stubbington *et al.*, 2016; Vander Vorste *et al.*, 2016) and there are likely complex  
236 interactions between dry/flowing (or terrestrial/aquatic) riverbed communities and ecosystem  
237 processes awaiting explanation. However, while there has historically been interest in  
238 studying community patterns at terrestrial-aquatic interfaces (e.g., Reich, 1991; O’Callaghan  
239 *et al.*, 2013; Langhans & Tockner, 2014), characterization of community dynamics involving  
240 complete terrestrial-aquatic shifts, as seen in IRs, has received considerably less attention (but  
241 see Moon 1956; Plum, 2005; Steward *et al.* 2012). Corti & Datry (2016) describe terrestrial  
242 and aquatic invertebrate communities from the active channel and the riparian zone of  
243 intermittent and perennial reaches along a French river. Aquatic and terrestrial taxa at  
244 intermittent reaches (during flowing and dry conditions, respectively) were largely subsets of  
245 the taxa at perennial reaches and the adjacent riparian zone, respectively, indicating strong  
246 longitudinal and lateral biological connections to upstream perennial reaches and bank  
247 habitats, respectively. Among-reach variation in community composition contributed most to  
248 overall terrestrial diversity, whereas within-reach variation was the greatest contributor to

249 overall aquatic diversity. These findings deny the assumption that the dry phase of IRs is a  
250 lifeless period and emphasize that IRs are coupled terrestrial-aquatic ecosystems.

251

### 252 **IRs as models to test and develop metacommunity concepts**

253 Following current developments in community ecology and biodiversity research,  
254 metacommunity perspectives are increasingly being applied in IR studies (e.g. Cañedo-  
255 Arguelles *et al.*, 2015; Datry, Bonada & Heino, 2016). Patterns of nestedness and species  
256 turnover can be due to two non-mutually exclusive processes. Common species of high  
257 dispersal ability can colonise more patches in the network, leading to large population sizes  
258 and ranges (Albanese, Angermeier & Peterson, 2009), than can species with limited dispersal  
259 ability. Common species also tolerate harsh environmental conditions and persist throughout a  
260 wide range of habitats, resulting in low extinction rates and large population sizes and ranges  
261 (Schlosser, 1990; Taylor & Warren, 2001). Although these processes were integrated in a  
262 metacommunity model by Larned *et al.* (2010), stating that longitudinal patterns of nestedness  
263 across connected stream habitats are caused by dispersal limitation, whereas temporal patterns  
264 of nestedness within habitats during stream drying are caused by interspecies differences in  
265 environmental tolerance, there is still little empirical evidence for this model (but see Datry *et*  
266 *al.*, 2014b). Whitney *et al.* (2016) quantify species abundance distributions and the  
267 importance of nestedness and turnover to community dissimilarity in tallgrass prairie streams  
268 of eastern Kansas, U.S.A. Few species were common but nestedness drove community  
269 dissimilarity across sites, notably during the first phases of recolonisation. Although common  
270 species were the first to colonise and the last to go extinct locally, the study raises the  
271 question: is commonness predictive of rather than predicted by colonisation and extinction?

272

273 Datry *et al.* (2016 b) further examine the relative roles of dispersal and environmental filtering  
274 in structuring biological communities in dynamic landscapes. When one thinks of IRs,  
275 tributaries of the Amazon River typically don't come to mind. Datry *et al.* (2016 b) compare  
276 the local and regional diversity of aquatic invertebrate and fish communities from intermittent  
277 and perennial reaches of rivers in central Bolivia to see if natural drying has a similar effect  
278 on the structure and composition of neotropical communities as has been observed in other  
279 regions. Intermittent and perennial reaches had similar invertebrate assemblages but perennial  
280 reaches had higher fish densities and richness than intermittent reaches. Using  
281 metacommunity analyses, in combination with life history knowledge of the local fauna, the  
282 authors were able to infer the relative importance of dispersal compared to local  
283 environmental filtering in structuring aquatic invertebrate and fish communities across the  
284 study sites. The study further suggests that drying may act as a relatively mild disturbance for  
285 aquatic invertebrate communities of neotropical IRs.

286

287 While differences in the community composition among rivers with contrasting flow regimes  
288 are a consistent pattern in many climate regions worldwide, it is not clear whether such  
289 differences among flow regimes are consistent during and after periods of prolonged drought  
290 (*sensu* Lake, 2003) and how much these differences are affected by organismal dispersal  
291 modes and strengths (e.g. Leigh & Datry, 2016). Using biomonitoring data on aquatic  
292 invertebrate and fish communities in subtropical rivers in Australia, Rolls *et al.* (2016) tested  
293 whether beta diversity across naturally near-perennial, mildly intermittent and highly  
294 intermittent streams were greater during a three-year drought characterized by low rainfall  
295 than during a wetter post-drought phase. They also tested whether differences in beta diversity  
296 between phases would decrease with increasing dispersal strength of organisms (Cañedo-  
297 Arguelles *et al.*, 2015; Datry *et al.*, 2015). Except for locally dispersing fish, beta-diversity

298 differed among flow regimes for all dispersal groups of invertebrates and fish. Within flow-  
299 regime groups, beta-diversity was higher during the drought than post-drought for most  
300 invertebrate groups (but was not different for fish) and, for most dispersal groups, was driven  
301 predominantly by replacement of taxa among samples rather than nestedness (except for  
302 diadromous fish). Overall, the findings suggest that beta diversity was similar during both  
303 phases, possibly due to consistent shifts in average community composition during recovery  
304 from drought in all flow regime groups. These consistent shifts may reflect some community  
305 resistance to the effects of drying-wetting cycles (Leigh *et al.*, 2016 b) but also resilience and  
306 the presence of perennial refuges (e.g., water holes) in many of the rivers studied.

307

#### 308 **Where to next? A roadmap for ecological research on intermittent rivers**

309 Contemporary IR ecology is a multifaceted and maturing field of research at the interface  
310 between aquatic and terrestrial ecology. The research findings in this Special Issue contribute  
311 to freshwater and general ecology by testing and challenging concepts across a range of topics  
312 in highly dynamic systems. This issue is also timely because information on IRs is being  
313 sought by managers and policy makers faced with increasing flow intermittence in response to  
314 climate change and growing demands for fresh water. There is ongoing debate regarding the  
315 legal status of IRs in many countries despite the increasing recognition of their ubiquity, their  
316 influence on perennial waters, and human-induced shifts increasing their prevalence and  
317 prolonging droughts (Acuña *et al.*, 2014; Datry *et al.*, 2014b). From the insights provided by  
318 the studies presented in this Special Issue, we draw several conclusions and proposals to  
319 direct future research and management.

320

321 Drying imposes a series of strong local filters expressed as incremental  
322 physicochemical and biological constraints selecting for biota and governing ecosystem

323 processes (Williams, 1996; Boulton, 2003). Much of what is known about IR ecology has  
324 been informed by this perspective (Leigh *et al.*, 2016 a). Comparative studies have used this  
325 perspective to test predictions regarding biodiversity and ecosystem processes between  
326 perennial and intermittent rivers as well as across continua of intermittence (Datry *et al.*, 2016  
327 b; Stromberg & Merritt, 2016; Rolls *et al.*, 2016). Although this Special Issue defines “IRs” as  
328 any channel that periodically ceases to flow and dries, we recognize that IRs really represent a  
329 continuum with varying durations, frequencies, timing and expansion/contraction rates of  
330 drying (Stanley, Fisher & Grimm, 1997; Hughes, 2005; Costigan *et al.*, 2016). The study of  
331 these continua can therefore provide a deeper understanding and predictive capability  
332 regarding how drying influences biodiversity and ecosystem function. Experimental  
333 approaches that manipulate different dimensions of intermittency (Vander Vorste *et al.*, 2016)  
334 and the use of models (Fisher *et al.*, 1998; Datry *et al.*, 2016 a) will also provide focused  
335 mechanistic advances.

336

337         Drying is increasingly recognized as affecting flow continuity through time and flow  
338 connectivity through space (e.g. Larned *et al.*, 2011; Bogan, Boersma & Lytle, 2013; Jaeger *et*  
339 *al.*, 2014). This aligns well with mainstream ecology’s recent use of meta-system perspectives  
340 (e.g., Loreau, Mouquet & Holt, 2003; Datry *et al.*, 2016) and riverine ecologists’ growing  
341 interest in connectivity at the network scale (e.g., Carrara *et al.*, 2012; Zimmermann *et al.*,  
342 2014). A common thread across most the papers in this Special Issue is the role of  
343 hydrological (dis)connectivity in IR ecology, whether by affecting dispersal or material flows  
344 (e.g. Whitney *et al.*, 2016). Connectivity underlies processes across all scales, from local  
345 within-habitat (Vander Vorste *et al.*, 2016) to longitudinal segments (Marshall *et al.*, 2016) to  
346 entire networks (Datry *et al.*, 2016 a; Rolls *et al.* 2016; Welter & Fisher, 2016). Longitudinal  
347 connectivity along IRs may receive the most attention because surface water is the dominant



348 transport route for many riverine organisms and materials, however because of recurrent wet-  
349 dry cycles the vertical connectivity with ground water and atmosphere can be important  
350 (Siebers *et al.*, 2016; Vander Vorste *et al.* 2016; Welter & Fisher, 2016). In spite of the role  
351 surface-groundwater interactions play in shaping drying patterns in IRs, disruption of vertical  
352 connectivity has attracted little interest from ecologists (Leigh *et al.*, 2016 a), reflecting the  
353 lag in recognition of the functional significance of hyporheic zone in perennial systems  
354 (Boulton *et al.*, 2010). Although rivers are linear features, lateral connectivity is critical in  
355 understanding resource subsidies (McCluney & Sabo, 2012) and community dynamics for  
356 floodplain systems (Fernandes *et al.*, 2014). Less studied has been lateral movement by  
357 organisms that inhabit or use dry stream beds, and more research is needed to inform  
358 understanding of their persistence in IRs (Corti & Datry, 2016). In addition to movement  
359 across space, storage or the lack of movement can be critical in understanding the distribution  
360 and abundance of materials and organisms in IRs. Numerous species inhabiting IRs have  
361 resting stages and adaptations that enable them to withstand (resist) the drying conditions in  
362 situ and resume growth and reproduction after rewetting (Stromberg & Merritt, 2016;  
363 Stubbington *et al.*, 2016). The importance of resistance or storage to the persistence or  
364 dynamics of populations and communities in IRs relative to other ecosystems, such as  
365 temporary pools, estuaries, or forest soils, is unknown. The papers presented here will  
366 encourage modification of existing approaches and development of novel approaches for  
367 investigating the (dis)continuity and (dis)connectivity in IRs and the degree to which these  
368 factors, as well as environmental filtering, govern biodiversity and biogeochemical patterns  
369 across ecosystems.

370

371           The study of IRs is situated at the interface of aquatic and terrestrial ecology. Most  
372 papers in this Special Issue emphasise the wet rather than the dry phase, however there is

373 growing interest in dry phases and the terrestrial vegetation and invertebrate assemblages  
374 living in and along IR channels. Biogeochemistry and microbial studies are also areas where  
375 the dry phase is being incorporated into a more complete understanding of IR ecosystems.  
376 Interdisciplinary studies on IRs should be encouraged to further blur the demarcation between  
377 aquatic and terrestrial ecology (Datry *et al.*, 2014 a). IRs are also extreme examples of  
378 systems where ecological patterns and processes are shaped by temporal environmental  
379 fluctuation. Therefore, IRs can be considered useful models for understanding seasonal food  
380 web shifts over time (McMeans *et al.*, 2015) and where / how resource booms and busts  
381 interact and alternate among members of flowing and dry channel communities (Balcombe *et*  
382 *al.*, 2015). The compression of interactions and flows of materials and energy to particular  
383 points in time and space that may vary in their predictability is certainly an area where IR  
384 research can contribute to aquatic and general ecology (Datry *et al.*, 2016 a).

385

386         As a result of ongoing climate change and human modification of landscapes and  
387 waterways, flooding and drought are expected to become more extreme and possibly more  
388 frequent (Ledger & Milner, 2015). Although flooding can be detrimental to society and  
389 riverine ecosystems, drying of formerly perennial rivers is expected to be more adverse and  
390 more difficult to mitigate through management actions (Palmer *et al.*, 2008). Shifts in  
391 streamflow regimes from perennial to intermittent and extension of the duration and  
392 frequency of dry phases in IRs could strongly affect river ecosystems and the services they  
393 provide (Costigan *et al.* 2016; Datry *et al.*, 2016). While this Special Issue testifies to recent  
394 advances in IR ecology, scientific aspects are certainly yet to be uncovered, and foreseeable  
395 challenges for their protection and restoration indicate there is still much room for growth and  
396 innovation.

397

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410

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632

633 **Figure captions**

634 **Fig. 1:** Number of IR-related publications on the combined topics of fish ecology, invertebrate  
635 ecology, biogeochemistry, hydrological assessment and ecological-condition assessment  
636 appearing in freshwater and ecology journals, and *Freshwater Biology* specifically, through  
637 time. Freshwater journals include any journal with the character string \*water or aquatic in the  
638 title, ecology journals include the string \*ecol in their titles, and freshwater and ecology  
639 journals include one or more of these three strings in their titles. Data taken from a Web of  
640 Science literature search conducted by Leigh et al. (2016 a).

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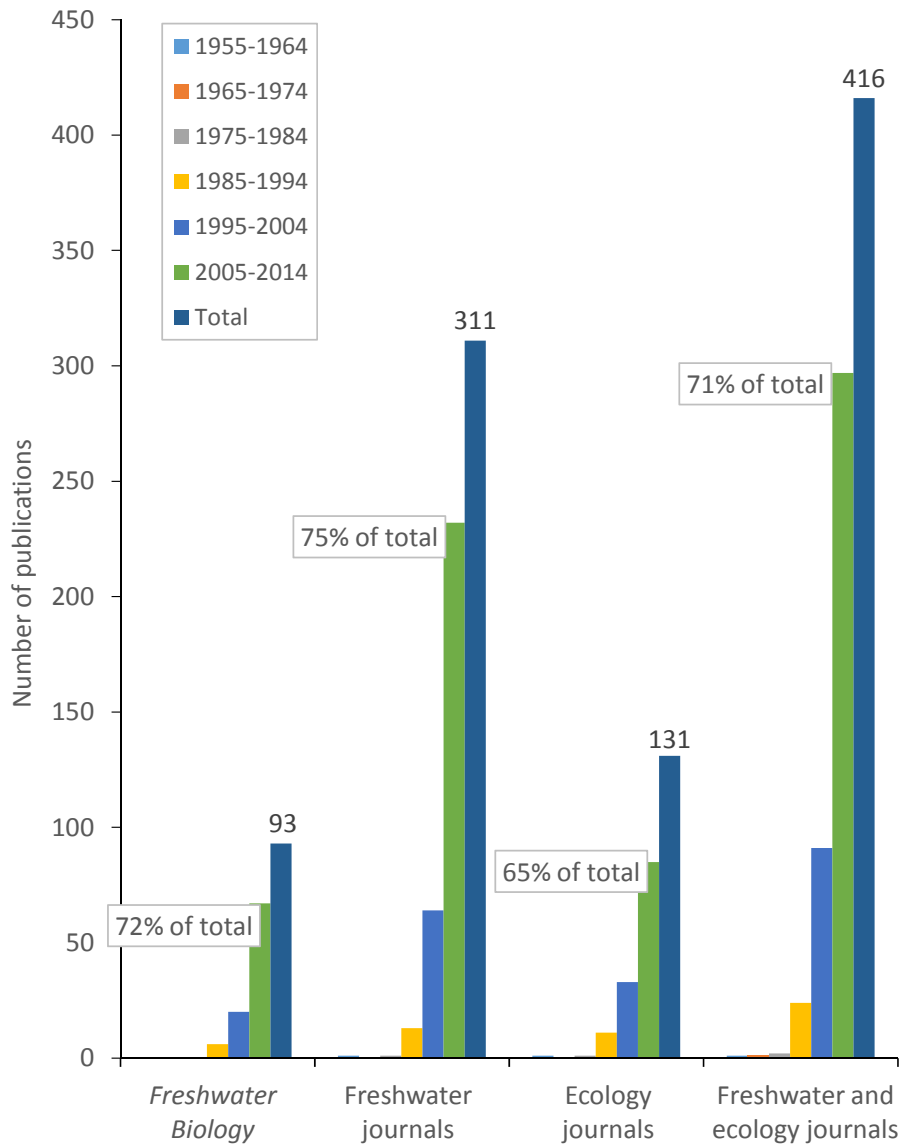
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648 **Figure 1.**

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