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1 **Towards understanding the organisation of metacommunities in highly**  
2 **dynamic ecological systems**

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13

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15

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32

33 **Abstract**

34 Community ecology recognises today that local biological communities are not only  
35 affected by local biotic interactions and abiotic environmental conditions, but also by  
36 regional processes (e.g. dispersal). While much is known about how metacommunities  
37 are organised in space in terrestrial, marine and freshwater ecological systems, their  
38 temporal variations remain poorly studied. Here, we address the question of the  
39 dynamics of metacommunities in highly variable systems, using intermittent rivers  
40 (IRs), those rivers which temporarily stop flowing or dry up, as a model system. We  
41 first review how habitat heterogeneity in space and time influences metacommunity  
42 organisation. Second, we compare the metacommunities in IRs to those in perennial  
43 rivers (PRs) and develop the idea that IRs could undergo highly dynamic shifts due to  
44 the temporal variability in local and regional community processes. Third, we develop  
45 the idea that in IRs, metacommunities of the wet and dry phases of IRs are closely  
46 intertwined, thereby increasing even more their respective temporal dynamics. Last, we  
47 provide a roadmap to stimulate further conceptual and empirical developments of  
48 metacommunity research and identify possible applications for improving the  
49 management of IRs and other highly dynamic ecological systems.

50

## 51 **1. Introduction**

52 Community ecology has progressed rapidly in recent years owing to the recognition  
53 that local communities are not spatially closed and temporally stable (Leibold et al.  
54 2004; Ricklefs 2008). Current views thus emphasise that local communities are not only  
55 affected by local abiotic environmental conditions and biotic interactions, but also by  
56 processes external to local ecological systems and operating at a regional scale, such as  
57 speciation, extinction, immigration and emigration (Hubbell 2001). Although the  
58 foundation of this idea dates back several decades (MacArthur & Wilson 1967), a shift  
59 from purely local views of community organisation to those that also acknowledge the  
60 importance of regional processes has been increasingly evident in the past years  
61 (Hubbell 2001; Leibold et al. 2004). Sets of local communities linked by dispersal, or  
62 metacommunities (**Table 1**), have been studied intensively in various ecological  
63 systems (Logue et al. 2011), including terrestrial (e.g. Meynard et al. 2013), marine (e.g.  
64 Moritz et al. 2013), and freshwater (e.g. Heino 2013) systems, and the number of  
65 studies on the topic continues to increase rapidly (Heino et al. 2015). The  
66 metacommunity framework has thus become a conceptually sound and empirically  
67 well-explored framework to study the spatio-temporal organisation of communities.

68

69 As an outcome of developments in spatial and dispersal ecology, different  
70 metacommunity models have been proposed to explain how both environmental  
71 filtering (i.e. local biotic interactions and abiotic environmental conditions, **Table 1**),  
72 and dispersal processes (i.e. the movement of individuals from one site to another  
73 within a region, **Table 1**), interact to shape local community structure (Vellend 2010,  
74 Logue et al. 2011; Winegardner et al. 2012). For example, “mass effects” models  
75 predict that high rates of dispersal can obscure the effect of environmental filtering,

76 while the “patch dynamic” models assume that the best dispersers arrive first and  
77 occupy the patches (sensu Logue et al. 2011) as long as no more competitive species  
78 have arrived (Logue et al. 2011). Although the potential differences between these  
79 various models have often been emphasised (Leibold et al. 2004; Logue et al. 2011;  
80 Winegardner et al. 2012), very few observational studies have succeeded in offering  
81 unambiguous explanations for their relative importance in nature (Cottenie 2005;  
82 Beisner et al. 2006; Bonada et al. 2012). One explanation stems from the fact that it is  
83 highly difficult to measure dispersal directly and that separating the effects of  
84 environmental filtering vs. dispersal processes is complex since most environmental  
85 factors are spatially autocorrelated (Legendre et al. 2005; Tuomisto & Ruokolainen  
86 2006; Jacobson & Peres-Neto 2010, Gilbert & Bennett 2010; Bonada et al. 2012).  
87 Another explanation is that a number of metacommunity studies considered spatial  
88 patterns of local communities as static within a given landscape (Leibold et al. 2004;  
89 Presley et al. 2010), while communities can be very dynamic with abrupt and constant  
90 change in richness and composition over very short scales (Chesson & Huntly 1989;  
91 Azeria & Kolasa 2008; Erös et al. 2012; Aiken & Navarette 2014; Fernandes et al.  
92 2014).

93

94 Logue et al. (2011) suggested that broadening the types of focal habitats and  
95 organisms in metacommunity studies would provide a better understanding of the  
96 variability of metacommunity organisation (**Table 1**). They specifically pointed out that  
97 metacommunity studies should go beyond those focusing on insular habitats with  
98 discrete boundaries and those using large organisms as models. Different types of  
99 aquatic systems (e.g. marine, coastal, temporary ponds, estuaries, and running waters)  
100 provide excellent opportunities for such additional studies because they harbour highly

101 disparate organismal groups, vary widely in their degree of connectivity, and exhibit  
102 wide spatial and temporal variability in local habitat conditions (Heino et al. 2015).  
103 However, previous focus on purely aquatic communities has provided limited  
104 perspectives on highly dynamic ecological systems, such as intermittent rivers (IRs), the  
105 rivers which cease to flow or dry up in time and space. IRs provide especially suitable  
106 arenas for examining metacommunity organisation in highly dynamic ecological  
107 systems because they are mosaics of aquatic and terrestrial habitats shifting constantly  
108 in time and space (Larned et al. 2010; Datry et al. 2014a). This dynamism, combined  
109 with the fact that nearly 50% of lengths of rivers across the globe are characterized by  
110 intermittent flow (Acuña et al. 2014; Datry et al. 2014a), calls for addressing  
111 metacommunity organisation in IRs and other highly dynamic systems.

112

113 Here, we address the question of how communities are organized in time and space  
114 in highly dynamic systems. We use IRs as model ecological systems because of their  
115 high dynamism and apply the metacommunity concept because of the possibility to  
116 distinguish between local and regional processes in river systems (e.g. Brown & Swan  
117 2010; Logue et al. 2011; Heino 2013). We first review the effects of habitat variability  
118 on metacommunities in various dynamic systems. Second, we compare  
119 metacommunities in IRs to those in perennial rivers (PRs) and develop the idea that IRs  
120 could undergo constant and severe shifts due to the variability in environmental filtering  
121 and dispersal processes. Third, we develop the idea that in IRs, metacommunities of the  
122 wet and dry phases of IRs are closely intertwined, which enhances their respective  
123 temporal dynamics. Last, we provide a roadmap to stimulate further conceptual and  
124 empirical developments of metacommunity research and identify possible applications  
125 for improving the management of IRs and other highly dynamic ecological systems.

126

127 **2. The importance of spatial and temporal dynamics for metacommunity**  
128 **organisation**

129 In the metacommunity framework, landscapes are considered as networks of  
130 interconnected focal habitats in a matrix of unsuitable habitats, i.e. they are spatially  
131 heterogeneous (Leibold et al. 2004; Holyoak et al. 2005). However, many conceptual  
132 and empirical developments have considered metacommunities as relatively stable  
133 entities (e.g. Leibold et al. 2004; Presley et al. 2010; Carrara et al. 2012; Altermatt  
134 2013), although local communities and their environments can be temporally variable  
135 (Azeria & Kolasa 2008; Erös et al. 2012; Aiken & Navarette 2014; Fernandes et al.  
136 2014). Factors that control metacommunity organisation, including habitat availability,  
137 local environmental conditions, and spatial connectivity, vary in space and time (Aiken  
138 & Navarette 2014). The most extreme aquatic systems are arguably those that alternate  
139 between aquatic and terrestrial conditions on a short time scale, for which high  
140 variability may be the predominant rule. This category includes rocky marine  
141 shorelines, tidal zones, small freshwater rock pools, temporary wetlands, vernal pools,  
142 floodplains, and IRs. In such systems, environmental conditions vary both spatially and  
143 temporally on a short-term basis. For example, the surface areas and connectivity of  
144 floodplain aquatic habitats vary considerably during periods of weeks to months  
145 between alternating wet and dry phases (Fernandes et al. 2014). Tide cycles generate  
146 short pulses of aquatic habitat expansion and contraction on a daily basis (Kirwan &  
147 Murray 2007). In such systems, and more generally in other systems exhibiting high  
148 environmental variability, a static view of metacommunity organisation is likely to be  
149 inaccurate.

150

151 In dynamic systems (i.e., systems experiencing constant and severe changes) the  
152 various mechanisms shaping local communities, as well as their respective importance,  
153 are constantly varying. For example, the contribution of dispersal will increase heavily  
154 after a disturbance to allow for recolonization of a given patch (defined as a discrete  
155 area with favourable environmental conditions, typically a flowing section in a river for  
156 a fish or aquatic invertebrates, but see Cavanaugh et al. 2014). Yet, after most colonists  
157 have reached the patch, environmental filtering will become more important in  
158 explaining the local community organisation in the absence of mass effects. In systems  
159 experiencing variable environmental conditions, such shifts between environmental  
160 filtering vs. dispersal processes may be common and generate dynamic patterns in  
161 community structure including short-term instabilities (Drake 1990; Chesson & Huntly  
162 1989; Aiken & Navarrete 2014).

163

164 Understanding and predicting the dynamics of metacommunities will be essential to  
165 managing, conserving, and restoring biodiversity in all ecological systems, including in  
166 freshwater ecological systems which have been drastically altered by global changes  
167 (Dudgeon et al. 2006). Because extreme climatic events and disturbances to ecological  
168 systems are occurring more frequently (Easterling et al. 2000; Parmesan, 2006), current  
169 static views of community organisation are becoming less and less useful and, given  
170 these limitations, we may fail to predict biodiversity loss accurately in disturbed  
171 systems. Moreover, most current management, conservation and restoration applications  
172 do not fully recognize the fact that maintaining the spatial and temporal dynamics of  
173 entire ecological systems is essential (Heino 2013; Tonkin et al. 2014). This recognition  
174 is certainly very important in the context of highly dynamic systems, where  
175 communities are restructured again and again within a short period of time.



176

177 **3. Intermittent rivers as model systems to explore the dynamics of**  
178 **metacommunities**

179 IRs occur under all types of climates on all continents, including Antarctica, and  
180 make up the majority of river networks in terms of length in many regions (Acuña et al.  
181 2014; Datry et al. 2014a). Globally, IRs represent 69% of the low-order streams south  
182 of 60°N latitude and from 30 to 40% of the larger river basins (Raymond et al. 2013). In  
183 the coming decades, the number and length of IRs will increase in many regions that  
184 experience drying trends due to climate and land-cover change, and increasing water  
185 abstraction for irrigation and other economic uses (Palmer et al. 2008; Larned et al.  
186 2010).

187

188 Most conceptual and empirical developments in freshwater ecology, including the  
189 application of metacommunity models (e.g. Brown & Swan 2010; Altermatt et al. 2011;  
190 Heino et al. 2015), have emerged from and been produced for perennial river systems  
191 (Datry et al. 2014a). Consequently, metacommunity ecology is still in its infancy in IRs,  
192 and this contrasts with temporary lentic systems which have been widely used to test  
193 predictions from metapopulation and metacommunity ecology (e.g. Kolasa & Romanuk  
194 2005; Vanschoenwinkel et al. 2007) or have provided new insights into these fields (e.g.  
195 Smol & Douglas 2007; Vanschoenwinkel et al. 2010). One important difference with  
196 temporary lentic systems is that rivers occur as dendritic networks, which consist of  
197 linearly-arranged, hierarchical and branching habitat elements (Fagan 2002; Grant et al.  
198 2007; Altermatt 2013). Headwaters are more isolated than mainstem reaches and this  
199 possibly results in spatial differences in the relative importance of community assembly  
200 processes (Brown & Swan 2010). Moreover, unidirectional flow and directionally-

201 biased dispersal can exacerbate the effects of disturbance (drying) on species  
202 coexistence (Altermatt et al. 2011).

203

204 IRs are dynamic shifting habitat mosaics of flowing, non-flowing and dry patches  
205 (**Figure 1**), the extent and connectivity of which constantly vary across drainage basins  
206 in response to river discharge and groundwater levels (Stanley et al. 1997; Jaeger et al.  
207 2014; Datry et al. 2015, **Figure 2**). This spatially complex and temporally dynamic  
208 habitat template is inhabited by both aquatic (e.g. fish, invertebrates, microbes, fungi,  
209 algae) and terrestrial (e.g. birds, mammals, arthropods, microbes, fungi) organisms, the  
210 communities of which alternate, coexist, interact, and experience extreme disturbances  
211 in terms of drying and rewetting phases (Stanley et al. 1997; Datry et al. 2014a).  
212 Aquatic and terrestrial communities can show intense biotic interactions. Predation by  
213 terrestrial organisms on aquatic organisms trapped in drying pools can be an important  
214 mortality factor in addition to interactions among fully aquatic organisms (Larned et al.  
215 2010). Some large, lentic specialist predators, such as giant water bugs or diving  
216 beetles, can also colonize the pools to prey on the stranded organisms, thereby  
217 enhancing aquatic interactions (Gasith & Resh 1999; Boulton 2003). Altogether, local  
218 environmental conditions, biotic interactions and accessibility to patches vary  
219 continuously in IRs, challenging the current static views of metapopulation and  
220 metacommunity approaches. Here, we make the case that IRs provide suitable arenas to  
221 explore the temporal dynamics of metacommunities and notably the idea that  
222 communities can experience highly dynamic shifts in structure and composition due to  
223 the variability in environmental filtering and dispersal processes.

224

225 **4. Uniqueness of intermittent rivers and implications for metacommunity**  
226 **dynamics**

227 IRs have some unique features that challenge current views of metacommunity  
228 organisation in river systems, which are mostly derived from research in PRs. While  
229 **Table 2** synthesises these features and their possible implications for metacommunity  
230 organisation, the different hydrological phases through which IR communities have to  
231 persist are presented below.

232 **Flow cessation: shifts from lotic to lentic conditions**

233 The most striking difference between PRs and IRs is that the flow ceases  
234 periodically in IRs, and surface water can disappear completely from IR channels  
235 (**Figure 1, Table 2**). Flow cessation gradually converts flowing river channels into  
236 chains of disconnected pools of standing waters, which face increased water  
237 temperatures and solute concentrations, and decreased pH and dissolved oxygen levels  
238 (Boulton 2003). As these pools decrease in size, the densities of organisms can increase  
239 dramatically, leading to strong intra- and interspecific interactions, such as competition  
240 or predation. Some large pools can persist throughout dry phases and represent essential  
241 refugia for aquatic organisms (Sheldon et al. 2010) and can be important “stepping  
242 stones” facilitating the continued existence of populations and communities across an  
243 IR network by connecting refuges and allowing recolonization of re-wetted sites by  
244 actively flying or passively dispersing aquatic organisms (Bogan & Boersma 2012;  
245 Cañedo-Argüelles et al. 2015). These shifts from lotic to lentic conditions occurring in  
246 many IRs challenge the view that riverine systems, in general, are dominated by  
247 physical constraints related to unidirectional flow (e.g. water velocity, shear stress)  
248 (Fagan 2002; Altermatt et al. 2011). During the lentic phase, biotic interactions may be

249 the dominant processes structuring aquatic communities (Gasith & Resh 1999; Boulton  
250 2003).

### 251 **Streambed drying**

252 In many IR systems, riffles dry first, after which remnant pools progressively dry  
253 up, thus converting river channel into terrestrial habitat and leading to the disappearance  
254 of aquatic communities (**Table 2**). Physiological tolerance to loss of water has been  
255 well documented in organisms of temporary ponds and pools (Wiggins et al. 1980) and  
256 a variety of species have also evolved physiological resistance strategies to cope with  
257 desiccation in IRs (**Table 2**). This “invertebrate seedbank” contributes to community  
258 recovery upon flow resumption, although its efficiency in such contribution is variable  
259 and not completely understood (Warner & Chesson 1985; Snyder 2006; Stubbington &  
260 Datry 2013). Described as the storage effect (**Table 1**), this mechanism contributes  
261 strongly to species coexistence when resources are limiting and recruitment fluctuates  
262 (Warner & Chesson 1985; Snyder 2006), thus promoting the resistance (defined as the  
263 capacity to persist unchanged through a disturbance) of IR communities to drying.  
264 During these dry phases, dry riverbeds are also being colonised by rich and abundant  
265 terrestrial biotas, including microbes, plants, arthropods, birds, and mammals (Steward  
266 et al. 2012). In spite of a recent increase in research on dry riverbed communities, they  
267 still represent *terra incognita* from an ecological perspective (Steward et al. 2012).

### 268 **Rewetting**

269 Rewetting of previously dry patches is often sudden and unpredictable and can take  
270 the form of impressive flood bores (a video can be found here: [www.irstea.fr/en/datry](http://www.irstea.fr/en/datry)).  
271 Myriads of terrestrial invertebrates have been reported on these advancing fronts, with  
272 densities typically reaching  $> 5000$  individuals/m<sup>3</sup> (Corti & Datry 2012; Rosado et al.  
273 2014). Many of these organisms have the ability to float or resist submersion for short

274 periods of time and are thus deposited alive further downstream. Such events could be  
275 mass dispersal events for terrestrial organisms.

276

## 277 **5. A dynamic view of metacommunities**

278 The above features (**Table 2**) and resulting effects on environmental filtering and  
279 dispersal processes can be used to build a new conceptual model of metacommunity  
280 organisation in highly dynamic systems. We propose that (1) metacommunities are very  
281 dynamic owing to temporal variations of habitat availability, environmental  
282 heterogeneity, and connectivity between patches; (2) these dynamics vary spatially  
283 within systems, depending on where environmental variability is the highest, where  
284 potential sources of colonists are located, and how much their dispersal is limited by  
285 distances between patches; and (3) metacommunities from aquatic and terrestrial phases  
286 interact and may have intertwined dynamics.

287

### 288 **5.1. Metacommunity organisation can be very variable**

289 Alternating wet and dry cycles create contrasting terrestrial and aquatic habitat  
290 phases in IRs (**Figure 3a**). As presented above, each of these phases is associated with  
291 the predominance of community processes operating locally or regionally. For example,  
292 shifts from lotic to lentic conditions are followed by an immediate increase in the  
293 importance of environmental filtering processes, including adaptations to lentic  
294 conditions, enhanced biotic interactions within contracting pools and very strong  
295 predation pressure by terrestrial organisms (**Table 2**). Later, the relative importance of  
296 dispersal processes to explain community structure and composition increases with the  
297 arrival of large specialist predators such as dragonflies (Odonata), diving beetles  
298 (Coleoptera) and some true bugs (Heteroptera), which are generally strong fliers and

299 colonize suitable habitats rapidly (Bogan & Boersma 2012; Bonada et al. 2012).  
300 Conversely, upon rewetting, dispersal processes may first predominate to allow  
301 colonisation of rewetted habitats by dispersal from refuges (Datry et al. 2014b). Soon  
302 after, the communities may be influenced by storage effects from the emergence of  
303 desiccation-resistant forms from the rewetted sediments (Stubbington & Datry 2013).  
304 After the initial colonisation events, environmental filtering should become gradually  
305 more important (**Figure 3b**). High dynamism may also characterize terrestrial  
306 communities in IRs, although community-structuring processes involved during each  
307 phase shift have been inadequately explored.

308

309 Over time, the structure of metacommunities should show imprints of the high  
310 temporal variability in the relative roles of community assembly processes. The most  
311 obvious example is probably the respective portions, at a given location, of lotic, lentic,  
312 and terrestrial species (**Figure 3c**). Community structure may thus vary sharply during  
313 the different phases, with notable dominance by lotic species during flowing phases,  
314 dominance by lentic species during non-flowing phases, and dominance by terrestrial  
315 species during dry phases (**Figure. 3c**). Although this is speculative, there are some  
316 datasets supporting these ideas in IRs (e.g. Bonada et al. 2007; Anna et al. 2008; Corti  
317 & Datry 2015). For example, Corti & Datry (2015) described how aquatic and terrestrial  
318 successions alternate following hydrological phases in one French IR. Other metrics of  
319 community structure, such as taxonomic richness, species abundance, or the proportion  
320 of predatory species should also change abruptly and include “a step-change” following  
321 phase shift.

322

323 The strong temporal variability in the relative roles of community assembly  
324 processes should also generate predictable spatial patterns of metacommunities. During  
325 phases dominated by dispersal processes from patches to other patches, communities  
326 should be predominantly nested, particularly for weak to moderate dispersers, while  
327 species turnover may dominate in phases dominated by environmental filtering  
328 operating locally to determine species coexistence (**Figure 3d**). However, these patterns  
329 are likely to alternate on short time scales, jeopardizing attempts to infer on  
330 communities processes from snap-shot spatial views of metacommunities. Lines of  
331 evidence from various systems support these predictions. For example, frequent  
332 hurricanes temporarily reduce the degree of nestedness of gastropod assemblages in  
333 tropical wet forests (Bloch et al. 2007). Fish in seasonal floodplains show differences in  
334 the metacommunity structure between the initial and late phases of the flooding period  
335 in response to a shift in the importance of connectivity versus local environmental  
336 conditions in structuring local communities (Fernandes et al. 2014). In PRs, different  
337 metacommunity models apply along a gradient of disturbance level (Campbell et al.  
338 2015). In temporary ponds, shifts from terrestrial to aquatic phases modulate  
339 community processes, and the importance of environmental filtering decreases with  
340 inundation time (Vanschoenwinkel et al. 2010).

341

## 342 **5.2. The temporal dynamics of metacommunities in dendritic structures**

343 In dendritic structures experiencing drying events, the spatial scale of  
344 metacommunities can be defined through the competitive process and/or the spatial  
345 scale of the disturbance, if wet and dry phases occur more rapidly than competitive  
346 exclusion (Massol et al. 2011). In this context, the dynamics of metacommunities likely  
347 varies spatially within ecosystems with hierarchical structure, notably in case of

348 directionally-biased dispersal (Brown & Swan 2010; Altermatt et al. 2011). For  
349 example, in the case of IR networks, the temporal variability of communities may differ  
350 according to where drying events (i.e. disturbance) prevail. There are five types of  
351 spatial drying configurations in river systems (**Figure 4**), each being potentially  
352 associated to a different spatial structuration of the temporal community dynamics.  
353 Contrary to the paradigm that headwater communities are being driven purely by  
354 environmental filtering and those of downstream, lowland reaches by mass effects due  
355 to convergence of all branches and downstream water flow (Brown & Swan 2010),  
356 more complex patterns may emerge for each drying configuration. For example, rivers  
357 drying completely or partly in their headwaters should have headwater communities  
358 driven essentially by dispersal (and perhaps by storage effects), as the source of  
359 colonists may be located downstream or in the saturated or dry underlying sediments  
360 (see section 3). For the different drying configurations, the degree of connectivity and  
361 resulting dispersal rates between patches is probably a key factor, as very high dispersal  
362 rates may decouple communities from purely local environmental control (Mouquet &  
363 Loreau 2003; Ng et al. 2009; for riverine systems, see also Heino & Peckarsky 2014).  
364 At the river network scale, the communities may show contrasting spatial patterns, with  
365 community nestedness being more predominant in mid-reach or downstream drying  
366 systems (e.g. Datry et al. 2014b), and environmental filtering dominating in headwaters  
367 or complete drying systems (e.g. Grant et al. 2007; Clarke et al. 2008; Brown & Swan  
368 2010).

369

### 370 **5.3. Terrestrial and aquatic metacommunities have intertwined dynamics**

371 Biotic interactions between species forming aquatic and terrestrial communities in  
372 IRs are localised in space (i.e. drying and rewetting sections) and time (i.e. drying and



373 rewetting phases) (see section 4). These discrete and punctuated interactions may  
374 enhance the temporal variability in the structure of both aquatic and terrestrial  
375 metacommunities. For example, aquatic species in drying reaches may be heavily  
376 preyed upon by terrestrial predators (e.g. beetles, spiders), further reducing the number  
377 of species able to survive flow cessation events (McHugh et al. 2014). Conversely, the  
378 myriad of terrestrial invertebrates colonising dry riverbeds are entrained by advancing  
379 rewetting fronts to downstream river sections, where they may provide subsidies to  
380 aquatic food webs and influence aquatic community dynamics (Corti & Datry 2012;  
381 Rosado et al. 2014). From a terrestrial perspective, these mass dispersal events could  
382 also homogenize terrestrial metacommunities, which could thus be dominated by  
383 dispersal processes in IRs rather than by local processes. Yet, aquatic and terrestrial  
384 metacommunities show contrasting spatial organisations in IRs, with aquatic  
385 metacommunities being longitudinally organised along river networks and terrestrial  
386 metacommunities being laterally organised by riparian and upland processes away from  
387 river channels (Corti & Datry 2015). Understanding the complex interaction between  
388 the respective temporal dynamics and spatial organisation of aquatic and terrestrial  
389 metacommunities offers a unique opportunity for integrating aquatic and terrestrial  
390 ecology (Datry et al. 2014a).

391

## 392 **6. A roadmap for future research on metacommunities in intermittent rivers and** 393 **other highly dynamic ecological systems**

394 As a first step, the questions associated with our conceptual models shown above  
395 should be tested, particularly because datasets may be now or will be soon available  
396 following the growing interest in IRs (e.g. Larned et al. 2010; Datry et al. 2014a, Acuña  
397 et al. 2014). Below, we list specific research questions and indicate their relevance to

398 furthering our understanding of metacommunities in IRs. Most of these research  
399 questions could be also adapted to other highly dynamic ecological systems.

400

401 *How temporally variable are metacommunities of dynamic systems?*

402 Fine-scale descriptions of the temporal dynamics of metacommunities during  
403 typical flowing/non-flowing/dry/flowing phase cycles (**Figure 3a**) are necessary to  
404 identify if high dynamism of local communities and metacommunities is a general rule.  
405 This would be useful for both aquatic and terrestrial communities and address current  
406 limitations in the static view of metacommunities (Erös et al. 2012, 2014). Such  
407 temporal descriptions of communities across multiple systems would help to determine  
408 if thresholds in phase duration, frequency or timing leading to alternative states of  
409 community organisation exist (Bogan & Lytle 2011). Describing and understanding  
410 such thresholds is crucial to predict biodiversity change in the context of climate change  
411 (Parmesan, 2006; Palmer et al. 2008; Jaeger et al. 2014). Empirical developments  
412 should in turn foster conceptual development of metacommunity models suitable for  
413 highly dynamic systems.

414

415 *How the dendritic nature of river systems influences the dynamics of metacommunities?*

416 Previous attempts to explore the spatial dynamics of communities in ecosystems,  
417 including rivers (e.g., Brown & Swan 2010) have been limited due to the low power of  
418 distance matrix-based approaches (Legendre et al. 2005). The development of spatial  
419 modelling in the context of constrained ordination (Cottenie 2005; Legendre et al. 2005;  
420 Muneeppeerakul et al. 2007; Heino et al. 2015) and in particular those accounting for  
421 directionally-biased dispersal (Blanchet et al. 2008) provide better opportunities to  
422 understand the spatial organisation of communities in dynamic ecosystems. Yet,

423 constrained ordination and associated spatial models assume a sort of equilibrium in  
424 communities, and further developments, such as cost distance-based methods used to  
425 model the dispersal of large terrestrial species (Larkin et al. 2004; LaRue & Nieslen  
426 2008; Erős & Campbell Grant 2015), represent a more relevant alternative approach.

427

428 *How significant is the storage effect in promoting community dynamics in IRs?*

429 The contribution of the invertebrate seedbank to community recovery has been  
430 shown to be significant, although highly variable across IR systems (Stubington &  
431 Datry 2013). Yet, its role in driving metacommunity dynamics in IRs is still unknown  
432 and notably, whether or not it can compensate for dispersal is an open question (Snyder  
433 2006). Manipulative approaches, such as common-garden experiments manipulating the  
434 invertebrate seedbank and/or the dispersal of organisms in water and the air could be  
435 helpful to address this question. Alternatively, cross-system comparisons of  
436 metacommunity dynamics in systems with contrasting drying patterns (i.e. with and  
437 without perennial refuges) may help disentangle the respective role of storage effects  
438 and dispersal in promoting community dynamics. From a modelling perspective,  
439 mechanistic approaches, for example using multi-occupancy models (e.g. Lamy et al.  
440 2013) applied to more than one species, would allow accounting for storage effects in  
441 estimating colonization and persistence rates, thus assessing the extent of cryptic  
442 dormant stages in metacommunities.

443

444 *Do interactions between aquatic and terrestrial metacommunities alter their respective*  
445 *dynamics?*

446 Understanding how biotic interactions between aquatic and terrestrial  
447 metacommunities influence their respective temporal dynamics requires further

448 quantification in IRs. Yet, studies describing synoptically aquatic and terrestrial  
449 metacommunities in IRs or other aquatic-terrestrial systems (e.g. wetlands, tidal  
450 marshes) remain scarce (but see Corti & Datry 2015). Considering simultaneously  
451 aquatic and terrestrial metacommunities in IRs would provide a way forward to account  
452 for the linkages between these two components, as well as to bring terrestrial and  
453 aquatic ecologists together in metacommunity research.

454

455 *Is there mass dispersal of terrestrial organisms during rewetting events?*

456 While recent studies have reported how dramatic rewetting events in IRs can be and  
457 how much large quantities of terrestrial organisms are being entrained downstream of a  
458 river network, it is still unknown how strong roles these events play in terrestrial or  
459 aquatic community dynamics (Corti & Datry 2012; Rosado et al. 2014). Typically, such  
460 events could produce a mass effect for downstream riparian communities, thereby  
461 obscuring local environmental filtering processes. To address this question, field  
462 experiments could monitor the fate of the entrained organisms on downstream  
463 communities using stable isotopes or molecular approaches. Also, the amount and type  
464 of terrestrial inputs to these rewetting fronts could be manipulated to examine their  
465 effects on aquatic and terrestrial communities.

466

467 *How can the metacommunity perspective help managers to conserve the biodiversity of*  
468 *IRs?*

469 The metacommunity perspective is a mechanistic route to relating biodiversity  
470 patterns to landscape features and exploring biodiversity conservation plans (Economo  
471 2011). Identifying the relative roles of environmental filtering and dispersal processes in  
472 metacommunities can help managers to better conserve these dynamic ecological

473 systems. If local communities are mainly governed by environmental filtering  
474 processes, management initiatives to maintain local habitats should be prioritized. If  
475 dispersal processes are predominant instead, management strategies should maintain  
476 landscape connectivity and natural disturbance regimes to promote “source” patches of  
477 biodiversity (Bengtsson 2010). In the specific case of IRs, this would require preserving  
478 the natural mosaic of shifting habitat types (Datry et al. 2015) and the local conditions  
479 of perennial headwater patches, which are considered as important sources of  
480 biodiversity (Cañedo-Argüelles et al. 2015). Additionally, the metacommunity  
481 framework applied to IRs will help to pinpoint keystone species or habitat-patches in  
482 the mosaic, on which managers should focus conservation and restoration efforts  
483 (Mouquet et al. 2013). Empirical studies analysing the metacommunity processes in IRs  
484 are thus urged to implement conservation actions specifically tailored to these dynamic  
485 systems.

486

## 487 **6. Conclusions**

488 While community ecology has progressed rapidly in recent years owing to the  
489 recognition that local communities are not spatially closed but form metacommunities  
490 (Logue et al. 2011; Winegardner et al. 2012), empirical studies have often reported  
491 ambiguous findings about the relative importance of underlying processes (Cottenie  
492 2005; Beisner et al. 2006; Logue et al. 2011). This could be partly due to the common  
493 consideration in metacommunity research that both biological communities and their  
494 habitats as relatively stable, whereas many ecological systems are actually highly  
495 dynamic in nature. Because IRs are common ecological systems across the globe and  
496 are dynamic shifting mosaics of lotic, lentic, and terrestrial habitats, they are ideal  
497 arenas for addressing the spatio-temporal variability of metacommunities in highly

498 dynamic settings. As developed here for IRs, the respective importance of  
499 environmental filtering and dispersal processes may shift abruptly or gradually over  
500 time in highly dynamic ecological systems, leading local community structure to vary  
501 constantly. This temporal variability is certainly enhanced by discrete and punctuated  
502 biotic interactions between aquatic and terrestrial communities in IRs and other coupled  
503 aquatic-terrestrial systems. In the case of dendritic systems with directionally-biased  
504 dispersal (Fagan 2002; Grant et al. 2007; Altermatt et al. 2011), the location and spatial  
505 extent of disturbances, such as drying, may interact with the temporal variations in  
506 community assembly processes to produce complex spatio-temporal variability in local  
507 community structure. We contend that addressing these questions in IRs may 1)  
508 substantially advance the metacommunity theory (Erös et al. 2012, 2014); 2) offer a  
509 unique opportunity for bridging the gap between aquatic and terrestrial community  
510 ecology (Datry et al. 2014a; Soininen et al. 2015); and 3) improve the management of  
511 ecological systems (Heino 2013; Tonkin et al. 2014). In the context of increasing  
512 extreme climatic events and ecosystem disturbances (Easterling et al. 2000; Parmesan  
513 2006), understanding how metacommunities are organised in highly dynamic systems is  
514 becoming a key research topic. Also, translating such research into efficient  
515 management guidelines is urgently needed.

516

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742 **Table 1. Definitions of terms used throughout the manuscript.**

<b>Term</b>	<b>Definition</b>
<b>Community (or local community)</b>	The individuals of all species that potentially interact within a single patch or local area of habitat (Leibold et al. 2004).
<b>Dispersal</b>	A regional process influencing metacommunity dynamics involving the movement of individuals from one site (i.e., emigration) to another (i.e., immigration) within a region (see also Leibold et al. 2004).
<b>Storage effect</b>	A local process involving the recruitment of many individuals from a single generation, allowing species coexistence in systems prone to disturbance (see also Warner & Chesson 1985; Snyder 2006).
<b>Flow intermittence</b>	Proportion of a given period, generally a year, during which a site in a river network is either under lentic or terrestrial phases (Datry et al. 2014).
<b>Local community structure</b>	A general term used to describe community characteristics resulting from the processes involved in its formation (e.g. species richness, dominance, etc.).
<b>Metacommunity</b>	A set of local communities that are linked by dispersal of multiple potentially interacting species (Leibold et al. 2004).
<b>Metacommunity dynamics</b>	The dynamics that arise within metacommunities; these consist of spatial dynamics, temporal dynamics, and community dynamics (multispecies interactions or the emergent properties arising from them within communities), and the interaction of these three dynamics (see also Leibold et al. 2004).
<b>Metacommunity organisation</b>	A term that refers to the processes that explain metacommunities, i.e., environmental filtering or dispersal (Heino et al. 2015).
<b>Environmental filtering</b>	A local, niche-based process influencing metacommunity dynamics and encompassing (i) the effects of local abiotic factors on species survival and (ii) local species interactions (see also species sorting in Leibold et al. 2004).
<b>Nestedness</b>	The species of communities with smaller numbers of species are subsets of species-richer communities, reflecting a non-random process of species loss or gain as a consequence of any factor that promotes the orderly disaggregation (or aggregation) of community (Baselga 2010).
<b>Turnover</b>	The replacement of some species by others between communities is a consequence of environmental filtering or spatial and historical constraints. Different from nestedness, the gain of one species is necessarily accompanied by a loss of a second species (Baselga 2010).

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