1   **Biodiversity in perennial and intermittent rivers: a meta-analysis**

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Abstract

Comprehensive knowledge of the effects of disturbances on biodiversity is

crucial for conservation and management, not least because ecosystems with

low biodiversity may be the most vulnerable. In rivers, the role of disturbance in

shaping aquatic biodiversity has mainly focused on floods. Perennial rivers

(PRs) often flood, whereas intermittent rivers (IRs) flood, stop flowing and dry.

Despite the recent and significant increase in research on IRs, controversy

remains about whether they are more or less biodiverse than PRs. Our aim was

to determine (Q1) if PRs and IRs differ in biodiversity and (Q2) if the direction

and magnitude of the differences (effect sizes) are related to environmental

(climate, season, habitat, longitudinal zonation and anthropogenic disturbance)

and/or biological factors (taxonomic group). We conducted a meta-analysis on

44 published studies of PR and IR biodiversity that had replicated data. We

applied random effects models to the data to obtain weighted mean effect sizes

for differences between PRs and IRs, and their confidence intervals, by first

considering all studies and then by splitting studies into groups on the basis of

the above factors. We found that biodiversity was significantly higher in PRs

than in IRs (Q1). We also detected significant differences (PRs>IRs) in studies

of macroinvertebrates, in those conducted within arid and temperate climates,

dry and wet sampling seasons, headwaters, and regions subject to different

levels of anthropogenic disturbance (Q2). Our meta-analysis suggests that the

expected increase in the prevalence of IRs in certain regions of the world due to

global change could result in a decrease in freshwater biodiversity. To better

manage and preserve aquatic biodiversity under future global change scenarios

52 and to avoid potential ecosystem consequences of biodiversity loss,

53 conservation efforts should be targeted towards those environmental conditions

54 or taxonomic groups with significant differences (PRs>IRs).

55

56 **Keywords:** disturbance, flow intermittence, fluvial ecosystems, global change,

57 temporary rivers

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Introduction

Understanding how disturbance influences biodiversity is a recurrent topic in community ecology (Pianka 1966, Huston 1979, Hughes et al. 2007). Disturbance includes a wide variety of phenomena acting at multiple temporal (e.g. from days to eons) and spatial (e.g. from local to biogeographical) scales, with multiple potential consequences for populations, communities and ecosystems (Dornelas 2010). Ecologists hypothesised many years ago that disturbance decreased biodiversity and favoured ecological succession (Clements 1916) and that intermediate levels of disturbance enhanced biodiversity (Connell 1978, but see Fox 2013). Effects of disturbance on biodiversity have been studied in many ecosystems and across multiple taxonomic groups (e.g. Horner-Devine et al. 2004, Granham et al. 2009, Barlow et al. 2016). Most studies highlight the negative effects of disturbance on biodiversity (e.g. Loreau et al. 2001, Wardle et al. 2011, Hooper et al. 2012), while only few show the contrary pattern (e.g. Thom and Seidl 2015, Brunbjerg et al. 2015). Understanding and predicting when and how biodiversity might change following disturbance is crucial for effective conservation and management (Dornelas 2010).

The role of disturbance in shaping aquatic biodiversity has focused mainly on flood and drying events (Resh et al. 1988, Giller 1996). Flood events are pulse disturbances that occur relatively quickly (Junk et al. 1989, Ward and Stanford 1995), disrupting habitat conditions and eliminating individuals (Poff et al. 1997, Lake 2000). In contrast, drying events are ramp disturbances that

85   reduce aquatic habitat and eventually result in flow cessation and/or complete

86   loss of surface water from the streambed, and can reduce aquatic biodiversity

87   drastically (Williams 1996, Lake 2000). Floods enhance connectivity among

88   aquatic habitats, whereas drying fragments them (Stanley et al. 1997, Boulton

89   2003). Although it is widely known that floods and drying events affect the

90   structure and function of rivers (Bonada et al. 2007a, Reich and Lake 2015) and

91   that research on drying events has significantly increased during the last

92   decade (Leigh et al. 2016a), the effects of floods have been more frequently

93   reported that those of drying events (e.g. Datry et al. 2007, Lake et al. 2007).

94   This may be because floods occur in all river types, whereas drying events are

95   particular to intermittent rivers (IRs), in which surface flow ceases at some point

96   in time and space (Acuña et al. 2014, Datry et al. 2014a, Leigh et al. 2016a). In

97   contrast, perennial rivers (PRs) are characterized by continuous flow.

98

99   IRs are probably the most common fluvial ecosystems in the world (Datry

100 et al. 2016a), and therefore drying events are probably more ubiquitous than

101 previously thought. In addition, many PRs are expected to transition to IRs in

102 the near future as a result of global change and increased human demand for

103 fresh water (Palmer et al. 2008, Döll and Schmied 2012), increasing the

104 importance and relative contribution of IR ecosystems to global aquatic

105 biodiversity. However, although research on IRs is in what has been described

106 as a boom phase (Datry et al. 2011, Leigh et al. 2016a), debate remains over

107 whether IRs are more or less biodiverse than PRs. Some studies find that IRs

108 are less biodiverse (e.g. Del Rosario and Resh 2000, Storey and Quinn 2008,

109 Bogan et al. 2013), whereas others find the opposite (e.g. Dietrich and

110   Anderson 2000), or no difference between IR and PR biodiversity (e.g. Miller

111   and Golladay 1996, Casas and Langton 2008, Santos and Stevenson 2011).

112   Clearly, a more thorough understanding and test of the biodiversity difference

113   between PRs and IRs is required.

114

115   Biodiversity between PRs and IRs might differ depending on several

116   factors. First, biodiversity in IRs can depend on how flow regime characteristics,

117   which change among climatic zones, forge adaptations to drying (Boulton 2003,

118   Lytle and Poff 2004). For example, the higher number of unique taxa in IRs than

119   PRs in Mediterranean climates has been related to their predictable flow

120   regimes (Bêche et al. 2006, Munné and Prat 2011). Second, biodiversity

121   between PRs and IRs can vary seasonally. During the wet season, when both

122   PRs and IRs flow, their biodiversity is more likely to be similar (Delucchi 1988,

123   Garcia-Roger et al. 2011), whereas during the dry season, IRs will likely have

124   lower aquatic habitat availability than PRs, and thus lower aquatic biodiversity.

125   Third, as biodiversity varies among habitats in PRs and IRs (Garcia-Roger et al.

126   2013), habitat type is another relevant factor to consider. Riffles in IRs might

127   host a lower biodiversity than in PRs because this habitat is the first to

128   disappear during drying (Bonada et al. 2006a), whereas pools might show the

129   contrary pattern if isolated pools remain in IRs during drying (Bonada et al.

130   2006a, Leigh and Sheldon 2009, Boersma et al. 2014). Fourth, biodiversity

131   differences between PRs and IRs may vary with longitudinal zonation. IR

132   headwaters might have lower biodiversity than PR headwaters because their

133   greater isolation might hamper recolonization after drying (Finn et al. 2011,

134   Datry et al. 2016b, c), whereas no significant landscape barriers would affect

135   recolonization of middle reaches (of free-flowing rivers, at least). However, and

136   fifthly, anthropogenic disturbance may dampen differences in biodiversity

137   between PRs and IRs by homogenizing and simplifying communities (Rahel

138   2002) regardless of flow regime, climate, habitat, season, or the taxonomic

139   group considered. Finally, the magnitude of change between biodiversity in PRs

140   and IRs may vary depending on the taxonomic group considered (i.e.

141   macroinvertebrates, fish, algae or macrophytes) because despite some taxa

142   within all groups having traits of resistance and/or resilience to drying (Bonada

143   and Resh 2013), their evolutionary history, species biodiversity and ecological

144   tolerance varies. For example, although algae and macrophyte species are

145   much more widespread than other freshwater groups, they have a limited set of

146   biological adaptations to flow variation (e.g. see Lange et al. 2016 for algae in

147   comparison to Tachet et al. 2002 for macroinvertebrates).

148

149   Here, we investigated the above hypotheses by comparing biodiversity in

150   PRs and IRs using a meta-analytic approach. Specifically, we sought to

151   determine (Q1) whether PR and IR biodiversity differ and (Q2) whether the

152   direction and magnitude of any difference is related to the environmental (i.e.

153   climate, season, habitat, longitudinal zonation, anthropogenic disturbance) or

154   biological factors (i.e. taxonomic group) hypothesised to affect biodiversity

155   patterns in river ecosystems. For our main question (Q1), we hypothesized that

156   biodiversity should be lower in IRs than in PRs (e.g. Fritz and Dodds 2002,

157   Storey and Quinn 2008, Bogan et al. 2013) because IRs are subject to drying

158   events that act primarily as a disturbance decreasing aquatic biodiversity (Leigh

159   and Datry 2016). However, if this loss of taxa in IRs is compensated by taxa

160 with resistance and resilience traits to cope with drying (Bonada et al. 2007b,

161 Grubbs 2011, Vander Vorste et al. 2016), biodiversity in PRs and IRs may be

162 similar or IR biodiversity may be higher. Assessing the differences in

163 biodiversity between PRs and IRs and understanding the conditions under

164 which those differences differ is increasingly important for predicting aquatic

165 biodiversity changes in the face of global change.

166

167

168 **Methods**

169

170 **Data selection**

171 We identified published studies that recorded biodiversity of PRs and IRs from

172 an ISI Web of Knowledge (https://www.accesowok.fecyt.es/) literature search

173 considering a time span from the 1900s to the 21st of August 2014 (Leigh et al.

174 2016a). Leigh et al (2016a) used a comprehensive search string of multiple

175 terms for IRs which resulted in 10800 records and then filtered these

176 publications using further search terms associated with key topics of research

177 on IR ecology and management: invertebrate ecology, fish ecology,

178 biogeochemistry, and ecological and hydrological assessment. They then

179 screened the resultant groups of records manually to ensure relevancy to the

180 topics and IR research more generally (e.g. removing studies in the medical

181 field), obtaining 1237 publications (see Table S2 in Leigh et al. 2016a for full

182 details of search parameters and screening criteria).

183

184   For this study, we re-screened each of the 1237 publications to select

185   those relevant for the meta-analysis according to the following criteria: the

186   publication had to discuss or provide direct insight into the ecology and/or

187   management of PRs and IRs, the sampling design had to include sites which

188   were not located along the same river (i.e. sites must be hydrologically

189   independent), and the publication had to include means and standard

190   deviations (SDs) of biodiversity measures (e.g. taxonomic richness, Shannon-

191   Wiener diversity index) for each river type (PRs and IRs) or enough information

192   to calculate these values. This selection resulted in a total of 63 publications, 44

193   with replicated data (i.e. studies with more than one PR and IR each from which

194   the means and SDs were obtained) and 19 with non-replicated data (i.e. only

195   one PR or IR from which biodiversity data was obtained) (see Appendixes S1

196   and S2 for the full reference details of these publications). Most studies were

197   conducted in North America, Europe and Australia. Very few studies were from

198   Africa and Asia, and none were from South America (Figure 1). For studies

199   investigating biodiversity in more than one distinct region (e.g. South Africa and

200   Australia) we derived biodiversity data separately for each region, whereas for

201   studies which investigated multiple groups of organisms (e.g. fish, invertebrates,

202   diatoms), we randomly chose one group only. Each of these individual

203   investigations are referred to and counted as one study for simplicity.

204

205   We most commonly extracted means, SDs, and number of sites (n)

206   directly, computed them from text and/or tables in the studies (27 studies), or

207   obtained them directly from authors (26 studies). For the remaining 10 studies,

208   we extracted data from figures using Plot Digitiser

209 (www.plotdigitizer.sourceforge.net/). Where multiple measures of biodiversity

210 (e.g. taxonomic richness, evenness, Shannon-Wiener diversity index) were

211 available, we preferentially extracted richness data due to it being the most

212 commonly reported measure across all studies. Only one study reported the

213 Shannon-Wiener diversity index alone. We included both these measures (i.e.

214 richness and the Shannon-Wiener diversity index) together in our analysis

215 because our aim was to provide a general summary of the difference in

216 biodiversity among groups (i.e. PRs and IRs) (Scheiner and Gurevitch 2001).

217 Then, for each individual publication, we obtained information on site or

218 sampling characteristics. In particular, we considered the following 6 factors,

219 each with several levels within: climate, sampling season, habitat, longitudinal

220 zonation, level of anthropogenic disturbance, and taxonomic group (Table 1,

221 Appendix S3). We created different subsets of data using the levels of these

222 factors and analysed them separately.

223

224 **Effect size estimate**

225 For replicated studies (with n > 1 PRs and n > 1 IRs, n_{PR} and n_{IR}, respectively),

226 we obtained effect sizes using Hedge's g, which corresponds to the difference

227 between the means of biodiversity in PRs and IRs ($\overline{PR} - \overline{IR}$) divided by the

228 pooled standard deviation (S_{within}) and with a correction for small sample bias (J)

229 (Rosenberg et al. 2000, Borenstein et al. 2009):

230 $$g = \frac{\overline{PR} - \overline{IR}}{S_{within}}J, \quad S_{within} = \sqrt{\frac{(n_{PR}-1)SD_{PR}^2 + (n_{IR}-1)SD_{IR}^2}{n_{PR} + n_{IR} - 2}}, \quad J = 1 - \frac{3}{4(n_{PR} + n_{IR} - 2) - 1}$$

231 The variance of g was given by:

232 $$V_g = \left(\frac{n_{PR} + n_{IR}}{n_{PR} n_{IR}} + \frac{\left(\frac{\overline{PR} - \overline{IR}}{S_{within}} \right)^2}{2(n_{PR} + n_{IR})} \right) J^2$$

233   For non-replicated studies, where means and standard deviations were

234 not available, we obtained effect sizes using log(PR/IR), known as the response

235 ratio. Following Hedges et al. (1999; see also equation 4.30 and 4.31 in

236 Borenstein et al. 2009), we also computed the response ratio for replicated

237 studies for comparison with the non-replicated studies, but we did not include it

238 in the estimation of weighted effect sizes.

239

240 **Weighted mean effect size**

241 We used random effects models in all cases because we assumed that the true

242 effect sizes vary among studies (Borenstein et al. 2009). This assumption is

243 justifiable as our meta-analysis included a wide variety of studies that, for

244 example, investigated different organisms or were conducted using different

245 sampling methods. Statistically, this choice of meta-analytic model consists in

246 estimating (i) the between-studies variance (T^2; see equations 12.2, 12.3, 12.4

247 and 12.5 in Borenstein et al. 2009) and (ii) the total variance ($V_i = V_g + T^2$) to (iii)

248 assign the weight of each study ($W_i = 1/V_i$). Model outputs included the

249 weighted mean effect size (wES) and its confidence interval, and a test of the

250 hypothesis that the true wES is zero, following standard methods described in

251 Borenstein et al. (2009). We estimated wES for the entire dataset (e.g.

252 considering all replicated data in the one random effects model) and for each of

253 the subsets of data separated by the 6 factors listed above (Table 1). For these

11

254 subset analyses, the models were estimated without the intercept (Viechtbauer

255 2010). With this parameterization, a pooled value of T^2 was used, a procedure

256 recommended by Borenstein et al. (2009) to increase the accuracy of the

257 estimate of the between-studies variance.

258

259   We used a forest plot to illustrate the results of the meta-analysis. This

260 plot shows the effect sizes and confidence intervals of each study and the wES

261 (Gates 2002). A significant model (or a wES whose confidence interval does not

262 include zero) indicates a significant difference between PR and IR biodiversity.

263 The magnitude of the wES indicates the amount of difference between the two

264 river types. Here, a positive wES indicates that biodiversity in PRs is higher than

265 in IRs.

266

267 **Publication bias**

268 First, we visually assessed publication bias in the replicated studies using a

269 funnel plot of effect size against a measure of study size or precision (e.g. the

270 standard error of the effect size) (Sterne et al. 2011). Visually asymmetrical

271 funnel plots usually indicate publication bias, whereas symmetrical ones

272 indicate negligible publication bias. Second, we calculated the fail-safe number

273 according to Orwin's equation (Orwin 1983), which gives the number of studies

274 needed to reduce the average effect size to a pre-specified value, which is

275 considered unimportant. We tested a range of values (with steps of 0.2) from

276 0.2 to 0.8 (corresponding, approximately, to half of the unweighted mean effect

277 size). Third, we calculated the fail-safe number according to Rosenthal's

278 approach ("file drawer analysis"). This indicates the number of missing studies

279   (i.e. those unpublished or available but not captured by the literature search and

280   selection process) needed to be retrieved and incorporated in the analysis to

281   eliminate bias (Borenstein et al. 2009). A high value indicates that a meta-

282   analysis (i.e. estimated effect size) is robust to publication bias, given that we

283   would need a large number of studies to nullify the effect size. Finally, as a

284   sensitivity analysis, we applied the trim-and-fill method (Duval and Tweedie

285   2000a, b). This method estimates and adjusts meta-analysis results for the

286   numbers and outcomes of missing studies.

287

288   We checked our meta-analysis against the quality criteria provided by

289   Koricheva et al. (2013). We fulfilled all applicable criteria. We computed all

290   statistics using the R 3.3.1 freeware (R Core Team 2015) and the libraries

291   metafor (Viechtbauer 2010) and rmeta (Lumley 2012).

292

293

294   **Results**

295

296   **Overall differences between IRs and PRs**

297   The overall meta-analysis revealed a statistically significant difference in PR

298   and IR biodiversity (considering all replicate studies together), with a positive

299   overall effect size (wES = 0.879, Table 2), thus indicating a significantly higher

300   biodiversity in PRs than in IRs (Figure 2). Positive effect sizes for the individual

301   studies ranged from 0.01 to 7.95; negative effect sizes were smaller, ranging

302   from -1.10 to -0.04 (Figure 2). Accordingly, heterogeneity among studies was

303   highly significant (Q = 89.317, df = 43; P < 0.0001).

304

305   Log response ratios estimated for replicated (weighted mean effect size

306 [log(PR/IR)] = 0.38 ± 0.05 SE) and non-replicated (unweighted mean effect size

307 [log(PR/IR)] = 0.25 ± 0.08 SE) studies were also positive (Appendix S4). The

308 majority of non-replicated studies had effect sizes located in the positive side of

309 the forest plot (Appendix S4), again indicating that biodiversity in PRs was, in

310 most cases, higher than in IRs.

311

312 **Specific differences in biodiversity between IRs and PRs**

313 For most levels of the 6 factors, wES was significantly positive (Table 2),

314 indicating higher biodiversity in PRs than IRs. We detected differences between

315 PR and IR biodiversity for studies conducted within arid (B), temperate (C), cold

316 (D) or multiple climate zones; within studies that considered dry, wet, or multiple

317 seasons; a multi-habitat sampling regime; samples from headwaters or multiple

318 longitudinal zones; sites subject to low and medium-high levels of

319 anthropogenic disturbance; and that included macroinvertebrates (Table 2). We

320 found non-significant results for polar climates (E); riffle, pool, and stone

321 habitats; middle reaches; fish, algae and macrophytes (Table 2).

322

323 **Publication bias**

324 Although the funnel plot visually approached asymmetry (Figure 3a), fail-safe

325 numbers and the sensitivity analysis indicated minimal bias. According to

326 Orwin's method, even if a substantial effect size (0.8) is conservatively assumed

327 as unimportant, a large number of unpublished studies would still be needed

328 (Orwin's fail safe N = 38 studies) with no differences between the types of rivers

329   for the estimated effect size to be reduced to an "unimportant" value. As

330   expected, this number increases substantially when lower effect sizes (i.e. 0.6,

331   0.4, and 0.2) are used in Orwin's equation (Orwin's fail safe N = 67, 124, and

332   295, respectively). According to Rosenthal's approach, the fail-safe number was

333   1352, suggesting that a large number of studies with non-significant differences

334   between types of rivers would be needed to reverse the conclusion that PRs

335   were more biodiverse than IRs. According to the trim and fill approach, only 6

336   studies were potentially missing from our analysis that if present would produce

337   a symmetrical funnel plot (Figure 3b). The wES estimated by this method was

338   similar to the one reported above (trim and fill wES = 0.776 ± 0.178; 95 % CI =

339   0.427 to 1.125).

340

341

342   ## Discussion

343

344   The studies analysed here compared biodiversity in PRs and IRs across a wide

345   range of environmental conditions. We found a significantly higher biodiversity

346   in PRs than in IRs, which confirmed our primary hypothesis . This finding

347   agrees with individual studies showing that PRs are more species-rich than IRs

348   and that flow intermittence is a disturbance that constrains a aquatic biodiversity

349   (e.g. Del Rosario and Resh, 2000, Storey and Quinn 2008, Bogan et al. 2013).

350   However, several individual studies included in our meta-analysis found similar

351   values of biodiversity in PRs and IRs; in these cases, the characteristic taxa

352   found in IRs during the dry period compensated for the loss of taxa present

353   during flow (e.g. Miller and Golladay 1996, Casas and Langton 2008, Santos

354 and Stevenson 2011). Few of the studies analysed here had higher biodiversity

355 in IRs than in PRs (e.g. Price et al. 2003, Bonada et al. 2007, Alexandre et al.

356 2013). The persistence of isolated pools during the dry season in IRs, which

357 favours the presence of a wide variety of species found exclusively in lentic

358 waters and/or that prefer such habitat, may have increased IR biodiversity in

359 these cases (Bonada et al. 2006a).

360

361 　　　　Although we found overall support for the hypothesis that PR biodiversity

362 is higher than IR biodiversity, IRs occur throughout the globe, including many in

363 regions in Africa, Asia or South America not covered by our meta-analysis

364 (Datry et al. 2016a, Leigh et al. 2016a). In addition, most of the papers analysed

365 here consider the most commonly studied taxonomic groups in river ecology

366 (i.e. macroinvertebrates, fish, algae and macrophytes); no papers examining

367 other highly diverse groups such as microbes (Palmer et al. 2000) fulfilled our

368 selection criteria. To increase the robustness of our meta-analysis, there is a

369 need for future research on studies comparing PRs and IRs biodiversity in

370 regions beyond those included here and across a wider variety of taxonomic

371 groups. This would provide a more comprehensive view of the effects of flow

372 intermittence on aquatic biodiversity and the potential effects of current and

373 future global change.

374

375 　　　　Our finding that PR biodiversity was higher than IR biodiversity within

376 cold, arid and temperate (which includes Mediterranean) climates agrees with

377 several studies from arid (e.g. Beugly and Pyron 2010, Leigh 2013, De Jong et

378 al. 2013) and Mediterranean-temperate regions (Progar and Moldenke 2002,

379   Roux et al. 2008, Storey and Quinn 2008). Flow predictability, which is related

380   to climate predictability, plays an important role in shaping species adaptations

381   and thus biodiversity (Lytle and Poff 2004); highly predictable environments

382   (e.g. in predictably seasonal Mediterranean-climate regions) are considered to

383   support higher biodiversity than less predictable ones. However, despite dry

384   riverbeds providing habitat and refuge for terrestrial organisms (Steward et al.

385   2012, Corti et al. 2013, Corti & Datry 2016) and their disconnected pools acting

386   as refuges for aquatic organisms (Bonada et al. 2007a, b, Sheldon et al. 2010,

387   Datry et al. 2014a), flow intermittence is a strong disturbance even in

388   predictable climates (Datry et al. 2014b, Leigh and Datry 2016). Indeed,

389   although some aquatic organisms have traits to cope with flow intermittence

390   (e.g. Bêche et al. 2006, Bonada et al. 2008, Blanchette and Pearson 2012),

391   resistance traits acquired through evolution as a response to drying are much

392   less frequent than resilience traits in IRs (Datry et al. 2014b, Leigh et al. 2016a,

393   Vander Vorste et al. 2016), which would explain our overall result. Of particular

394   concern is our finding of comparatively low biodiversity in arid-zone IRs given

395   aridity is projected to increase in several regions of the world (e.g. the already

396   arid southwest region of USA; Seager et al. 2013).

397

398   Our results do not support the view that differences in biodiversity

399   between PRs and IRs are negligible during the wet season. However, despite

400   the low number of studies considered, we did find support for the hypothesis

401   that biodiversity in PRs is higher than in IRs during the dry season. In this latter

402   case, the low habitat availability in IRs compared to PRs will reduce biodiversity

403   unless isolated pools remain for long periods allowing many species to colonize

404 and increase community variability among pools within reaches (Bonada et al.

405 2006a; Leigh and Sheldon 2009). By contrast, during the wet season, despite

406 IRs having similar habitat availability as PRs, some studies have also shown

407 that biodiversity may remain relatively low in IRs because fewer species may be

408 available and able to colonize these habitats and/or because of alterations to

409 food web structure and dimensions (Datry 2012, McHugh et al. 2015).

410

411   Aquatic organisms (i.e. macroinvertebrate, fish, algae and macrophytes)

412 have adaptations to particular instream habitats, from riffles to pools (Bonada et

413 al. 2006a, Dallas 2007, Bonada et al. 2008). Most likely due to the small

414 number of studies in the subsets, our hypothesis regarding habitat (i.e.

415 biodiversity in PR riffles may be higher than in IR riffles, whereas the opposite

416 pattern may be observed in pools) was not supported. However, studies

417 sampling multiple habitats showed a higher biodiversity in PRs than in IRs,

418 which agrees with findings from Graça et al. (2004), Belmar et al. (2013) and

419 Leigh et al. (2013a). Multi-habitat sampling may be a better method to account

420 for biodiversity of rivers (Leitão et al. 2014) because species characteristic of

421 individual habitats may not occur across all habitat types (Bonada et al. 2006b;

422 Cid et al. 2016).

423

424   The aquatic biodiversity of a particular reach not only depends on

425 instream habitat characteristics, but also on the regional biodiversity and the

426 balance between dispersal and abiotic/biotic factors. The river network structure

427 plays an essential role for the dispersion of aquatic organisms and thus helps

428 determine aquatic biodiversity patterns (Altermatt 2013). In PRs, biodiversity in

429   lowland reaches is driven by mass effects whereas abiotic/biotic factors are

430   considered more important in their headwaters (Brown and Swan 2010). In IRs,

431   the relative role of dispersal versus abiotic/biotic factors depends not only on

432   the hydrological phase of the reach (i.e. flowing, non-flowing, dry) but also on

433   where the drying event occurs along the river network (Datry et al. 2014b,

434   2016c, d). We were unable to test how different configurations of drying events

435   affect a aquatic biodiversity but, although more studies are needed for middle

436   reaches, our results on longitudinal zonation agreed with our initial hypothesis.

437   Flow and river characteristics change with longitudinal zonation and, according

438   to the River Continuum Concept, alpha-diversity is expected to peak at middle

439   reaches (Vannote et al. 1980, Finn et al. 2011). Indeed, the low alpha

440   biodiversity in headwaters and their high isolation make them highly vulnerable

441   to biodiversity loss by flow intermittence and hampers recolonization after flow

442   resumption unless communities in IR headwaters are dominated by resistance

443   strategies to drying (Datry et al. 2014b, 2016a). In contrast, middle reaches

444   have higher alpha biodiversity and less isolation (Finn et al. 2011), resulting in

445   no differences between PRs and IRs. On the other hand, headwaters make up

446   a large proportion of all river networks (Naiman 1983, Benda et al. 2005) and

447   the studies included in our analyses that were conducted in multiple reaches

448   also included a higher proportion of headwater sites, supporting the hypothesis

449   that PRs have a higher biodiversity than IRs when examined across multiple

450   reaches (i.e. at large spatial scales). We suggest, however, that these

451   interpretations should be viewed with caution due to the small number of

452   studies in middle reaches.

453

454   Anthropogenic disturbances often decrease biodiversity by homogenising

455   communities (Rahel 2002). Despite this, we found higher biodiversity in PRs

456   than in IRs regardless of the level of anthropogenic disturbance (i.e. low or

457   medium-high). We acknowledge, however, that our categorization of

458   anthropogenic disturbances was coarse and more studies comparing

459   biodiversity in PRs and IRs under more explicit and different disturbance

460   categories are needed. The effect of anthropogenic disturbances on IRs is a

461   relatively novel topic that is being considered in terms of management and

462   conservation of river ecosystems (e.g. Skoulikidis et al. 2017). Current

463   bioassessment methods are designed to detect the impacts of anthropogenic

464   disturbances (Bonada et al. 2006b) but typically fail when applied to IRs. This

465   means that the lower biodiversity of IRs compared to PRs cannot simply be

466   interpreted as indicative of anthropogenic impairment. New methods for IR

467   bioassessment must be designed that can disentangle natural from

468   anthropogenic disturbances (Prat et al. 2004, Leigh et al. 2013b).

469

470   Biodiversity has been related to ecosystem resilience (defined by Holling

471   1973, "as the magnitude of disturbance that a system can experience before it

472   shifts into a different state"), however, there is uncertainty about how ecosystem

473   resilience will respond to increases in levels of anthropogenic disturbance and

474   consequent impacts on biodiversity (Steffen et al. 2004). Walker and Meyer

475   (2004) suggested that ecosystems might respond gradually to biodiversity loss,

476   whereas Gunderson and Pritchard (2002) suggested that ecosystems will

477   respond strongly, because crossing the threshold of biodiversity loss will

478   produce sudden and dramatic changes in the responding state factors. Indeed,

479   higher numbers of species are expected to increase the ability to recover from

480   disturbances (Holling 1978, Folke et al. 2004). If IRs have significantly lower

481   biodiversity than PRs, as found by us, ecosystem resilience could be affected.

482   However, IR taxa have particular adaptations for surviving and recovering from

483   drying (Lake 2011, Blanchette and Pearson 2012; Leigh et al. 2016b), which

484   may help to mitigate the effects of future co-occurring disturbances (Mori et al.

485   2013, Vander Vorste et al. 2016). Although a growing number of studies on IRs

486   consider ecosystem resilience (e.g. using functional characteristics of species;

487   Bruno et al. 2016, Vander Vorste et al. 2016), the ecosystem effects of

488   biodiversity loss in these systems needs to be investigated.

489

490   As a result of global change, extreme climatic events are expected to

491   increase in frequency and intensity, with an increase in drying frequency,

492   duration, and/or intensity in many regions (Beniston et al. 2007, Palmer et al.

493   2008, Döll and Schmied 2012). Some regions will experience shifts from PRs to

494   IRs, whereas other regions will show the contrary pattern (Döll and Schmied

495   2012). If these hydrological regime shifts occur faster than the evolutionary

496   scale at which species acquire adaptive traits (Filipe et al. 2013), dramatic

497   effects on aquatic biodiversity and ecosystem processes and services will result

498   (Datry et al. 2014a, IPCC 2014, Ledger and Milner, 2015). In regions where

499   PRs will shift to IRs, loss of species poorly adapted to dry conditions can be

500   expected (Phillipsen and Lytle 2013, Jaeger et al. 2014). Our findings suggest

501   such losses may be particularly relevant for certain taxonomic groups (i.e.

502   macroinvertebrates) and under particular environmental conditions or in certain

503   regions (e.g. in arid and temperate climate zones, and in headwaters).

504   However, IRs communities of species with strong dispersal capacity and high

505   fecundity may be minimally affected and able to colonize these novel IRs

506   (Arscott et al. 2010, Datry et al. 2014a, b). In regions where IRs will shift to PRs,

507   the expected increase in biodiversity in these novel PRs will ultimately depend

508   on the connectivity to other PRs. PRs highly connected to novel PRs might

509   maintain biodiversity, whereas the biodiversity in of highly isolated PRs may

510   decline. As highly dynamic metacommunities are expected to dominate in this

511   future scenario of IRs shifting to PRs and vice versa (Datry et al. 2016b),

512   conservation efforts to reduce the risk of undesired hydrological regime shifts

513   should be prioritized to avoid effects on ecosystem resilience (Folke et al. 2004)

514   and could be targeted towards those environmental conditions or taxonomic

515   groups with significant differences between PR and IR biodiversity.

516

517

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519

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530

531

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533

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Table 1. Description of the environmental and biological factors and levels

within each factor, identified from individual publications and used in our meta-

analysis with replicated data.

ENVIRONMENTAL FACTORS	Levels	Observations
Climate	B, C, D, E, Multiple	Dominant climate of each system was determined according to the Köppen classification of Peel et al. (2007), which considers 5 general climates: tropical (A), arid (B), temperate (C), cold (D), and polar (E). No studies were carried out in the tropical (A) climate and thus it is not included here. Multiple includes a combination of these climates.
Sampling season	Dry, Wet, Multiple	Multiple refers to studies that sampled in both dry and wet seasons, or at multiple times of year in regions that cannot be described simply in terms of dry-wet seasonality
Habitat	Riffles, Pools, Stones, Multihabitat	Multihabitat includes riffles and pools. Stones refer to rock fragments of more than 25 cm.
Longitudinal Zonation	Headwaters, Middle, Multiple	Headwater reaches refer to a catchment area <100km^2, or a stream order equal to or less than 3. Middle refers to reaches with a catchment area between 100 and 1000 km^2 or a stream order of 4-6. Large refers to a catchment area >1000km^2. Multiple

		includes headwaters, middle and large reaches.
Anthropogenic disturbance	Low, Medium-High	This factor was considered very general and did not distinguishspecific types of disturbance (e.g. hydrological vs morphological). Low levels were distinguished from Medium-High levels on the basis of information available in the published studies (e.g. Low levels were assigned to sites within reserves; Medium-High to sites in urban areas). Medium and high levels of disturbance were difficult to differentiate based on information provided in studies and were thus combined .
BIOLOGICAL FACTORS	**Levels**	
Taxonomic group	Macroinvertebrates, Fish, Algae/Macrophytes	

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868   Table 2. Results of the random effects models for the overall design (with and

869   without trim-and-fill) and for the levels of the 6 factors. Bold typeface indicates p

870   < 0.005. N = number of studies considered in each level; wES = weighted mean

871   effect size; SE = Standard Error of the estimates; ci.lb and ci.ub = confidence

872   interval (lower and upper limits, respectively). See Table 1 for a description of

873   the factors and levels.

			Model Results				
		N	wES	SE	p-value	ci.lb	ci.ub
OVERALL DESIGN		44	0.879	0.169	**<0.0001**	0.549	1.209
ENVIRONMENTAL FACTORS	**LEVELS**						
Climate	**B**	6	0.946	0.454	**0.0373**	0.056	1.836
	C	28	0.735	0.203	**0.0003**	0.336	1.133
	D	4	1.766	0.726	**0.0150**	0.343	3.188
	E	3	1.369	1.204	0.2556	-0.991	3.729
	Multiple	3	1.244	0.556	**0.0254**	0.153	2.334
Sampling season	**Dry**	10	1.304	0.387	**0.0007**	0.546	2.061
	Wet	7	0.964	0.400	**0.0159**	0.180	1.748
	Multiple	27	0.719	0.222	**0.0012**	0.283	1.155
Habitat	Riffles	4	0.754	0.600	0.2089	-0.422	1.929
	Pools	2	0.734	1.123	0.5132	-1.467	2.935
	Stones	1	0.009	0.777	0.9912	-1.515	1.532
	Multihabitat	32	0.994	0.194	**<0.0001**	0.613	1.375
Longitudinal zonation	**Headwaters**	24	0.988	0.263	**0.0002**	0.472	1.504
	Middle	1	-0.588	1.390	0.6723	-3.312	2.137
	Multiple	11	1.028	0.295	**0.0005**	0.451	1.605
Anthropogenic disturbance	**Low**	27	0.783	0.210	**0.0002**	0.372	1.195
	Medium-High	14	1.016	0.293	**0.0005**	0.443	1.590
BIOLOGICAL FACTORS	**LEVELS**						
Taxonomic group	**Macroinvertebrate**	36	1.059	0.181	**<0.0001**	0.704	1.413
	Fish	6	0.446	0.411	0.2783	-0.360	1.252
	Algae/Macrophytes	2	0.024	0.509	0.9619	-0.974	1.022

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Figure legends

Figure 1. Distribution of publications, identified from an ISI Web of Knowledge literature search by Leigh et al. (2016a), that examined biodiversity in hydrologically independent perennial and intermittent rivers (PRs and IRs, respectively). White stars refer to studies with non-replicated data for PRs and/or IRs (n = 19), whereas black stars refer to studies with replicated data for PRs and IRs (n = 44).

Figure 2. Forest plot for the overall design of the original model (without trim-and-fill) considering the 44 replicated studies ordered by increasing effect size from the top to the bottom. Each study is indicated in the left column with the first author and the year of publication (see Appendix 1 for the complete reference). Effect sizes of each study (using the standardized mean difference) with their corresponding confidence intervals are displayed in the centre of the plot with the exact values on the right. The filled diamond at the bottom shows the weighted mean effect size (wES) estimated by the model with the edges of the diamond showing the corresponding confidence interval.

Figure 3. Funnel plots for the overall design using replicated studies without and with trim-and-fill, (a) and (b) panels, respectively. Filled circles represent the individual replicated studies, whereas open circles represent the missing studies required to produce a symmetrical plot.