

Biodiversity in perennial and intermittent rivers: a meta-analysis

Maria Soria, Catherine Leigh, Thibault Datry, Luis Mauricio Bini and Núria Bonada

M. Soria (<http://orcid.org/0000-0001-9379-7626>) (mariasoriaextremera@gmail.com) and N. Bonada (<http://orcid.org/0000-0002-2983-3335>), Dept de Biologia Evolutiva, Ecologia i Ciències Ambientals, Facultat de Biologia, Inst. de Recerca de la Biodiversitat (IRBio), Univ. de Barcelona, ES-08028 Barcelona, Catalonia, Spain. – C. Leigh (<http://orcid.org/0000-0003-4186-1678>) and T. Datry (<http://orcid.org/0000-0003-1390-6736>), Irstea, UR MALY, Centre de Lyon-Villeurbanne, Villeurbanne Cedex, France. CL also at: Australian Rivers Inst. and Griffith School of Environment, Griffith Univ., Nathan, QLD, Australia. – L. M. Bini (<http://orcid.org/0000-0003-3398-9399>), Inst. de Ciências Biológicas, Depto de Ecologia, Univ. Federal de Goiás, Goiânia/GO, Brazil.

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 and to avoid potential ecosystem consequences of biodiversity loss, conservation efforts should be targeted towards those environmental conditions or taxonomic groups with significant differences (PRs > IRs).

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 (Horner-Devine et al. 2004, Graham et al. 2009, Barlow

et al. 2016). Most studies highlight the negative effects of disturbance on biodiversity (Loreau et al. 2001, Wardle et al. 2011, Hooper et al. 2012), while only few show the contrary pattern (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 et al. 2000). In contrast, drying events are ramp disturbances that reduce aquatic habitat

and eventually result in flow cessation and/or complete loss of surface water from the streambed, and can reduce aquatic biodiversity drastically (Williams 1996, Lake et al. 2000). Floods enhance connectivity among aquatic habitats, whereas drying fragments them (Stanley et al. 1997, Boulton 2003). Although it is widely known that floods and drying events affect the structure and function of rivers (Bonada et al. 2007a, Reich and Lake 2015) and that research on drying events has significantly increased during the last decade (Leigh et al. 2016a), the effects of floods have been more frequently reported than those of drying events (Datry et al. 2007, Lake et al. 2007). This may be because floods occur in all river types, whereas drying events are particular to intermittent rivers (IRs), in which surface flow ceases at some point in time and space (Acuña et al. 2014, Datry et al. 2014a, Leigh et al. 2016a). In contrast, perennial rivers (PRs) are characterized by continuous flow.

IRs are probably the most common fluvial ecosystems in the world (Datry et al. 2016a), and therefore drying events are probably more ubiquitous than previously thought. In addition, many PRs are expected to transition to IRs in the near future as a result of global change and increased human demand for fresh water (Palmer et al. 2008, Döll and Schmied 2012), increasing the importance and relative contribution of IR ecosystems to global aquatic biodiversity. However, although research on IRs is in what has been described as a boom phase (Datry et al. 2011, Leigh et al. 2016a), debate remains over whether IRs are more or less biodiverse than PRs. Some studies find that IRs are less biodiverse (Del Rosario and Resh 2000, Storey and Quinn 2008, Bogan et al. 2013), whereas others find the opposite (Dieterich and Anderson 2000), or no difference between IR and PR biodiversity (Miller and Golladay 1996, Casas and Langton 2008, Santos and Stevenson 2011). Clearly, a more thorough understanding and test of the biodiversity difference between PRs and IRs is required.

Biodiversity between PRs and IRs might differ depending on several factors. First, biodiversity in IRs can depend on how flow regime characteristics, which change among climatic zones, forge adaptations to drying (Boulton 2003, Lytle and Poff 2004). For example, the higher number of unique taxa in IRs than PRs in Mediterranean climates has been related to their predictable flow regimes (Bêche et al. 2006, Munné and Prat 2011). Second, biodiversity between PRs and IRs can vary seasonally. During the wet season, when both PRs and IRs flow, their biodiversity is more likely to be similar (Delucchi 1988, García-Roger et al. 2011), whereas during the dry season, IRs will likely have lower aquatic habitat availability than PRs, and thus lower aquatic biodiversity. Third, as biodiversity varies among habitats in PRs and IRs (García-Roger et al. 2013), habitat type is another relevant factor to consider. Riffles in IRs might host a lower biodiversity than in PRs because this habitat is the first to disappear during drying (Bonada et al. 2006a), whereas pools might show the contrary pattern if isolated pools remain in IRs during drying (Bonada et al. 2006a, Leigh and Sheldon 2009, Boersma et al. 2014). Fourth, biodiversity differences between PRs and IRs may vary with longitudinal zonation. IR headwaters might have lower biodiversity than PR headwaters because their greater isolation might hamper recolonization after drying (Finn et al. 2011, Datry et al. 2016b,

c), whereas no significant landscape barriers would affect recolonization of middle reaches (of free-flowing rivers, at least). However, and fifthly, anthropogenic disturbance may dampen differences in biodiversity between PRs and IRs by homogenizing and simplifying communities (Rahel 2002) regardless of flow regime, climate, habitat, season, or the taxonomic group considered. Finally, the magnitude of change between biodiversity in PRs and IRs may vary depending on the taxonomic group considered (i.e. macroinvertebrates, fish, algae or macrophytes) because despite some taxa within all groups having traits of resistance and/or resilience to drying (Bonada and Resh 2013), their evolutionary history, species biodiversity and ecological tolerance varies. For example, although algae and macrophyte species are much more widespread than other freshwater groups, they have a limited set of biological adaptations to flow variation (e.g. see Lange et al. 2016 for algae in comparison to Tachet et al. 2002 for macroinvertebrates).

Here, we investigated the above hypotheses by comparing biodiversity in PRs and IRs using a meta-analytic approach. Specifically, we sought to determine (Q1) whether PR and IR biodiversity differ and (Q2) whether the direction and magnitude of any difference is related to the environmental (i.e. climate, season, habitat, longitudinal zonation, anthropogenic disturbance) or biological factors (i.e. taxonomic group) hypothesised to affect biodiversity patterns in river ecosystems. For our main question (Q1), we hypothesized that biodiversity should be lower in IRs than in PRs (Fritz and Dodds 2002, Storey and Quinn 2008, Bogan et al. 2013) because IRs are subject to drying events that act primarily as a disturbance decreasing aquatic biodiversity (Leigh and Datry 2016). However, if this loss of taxa in IRs is compensated by taxa with resistance and resilience traits to cope with drying (Bonada et al. 2007b, Grubbs 2011, Vander Vorste et al. 2016), biodiversity in PRs and IRs may be similar or IR biodiversity may be higher. Assessing the differences in biodiversity between PRs and IRs and understanding the conditions under which those differences differ is increasingly important for predicting aquatic biodiversity changes in the face of global change.

Methods

Data selection

We identified published studies that recorded biodiversity of PRs and IRs from an ISI Web of Knowledge (< www.accesswok.fecyt.es/ >) literature search considering a time span from the 1900s to the 21 of August 2014 (Leigh et al. 2016a). Leigh et al (2016a) used a comprehensive search string of multiple terms for IRs which resulted in 10 800 records and then filtered these publications using further search terms associated with key topics of research on IR ecology and management: invertebrate ecology, fish ecology, biogeochemistry and ecological and hydrological assessment. They then screened the resultant groups of records manually to ensure relevancy to the topics and IR research more generally (e.g. removing studies in the medical field), obtaining 1237 publications (see Table S2 in Leigh et al. 2016a for full details of search parameters and screening criteria).

For this study, we re-screened each of the 1237 publications to select those relevant for the meta-analysis according to the following criteria: the publication had to discuss or provide direct insight into the ecology and/or management of PRs and IRs, the sampling design had to include sites which were not located along the same river (i.e. sites must be hydrologically independent), and the publication had to include means and standard deviations (SDs) of biodiversity measures (e.g. taxonomic richness, Shannon–Wiener diversity index) for each river type (PRs and IRs) or enough information to calculate these values. This selection resulted in a total of 63 publications, 44 with replicated data (i.e. studies with more than one PR and IR each from which the means and SDs were obtained) and 19 with non-replicated data (i.e. only one PR or IR from which biodiversity data was obtained) (see Supplementary material Appendix 1 and 2 for the full reference details of these publications). Most studies were conducted in North America, Europe and Australia. Very few studies were from Africa and Asia, and none were from South America (Fig. 1). For studies investigating biodiversity in more than one distinct region (e.g. South Africa and Australia) we derived biodiversity data separately for each region, whereas for studies which investigated multiple groups of organisms (e.g. fish, invertebrates, diatoms), we randomly chose one group only. Each of these individual investigations are referred to and counted as one study for simplicity.

We most commonly extracted means, SDs, and number of sites (n) directly, computed them from text and/or tables in the studies (27 studies), or obtained them directly from authors (26 studies). For the remaining 10 studies, we extracted data from figures using Plot Digitiser (<www.plotdigitizer.sourceforge.net/>). Where multiple measures

of biodiversity (e.g. taxonomic richness, evenness, Shannon–Wiener diversity index) were available, we preferentially extracted richness data due to it being the most commonly reported measure across all studies. Only one study reported the Shannon–Wiener diversity index alone. We included both these measures (i.e. richness and the Shannon–Wiener diversity index) together in our analysis because our aim was to provide a general summary of the difference in biodiversity among groups (i.e. PRs and IRs) (Scheiner and Gurevitch 2001). Then, for each individual publication, we obtained information on site or sampling characteristics. In particular, we considered the following six factors, each with several levels within: climate, sampling season, habitat, longitudinal zonation, level of anthropogenic disturbance, and taxonomic group (Table 1, Supplementary material Appendix 3). We created different subsets of data using the levels of these factors and analysed them separately.

Effect size estimate

For replicated studies (with $n > 1$ PRs and $n > 1$ IRs, n_{PR} and n_{IR} , respectively), we obtained effect sizes using Hedge's g , which corresponds to the difference between the means of biodiversity in PRs and IRs ($PR - IR$) divided by the pooled standard deviation (S_{within}) and with a correction for small sample bias (J) (Rosenberg et al. 2000, Borenstein et al. 2009):

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

$$J = 1 - \frac{3}{4(n_{PR} + n_{IR} - 2) - 1}$$



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 ($n = 44$).

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/biological 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 five 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 < 100 km 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 > 1000 km ² . Multiple includes headwaters, middle and large reaches.
Anthropogenic disturbance	low, medium-high	This factor was considered very general and did not distinguish specific types of disturbance (e.g. hydrological versus 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.
Taxonomic group	macroinvertebrates, fish, algae/macrophytes	

The variance of g was given by:

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

For non-replicated studies, where means and standard deviations were not available, we obtained effect sizes using $\log(PR/IR)$, known as the response ratio. Following Hedges et al. (1999; see also Eq. 4.30 and 4.31 in Borenstein et al. 2009), we also computed the response ratio for replicated studies for comparison with the non-replicated studies, but we did not include it in the estimation of weighted effect sizes.

Weighted mean effect size

We used random effects models in all cases because we assumed that the true effect sizes vary among studies (Borenstein et al. 2009). This assumption is justifiable as our meta-analysis included a wide variety of studies that, for example, investigated different organisms or were conducted using different sampling methods. Statistically, this choice of meta-analytic model consists in estimating 1) the between-studies variance (T^2 ; see Eq. 12.2, 12.3, 12.4 and 12.5 in Borenstein et al. 2009) and 2) the total variance ($V_i = V_g + T^2$) to 3) assign the weight of each study ($W_i = 1/V_i$). Model outputs included the weighted mean effect size (wES) and its confidence interval, and a test of the hypothesis that the true wES is zero, following standard methods described in Borenstein et al. (2009). We estimated wES for the entire dataset (e.g. considering all replicated data in the one random effects model) and for each of the subsets

of data separated by the six factors listed above (Table 1). For these subset analyses, the models were estimated without the intercept (Viechtbauer 2010). With this parameterization, a pooled value of T^2 was used, a procedure recommended by Borenstein et al. (2009) to increase the accuracy of the estimate of the between-studies variance.

We used a forest plot to illustrate the results of the meta-analysis. This plot shows the effect sizes and confidence intervals of each study and the wES (Gates 2002). A significant model (or a wES whose confidence interval does not include zero) indicates a significant difference between PR and IR biodiversity. The magnitude of the wES indicates the amount of difference between the two river types. Here, a positive wES indicates that biodiversity in PRs is higher than in IRs.

Publication bias

First, we visually assessed publication bias in the replicated studies using a funnel plot of effect size against a measure of study size or precision (e.g. the standard error of the effect size) (Sterne et al. 2011). Visually asymmetrical funnel plots usually indicate publication bias, whereas symmetrical ones indicate negligible publication bias. Second, we calculated the fail-safe number according to Orwin's equation (Orwin 1983), which gives the number of studies needed to reduce the average effect size to a pre-specified value, which is considered unimportant. We tested a range of values (with steps of 0.2) from 0.2 to 0.8 (corresponding, approximately, to half of the unweighted mean effect size). Third, we calculated the fail-safe number according to Rosenthal's approach ('file drawer analysis'). This indicates the number of missing studies (i.e. those unpublished or available but not captured by the literature search and selection process) needed to be

retrieved and incorporated in the analysis to eliminate bias (Borenstein et al. 2009). A high value indicates that a meta-analysis (i.e. estimated effect size) is robust to publication bias, given that we would need a large number of studies to nullify the effect size. Finally, as a sensitivity analysis, we applied the trim-and-fill method (Duval and Tweedie 2000a, b). This method estimates and adjusts meta-analysis results for the numbers and outcomes of missing studies.

We checked our meta-analysis against the quality criteria provided by Koricheva et al. (2013). We fulfilled all applicable criteria. We computed all statistics using the R ver. 3.3.1 (< www.r-project.org >) and the libraries metafor (Viechtbauer 2010) and rmeta (Lumley 2012).

Data deposition

Data available from the Dryad Digital Repository: < <http://dx.doi.org/10.5061/dryad.559cs> > (Soria et al. 2017).

Results

Overall differences between IRs and PRs

The overall meta-analysis revealed a statistically significant difference in PR and IR biodiversity (considering all replicate studies together), with a positive overall effect size ($wES = 0.879$, Table 2), thus indicating a significantly higher biodiversity in PRs than in IRs (Fig. 2). Positive effect sizes for the individual studies ranged from 0.01 to 7.95; negative effect sizes were smaller, ranging from -1.10 to -0.04 (Fig. 2). Accordingly, heterogeneity among

studies was highly significant ($Q = 89.317$, $df = 43$, $p < 0.0001$).

Log response ratios estimated for replicated (weighted mean effect size [$\log(PR/IR)$] = 0.38 ± 0.05 SE) and non-replicated (unweighted mean effect size [$\log(PR/IR)$] = 0.25 ± 0.08 SE) studies were also positive (Supplementary material Appendix 4). The majority of non-replicated studies had effect sizes located in the positive side of the forest plot (Supplementary material Appendix 4), again indicating that biodiversity in PRs was, in most cases, higher than in IRs.

Specific differences in biodiversity between IRs and PRs

For most levels of the six factors, wES was significantly positive (Table 2), indicating higher biodiversity in PRs than IRs. We detected differences between PR and IR biodiversity for studies conducted within arid (B), temperate (C), cold (D) or multiple climate zones; within studies that considered dry, wet, or multiple seasons; a multi-habitat sampling regime; samples from headwaters or multiple longitudinal zones; sites subject to low and medium-high levels of anthropogenic disturbance; and that included macroinvertebrates (Table 2). We found non-significant results for polar climates (E); riffle, pool, and stone habitats; middle reaches; fish, algae and macrophytes (Table 2).

Publication bias

Although the funnel plot visually approached asymmetry (Fig. 3a), fail-safe numbers and the sensitivity analysis indicated minimal bias. According to Orwin's method, even if

Table 2. Results of the random effects models for the overall design (with and without trim-and-fill) and for the levels of the six factors. Bold typeface indicates $p < 0.005$. n = number of studies considered in each level; wES = weighted mean effect size; SE = standard error of the estimates; $ci.lb$ and $ci.ub$ = confidence interval (lower and upper limits, respectively). See Table 1 for a description of 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	
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	
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	

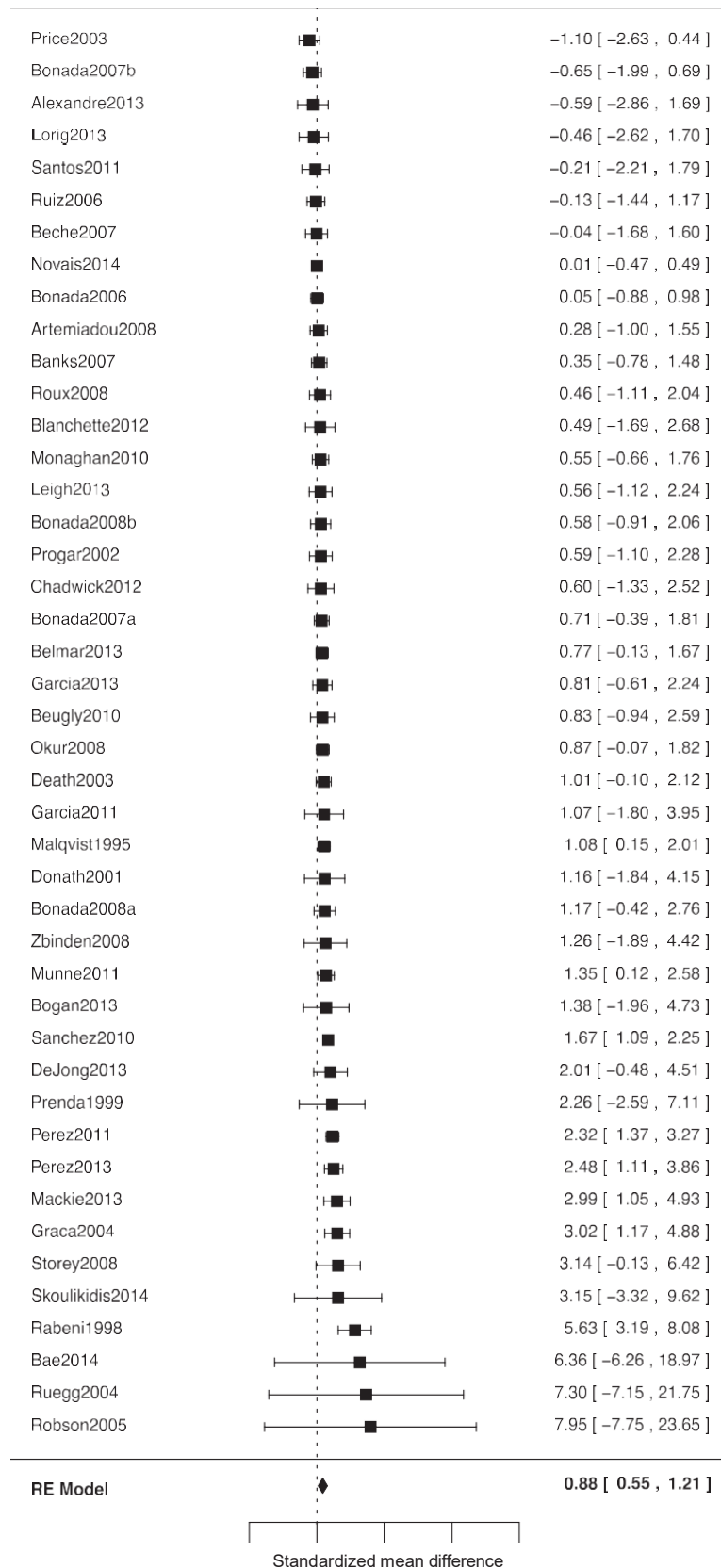


Figure 2. Forest plot for the overall design of the original model (without trim-and-fill) considering the 44 replicated studies ordered by increasing effect size from the top to the bottom. Each study is indicated in the left column with the first author and the year of publication (see Supplementary material 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.

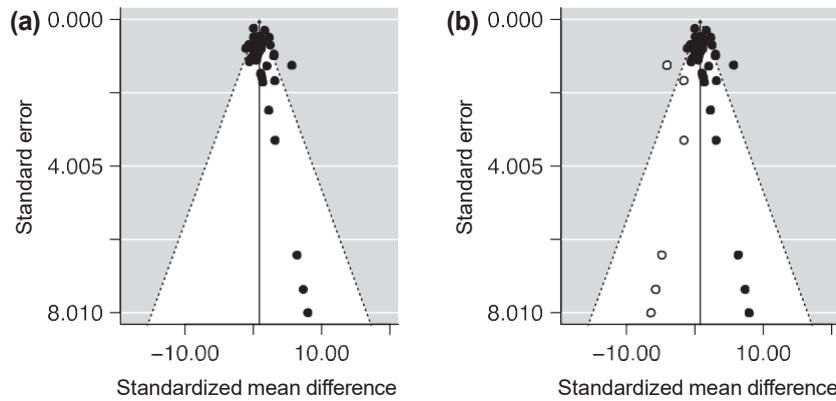


Figure 3. Funnel plots for the overall design using replicated studies without and with trim-and-fill, (a) and (b) panels, respectively. Filled circles represent the individual replicated studies, whereas open circles represent the missing studies required to produce a symmetrical plot.

a substantial effect size (0.8) is conservatively assumed as unimportant, a large number of unpublished studies would still be needed (Orwin's fail safe $N = 38$ studies) with no differences between the types of rivers for the estimated effect size to be reduced to an 'unimportant' value. As expected, this number increases substantially when lower effect sizes (i.e. 0.6, 0.4 and 0.2) are used in Orwin's equation (Orwin's fail safe $N = 67, 124$ and 295 , respectively). According to Rosenthal's approach, the fail-safe number was 1352, suggesting that a large number of studies with non-significant differences between types of rivers would be needed to reverse the conclusion that PRs were more biodiverse than IRs. According to the trim and fill approach, only six studies were potentially missing from our analysis that if present would produce a symmetrical funnel plot (Fig. 3b). The wES estimated by this method was similar to the one reported above (trim and fill wES = 0.776 ± 0.178 ; 95% CI = 0.427 to 1.125).

Discussion

The studies analysed here compared biodiversity in PRs and IRs across a wide range of environmental conditions. We found a significantly higher biodiversity in PRs than in IRs, which confirmed our primary hypothesis. This finding agrees with individual studies showing that PRs are more species-rich than IRs and that flow intermittence is a disturbance that constrains aquatic biodiversity (Del Rosario and Resh 2000, Storey and Quinn 2008, Bogan et al. 2013). However, several individual studies included in our meta-analysis found similar values of biodiversity in PRs and IRs; in these cases, the characteristic taxa found in IRs during the dry period compensated for the loss of taxa present during flow (Miller and Golladay 1996, Casas and Langton 2008, Santos and Stevenson 2011). Few of the studies analysed here had higher biodiversity in IRs than in PRs (Price et al. 2003, Bonada et al. 2007a, Alexandre et al. 2013). The persistence of isolated pools during the dry season in IRs, which favours the presence of a wide variety of species found exclusively in lentic waters and/or that prefer such habitat, may have increased IR biodiversity in these cases (Bonada et al. 2006a).

Although we found overall support for the hypothesis that PR biodiversity is higher than IR biodiversity, IRs occur throughout the globe, including many in regions in Africa, Asia or South America not covered by our meta-analysis (Datry et al. 2016a, Leigh et al. 2016a). In addition, most of the papers analysed here consider the most commonly studied taxonomic groups in river ecology (i.e. macroinvertebrates, fish, algae and macrophytes); no papers examining other highly diverse groups such as microbes (Palmer et al. 2000) fulfilled our selection criteria. To increase the robustness of our meta-analysis, there is a need for future research on studies comparing PRs and IRs biodiversity in regions beyond those included here and across a wider variety of taxonomic groups. This would provide a more comprehensive view of the effects of flow intermittence on aquatic biodiversity and the potential effects of current and future global change.

Our finding that PR biodiversity was higher than IR biodiversity within cold, arid and temperate (which includes Mediterranean) climates agrees with several studies from arid (Beugly and Pyron 2010, Leigh 2013, De Jong et al. 2013) and Mediterranean-temperate regions (Progar and Moldenke 2002, Roux et al. 2008, Storey and Quinn 2008). Flow predictability, which is related to climate predictability, plays an important role in shaping species adaptations and thus biodiversity (Lytle and Poff 2004); highly predictable environments (e.g. in predictably seasonal Mediterranean-climate regions) are considered to support higher biodiversity than less predictable ones. However, despite dry riverbeds providing habitat and refuge for terrestrial organisms (Steward et al. 2012, Corti et al. 2013, Corti and Datry 2016) and their disconnected pools acting as refuges for aquatic organisms (Bonada et al. 2007a, b, Sheldon et al. 2010, Datry et al. 2014a), flow intermittence is a strong disturbance even in predictable climates (Datry et al. 2014b, Leigh and Datry 2016). Indeed, although some aquatic organisms have traits to cope with flow intermittence (Bêche et al. 2006, Bonada et al. 2008, Blanchette and Pearson 2012), resistance traits acquired through evolution as a response to drying are much less frequent than resilience traits in IRs (Datry et al. 2014b, Leigh et al. 2016a, Vander Vorste et al. 2016), which would explain our overall result. Of particular concern is our

finding of comparatively low biodiversity in arid-zone IRs given aridity is projected to increase in several regions of the world (e.g. the already arid southwest region of USA; Seager et al. 2013).

Our results do not support the view that differences in biodiversity between PRs and IRs are negligible during the wet season. However, despite the low number of studies considered, we did find support for the hypothesis that biodiversity in PRs is higher than in IRs during the dry season. In this latter case, the low habitat availability in IRs compared to PRs will reduce biodiversity unless isolated pools remain for long periods allowing many species to colonize and increase community variability among pools within reaches (Bonada et al. 2006a, Leigh and Sheldon 2009). By contrast, during the wet season, despite IRs having similar habitat availability as PRs, some studies have also shown that biodiversity may remain relatively low in IRs because fewer species may be available and able to colonize these habitats and/or because of alterations to food web structure and dimensions (Datry 2012, McHugh et al. 2015).

Aquatic organisms (i.e. macroinvertebrate, fish, algae and macrophytes) have adaptations to particular instream habitats, from riffles to pools (Bonada et al. 2006a, 2008, Dallas 2007). Most likely due to the small number of studies in the subsets, our hypothesis regarding habitat (i.e. biodiversity in PR riffles may be higher than in IR riffles, whereas the opposite pattern may be observed in pools) was not supported. However, studies sampling multiple habitats showed a higher biodiversity in PRs than in IRs, which agrees with findings from Graça et al. (2004), Belmar et al. (2013) and Leigh et al. (2013a). Multi-habitat sampling may be a better method to account for biodiversity of rivers (Leitão et al. 2014) because species characteristic of individual habitats may not occur across all habitat types (Bonada et al. 2006b, Cid et al. 2016).

The aquatic biodiversity of a particular reach not only depends on instream habitat characteristics, but also on the regional biodiversity and the balance between dispersal and abiotic/biotic factors. The river network structure plays an essential role for the dispersion of aquatic organisms and thus helps determine aquatic biodiversity patterns (Altermatt 2013). In PRs, biodiversity in lowland reaches is driven by mass effects whereas abiotic/biotic factors are considered more important in their headwaters (Brown and Swan 2010). In IRs, the relative role of dispersal versus abiotic/biotic factors depends not only on the hydrological phase of the reach (i.e. flowing, non-flowing, dry) but also on where the drying event occurs along the river network (Datry et al. 2014b, 2016c, d). We were unable to test how different configurations of drying events affect aquatic biodiversity but, although more studies are needed for middle reaches, our results on longitudinal zonation agreed with our initial hypothesis. Flow and river characteristics change with longitudinal zonation and, according to the River continuum concept, alpha-diversity is expected to peak at middle reaches (Vannote et al. 1980, Finn et al. 2011). Indeed, the low alpha biodiversity in headwaters and their high isolation make them highly vulnerable to biodiversity loss by flow intermittence and hampers recolonization after flow resumption unless communities in IR headwaters are dominated by resistance strategies to

drying (Datry et al. 2014b, 2016a). In contrast, middle reaches have higher alpha biodiversity and less isolation (Finn et al. 2011), resulting in no differences between PRs and IRs. On the other hand, headwaters make up a large proportion of all river networks (Naiman 1983, Benda et al. 2005) and the studies included in our analyses that were conducted in multiple reaches also included a higher proportion of headwater sites, supporting the hypothesis that PRs have a higher biodiversity than IRs when examined across multiple reaches (i.e. at large spatial scales). We suggest, however, that these interpretations should be viewed with caution due to the small number of studies in middle reaches.

Anthropogenic disturbances often decrease biodiversity by homogenising communities (Rahel 2002). Despite this, we found higher biodiversity in PRs than in IRs regardless of the level of anthropogenic disturbance (i.e. low or medium-high). We acknowledge, however, that our categorization of anthropogenic disturbances was coarse and more studies comparing biodiversity in PRs and IRs under more explicit and different disturbance categories are needed. The effect of anthropogenic disturbances on IRs is a relatively novel topic that is being considered in terms of management and conservation of river ecosystems (Skoulikidis et al. 2017). Current bioassessment methods are designed to detect the impacts of anthropogenic disturbances (Bonada et al. 2006b) but typically fail when applied to IRs. This means that the lower biodiversity of IRs compared to PRs cannot simply be interpreted as indicative of anthropogenic impairment. New methods for IR bioassessment must be designed that can disentangle natural from anthropogenic disturbances (Prat et al. 2004, Leigh et al. 2013b).

Biodiversity has been related to ecosystem resilience (defined by Holling 1973, “as the magnitude of disturbance that a system can experience before it shifts into a different state”), however, there is uncertainty about how ecosystem resilience will respond to increases in levels of anthropogenic disturbance and consequent impacts on biodiversity (Steffen et al. 2004). Walker and Meyers (2004) suggested that ecosystems might respond gradually to biodiversity loss, whereas Gunderson and Pritchard (2002) suggested that ecosystems will respond strongly, because crossing the threshold of biodiversity loss will produce sudden and dramatic changes in the responding state factors. Indeed, higher numbers of species are expected to increase the ability to recover from disturbances (Holling 1978, Folke et al. 2004). If IRs have significantly lower biodiversity than PRs, as found by us, ecosystem resilience could be affected. However, IR taxa have particular adaptations for surviving and recovering from drying (Lake 2011, Blanchette and Pearson 2012, Leigh et al. 2016b), which may help to mitigate the effects of future co-occurring disturbances (Mori et al. 2013, Vander Vorste et al. 2016). Although a growing number of studies on IRs consider ecosystem resilience (e.g. using functional characteristics of species; Bruno et al. 2016, Vander Vorste et al. 2016), the ecosystem effects of biodiversity loss in these systems needs to be investigated.

As a result of global change, extreme climatic events are expected to increase in frequency and intensity, with an increase in drying frequency, duration, and/or intensity in

many regions (Beniston et al. 2007, Palmer et al. 2008, Döll and Schmied 2012). Some regions will experience shifts from PRs to IRs, whereas other regions will show the contrary pattern (Döll and Schmied 2012). If these hydrological regime shifts occur faster than the evolutionary scale at which species acquire adaptive traits (Filipe et al. 2013), dramatic effects on aquatic biodiversity and ecosystem processes and services will result (Datry et al. 2014a, IPCC 2014, Ledger and Milner 2015). In regions where PRs will shift to IRs, loss of species poorly adapted to dry conditions can be expected (Phillipsen and Lytle 2013, Jaeger et al. 2014). Our findings suggest such losses may be particularly relevant for certain taxonomic groups (i.e. macroinvertebrates) and under particular environmental conditions or in certain regions (e.g. in arid and temperate climate zones, and in headwaters). However, IRs communities of species with strong dispersal capacity and high fecundity may be minimally affected and able to colonize these novel IRs (Arscott et al. 2010, Datry et al. 2014a, b). In regions where IRs will shift to PRs, the expected increase in biodiversity in these novel PRs will ultimately depend on the connectivity to other PRs. PRs highly connected to novel PRs might maintain biodiversity, whereas the biodiversity in of highly isolated PRs may decline. As highly dynamic metacommunities are expected to dominate in this future scenario of IRs shifting to PRs and vice versa (Datry et al. 2016b), conservation efforts to reduce the risk of undesired hydrological regime shifts should be prioritized to avoid effects on ecosystem resilience (Folke et al. 2004) and could be targeted towards those environmental conditions or taxonomic groups with significant differences between PR and IR biodiversity.

Acknowledgements – We thank all authors that provided original data: Antoni Munné, María del Mar Sánchez, Esther Mas-Martí and Oscar Belmar.

Funding – This work is one aspect of the international research project “Intermittent River Biodiversity Analysis and Synthesis” (IRBAS, irbas.cesab.org). The IRBAS research project is supported by the Center for Synthesis and Analysis of Biodiversity (CESAB), which is funded jointly by the French Foundation for Research on Biodiversity (FRB) and the French National Agency for Water and Aquatic Environments (ONEMA). Financial support was received from the Centre for Synthesis and Analysis of Biodiversity (CESAB) and the Intermittent River Biodiversity Analysis and Synthesis working group (IRBAS).

References

- Acuña, V. et al. 2014. Why should we care about temporary waterways? – *Science* 343: 1080–1081.
- Alexandre, C. M. et al. 2013. Fish assemblages in non-regulated and regulated rivers from permanent and temporary Iberian systems. – *River Res. Appl.* 29: 1042–1058.
- Altermatt, F. 2013. Diversity in riverine metacommunities: a network perspective. – *Aquat. Ecol.* 47: 365–377.
- Arscott, D. B. et al. 2010. Aquatic invertebrate community structure along an intermittence gradient: Selwyn River, New Zealand. – *J. N. Am. Benthol. Soc.* 29: 530–545.
- Barlow, J. et al. 2016. Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. – *Nature* 535: 144–147.
- Bêche, L. A. et al. 2006. Long-term seasonal variation in the biological traits of benthic-macroinvertebrates in two Mediterranean-climate streams in California, USA. – *Freshwater Biol.* 51: 56–75.
- Belmar, O. et al. 2013. The influence of natural flow regimes on macroinvertebrate assemblages in a semiarid Mediterranean basin. – *Ecohydrology* 6: 363–379.
- Benda, L. et al. 2005. Geomorphology of steep-land headwaters: the transition from hillslopes to channels. – *J. Am. Water Resour. Assoc.* 41: 835–851.
- Beniston, M. et al. 2007. Future extreme events in European climate: an exploration of regional climate model projections. – *Climatic Change* 81: 71–95.
- Beugly, J. and Pyron, M. 2010. Variation in fish and macroinvertebrate assemblages among seasonal and perennial headwater streams. – *Am. Midl. Nat.* 163: 2–13.
- Blanchette, M. L. and Pearson, R. G. 2012. Macroinvertebrate assemblages in rivers of the Australian dry tropics are highly variable. – *Freshwater Sci.* 31: 865–881.
- Boersma, K. S. et al. 2014. Invertebrate assemblages of pools in arid-land streams have high functional redundancy and are resistant to severe drying. – *Freshwater Biol.* 59: 491–501.
- Bogan, M. T. et al. 2013. Flow intermittency alters longitudinal patterns of invertebrate diversity and assemblage composition in an arid-land stream network. – *Freshwater Biol.* 58: 1016–1028.
- Bonada, N. and Resh, V. H. 2013. Mediterranean-climate streams and rivers: geographically separated but ecological comparable freshwater systems. – *Hydrobiologia* 719: 1–29.
- Bonada, N. et al. 2006a. Benthic macroinvertebrate assemblages and macrohabitat connectivity in Mediterranean-climate streams of northern California. – *J. N. Am. Benthol. Soc.* 25: 32–43.
- Bonada, N. et al. 2006b. Developments in aquatic insect biomonitoring: a comparative analysis of recent approaches. – *Annu. Rev. Entomol.* 51: 495–523.
- Bonada, N. et al. 2007a. Taxonomic and biological trait differences of stream macroinvertebrate communities between Mediterranean and temperate regions: implications for future climatic scenarios. – *Global Change Biol.* 13: 1658–1671.
- Bonada, N. et al. 2007b. Macroinvertebrate community structure and biological traits related to flow permanence in a Mediterranean river network. – *Hydrobiologia* 589: 91–106.
- Bonada, N. et al. 2008. Multi-scale assessment of macroinvertebrate richness and composition in Mediterranean-climate rivers. – *Freshwater Biol.* 53: 772–788.
- Borenstein, M. et al. 2009. Introduction to meta-analysis. – Wiley.
- Boulton, A. J. 2003. Parallels and contrasts in the effects of drought on stream macroinvertebrate assemblages. – *Freshwater Biol.* 48: 1173–1185.
- Brown, B. L. and Swan, C. M. 2010. Dendritic network structure constrains metacommunity properties in riverine ecosystems. – *J. Animal Ecol.* 79: 571–580.
- Brunbjerg, A. K. et al. 2015. Disturbance in dry coastal dunes in Denmark promotes diversity of plants and arthropods. – *Biol. Conserv.* 182: 243–253.
- Bruno, D. et al. 2016. Impacts of environmental filters on functional redundancy in riparian vegetation. – *J. Appl. Ecol.* 53: 846–855.
- Casas, J. J. and Langton, P. H. 2008. Chironomid species richness of a permanent and a temporary Mediterranean stream: a long-term comparative study. – *J. N. Am. Benthol. Soc.* 27: 746–759.
- Cid, N. et al. 2016. A biological tool to assess flow connectivity in reference temporary streams from the Mediterranean Basin. – *Sci. Total Environ.* 540: 178–190.

- Clements, F. E. 1916. Plant succession: an analysis of the development of vegetation. – Carnegie Inst. of Washington.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. – *Science* 199: 1302–1310.
- Corti, R. and Datry, T. 2016. Terrestrial and aquatic invertebrates in the riverbed of an intermittent river: parallels and contrasts in community organisation. – *Freshwater Biol.* 61: 1308–1320.
- Corti, R. et al. 2013. A comparison of pitfall-trap and quadrat methods for sampling ground-dwelling invertebrates in dry riverbeds. – *Hydrobiologia* 717: 13–26.
- Dallas, H. F. 2007. The influence of biotope availability on macroinvertebrate assemblages in South African rivers: implications for aquatic bioassessment. – *Freshwater Biol.* 52: 370–380.
- Datry, T. 2012. Benthic and hyporheic invertebrate assemblages along a flow intermittence gradient: effects of duration of dry events. – *Freshwater Biol.* 57: 563–574.
- Datry, T. et al. 2007. Responses of hyporheic invertebrate assemblages to large-scale variation in flow permanence and surface–subsurface exchange. – *Freshwater Biol.* 52: 1452–1462.
- Datry, T. et al. 2011. Recent perspectives on temporary river ecology. – *Aquat. Sci.* 73: 453–457.
- Datry, T. et al. 2014a. Intermittent rivers: a challenge for freshwater ecology. – *Bioscience* 64: 229–235.
- Datry, T. et al. 2014b. Broad-scale patterns of invertebrate richness and community composition in temporary rivers: effects of flow intermittence. – *Ecography* 37: 94–104.
- Datry, T. et al. 2016a. Challenges, developments and perspectives in intermittent river ecology. – *Freshwater Biol.* 61: 1171–1180.
- Datry, T. et al. 2016b. Towards understanding the organisation of metacommunities in highly dynamic ecological systems. – *Oikos* 125: 149–159.
- Datry, T. et al. 2016c. Determinants of local and regional communities in intermittent and perennial headwaters of the Bolivian Amazon. – *Freshwater Biol.* 61: 1335–1349.
- Datry, T. et al. 2016d. Metacommunity patterns across three Neotropical catchments with varying environmental harshness. – *Freshwater Biol.* 61: 277–292.
- De Jong, G. D. et al. 2013. Riffle beetle communities of perennial and intermittent streams in northern Nevada, USA, with a new state record for *Optioservus castaneipennis* (Fall) (Coleoptera: Elmidae). – *Coleopts. Bull.* 67: 293–301.
- Del Rosario, R. B. and Resh, V. H. 2000. Invertebrates in intermittent and perennial streams: is the hyporheic zone a refuge from drying? – *J. N. Am. Benthol. Soc.* 19: 680–696.
- Delucchi, C. M. 1988. Comparison of community structure among streams with different temporal flow regimes. – *Can. J. Zool.* 66: 579–586.
- Dieterich, M. and Anderson, N. H. 2000. The invertebrate fauna of summer-dry streams in western Oregon. – *Fundam. Appl. Limnol.* 147: 273–295.
- Döll, P. and Schmied, H. M. 2012. How is the impact of climate change on river flow regimes related to the impact on mean annual runoff? A global-scale analysis. – *Environ. Res. Lett.* 7: 14–37.
- Dornelas, M. 2010. Disturbance and change in biodiversity. – *Phil. Trans. R. Soc. B.* 365: 3719–3727.
- Duval, S. and Tweedie, R. 2000a. A nonparametric “trim and fill” method of accounting for publication bias in meta-analysis. – *J. Am. Stat. Assoc.* 95: 89–98.
- Duval, S. and Tweedie, R. 2000b. Trim and fill: a simple funnel-plot-based method of testing and adjusting for publication bias in meta-analysis. – *Biometrics* 56: 455–463.
- Filipe, A. F. et al. 2013. Vulnerability of stream biota to climate change in Mediterranean-climate regions: a synthesis of ecological responses and conservation challenges. – *Hydrobiologia* 719: 331–351.
- Finn, D. S. et al. 2011. Small but mighty: headwaters are vital to stream network biodiversity at two levels of organization. – *J. N. Am. Benthol. Soc.* 30: 963–980.
- Folke, C. et al. 2004. Regime Shifts, resilience, and biodiversity in ecosystem management. – *Annu. Rev. Ecol. Evol. Syst.* 35: 557–581.
- Fox, J. W. 2013. The intermediate disturbance hypothesis should be abandoned. – *Trends Ecol. Evol.* 28: 86–92.
- Fritz, K. M. and Dodds, W. K. 2002. Macroinvertebrate assemblage structure across a tallgrass prairie stream landscape. – *Fundam. Appl. Limnol.* 154: 79–102.
- García-Roger, E. et al. 2011. Do seasonal changes in habitat features influence aquatic macroinvertebrate assemblages in perennial versus temporary Mediterranean streams? – *Aquatic Sci.* 73: 567–579.
- García-Roger, E. et al. 2013. Spatial scale effects on taxonomic and biological trait diversity of aquatic macroinvertebrates in Mediterranean streams. – *Fundam. Appl. Limnol.* 183: 89–105.
- Gates, S. 2002. Review of methodology of quantitative reviews using meta-analysis in ecology. – *J. Anim. Ecol.* 71: 547–557.
- Giller, P. S. 1996. Floods and droughts: the effects of variations in water flow on streams and rivers. – In: Giller, P. S. and Myers, A. A. (eds), *Disturbance and recovery of ecological systems*. R. Irish Acad., pp. 1–19.
- Graça, M. A. et al. 2004. Factors affecting macroinvertebrate richness and diversity in Portuguese streams: a two-scale analysis. – *Int. Rev. Hydrobiol.* 89: 151–164.
- Graham, N. A. J. et al. 2009. Coral mortality versus structural collapse as drivers of corallivorous butterflyfish decline. – *Biodivers. Conserv.* 18: 3325–3336.
- Grubbs, S. A. 2011. Influence of flow permanence on headwater macroinvertebrate communities in a Cumberland Plateau watershed, USA. – *Aquat. Ecol.* 45: 185–195.
- Gunderson, L. H. and Pritchard, L. 2002. Resilience and the behavior of large-scale ecosystems. – Island Press.
- Hedges, L. V. et al. 1999. The meta-analysis of response ratios in experimental ecology. – *Ecology* 80: 1150–1156.
- Holling, C. S. 1973. Resilience and stability of ecological systems. – *Annu. Rev. Ecol. Syst.* 4: 1–23.
- Holling, C. S. 1978. The spruce-budworm/forest management problem. – In: Holling, C. S. (ed.), *Adaptive environmental assessment and management*. Wiley, pp. 143–182.
- Hooper, D. U. et al. 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. – *Nature* 486: 105–108.
- Horner-Devine, M. C. et al. 2004. An ecological perspective on bacterial biodiversity. – *Proc. R. Soc. B* 271: 113–122.
- Hughes, A. R. et al. 2007. Reciprocal relationships and potential feedbacks between biodiversity and disturbance. – *Ecol. Lett.* 10: 849–864.
- Huston, M. 1979. A general hypothesis of species diversity. – *Am. Nat.* 113: 81–101.
- IPCC 2014. Climate Change 2014. Part A. Global and sectoral aspects. Contribution of working group II to the fifth assessment report of the intergovernmental panel on climate change – In: Field C. B. et al. (eds), *Climate Change 2014: impacts, adaptation and vulnerability*. Cambridge Univ. Press, pp. 1–1132.
- Jaeger, K. L. et al. 2014. Climate change poised to threaten hydrologic connectivity and endemic fishes in dryland streams. – *Proc. Natl Acad. Sci. USA* 111: 13686–13687.
- Junk, W. J. et al. 1989. The flood pulse concept in river-floodplain systems. – In: Dodge, D. P. (ed.), *Proceedings of the international large river symposium*. Can. Spec. Publ. Fish. Aquat. Sci. pp. 110–127.
- Koricheva, J. et al. 2013. Handbook of meta-analysis in ecology and evolution. – Princeton Univ. Press.

- Lake, P. S. et al. 2000. Global change and the biodiversity of freshwater ecosystems: impacts on linkages between above-sediment and sediment biota. – *BioScience* 50: 1099–1107.
- Lake, P. S. et al. 2007. Linking ecological theory with stream restoration. – *Freshwater Biol.* 52: 597–615.
- Lake, P. S. 2011. Drought and aquatic ecosystems: effects and responses. – Wiley-Blackwell.
- Lange, K. et al. 2016. A trait-based framework for stream algal communities. – *Ecol. Evol.* 6: 23–36.
- Ledger, M. E. and Milner, A. M. 2015. Extreme events in running waters. – *Freshwater Biol.* 60: 2455–2460.
- Leigh, C. 2013. Dry season changes in macroinvertebrate assemblages of highly seasonal rivers: responses to low flow, no flow and antecedent hydrology. – *Hydrobiologia* 703: 95–112.
- Leigh, C. and Sheldon, F. 2009. Hydrological connectivity drives patterns of macroinvertebrate biodiversity in floodplain rivers of the Australian wet/dry tropics. – *Freshwater Biol.* 54: 549–571.
- Leigh, C. and Datry, T. 2016. Drying as a primary hydrological determinant of biodiversity in river systems: a broad-scale analysis. – *Ecography* 39: 1–13.
- Leigh, C. et al. 2013a. High potential subsidy of dry-season aquatic fauna to consumers in riparian zones of wet–dry tropical rivers. – *Inland Waters* 3: 411–420.
- Leigh, C. et al. 2013b. Hyporheic invertebrates as bioindicators of ecological health in temporary rivers: a meta-analysis. – *Ecol. Indic.* 32: 62–73.
- Leigh, C. et al. 2016a. Ecological research and management of intermittent rivers: an historical review and future directions. – *Freshwater Biol.* 61: 1181–1199.
- Leigh, C. et al. 2016b. Invertebrate assemblage responses and the dual roles of resistance and resilience to drying in intermittent rivers. – *Aquatic Sci.* 78: 291–301.
- Leitão, F. et al. 2014. Habitat-oriented sampling of macroinvertebrates affects the determination of ecological status in temporary Mediterranean river systems. – *River Res. Appl.* 30: 1233–1247.
- Loreau, M. et al. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. – *Science* 26: 804–808.
- Lytle, D. A. and Poff, N. L. 2004. Adaptation to natural flow regimes. – *Trends Ecol. Evol.* 19: 94–100.
- Lumley, T. 2012. Rmeta: meta-analysis. – R package ver. 2.16. <<https://CRAN.R-project.org/package=rmeta>>.
- Miller, A. M. and Golladay, S. W. 1996. Effects of spates and drying on macroinvertebrate assemblages of an intermittent and a perennial prairie stream. – *J. N. Am. Benthol. Soc.* 14: 670–689.
- Mori, A. S. et al. 2013. Response diversity determines the resilience of ecosystems to environmental change. – *Biol. Rev.* 88: 349–364.
- Munné, A. and Prat, N. 2011. Effects of Mediterranean-climate annual variability on stream biological quality assessment using macroinvertebrate communities. – *Ecol. Indic.* 11: 651–662.
- McHugh, P. A. et al. 2015. Habitat size influences food web structure in drying streams. – *Ecography* 38: 700–712.
- Naiman, R. J. 1983. The annual pattern and spatial distribution of aquatic oxygen metabolism in boreal forest watersheds. – *Ecol. Monogr.* 53: 73–94.
- Orwin, R. G. 1983. A fail-safe N for effect size in meta-analysis. – *J. Educ. Stat.* 8: 157–159.
- Palmer, M. A. et al. 2000. Linkages between aquatic sediment biota and life above sediments as potential drivers of biodiversity and ecological processes. – *BioScience* 50: 1062–1075.
- Palmer, M. A. et al. 2008. Climate change and the world's river basins: anticipating management options. – *Front. Ecol. Environ.* 6: 81–89.
- Peel, M. C. et al. 2007. Updated world map of the Köppen–Geiger climate classification. – *Hydrol. Earth Syst. Sci.* 11: 1633–1644.
- Phillipsen, I. C. and Lytle, D. A. 2013. Aquatic insects in a sea of desert: population genetic structure is shaped by limited dispersal in a naturally fragmented landscape. – *Ecography* 36: 731–743.
- Pianka, E. R. 1966. Latitudinal gradients in species diversity: a review of concepts. – *Am. Nat.* 100: 33–46.
- Poff, N. L. et al. 1997. The natural flow regime. – *BioScience* 47: 769–784.
- Prat, N. et al. 2004. The mirage toolbox: an integrated assessment tool for temporary streams. – *River Res. Appl.* 30: 1318–1334.
- Price, K. et al. 2003. Communities of aquatic insects of old-growth and clearcut coastal headwater streams of varying flow persistence. – *Can. J. For. Res.* 33: 1416–1432.
- Progar, R. A. and Moldenke, A. R. 2002. Insect production from temporary and perennially flowing headwater streams in western Oregon. – *J. Freshwater Ecol.* 17: 391–407.
- Rahel, F. J. 2002. Homogenization of freshwater faunas. – *Annu. Rev. Ecol. Syst.* 33: 291–315.
- Reich, P. and Lake, P. S. 2015. Extreme hydrological events and the ecological restoration of flowing waters. – *Freshwater Biol.* 60: 2639–2652.
- Resh, V. et al. 1988. The role of disturbance in stream ecology. – *J. N. Am. Benthol. Soc.* 7: 433–455.
- Rosenberg, M. S. et al. 2000. MetaWin: statistical software for meta-analysis: ver. 2.0. – Sinauer Assoc.
- Roux, D. J. et al. 2008. Designing protected areas to conserve riverine biodiversity: Lessons from a hypothetical redesign of the Kruger National Park. – *Biol. Conserv.* 141: 100–117.
- Santos, A. N. and Stevenson, R. D. 2011. Comparison of macroinvertebrate diversity and community structure among perennial and non-perennial headwater streams. – *Northeast. Nat.* 18: 7–26.
- Scheiner, S. M. and Gurevitch, J. 2001. Design and analysis of ecological experiments, 2nd edn. – Oxford Univ. Press.
- Seager, R. M. et al. 2013. Projections of declining surface-water availability for the southwestern United States. – *Nat. Clim. Change* 3: 482–486.
- Sheldon, F. et al. 2010. Ecological roles and threats to aquatic refugia in arid landscapes: dryland river waterholes. – *Mar. Freshwater Res.* 61: 885–895.
- Skoulikidis, N. T. et al. 2017. Non-perennial Mediterranean rivers in Europe: status, pressures, and challenges for research and management. – *Sci. Total Environ.* 577: 1–18.
- Soria, M. et al. 2017. Data from: Biodiversity in perennial and intermittent rivers: a meta-analysis. – Dryad Digital Repository, <<http://dx.doi.org/10.5061/dryad.559cs>>.
- Stanley, E. H. et al. 1997. Ecosystem expansion and contraction in streams. – *BioScience* 47: 427–435.
- Steffen, W. et al. 2004. Global change and the earth system: a planet under pressure. – Springer.
- Sterne, J. A. et al. 2011. Recommendations for examining and interpreting funnel plot asymmetry in meta-analyses of randomised controlled trials. – *BMJ* 342: d4002.
- Steward, A. L. et al. 2012. When the river runs dry: human and ecological values of dry riverbeds. – *Front. Ecol. Environ.* 10: 202–209.
- Storey, R. G. and Quinn, J. M. 2008. Composition and temporal changes in macroinvertebrate communities of intermittent streams in Hawke's Bay, New Zealand. – *N. Z. J. Mar. Freshwater Res.* 42: 109–125.

- Tachet, H. et al. 2002. Invertebrés d'eau douce (2nd corrected impression). – CNRS editions.
- Thom, D. and Seidl, R. 2015. Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal forests. – *Biol. Rev.* 91: 760–781.
- Vander Vorste, R. V. et al. 2016. Invertebrate communities in gravel-bed, braided rivers are highly resilient to flow intermittence. – *Freshwater Sci.* 35: 164–177.
- Vannote, R. L. et al. 1980. The river continuum concept. – *Can. J. Fish. Aquat. Sci.* 37: 130–137.
- Viechtbauer, W. 2010. Conducting meta-analyses in R with the metaphor package. – *J. Stat. Softw.* 36: 1–48.
- Walker, B. H. and Meyers, J. A. 2004. Thresholds in ecological and social-ecological systems: a developing database. – *Ecol. Soc.* 9: 3.
- Ward, J. V. and Stanford, J. A. 1995. Ecological connectivity in alluvial river ecosystems and its disruption by flow regulation. – *Regul. Rivers Res. Manage.* 11: 105–119.
- Wardle, D. A. et al. 2011. Terrestrial ecosystem responses to species gains and losses. – *Science* 332: 1273–1277.
- Williams, D. 1996. Environmental constraints in temporary fresh waters and their consequences for the insect fauna. – *J. N. Am. Benthol. Soc.* 15: 634–650.

Supplementary material (available online as Appendix oik-04118 at < www.oikosjournal.org/appendix/oik-04118 >). Appendix 1–4.