



HAL
open science

Drying as a primary hydrological determinant of biodiversity in river systems: a broad-scale analysis

C. Leigh, T. Datry

► **To cite this version:**

C. Leigh, T. Datry. Drying as a primary hydrological determinant of biodiversity in river systems: a broad-scale analysis. *Ecography*, 2017, 40 (4), pp.487-499. 10.1111/ecog.02230 . hal-02604737

HAL Id: hal-02604737

<https://hal.inrae.fr/hal-02604737v1>

Submitted on 16 Aug 2024

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Queensland University of Technology
Brisbane Australia

This may be the author's version of a work that was submitted/accepted for publication in the following source:

[Leigh, Catherine](#) & Datry, Thibault
(2017)

Drying as a primary hydrological determinant of biodiversity in river systems: a broad-scale analysis.

Ecography, 40(4), pp. 487-499.

This file was downloaded from: <https://eprints.qut.edu.au/119724/>

© Consult author(s) regarding copyright matters

This work is covered by copyright. Unless the document is being made available under a Creative Commons Licence, you must assume that re-use is limited to personal use and that permission from the copyright owner must be obtained for all other uses. If the document is available under a Creative Commons License (or other specified license) then refer to the Licence for details of permitted re-use. It is a condition of access that users recognise and abide by the legal requirements associated with these rights. If you believe that this work infringes copyright please provide details by email to qut.copyright@qut.edu.au

Notice: *Please note that this document may not be the Version of Record (i.e. published version) of the work. Author manuscript versions (as Submitted for peer review or as Accepted for publication after peer review) can be identified by an absence of publisher branding and/or typeset appearance. If there is any doubt, please refer to the published source.*

<https://doi.org/10.1111/ecog.02230>

Drying as a primary hydrological determinant of biodiversity in river systems: a broad-scale analysis

Authors

Catherine Leigh^{1,2,†*} and Thibault Datry^{1,3}

¹ Irstea, UR MALY, Centre de Lyon-Villeurbanne, Villeurbanne Cedex, France

² CESAB-FRB, Immeuble Henri Poincare, Aix-en-Provence Cedex, France

³ UMR “BOREA” CNRS 7208/IRD 207/MNHN/UPMC, DMPA, Museum National d’Histoire Naturelle, Paris Cedex, France

†Present address: Australian Rivers Institute, Griffith University, 170 Kessels Road, Nathan 4111, Queensland, Australia

* Corresponding author: catherine.leigh@irstea.fr

Abstract

Determining and understanding relationships between biodiversity and hydrology is a critical goal in ecology, particularly given biodiversity in the freshwater realm is in crisis. Despite the prevalence of rivers experiencing natural drying disturbances (which we collectively refer to as intermittent rivers), and projections of increased frequency and duration of drying events, the importance of drying relative to other flow-related determinants of river biodiversity remains understudied. We assessed the influence of drying on alpha- and beta-diversity using

discharge and macroinvertebrate data collated from Australia and southwest Europe over broad spatial and temporal scales, providing information on current and past drying events, and combining a wide variety of flow metrics. We found clear evidence that drying acts as a strong environmental filter and is a primary hydrological determinant of alpha-diversity; even when considering both intermittent and perennial rivers, drying-event conditions were its most important predictors. Macroinvertebrate richness declined with increasing durations of drying over the long-term (Australia) and recent (Australia and southwest Europe) history of river discharge, and with decreasing predictability of event timing (Australia). Our analysis also revealed that: responses can be taxon specific due to variation in traits of resistance and resilience to drying; some taxa may respond just as or more strongly to variation in other discharge components (e.g. high- or low-flow events) than to drying; and together these phenomena may result in differing community-level responses within and across regions. Patterns of beta-diversity across the wide biogeographical range of our study suggested that convergent and divergent niche-selection processes may act in combination on aquatic communities of rivers experiencing drying disturbances. However, strong ability to disperse by flight (not by water) weakened beta-diversity patterning among rivers. Our findings can be used to improve understanding of biodiversity organisation in disturbed systems, notably in those with dendritic features, including intermittent rivers.

Introduction

Ecosystem function and services to humans are fundamentally linked to biodiversity and are threatened by its loss, manifesting as declines in species richness (loss of alpha- or gamma-diversity) and/or biotic homogenization (loss of beta-diversity) (Cardinale et al. 2012). Biodiversity declines are occurring on global and local scales (Dirzo and Raven 2003; Balint et al. 2011) and, while the threats to freshwater biodiversity remain diverse, the diversity of life in fresh waters is in crisis (Vörösmarty et al. 2010). Of particular concern is the disturbance of river flow regimes, including that associated with climate change and human activities such as flow regulation and water abstraction (Dudgeon et al. 2006). Determining relationships between biodiversity and river hydrology, both naturally disturbed and anthropogenically modified, is thus vital for effective biodiversity conservation and natural resource management (Bunn and Arthington 2002; Poff et al. 2007; Rolls et al. 2012).

Natural disturbance regimes can act as strong environmental filters that, according to niche-based concepts of biodiversity patterns, non-randomly delimit regional species pools (Keddy 1992; Poff 1997; Weiher et al. 2011). These filters play a role in the distribution and evolution of traits that enable species to survive each individual disturbance (Díaz et al. 1998; Lytle 2001; Gutiérrez-Cánova et al. 2015) and, in turn, each disturbance modifies the quality, quantity and availability of habitat and resources, further determining the local species assemblage. Community homogenisation (convergence) may thus ensue under harsh environmental disturbance. As harshness increases, e.g. as the duration, frequency or spatial extent of disturbance increases, beta-diversity declines as species lacking resistance or resilience to the disturbance are progressively filtered from the regional pool and effects of stochastic assembly processes are weakened (McKinney and Lockwood 1999; Chase 2007; Jacobsen and Dangles 2012; cf. Connell 1978).

In rivers, natural hydrological disturbances including high-flow and dry phases that can modify or destroy habitat and kill or displace biota have long been considered among the most significant environmental filters (Power et al. 1988; Poff 1997; Lytle and Poff 2004; Matthews et al. 2013). However, evidence that dry phases structure communities as strongly as or more so than high-flow events is sparse (e.g. Bouton et al. 1992; Stubbington et al. 2009); floods can exert a dominant force on community assembly even where river drying occurs frequently (Fritz and Dodds, 2005). Perhaps in consequence, much work integral to determining relationships between hydrology and biodiversity includes minimal treatment of river drying (e.g. Konrad et al. 2008; Carlisle et al. 2010; Booker et al. 2015). This is surprising given rivers that dry naturally, herein intermittent rivers for simplicity, probably comprise at least 50% of the world's lotic freshwaters (Acuña et al. 2014; Datry et al. 2014a), with their prevalence likely to increase in many regions (Milly et al. 2005; Döll and Schmeid 2012; Seager et al. 2013). It is all the more surprising given research indicates river drying can trigger short- and long-term decline in alpha-diversity (e.g. Boulton 2003; Wood and Armitage 2004; Datry et al. 2014b; Bogan et al. 2015). Moreover, current understanding of the importance of river drying on biodiversity is primarily drawn from studies with restricted biogeographic and/or temporal coverage, or that focus on just one aspect of drying (e.g. duration), often in isolation from other components of hydrological disturbance (e.g. high-magnitude events) (Leigh et al. 2015a). While it is established that drying can act as an environmental filter (e.g. Bonada et al. 2007; Chase 2007; Bogan and Lytle 2011), the importance of drying relative to other, potential, hydrological determinants of river biodiversity remains understudied.

Our objective was to assess the influence of drying on river biodiversity, both in terms of alpha- and beta-diversity, relative to multiple, other components of hydrological disturbance using data collated over broad spatial and temporal scales from Australia and

southwest Europe, distant land masses encompassing multiple bioregions and a range of flow regimes. We hypothesised that drying disturbs aquatic communities, via loss and fragmentation of habitat, and is a primary hydrological determinant of biodiversity patterns in rivers. As such, we predict that alpha-diversity and assemblage composition vary foremost in response to drying (variation in its duration, frequency, timing and seasonality) and secondarily to other flow components (e.g. variation in high-flow characteristics), but due to variation in resistance and resilience to drying among taxa, not all taxa will respond to drying disturbances equally. We additionally hypothesised that increasing durations of drying progressively homogenise communities due to severe environmental filtering and selection of the most tolerant taxa from the regional species pool, but that this pattern may be modified by dispersal processes, namely that community homogenisation can also depend on the ability of and/or mode by which taxa disperse among habitats (Leibold et al. 2004; Cañedo-Argüelles et al. 2015; Datry et al. 2015a). When considering all taxa, we therefore predict beta-diversity to decline as the durations of dry phases increase, such that it is highest among rivers with continuous flow and lowest among rivers that are strongly intermittent; this general pattern will vary, however, among taxa grouped by dispersal characteristics. We used aquatic macroinvertebrates as our biotic subjects because they are known to vary in richness and community composition along a range of environmental disturbance gradients while contributing significantly to freshwater biodiversity, rendering them suitable surrogates of biodiversity in rivers (Malmqvist 2002; Turak et al. 2011).

Methods

Hydrological data and flow metrics

We obtained mean daily flow data from gauging stations in Australia from all states and territories, and in southwest Europe from mainland France (Banque Hydro;

hydro.eaufrance.fr) and northeast Spain (Catalan Water Agency, <http://aca-web.gencat.cat/aca>). All data were converted to a standard unit of measurement ($\text{m}^3 \text{s}^{-1}$). Gauges were screened to include only those on rivers with minimal modification of their natural flow regimes. For the Australia dataset, we only selected gauges pre-screened by Kennard et al. (2010) with little or no hydrologic modifications alterations attributable to human activities. For southwest Europe, personal communications with the gauges' managers and visual inspection of individual hydrographs and satellite images of gauge locations informed selection of gauges recording minimally altered flows (pers. comm. E. Sauquet, IRSTEA, France; see also Snelder et al. 2013). For example, gauges downstream of dams or weirs $> 2 \text{ m}$ in height or reservoirs $> 1 \text{ hm}^3$ in capacity were excluded.

From the standardised flow data, we calculated metrics that describe the critical components of hydrological variation influencing ecological and biological patterns and processes in rivers: magnitude, duration, frequency, timing or predictability, and rate of change or 'flashiness' (Poff et al. 1997; Olden and Poff 2003; Table 1). We calculated the metrics over the long term (for gauges with records of at least 30 y in length from 1970 onwards; Supplementary material Appendix 1) and over the 12 mo period antecedent to each biological sampling date (Supplementary material Appendix 1). Long-term hydrological conditions are an important environmental filter for community assembly in rivers and the 12-mo antecedent period is particularly relevant for describing changes in aquatic communities associated with recent, often extreme, hydrological conditions that can impose an additional structuring force (Lytle and Poff 2004; Fritz and Dodds 2005; Finn et al. 2009). Within each of these two groups (long-term and antecedent), we aimed to include, as far as practicable, a balanced number of metrics to describe the critical components of variation across average, low-flow, high-flow and zero-flow (ZF) conditions, drying disturbances being described by the ZF metrics. The inclusion of several ZF metrics which described multiple components of

variation and which were not subsumed within a “low flow” category (as typically occurs in flow-ecology analyses), was particularly important given our first hypothesis on responses to variation in drying conditions, beyond duration alone. Before analysis, all metrics describing flow magnitude ($\text{m}^3 \text{s}^{-1}$) were divided by the entire record’s mean daily flow (calculated from 1970 onwards for each respective paired hydrological-biological site; Supplementary material Appendix 3) to account for differences in upstream catchment size (Kennard et al. 2010; Olden et al. 2012; McManamay et al. 2015; catchment size was not available for all gauges). Long-term flow metrics could not be calculated for the southwest European dataset because gauged records were typically short in length ($\ll 30$ y post-1970 due to missing data, anthropogenic flow modification, and/or discontinuation); thus only antecedent flow metrics were used in analyses involving the southwest European dataset.

Flow metrics were calculated in RAP v3.0.7 (Marsh et al. 2003) based on calendar years (Kennard et al. 2010), except for antecedent flow metrics which were all based on the 12-mo period prior to each biological sampling date. Calendar years were chosen as a consistent, standard time period, rather than water years, because of the multiple different water years among and within Australia, France and Spain. We used the 10th and 90th percentiles of the mean daily flows to respectively describe low-flow and high-flow thresholds and in low-flow and high-flow spells calculations, default settings for Colwell’s predictability, and $0 \text{ m}^3 \text{ s}^{-1}$ for zero flow (Table 1). The metrics we calculated are described thoroughly elsewhere (e.g. Olden and Poff 2003; Kennard et al. 2010) with the exception of Sd6, a relatively new metric describing the 6-month seasonal predictability of ZF periods (Gallart et al. 2012). Sd6 ranges from 0 (no predictability) to 1 (total predictability). For example, a river typically experiencing zero flows throughout the year will have an Sd6 value approaching 0, whereas one experiencing zero flows within the same contiguous 6-month

period each year will have a value of 1. Rivers with no zero flows in their hydrological record over the period for which Sd6 is calculated will have a value of 1.

Biological data and biodiversity metrics

We collated macroinvertebrate count data from biomonitoring and assessment databases in Australia and southwest Europe (Australia: AUSRIVAS database, <http://ausrivas.ewater.org.au/>; France: eaufrance database, ONEMA, <http://www.onema.fr/>; northeast Spain: SIX database, Catalan Water Agency, <http://aca-web.gencat.cat/aca/>) from ‘reference condition’, minimally disturbed or least-disturbed sites only (see Supplementary material Appendix 2 for detail on methods of collection and taxonomic identification). The finest level of taxonomic resolution consistent across datasets was family, a level suitable for examining patterns in biodiversity (Heino 2011; Datry et al. 2014b). Any taxa identified to finer levels were aggregated to family, and taxa at coarser levels were excluded; all taxa could thus be treated equally in analyses (as recommended by Booker et al. 2015). Data from France and Spain were combined into a single southwest European dataset (Supplementary material Appendix 2). Rare taxa (occurring in 1 sample only or with an abundance of ≤ 3 across all samples; Worrall et al. 2014) were then removed from each of the Australian and southwest European datasets to reduce the effect of sampling frequency on detecting rare fauna (Snelder et al. 2012) and produce a subset of taxa with enough statistical power to analyse patterns of biodiversity (Vellend et al. 2008; Heino and Soininen 2010). We then standardised sampling effort across all samples (from both Australia and southwest Europe) by generating for each sample a random subsample of 200 individuals, without replication, using the R vegan package (Oksanen et al. 2015). This ensured no sample contained more than the lowest maximum per-sample count across the datasets (Supplementary material Appendix 2) and was important not only for standardisation within the combined southwest Europe dataset, but also for comparing results between Australia and southwest Europe.

The above procedures generated a final sample by taxon abundance matrix for each dataset, which was used to analyse relationships between community composition and antecedent flow metrics (both being measured at the scale of samples; 425 samples across 62 sites and 41 drainage basins in Australia and 43 samples across 10 sites and 8 drainage basins in southwest Europe). Taxonomic richness, a common surrogate for alpha-diversity with wide use in bioassessment and conservation (Vellend et al. 2008), was then calculated for each sample, matching the scale of the antecedent flow metrics. We also calculated the mean richness of samples at each site, generating a temporally-integrated richness value for each site, matching the scale of the long-term flow metrics.

Taxa were then grouped by their dispersal characteristics as *either* strong flight or strong water dispersers. These groups were mutually exclusive to facilitate interpretation of results, i.e. taxa with strong flight *and* strong water dispersal ability were not assigned to either group. Dispersal mode or ability could not be assigned for 17 families (5% of the total number of taxa represented by our datasets) and were likewise not assigned to either group. Information on dispersal characteristics was sourced from Tachet (2000), Poff et al. (2006a), Brooks et al. (2011) and Campbell et al. (2015) and applied following the method outlined in Supplementary material Appendix 2.

Pairing gauges with biomonitoring sites

There is a lack of paired hydrological-biological datasets worldwide (Booker et al. 2015). This is also true in Australia, France and northeast Spain, where hydrological gauges are rarely found in the same location as regularly sampled biomonitoring sites. Thus we paired gauges with nearby biomonitoring sites using ArcGIS 10.2 and stream network layers for France, Spain and Australia (Supplementary material Appendix 3). We used a maximum pairing distance of 10 km and considered gauges with an annual mean of > 5 zero-flow days

intermittent (after Kennard et al. 2010) and the remainder perennial. This ensured we would retain for analysis a suite of gauges located on intermittent rivers and that biomonitoring sites on perennial rivers were not paired with gauges on intermittent rivers, or vice versa.

Following strict selection criteria (Supplementary material Appendix 3), 62 gauges (31 intermittent and 31 perennial) were confidently paired with biomonitoring sites across the eastern Australian states of New South Wales, Queensland, South Australia and Victoria, and 10 gauges (7 intermittent and 3 perennial) were confidently paired with biomonitoring sites across southwest Europe. Only 18% of these gauges were paired with biomonitoring sites within 200 m, but 46% were paired within 1 km, and < 1 % had biomonitoring sites within 5-10 km. We now refer to these pairs simply as sites (Supplementary material Appendix 3, Fig. A1).

Data analysis

We used the large hydrological and biological dataset from Australia to thoroughly explore our hypotheses and the comparatively smaller one from southwest Europe to determine if responses to drying were generalizable across regions.

Hypothesis 1: drying is a primary hydrological determinant of biodiversity patterns in rivers; alpha-diversity and assemblage composition therefore vary foremost in response to drying and secondarily to other flow components

We used random forests (RFs) and gradient forests (GFs) to explore our first hypothesis (Supplementary material Appendix 4; Ellis et al. 2012; Pitcher et al. 2012). These methods are highly flexible regression techniques suitable for modelling response variables (e.g. richness and abundance) that have complex relationships with predictor variables (e.g. river discharge) (Leigh et al. 2012; Booker et al. 2015). RFs are invariant to monotonic transformations of predictor variables and provide both an overall goodness-of-fit measure

(R^2) and a measure of importance of each predictor in the model, the latter being analogous to the error resulting from dropping a term from a linear model (Cutler et al. 2007; Ellis et al. 2012). GFs extend the RF approach to multivariate responses and have recently found use in ecological applications (Ellis et al. 2012; Pitcher et al. 2012). They can model responses of whole communities (including non-linear and threshold responses) to environmental gradients (Pitcher et al. 2012) by producing an RF for each taxon in a community (where the taxon's abundance is the response variable) and aggregating the results of each RF to give the cumulative and overall importance of each predictor along with an aggregated R^2 value of goodness-of-fit.

To test the prediction that variation in drying conditions (e.g. change in zero-flow duration, frequency, timing and seasonality) would be a stronger driver of variation in macroinvertebrate richness and composition of rivers than variation in other flow components, we modelled responses of the macroinvertebrate fauna to drying in intermittent rivers alone, or in combination with perennial rivers, and compared models with and without zero-flow predictor variables. We used RFs to model changes in taxonomic richness and GFs to model 'compositional turnover' (*sensu* Ellis et al. 2012), i.e. changes in the abundances of multiple taxa, along gradients of zero-flow and other hydrological conditions. We used long-term flow metrics to model changes in site-scale richness and antecedent flow metrics to model changes in sample-scale richness and compositional turnover. Models were run with all (long-term or antecedent) flow metrics, without (long-term or antecedent) ZF metrics and with only (long-term or antecedent) ZF metrics, and as dependent on dataset constraints (e.g. only the Australian dataset had long-term flow metrics and a sufficient number of perennial sites for models run with long-term metrics and/or data from perennial sites). We used the R packages `extendedForest` to implement RFs and `gradientForest` to implement GFs (Liaw & Wiener 2002; Ellis et al. 2012), which both allowed us to calculate conditional importance to

account for correlation among predictor variables (Strobl et al. 2008; Supplementary material Appendix 4). This is essential when modelling biological responses to hydrological variation because flow metrics are typically inter-correlated, and represents an alternative to pre-analysis redundancy-minimisation (Olden and Poff 2003). We used default settings (e.g. for the numbers of trees to grow and predictors to randomly sample as candidates at each split), with conditional permutation for importance computation based on a correlation threshold of 0.5 (Kendall's tau; Ellis et al. 2012) and a maximum number of splits per tree as per the formula in Pitcher et al. (2012). Abundances were $\log_{10}(x+1)$ transformed prior to analysis.

Hypothesis 2: increasing durations of drying progressively homogenise communities; beta-diversity therefore declines as dry-phase durations increase, such that it is highest among rivers with continuous flow and lowest among rivers that are strongly intermittent, but this general pattern will vary depending on dispersal characteristics of the taxa

To explore our second hypothesis and test the prediction that beta-diversity among rivers would decline with increasing durations of ZF events, we compared beta-diversity among four classes of river using the PERMDISP routine in PRIMER + PERMANOVA v6, a dissimilarity-based multivariate extension of Levene's test that analyses homogeneity of multivariate dispersions based on any resemblance measure (Anderson 2006; Anderson et al. 2008). First, we generated classes of increasing ZF duration in R (R Core Team 2015) using k-means clustering on site-averaged, $\log_{10}(x + 1)$ transformed ant_mDurZFspells (Table 1) calculated from intermittent rivers only (from Australia and southwest Europe combined). A k of 3 minimised the within-class sum of squares (relative to k = 2, 4 or 5), with the resultant classes having mean ant_mDurZFspells values of 0.4 d, 11 d and 92 d, respectively, corresponding to weakly (n=6), moderately (n= 16) and strongly (n=16) intermittent conditions antecedent to macroinvertebrate sampling. The fourth class comprised perennial rivers (n=34). In PRIMER + PERMANOVA v6, we then produced three resemblance

matrices of compositional similarity between all pairs of macroinvertebrate samples from Australia and southwest Europe using the Bray-Curtis similarity measure on $\log_{10}(x + 1)$ transformed abundance data: one considering all taxa, one considering only strong flight dispersers, and one considering only strong water dispersers. To preserve the Bray-Curtis measure but conduct the analysis on compositional similarity between sites (rather than samples) we then calculated distances among centroids grouped by site, as recommended by Anderson (2006), for each matrix. Using the resultant site-based resemblance matrices, we ran PERMDISP to test for between-class differences in beta-diversity, calculating distances to spatial medians and obtaining *P*-values using permutation.

Results

Macroinvertebrate richness and composition

The southwest European dataset comprised 70 families of macroinvertebrates, with sample richness of intermittent rivers (66 families in 28 samples from 7 sites) ranging from 7 to 31, and of perennial rivers (53 families in 12 samples from 3 sites) from 2 to 21 (Supplementary material Appendix 2, Fig. A1). The Australian dataset comprised 110 families, with sample richness of intermittent rivers (100 families in 171 samples from 31 sites) ranging from 2 to 37, and of perennial rivers (97 families in 254 samples from 31 sites) from 5 to 31 (Supplementary material Appendix 2, Fig. A1). Forty-four families were common to the Australian and southwest European datasets, 66 being unique to the Australian and 26 unique to southwest European datasets (Supplementary material Appendix 2).

Hypothesis 1

When modelling changes in richness in intermittent rivers, RFs only including ZF metrics always explained a similar or greater amount of variation than those including ZF and non-ZF metrics combined or non-ZF metrics alone, in the Australian and southwest European

datasets (Fig. 1). Although the combined intermittent and perennial river models were distinct in that more variation was explained by a combination of ZF and non-ZF metrics than by ZF metrics alone, the latter model explained a similar amount of variation as did the non-ZF metrics model and suggested that ZF metrics are meaningful and important to include in combined intermittent-perennial models (Fig. 1). This was confirmed by predictor-importance results; for example, at least two out of the three most important predictors in all models using both ZF and non-ZF metrics, including the intermittent-perennial river model, were ZF metrics (Supplementary material Appendix 4, Fig. A3). Seasonal predictability of ZF events (Sd6) and/or ZF duration (maZer) were typically the most important metrics in RFs modelling changes in site-scale richness, even when considering intermittent and perennial rivers together, followed by the magnitude of high flows (maP90) and timing of high-flow maxima (maMeanJDMax; Supplementary material Appendix 4, Fig. A3). In both Australia and southwest Europe, the frequency of antecedent ZF-events (ant_NoZFspells) and their combined duration (ant_Zer) were important predictors of changes in richness at the sample-scale, along with the magnitude of antecedent low flows (ant_P10; Supplementary material Appendix 4, Fig. A3).

Richness declined as the long-term duration of zero flows (maZer) increased and long-term frequency of ZF events (maNoZFspells) increased (Fig. 2). For duration, sharp declines in richness occurred between ~ 100 and 150 days, whereas the decline associated with increasing event frequency was more gradual (Fig. 2). By contrast, the response to increasing ZF duration in the period antecedent to sampling (ant_Zer) was more variable, particularly when durations were < ~50 days, thereafter showing a steady decline in richness (Fig. 2). Richness responded similarly to increasing long-term and antecedent frequencies of ZF events (maNoZFspells and ant_NoZFspells), declining up to ~ 3-5 events over a 12-mo period. With increasing frequencies of antecedent ZF events, the Australian and southwest European

models suggest the initial decline in richness may be followed by a slight increase before embarking on a steady decline (Fig. 2). Sharp increases in richness occurred when the seasonality of zero flows became highly predictable ($Sd6 \sim 0.8$; Fig. 2). Regarding the important non-ZF predictors mentioned above, long-term high-flow magnitudes around twice that of the mean daily flow ($maP90 \sim 2$) and high-flow maxima ($maMeanJDMax$) in spring to early summer were associated with high richness at the site scale, and sample-scale richness increased with the magnitude of antecedent low flows (ant_P10) (figures not shown).

Relationships between drying and compositional turnover, as modelled by GFs, were not as strong as those between drying and richness. GFs with ZF metrics explained a lower or similar amount of variation in compositional turnover than those without ZF metrics, for both the Australian and southwest European datasets (Fig. 3, Supplementary material Appendix 4, Fig. A4). However, the percentage of Australian families for which flow metrics had some predictive power was highest (51%) when including only ZF metrics in the model (Fig. 3). Changes in composition of Australian families occurred reasonably steadily along the gradient of ZF-event frequency, but for southwest European families, changes were gradual along the gradient of ZF-event duration until ~ 40 d when substantial alterations occurred (Fig. 4). These patterns reflected changes in abundances of families such as Australian Elmidae and Leptophlebiidae, which both declined gradually as the number of ZF-events in intermittent rivers increased, and southwest European Baetidae and Nemouridae, which showed differing responses to increasing ZF-event duration (Fig. 4). While Baetidae declined gradually in abundance along the duration gradient, Nemouridae abundance dropped to zero when durations were > 40 -50 d (Fig. 4).

Hypothesis 2

Contrary to our prediction, communities that experienced longer ZF-event durations did not consistently have more homogeneous compositions than those experiencing shorter durations. Rather, we discerned a hump-shaped relationship between beta-diversity and ZF-event duration (Fig. 5). When considering all taxa, multivariate dispersion differed significantly between moderately intermittent and perennial rivers, with dispersion being higher in the intermittent-river class, reflecting greater beta-diversity among communities (pairwise $P = 0.008$). The difference was preserved when only considering strong water dispersers (pairwise $P = 0.003$) but not strong flight dispersers (pairwise $P < 0.05$; Fig. 5). Multivariate dispersions were comparable between perennial, weakly intermittent and strongly intermittent rivers in all cases (pairwise $P < 0.05$), except in the case of strong water dispersers, for which multivariate dispersion was higher in strongly intermittent than perennial rivers (pairwise $P = 0.004$).

Discussion

Drying disturbance, alpha-diversity and community composition

Our study reveals that drying disturbance is a strong hydrological determinant of alpha-diversity in river systems. Even when considering both intermittent and perennial rivers in analyses, conditions such as the timing and duration of ZF events were often the most important hydrological predictors of aquatic macroinvertebrate richness, being more important than average-, low- or high-flow predictors. The influence of drying was even more apparent when considering intermittent rivers alone. In this case, ZF metrics alone explained an equivalent or greater amount of variation in richness than in combination with metrics describing other flow conditions; a result consistent across regions as distant and biogeographically distinct as southwest Europe and Australia. Our results thus supported our prediction that alpha-diversity would vary foremost in response to drying and secondarily to

other flow components. From an applied perspective, this suggests ZF conditions should be included in predictive flow-ecology models even when considering perennial rivers in the analysis.

From a theoretical perspective, alpha-diversity is predicted to follow a unimodal pattern with increasing frequency and/or duration of disturbance, in keeping with Connell's (1978) intermediate disturbance hypothesis (IDH). In our study, however, richness declined with increasing durations of drying, both over the long-term (> 30-y; Australia) and recent (12-mo; Australia and southwest Europe) history of river discharge, and with decreasing predictability of event timing (Australia). Support for the IDH is limited (Fox 2013), notably from stream ecology studies, with cumulative evidence more strongly suggesting that hydrological disturbances remove aquatic organisms and lower richness (Death 2010). Our results also indicate that this latter pattern is dominant in stream ecosystems and concurs with previous research on intermittent rivers examining responses to dry-phase duration (Datry et al. 2014b).

However, our analysis of compositional turnover along multiple gradients of flow variation revealed that (i) the response to drying may be taxon specific due to variation in traits of resistance and resilience to drying, (ii) some taxa may respond just as or more strongly to other components of flow variation than to drying, and (iii) together these phenomena may result in differing community-level responses within and across regions (e.g. Leigh et al. 2015b; Vander Vorste et al. 2015a). In southwest Europe for example, Nemouridae (a family of northern-hemisphere stonefly) were only found in rivers where ZF events were not more than ~ 40 d in duration, whereas individuals of Baetidae (a globally-distributed mayfly family) were still present in rivers, albeit in low abundance, that had > 100 d of continuous zero flow. Several neumourid species have a desiccant-resistant egg stage and are known to aestivate in the moist sediments of dry streams (Earle 2004; Stubbington et al.

2009), although in many systems this requires only 1-3 months aestivation during a seasonal dry phase (e.g. Earle 2004). Longer dry phases may be prohibitive to their persistence. By contrast, the strong swimming ability of baetids together with their multi-voltinism (Tachet et al. 2000; Datry et al. 2014b) may allow these taxa to readily escape drying habitats and recolonise previously dry ones across a wider range of drying durations. Baetids are often among the first colonisers upon rewetting (e.g. Datry 2012, Ríos-Touma et al. 2012, Vander Vorste et al. 2015b) and are a dominant mayfly family in many intermittent systems (Moya et al. 2011, Grubbs 2011, Datry et al. 2014b).

Furthermore, changes in composition of Australian families were gradual along a drying gradient whereas changes in southwest European families were more stepped. This may reflect a difference in both the historical and recent conditions of disturbance (i.e. drying) to which the aquatic macroinvertebrates of Australian and southwest European rivers have been exposed. For example, the maximum duration of ZF events antecedent to sampling was much shorter in southwest Europe than Australia (110 vs. 272 d) and likely mirrors a regional difference in ZF durations over the longer term (de Vries et al. 2015). Australian river systems, including many of the country's intermittent rivers, are renowned for their highly variable and extreme flow conditions, whereas historical alternation between the wet- and dry-phases of southwest European rivers may be less 'flashy' and comparatively predictable (Puckridge et al. 1998; Poff et al. 2006b). The evolution of traits that enable species to survive drying disturbances (Lytle and Poff 2004) likely varies between Australia and southwest Europe, and probably also within each of these regions (e.g. Bonada et al. 2007). Such variation serves to further highlight our findings of the dominating force river drying exerts on aquatic biodiversity. Nevertheless, continued gathering of macroinvertebrate data from rivers encompassing wide ranges of dry-phase conditions, particularly in Europe where our intermittent-river dataset was limited to 7 sites, and finer-scale taxonomic resolution for

groups of interest such as baetids and nemourids, will improve our ability to contrast or generalise findings within and across regions. More generally, our results indicate that long-term persistence of harsh disturbance regimes (e.g. in Australian intermittent rivers) may promote the acquisition of tolerance to disturbance, and potentially some buffering against novel disturbances (Gutiérrez-Cánovas et al. 2015; Vander Vorste et al. 2015a).

Drying disturbance and beta-diversity

Disturbance can have variable effects on beta-diversity (Chase 2003; Datry et al. 2016a); it can increase beta-diversity by increasing habitat filtering across environmental gradients (= divergent niche-selection) or alternatively decrease beta-diversity by increasing selection of disturbance-tolerant species (= convergent niche-selection) (Myers et al. 2015). Although we predicted that niche-selection of the convergent type would be acting on macroinvertebrate communities to decrease beta-diversity as drying duration increased, our finding that beta-diversity was highest in moderately-intermittent rivers but low in severely-intermittent rivers appears more consistent with the above ‘variable effects’ concept.

Drying causes the fragmentation and loss of aquatic habitat as surface waters contract and then disconnect or disappear across an increasingly large spatial expanse as the duration of the dry phase lengthens (Jaeger et al. 2014; Datry et al. 2015b) and this spatial-temporal interplay may help explain why beta-diversity did not decline as expected. For example, Sheldon et al. (2010) predicted that dissimilarity among aquatic communities in intermittent rivers of dryland regions would be highest during the early phases of habitat disconnection (i.e. under moderate drying durations) when aquatic habitat diversity across the landscape is high (= divergent niche-selection), and lowest after prolonged disconnection (i.e. under extended drying durations) when virtually all aquatic habitats remaining in the landscape have become environmentally harsh and dominated by tolerant generalists (= convergent niche-

selection). Our finding thus suggests these two niche-selection processes may act together to determine beta-diversity patterns among intermittent river communities, not only in drylands but across a wide biogeographical range. In a context of global change, understanding how beta-diversity varies in space and time, notably in disturbed systems, is becoming a key research topic, which will certainly translate into conservation and restoration applications (Datry et al. 2015a, 2016a).

However, beta-diversity patterns can also differ along gradients of disturbance according to the dispersal modes and abilities of the taxa considered (Sheldon et al. 2010; Cañedo-Argüelles et al. 2015, Campbell et al. 2015). Beta-diversity was highest in moderately intermittent rivers when considering all taxa, but when dispersal was accounted for, this pattern was preserved only for strong water dispersers; beta-diversity among assemblages of strong flight dispersers was similar among river types. Water dispersers, even strong ones (e.g. baetids), are more constrained by spatio-temporal variation in surface water availability than flight dispersers due to the latter group's ability to disperse both along and across channels, and across drainage divides (Cañedo-Argüelles et al. 2015; Datry et al. 2016a). Beta-diversity patterns may thus be less well explained by environmental filtering for the latter group than the former, as evidenced by our results and reported in intermittent rivers from South America (Datry et al. 2015b).

Very dynamic ecosystems such as intermittent rivers provide interesting arenas to explore further how beta-diversity patterns vary with disturbance frequency and magnitude and species dispersal. Although beta-diversity patterns have been generally viewed as relatively static (e.g. Leibold et al. 2004; Presley et al. 2010; Carrara et al. 2012), the emerging acceptance that many ecosystems and communities are temporally variable (e.g. Azeria & Kolasa 2008; Aiken & Navarette 2014; Datry et al. 2016a) is triggering new developments and challenges in metacommunity ecology (e.g. Fernandes et al. 2014;

Campbell et al. 2015; Datry et al. 2015a). In river systems, exploring how community processes and subsequent beta-diversity patterns vary temporarily in response to environmental changes (including disturbances) is complicated by the dendritic structure of river networks and the multitude of dispersal modes and abilities shown by aquatic organisms (Erös & Campbell Grant 2015; Tonkin et al. 2015 Datry et al. 2016a,b). For example, strong water and aerial dispersers could reach all sites within a network and be more prone to convergent or divergent niche-selection, while the coexistence of weak dispersers may be solely driven by dispersal processes (e.g. Datry et al. 2016a). Conservation and restoration efforts in dynamic ecosystems should seek to account for such differences for sake of efficiency and relevance, particularly, given our findings, that unnaturally prolonged durations of drying will likely not only reduce aquatic alpha-diversity but potentially also beta-diversity, threatening freshwater biodiversity and the provision of associated ecosystem services.

Acknowledgements

We are grateful to the many people who supplied data and helped us compile the datasets and metrics used in this study. In particular, we thank Mark Kennard, Antoni Munné, Núria Bonada and Eric Sauquet for assisting with collation of hydrological data and verification of the hydrological-modification status of gauges; Evan Harrison, Antoni Munné, Núria Bonada, Martial Ferreol and Marta Prieto-Montes for assisting with collation of biological data; Stefan de Vries, Jasper Hoeve and Alex Niese for assistance with flow-metric calculations; Quitterie Blanchard for calculating flow-path distances between hydrological and biological sites; Andrew Boulton, Ken Fritz, Scott Larned and the IRBAS (Intermittent River Biodiversity Analysis and Synthesis) working group for discussions on flow-ecology relationships. CL was funded through the IRBAS project (www.irbas.fr), led by TD and supported by the Centre for Synthesis and Analysis of Biodiversity (CESAB) and funded jointly by the French Foundation for Research and Biodiversity (FRB) and the French National Agency for Water

and Aquatic Environments (ONEMA). Earlier versions of this manuscript benefited from comments by N. LeRoy Poff, Paul Wood and two anonymous reviewers.

References

- Acuña, V. et al. 2014. Why should we care about temporary waterways? – *Science* 343: 1080–1081.
- Aiken, C. M. and Navarrete, S. A. 2014. Coexistence of competitors in marine metacommunities: environmental variability, edge effects, and the dispersal niche. – *Ecology* 95: 2289–2302.
- Anderson, M. J. 2006. Distance-based tests for homogeneity of multivariate dispersions. – *Biometrics* 62: 245–253.
- Anderson, M. J. et al. 2008. PERMANOVA+ for PRIMER: guide to software and statistical methods. PRIMER-E. Plymouth, UK.
- Azeria, E. T. and Kolasa, J. 2008. Nestedness, niche metrics and temporal dynamics of a metacommunity in a dynamic natural model system. – *Oikos* 117: 1006–1019.
- Balint, M. et al. 2011. Cryptic biodiversity loss linked to global climate change. – *Nature Clim. Change*. 1: 313–318.
- Bogan, M. T. and Lytle, D. A. 2011. Severe drought drives novel community trajectories in desert stream pools. – *Freshwater Biol.* 56: 2070–2081.
- Bogan, M. T. et al. 2015. Resistance and resilience of invertebrate communities to seasonal and suprasedonal drought in arid-land headwater streams. – *Freshwater Biol.* 60: 2547–2558

- Bonada, N. et al. 2007. Macroinvertebrate community structure and biological traits related to flow permanence in a Mediterranean river network. – *Hydrobiologia* 589: 91–106.
- Booker, D. J. et al. 2015. Relationships between invertebrate communities and both hydrological regime and other environmental factors across New Zealand's rivers. – *Ecohydrology* 8: 13–32.
- Boulton, A. J. 2003. Parallels and contrasts in the effects of drought on stream macroinvertebrate assemblages. – *Freshwater Biol.* 48:1173–1185.
- Boulton, A. J. et al. 1992. Stability of an aquatic macroinvertebrate community in a multiyear hydrologic disturbance regime. – *Ecology* 73: 2192–2207.
- Brooks, A. J. et al. 2011. Macroinvertebrate traits distinguish unregulated rivers subject to water abstraction. – *J. N. Am. Benthol. Soc.* 30: 419–435
- Bunn, S. E. and Arthington, A. H. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. – *Environ. Manage.* 30: 492–507.
- Campbell, R. E. et al. 2015. Flow-related disturbance creates a gradient of metacommunity types within stream networks. – *Landsc. Ecol.* 30: 667–680.
- Cañedo-Argüelles, M. et al. 2015. Dispersal strength determines meta-community structure in a dendritic riverine network. – *J. Biogeogr.* 42: 778–790.
- Cardinale, B. J. et al. 2013. Biodiversity simultaneously enhances the production and stability of community biomass, but the effects are independent. – *Ecology* 94: 1697–1707.
- Carlisle, D. M. et al. 2010. Predicting the natural flow regime: models for assessing hydrological alteration in streams. – *River Res. Appl.* 26: 118–136.

- Carrara, F. et al. 2012. Dendritic connectivity controls biodiversity patterns in experimental metacommunities. – *Proc. Natl. Acad. Sci.* 109: 5761– 5766
- Chase, J. M. 2003. Community assembly: when should history matter? – *Oecologia* 136: 489–498.
- Chase, J. M. 2007. Drought mediates the importance of stochastic community assembly. – *Proc. Natl. Acad. Sci.* 104: 17430–17434.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. – *Science* 199: 1302–1310.
- Cutler, D. R. et al. 2007. Random forests for classification in ecology. – *Ecology* 88: 2783–2792.
- 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. 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. 2015a. Towards understanding the organisation of metacommunities in highly dynamic ecological systems. – *Oikos*. doi: 10.1111/oik.02922
- Datry, T. et al. 2015b. A landscape approach to advance intermittent river ecology. – *Freshwater Biol.* Accepted article, in press.

- Datry T. et al. 2016a. Metacommunity patterns vary with environmental harshness across three tropical headwater streams. – *Freshwater Biol.* doi:10.1111/fwb.12702
- Datry, T. et al. 2016. Determinants of local and regional communities in intermittent and perennial headwaters of the Bolivian Amazon. – *Freshwater Biol.* doi:10.1111/fwb.12706
- Death, R. G. 2010. Disturbance and riverine benthic communities: what has it contributed to general ecological theory? – *River Res. Appl.* 26: 15–25.
- de Vries, S. B. et al. 2015. Characterizing spatial and temporal patterns of intermittent rivers. – *Geophys. Res. Abstr.* 17. EGU General Assembly. Vienna, Austria.
- Díaz, S. et al. 1998. Plant functional traits and environmental filters at a regional scale. – *J. Veg. Sci.* 9: 113–122.
- 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.
- Dudgeon, D. et al. 2006. Freshwater biodiversity: importance, threats, status, and conservation challenges. – *Biol. Rev.* 81: 163–182.
- Earle, J. I. 2004. Stonefly (Plecoptera) species of an acidic intermittent stream in southwestern Pennsylvania, USA, comparison with a circumneutral perennial stream and consideration of survival strategies. – *Arch. Hydrobiol.* 159: 97–114.
- Ellis, N. et al. 2012. Gradient forests: calculating importance gradients on physical predictors. – *Ecology* 93: 156–168.

- Erős, T. and Campbell Grant, E. H. 2015. Unifying research on the fragmentation of terrestrial and aquatic habitats: patches, connectivity and the matrix in riverscapes. – *Freshwater Biol.* 60: 1487–1501.
- Finn, M. A. et al. 2009. Ecological responses to artificial drought in two Australian rivers with differing water extraction. – *Fund. Appl. Limnol. / Arch. Hydrobiol.* 175: 231–248.
- Fernandes, I. M. et al. 2014. Spatiotemporal dynamics in a seasonal metacommunity structure is predictable: the case of floodplain-fish communities. – *Ecography* 37: 464–475.
- Fox, J. W. 2013. The intermediate disturbance hypothesis should be abandoned. – *Trends Ecol. Evol.* 28: 86–92.
- Fritz, K. M. and Dodds, W. K. 2005. Harshness: characterisation of intermittent stream habitat over space and time. – *Mar. Freshwater Res.* 56: 13–23.
- Gallart, F. et al. 2012. A novel approach to analysing the regimes of temporary streams in relation to their controls on the composition and structure of aquatic biota. – *Hydrol. Earth Syst. Sci.* 16: 3165–3182.
- Grubbs, S. A. 2011. Influence of flow permanence on headwater macroinvertebrate communities in a Cumberland Plateau watershed, USA. – *Aquat. Ecol.* 45: 185–195.
- Gutiérrez-Cánovas, C. et al. 2015. Similarity in the difference: changes in community functional features along natural and anthropogenic stress gradients. – *Ecology* 96: 2458–2466.
- Heino, J. 2011. A macroecological perspective of diversity patterns in the freshwater realm. – *Freshwater Biol.* 56: 1703–1722

- Heino, J. and Soininen, J. 2010. Are common species sufficient in describing turnover in aquatic metacommunities along environmental and spatial gradients? – *Limnol. Oceanogr.* 55: 2397–2402.
- Jacobsen, D. and Dangles, O. 2012. Environmental harshness and global richness patterns in glacier-fed streams. – *Glob. Ecol. Biogeogr.* 21: 647–656.
- Jaeger, K. L. et al. 2014. Climate change poised to threaten hydrologic connectivity and endemic fishes in dryland streams. – *Proc. Natl. Acad. Sci.* 111: 13894–13899.
- Keddy, P. A. 1992. Assembly and response rules: two goals for predictive community ecology. – *J. Veg. Sci.* 3: 157–164.
- Kennard, M. J. et al. 2010. Classification of natural flow regimes in Australia to support environmental flow management. – *Freshwater Biol.* 55: 171–193.
- Konrad, C. P. et al. 2008. Assessing streamflow characteristics as limiting factors on benthic invertebrate assemblages in streams across the western United States. *Freshwater Biol.* 53: 1983–1998.
- Leibold, M. A. et al. 2004 The metacommunity concept: a framework for multi-scale community ecology. – *Ecol. Lett.* 7: 601–613.
- Liaw, A. and Wiener, M. 2002. Classification and regression by randomForest. – *R news* 2: 18–22.
- Lytle, D. A. and Poff, N. L. 2004. Adaptation to natural flow regimes. – *Trends Ecol. Evol.* 19: 94–100.
- Leigh C. et al. 2012. Understanding multiple ecological responses to anthropogenic disturbance: rivers and potential flow regime change. – *Ecol. Appl.* 22: 250–263.

- Leigh, C. et al. 2015a. Ecological research and management of intermittent rivers: an historical review and future directions. – *Freshwater Biol.* doi:10.1111/fwb.12646
- Leigh, C. et al. 2015b. Invertebrate assemblage responses and the dual roles of resistance and resilience to drying in intermittent rivers. – *Aquat. Sci.* doi: 10.1007/s00027-015-0427-2
- Marsh, N. A. et al. 2003. River Analysis Package. Cooperative Research Centre for Catchment Hydrology, Monash University. Melbourne, Australia.
- Matthews, W. J. et al. 2013. Disturbance and trajectory of change in a stream fish community over four decades. – *Oecologia* 173: 955–969.
- McKinney, M. L. and Lockwood, J. L. (1999). Biotic homogenization: a few winners replacing many losers in the next mass extinction. – *Trends Ecol. Evol.* 14: 450–453.
- McManamay, R. A. et al. 2015. Associations among hydrologic classifications and fish traits to support environmental flow standards. – *Ecohydrology* 8: 460–479.
- Milly, P. C. D. et al. 2005. Global pattern of trends in streamflow and water availability in a changing climate. – *Nature* 438: 347–350.
- Moya, N. et al. 2011. Macroinvertebrate-based multimetric predictive models for evaluating the human impact on biotic condition of Bolivian streams. – *Ecol. Indic.* 11: 840–847.
- Myers, J. A. et al. 2015. Disturbance alters beta-diversity but not the relative importance of community assembly mechanisms. – *J. Ecol.* 103: 1291–1299.
- Oksanen J. et al. 2015. Vegan: community ecology package. R package version 2.2-1. <<http://CRAN.R-project.org/package=vegan>>.

- Olden, J. D. et al. 2012. A framework for hydrologic classification with a review of methodologies and applications in ecohydrology. – *Ecohydrology* 5: 503–518.
- Olden, J. D. and Poff, N. L. 2003. Redundancy and the choice of hydrologic indices for characterizing streamflow regimes. – *River Res. Appl.* 19: 101–121.
- Pitcher, C. R. et al. 2012. Exploring the role of environmental variables in shaping patterns of seabed biodiversity composition in regional-scale ecosystems. – *J. Appl. Ecol.* 49: 670–679.
- Poff, N. L. 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. – *J. N. Am. Benthol. Soc.* 16: 391–409.
- Poff, N. L. et al. 1997. The natural flow regime: a paradigm for river conservation and restoration. – *BioScience* 47: 769–784.
- Poff, N. L. et al. 2006a. Functional trait niches of North American lotic insects: traits-based ecological applications in light of phylogenetic relationships. – *J. N. Am. Benthol. Soc.* 25: 730–755.
- Poff, N. L. et al. 2006b. Placing global stream flow variability in geographic and geomorphic contexts. – *River Res. Appl.* 22: 149–166.
- Poff, N. L. et al. 2007. Homogenization of regional river dynamics by dams and global biodiversity implications. – *Proc. Natl. Acad. Sci. U.S.A.* 104: 5732–5737.
- Power, M. E. et al. 1988. Biotic and abiotic controls in river and stream communities. – *J. N. Am. Benthol. Soc.* 7: 456–479.
- Presley, S. J. et al. 2010. A comprehensive framework for the evaluation of metacommunity structure. – *Oikos* 119: 908–917.

- Puckridge, J. T. et al. 1998. Flow variability and the ecology of large rivers. – *Mar. Freshwater Res.* 49: 55–72.
- R Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. <<http://www.R-project.org/>>.
- Ríos-Touma, B. et al. 2012. Invertebrate drift and colonization processes in a tropical Andean stream. – *Aquat. Biol.* 14: 233–246.
- Rolls, R. J., et al. 2012. Mechanistic effects of low-flow hydrology on riverine ecosystems: ecological principles and consequences of alteration. – *Freshwater Sci.* 31: 1163–1186.
- Seager, R. et al. 2013. Projections of declining surface-water availability for the southwestern United States. – *Nat. Clim. Chang.* 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.
- Snelder, T. et al. 2012. Can bottom-up procedures improve the performance of stream classifications? – *Aquat. Sci.* 74: 45–59.
- Snelder, T. H. et al. 2013. Characterization of regional patterns of flow intermittence from gauging station records. – *Hydrol. Earth Syst. Sci.* 17: 2685–2699.
- Strobl, C. et al. 2008. Conditional variable importance for random forests. *BMC Bioinformatics* 9: 307.
- Stubbington, R. et al. 2009. The response of perennial and temporary headwater stream invertebrate communities to hydrological extremes. – *Hydrobiologia* 630: 299–312.

- Tachet, H. et al. 2000. *Invertébrés d'eau douce: systématique, biologie, écologie*. – CNRS éditions. Paris, France.
- Tonkin, J. D. et al. 2015. Environmental controls on river assemblages at the regional scale: an application of the elements of metacommunity structure framework. – *PloS one* 10:e0135450.
- Townsend, C. R. et al. 1997. The intermediate disturbance hypothesis, refugia, and biodiversity in streams. – *Limnol. Oceanogr.* 42: 938–949.
- Vander Vorste, R. et al. 2015a. Invertebrate communities in gravel-bed, braided rivers are highly resilient to flow intermittence. – *Freshwater Sci.* doi:10.1086/683274
- Vander Vorste, R. et al. 2015b. Is drift the primary process promoting the resilience of river invertebrate communities? A manipulative field experiment in an intermittent alluvial river. – *Freshwater Biol.* doi: 10.1111/fwb.12658
- Vellend, M. et al. 2008. Using subsets of species in biodiversity surveys. – *J. Appl. Ecol.* 45: 161–169.
- Vörösmarty, C. J. et al. 2010. Global threats to human water security and river biodiversity. – *Nature* 467: 555–561.
- Weiher, E. et al. 2011. Advances, challenges and a developing synthesis of ecological community assembly theory. – *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 366: 2403–2413.
- Wood, P. J. and Armitage, P. D. 2004. The response of the macroinvertebrate community to low-flow variability and supra-seasonal drought within a groundwater dominated stream. – *Arch. Hydrobiol.* 161: 1–20.

Supplementary material

Supplementary material (Appendix EXXXXX at <www.oikosoffice.lu.se/appendix>).

Appendix 1–4.

Figure captions

Figure 1: Goodness-of-fit (R^2) of random forests modelling the richness of macroinvertebrate communities of intermittent and perennial rivers in Australia and southwest Europe, using different combinations of flow metrics as predictor variables, as indicated. ANT, antecedent flow conditions; I, intermittent; LT, long-term flow conditions; P, perennial.

Figure 2: Partial dependence plots showing the shapes of relationships between important zero-flow metric predictors describing seasonality, duration or frequency and richness of macroinvertebrate communities of intermittent and perennial rivers in Australia and southwest Europe, as modelled by random forests. Plots are based on models using zero-flow metrics only except when indicated by an asterisk, for which models were based on all flow metrics. See Table 1 for detail on flow metrics.

Figure 3: Performance statistics for gradient forests modelling compositional turnover of macroinvertebrate families of Australian and southwest European intermittent rivers, using log-transformed sample-scale abundances as response and antecedent flow metrics as predictor variables. No. families $R^2 > 20\%$, number of families with R^2 greater than 20%; % families +ve R^2 , percentage of families (out of the total number of families in the relevant dataset) with positive R^2 .

Figure 4: a-b) Cumulative importance curves showing overall pattern of compositional change, for all families with positive R^2 in gradient-forest models, along gradients of the two zero-flow metrics that were important predictors of compositional turnover in intermittent

rivers of Australia (ant_NoZFspells) and southwest Europe (ant_mDurrZFspells). Steep parts of curves indicate ranges of the predictors where composition changes and the flatter regions indicate more homogenous portions. Plots are based on models using antecedent zero-flow metrics as predictor variables. c-d) Abundances of macroinvertebrate families contributing strongly to the overall R^2 of models (individual family $R^2 \geq 70\%$ of the mean across all families with positive R^2) along gradients of the same two zero-flow metrics.

Figure 5: Dissimilarity, as measured by Bray–Curtis on $\log_{10}(x+1)$ -transformed abundance data, from each observation in full dimensional space to its group spatial median. Grey shading indicates the cases for which multivariate dispersion was significantly higher in the moderately intermittent river class than the perennial river class. MI, moderately intermittent; SI, strongly intermittent; P, perennial; WI, weakly intermittent.

Tables

Table 1: Flow metrics used in this study to describe average, low-flow, high-flow and zero-flow conditions across key components of hydrological variation, calculated from the 12-mo period antecedent to biological sampling or the ≥ 30 -y, long-term period from 1970 onwards.

Conditions	Component	Antecedent	Long-term	Units
Average-flow	Magnitude	ant_MDF*	maMDF*	unitless
	Magnitude (variation in)	ant_cvMDF	cv_maMDF	unitless
	Timing/predictability	-	Pred	unitless
	Rate of change/flashiness	ant_maRRise	maRRise	$\text{m}^3 \text{s}^{-2}$
	Rate of change/flashiness	ant_maRFall	maRFall	$\text{m}^3 \text{s}^{-2}$
Low-flow	Magnitude	ant_P10*	maP10*	unitless
	Timing/predictability	-	maMeanJDMin	unitless
	Frequency	ant_NoP10spells	maNoP10spells	count/y
	Duration	ant_mDURP10spells	maDURP10spells	d
High-flow	Magnitude	ant_P90*	maP90*	unitless
	Timing/predictability	-	maMeanJDMax	unitless
	Frequency	ant_NoP90spells	maNoP90spells	count/y
	Duration	ant_mDURP90spells	maDURP90spells	d
Zero-flow	Timing/predictability	-	Sd6	unitless

Frequency	ant_NoZFspells	maNoZFspells	count/y
Duration	ant_mDurZFspells	maDurZFspells	d
Duration	ant_Zer	maZer	d

cv, coefficient of variation; Dur, duration of; ma, mean annual; mDur, mean duration of; MDF, mean daily flow; MeanJDMin, mean Julian date of the minimum flow; MeanJDMax, mean Julian date of the maximum flow; No, number of; P10, 10th percentile; P90, 90th percentile; Pred, Colwell's predictability; RFall, rate of fall; RRise, rate of rise; Sd6, see text for details; Zer, total number of zero-flow days.

* Divided by the MDF calculated from the relevant gauge's entire record (from 1970 onwards).