



Extreme weather events threaten biodiversity and functions of river ecosystems: evidence from a meta-analysis

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ABSTRACT

Both gradual and extreme weather changes trigger complex ecological responses in river ecosystems. It is still unclear to what extent trend or event effects alter biodiversity and functioning in river ecosystems, adding considerable uncertainty to predictions of their future dynamics. Using a comprehensive database of 71 published studies, we show that event – but not trend – effects associated with extreme changes in water flow and temperature substantially reduce species richness. Furthermore, event effects – particularly those affecting hydrological dynamics – on biodiversity and primary productivity were twice as high as impacts due to gradual changes. The synthesis of the available evidence reveals that event effects induce regime shifts in river ecosystems, particularly affecting organisms such as invertebrates. Among extreme weather events, dryness associated with flow interruption caused the largest effects on biota and ecosystem functions in rivers. Effects on ecosystem functions (primary production, organic matter decomposition and respiration) were asymmetric, with only primary production exhibiting a negative response to extreme weather events. Our meta-analysis highlights the disproportionate impact of event effects on river biodiversity and ecosystem functions, with implications for the long-term conservation and management of river ecosystems. However, few studies were available from tropical areas, and our conclusions therefore remain largely limited to temperate river systems. Further efforts need to be directed to assemble evidence of extreme events on river biodiversity and functioning.

Key words: flow interruption, floods, temperature, species richness, abundance, river ecosystem.

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I. INTRODUCTION

Extreme weather events are becoming more frequent and unpredictable as global warming and human activities jointly alter the water cycle (Evans & Boyer-Souchet, 2012; Ummenhofer & Meehl, 2017; Best & Darby, 2020). Changes in rainfall and temperature patterns have led to prolonged heatwaves, abrupt decreases in water flow, or large floods, which are subsequently altering temporal patterns of water flow in river networks over large areas of the Earth (Messenger *et al.*, 2021). Low water flow periods have become longer (Döll & Zhang, 2010) and, as a result, river systems experience progressively stronger transitions towards slow-flowing phases (Sabater, 2008) or are completely interrupted (Messenger *et al.*, 2021). Furthermore, these hydrological changes have altered sedimentological processes (Inman & Jenkins, 1999), and increased water temperatures (Morrill, Bales & Conklin, 2005; Kaushal *et al.*, 2010). At the other extreme of hydrological events, large floods have become more frequent (Hirabayashi *et al.*, 2013; Arnell & Gosling, 2016), and already produce long-term effects in larger rivers of the world (e.g. Espinoza *et al.*, 2022). Large floods may transform the geomorphological setting of river networks and, when catastrophic, produce long-lasting impacts on river biodiversity (Woodward *et al.*, 2015). Thus the type and intensity of extreme events, principally hydrological and climatic events, likely affect the biodiversity and ecosystem functioning of river ecosystems, yet the magnitude and direction of their impacts remain to be comprehensively synthesized.

Extreme events, which frequently overlap in time and space (Bowler *et al.*, 2020), vary in their impacts on biodiversity and ecosystem functions (Rillig *et al.*, 2019). Ecosystems impacted by frequent disturbances, such as river networks, host ecological communities and provide ecosystem functions that respond directly to water flow patterns (Thorp, Thoms & Delong, 2006). River systems are increasingly affected by gradual changes (*trend effects*) and extreme events (*event effects*; Jentsch, Kreyling & Bejerkuhnlein, 2007) in their hydrology and climate patterns. While gradual changes in water flow and temperature can be classified as press disturbances, extreme events are equivalent to pulse disturbances (Lake, 2000; Harris *et al.*, 2018). The impacts of press disturbances on biodiversity may be seen as continuous and gradual, leading to shifts in species distributions and community structure (e.g. Mantua, Tohver & Hamlet, 2010). The pace of changes due to press disturbances may allow for some

degree of adaptation, at least for some species (Benedetti-Cecchi *et al.*, 2006; Heino, Virkkala & Toivonen, 2009). By contrast, the impacts of pulse disturbances may lead to abrupt changes in environmental conditions, disproportionately affecting species with limited opportunities for adaptation (Harris *et al.*, 2018; Ledger & Milner, 2015).

Press or pulse disturbances may differentially affect the capacity of ecosystems to resist and recover structurally and functionally (Jentsch & White, 2019). Changes to community structure due to trend and event effects may cascade to ecosystem functions, with unknown consequences for biodiversity–ecosystem function relationships (Biggs *et al.*, 2020). In terrestrial ecosystems such as experimental grassland communities, biodiversity consistently buffers variation in ecosystem functioning (productivity) for both extreme wet and dry events (Isbell *et al.*, 2015). Functional redundancy, i.e. the extent to which multiple species perform similar roles in a community, may moderate the impacts of extreme climate events on ecosystem functions (Woodward *et al.*, 2015). Quantifying the relative importance of the impacts of trend- and event-driven disturbances on biodiversity and ecosystem functions of river ecosystems is essential for developing data-driven adaptation and mitigation strategies.

Herein we perform a comprehensive meta-analysis that evaluates the relative impacts of trend and event weather effects on the biodiversity and ecosystem functions of river ecosystems. We compiled a database of 199 effect sizes, including both observational and experimental studies, to determine whether: (i) event effects have stronger, negative impacts than those of trend effects on diversity, abundance, and biomass of river communities, based on the assumption that pulse effects are stronger than press effects; (ii) hydrological anomalies lead to stronger or weaker impacts than temperature anomalies on river ecosystems; (iii) the impacts of trend and event effects on ecosystem functions (decomposition, respiration, primary production) are weaker than impacts on biodiversity, since ecosystem functions may be maintained at pre-disturbance levels where functional redundancy is high.

II. METHODS

(1) Data collection

We used the *Web of Science* and *Scopus* databases to perform a comprehensive search of relevant studies (Gusenbauer & Haddaway, 2020). Entries up to March 2021 were included using a composite search string with hydrological and

climatic descriptors considering different ecological communities and functions of river ecosystems (the complete set of Boolean terms is provided as online supporting information in Appendix S1). Our search returned 30,847 references, which was reduced to 1,235 unique records after removing duplicates (PRISMA diagram, Appendix S2). We only retained peer-reviewed papers testing the effects of climate change on biodiversity or ecosystem functions. These papers had to use standardized sampling methods (in the field or the laboratory), with at least one control and impact treatment and more than three samples for each. We included species richness, density (number of individuals per unit area), and biomass as descriptors of biodiversity, while organic matter decomposition, respiration, and primary production were included as descriptors of ecosystem functions (Hooper *et al.*, 2012).

We extracted mean values, standard deviations, standard errors, and the number of samples in control and impact treatments from tables, text, or figures. If the mean abundance or standard deviation were not reported, we derived these from the total abundance, sample size, and standard error, if possible. Data from figures were extracted using Webplot Digitizer 3.4 (Rohatgi, 2015). We also retrieved information on four moderators that we anticipated could affect biodiversity and ecosystem functions (Table S1). Following the information provided by the authors, for each extracted data point we collected information on the ecological community, type of effect (trend or event), anomaly type (increase or decrease in water flow; increase or decrease in water temperature), and study type (experimental or observational).

In total, we built a database of 199 effect sizes from 71 studies (each observational or experimental treatment was considered as a replication unit), of which only 21 had both biodiversity and ecosystem function data. All studies included in the meta-analysis are identified in the reference list with an asterisk. Effect sizes were calculated as standardized mean differences (Hedges' g) using means, standard deviations, and sample sizes retrieved from each study. We used the *escalc* function in the *metafor* package in R (Viechtbauer, 2010) to compute Hedges' g and its respective variance. To account for differences in sampling variance, we weighted the estimated effect sizes by their sample size as recommended by Hamman *et al.* (2018). Effect sizes are presented as units of the pooled standard deviation, such that a value of 0.5 represents a difference equivalent to half of a standard deviation. Thus, negative values indicate that climate change, whether trend or event, had a negative impact on the variables, while positive values indicate the opposite. The complete list of data sources, effect sizes, and moderators is available at <https://doi.org/10.5281/zenodo.7004412>.

(2) Data analysis

We used hierarchical Bayesian models to analyse variation in effect sizes, as implemented in the *brms* package in R (Bürkner, 2017). To distinguish between the effect of trend

versus event effects and the anomaly type, we fitted a univariate model for each predictor variable, excluding the intercept. We chose this approach because intercept models for categorical predictors with more than two levels use only one as the reference against all others (Doherty *et al.*, 2020). We considered predictor variables important for all models when the 95% credible intervals (CIs) of the posterior estimates did not overlap with zero. We did not evaluate interactions between fixed effects because some combinations of variables (e.g. extreme temperature decrease) were poorly replicated. We ran four chains of 10,000 iterations each for each model, with a burn-in of 1000 iterations, resulting in a total of 36,000 samples. We assessed convergence by inspecting trace plots and ensuring that the Gelman–Rubin statistic was <1.1 (Gelman & Rubin, 1992).

We specified non-informative normal priors ($\mu = 0$, $\sigma = 10$) for the fixed effects and weakly informative half Cauchy priors ($\mu = 0$, $\sigma = 1$) for the random effects (Bürkner, 2018). We fitted models assuming a normal distribution and included random effects for the study identity, type, and duration to account for non-independence between effect sizes from the same study or study type. By incorporating these categorical factors as random effects, we assume that the biodiversity and ecosystem function responses will be more similar within the same study (ID) and similar types of study (observational or experimental). To identify an appropriate structure of random effects, we fitted and ranked five nested models containing different combinations of study ID and type as random effects. The ecological community could not be included as a random effect factor because the number of samples per class was highly unbalanced. Model ranking using leave-one-out cross-validation (Vehtari, Gelman & Gabry, 2017) indicated different random effects structures for each response variable (Table S2).

To avoid potential confounding effects of unusually adverse events, we decided to exclude data points falling outside the ranges of the biodiversity (−10.3 to 9.1) and ecosystem function (0.04 to −7.7) aspects. These ranges accounted for the 1st percentile of the distribution of effect sizes in biodiversity (effect sizes less than −10) and ecosystem function variables (effect sizes less than −7). Specifically, we did not include some of the results from Romero *et al.* (2019) and Truchy *et al.* (2020) (Hedges' g for biomass between −14 and −244), Geraldès, Pascoal & Cassio (2012) (Hedges' g for decomposition greater than −10), and Oprei, Zlatanovic & Mutz (2019) (Hedges' g for respiration greater than −10). The inclusion of these studies increased the magnitude of the effect size for extreme events although did not alter the reported trends.

We used a combination of funnel plots and Egger's tests (Egger *et al.*, 1997) to assess potential publication bias. Visual inspection of the funnel plot suggested no systematic asymmetry in effect sizes (Fig. S1), a result also supported by the non-significance of Egger's tests (Table S3). To assess the sensitivity of our analysis to the use of Hedges' g , we also ran a parallel meta-analysis using the log-response ratio (LRR) as

the effect size. To calculate the LRR we divided values from impact treatments by those in the control treatments and took the logarithm of this number. We used the *escale* function for this computation. Table S4 shows that our results are robust to the selection of the effect size, as the magnitude and direction of the effect sizes did not change significantly when comparing Hedges' *g* and LRR results.

All analyses and figures were performed using R v. 4.0.3 (R Core Team, 2020). Code and data are available at <https://doi.org/10.5281/zenodo.7004412>. We provide a completed PRISMA for Ecology and Evolutionary Biology (PRISMA-EcoEvo; O'Dea *et al.*, 2021) checklist in Table S5.

III. RESULTS

We analyzed 199 effect sizes for components of biodiversity (62 studies) and 100 effect sizes for ecosystem functions (26 studies) (see Table S4 for a summary of the effect sizes and their respective 95% credible intervals). The geographical distribution of the studies is shown in Fig. 1. Most studies were distributed in temperate and boreal regions in North America and Europe; very few were from tropical or arctic regions.

Our analysis of multiple components of river biodiversity revealed negative impacts of weather changes on species richness (Fig. 2). A univariate model for weather anomalies (trend *versus* event) revealed that these negative impacts were mainly due to extreme events [posterior mean of event: -1.08 (95%CI: -1.78 to -0.42), posterior mean of trend: 0.07 (95%CI: -0.73 to 0.9)]. The between-study heterogeneity variance of this model was estimated at $\tau = 0.75$ (95%CI: 0.06 – 1.5). A separate model for anomaly type showed that decreases in water flow caused the most dramatic impacts

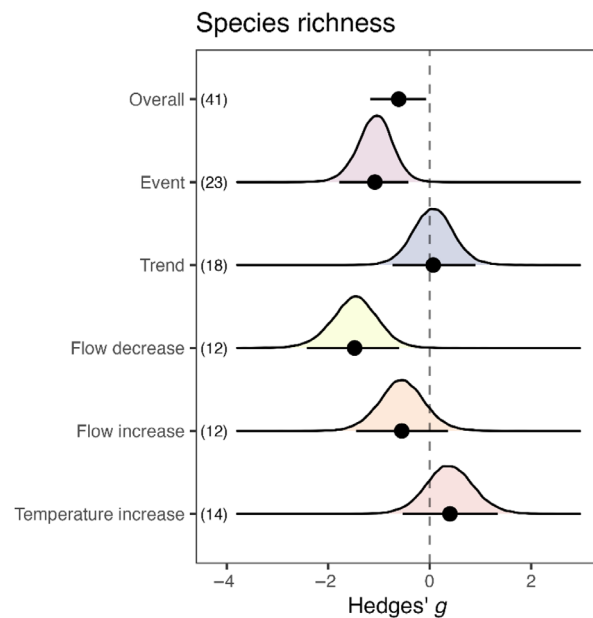


Fig. 2. Impacts of trend and event effects and anomaly type on species richness of river ecosystems. The distributions display the posterior probability of different effect sizes, dots corresponding to posterior means, and their horizontal bars to 95% credible intervals. The dashed line corresponds to an effect size of zero. Numbers in parentheses represent the sample size (i.e. number of effect sizes) for each predictor variable. Weather events, particularly flow decrease, had a significant impact on riverine species richness.

on species richness (posterior mean: -1.48 , CI: -2.42 to -0.60). The between-study heterogeneity variance of this model was estimated at $\tau = 0.83$ (95%CI: 0.18 – 1.46).

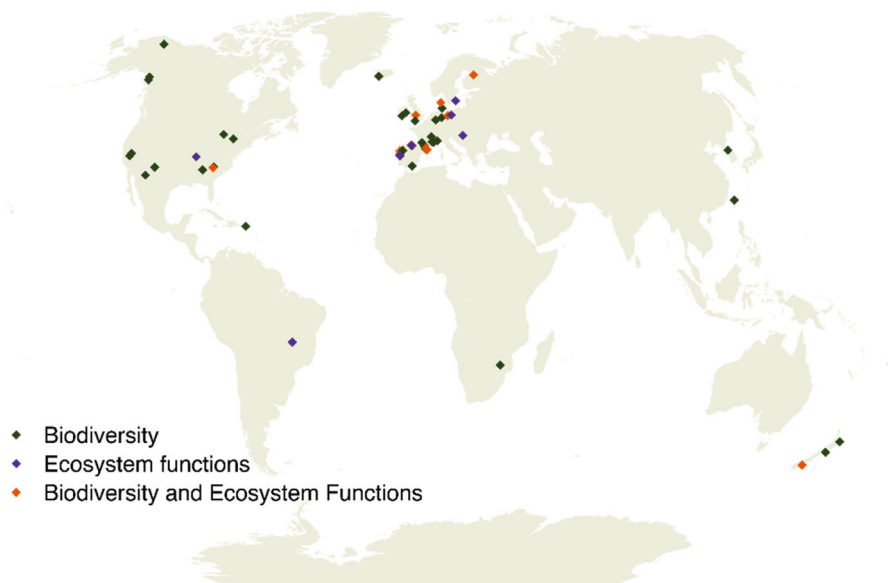


Fig. 1. Geographical distribution of the studies included in the meta-analysis. Different colours indicate whether studies contained data on biodiversity, ecosystem functions, or both.

Neither extreme increases in temperature nor water flow had detectable effects on species richness. In contrast to species richness, community density ($N = 85$) did not change consistently in response to trend or event effects (Table S4).

As was the case for species richness, community biomass showed an overall decrease in response to event effects and anomaly types (Fig. 3A, model's $\tau = -0.74$, 95%CI: -1.17 to -0.31). The decrease in community biomass was not significantly associated with trend effects (posterior mean: -0.62 , CI: -1.28 to 0.04), but the relationship was significant for event effects (posterior mean: -1.13 , CI: -1.84 to -0.41). A second model revealed that reduction in biomass is associated with increases in temperature and decreases in flow (Fig. 3A, model's $\tau = -1.04$, 95%CI: -1.89 to -0.19). However, the response of community biomass was not consistent across taxonomic groups. Independent models indicate that trend changes do not impair benthic algal

(biofilm) biomass (Fig. 3B), and that only extreme weather events affect fungal (posterior mean: -1.75 , CI: -3.41 to -0.09 ; model's $\tau = 1.08$, 95%CI: 0.04 – 2.96) (Fig. 3C) and invertebrate biomass (posterior mean: -1.46 , CI: -2.37 to -0.54 ; model's $\tau = 1.34$, 95%CI: 0.89 – 3.45) (Fig. 3D). We also found significant impacts of temperature increases and flow decreases on invertebrate biomass (model's $\tau = -1.48$, 95%CI: -2.53 to -0.43) (Fig. 3D).

Finally, our results did not show effects of anomaly type on most of the ecosystem functions (Fig. 4). Respiration (Fig. 4C) and organic matter decomposition (Fig. 4B) were not affected by either event or trend effects or anomaly type. The between-study heterogeneity variance of these models (type of effect: trend *versus* event) was estimated at $\tau = 0.98$ (95%CI: 0.06 – 2.20) for respiration; $\tau = 1.62$ (95%CI: 1.03 – 2.46) for decomposition; and $\tau = 0.83$ (95%CI: 0.03 – 2.61) for primary productivity. However, we found that

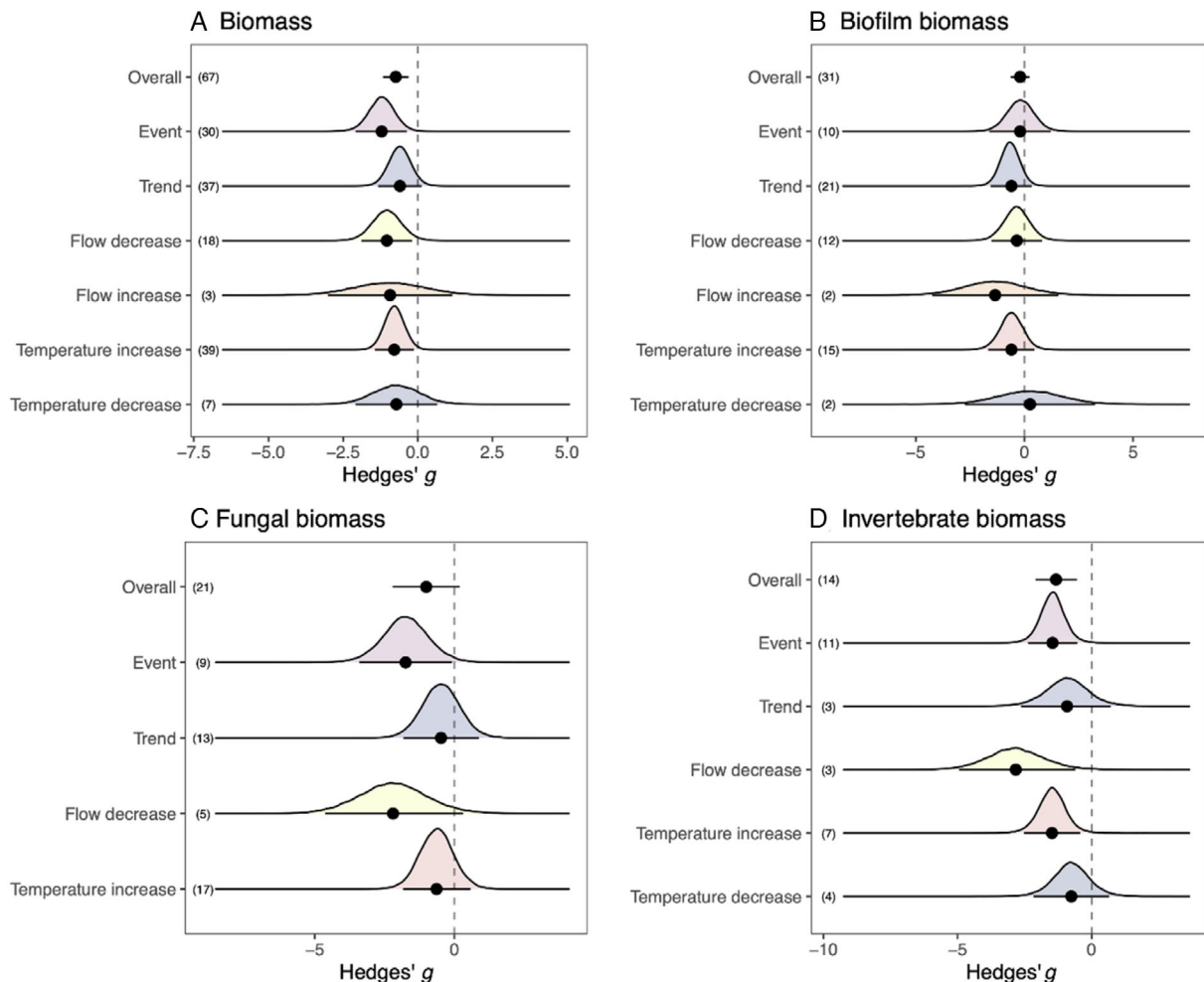


Fig. 3. Impacts of trend and event effects and anomaly type on the biomass of communities of river ecosystems (A), and on the biomass of biofilm (B), fungi (C) and invertebrate (D) communities. The distributions display the posterior probability of different effect sizes, with dots corresponding to posterior means and their horizontal bars to 95% credible intervals. The dashed line corresponds to an effect size of zero. Numbers in parentheses represent the sample size (i.e. number of effect sizes) for each predictor variable. Weather events (flow decrease) had a significant impact on biomass, mostly on that of invertebrates and fungi, but not on biofilm.

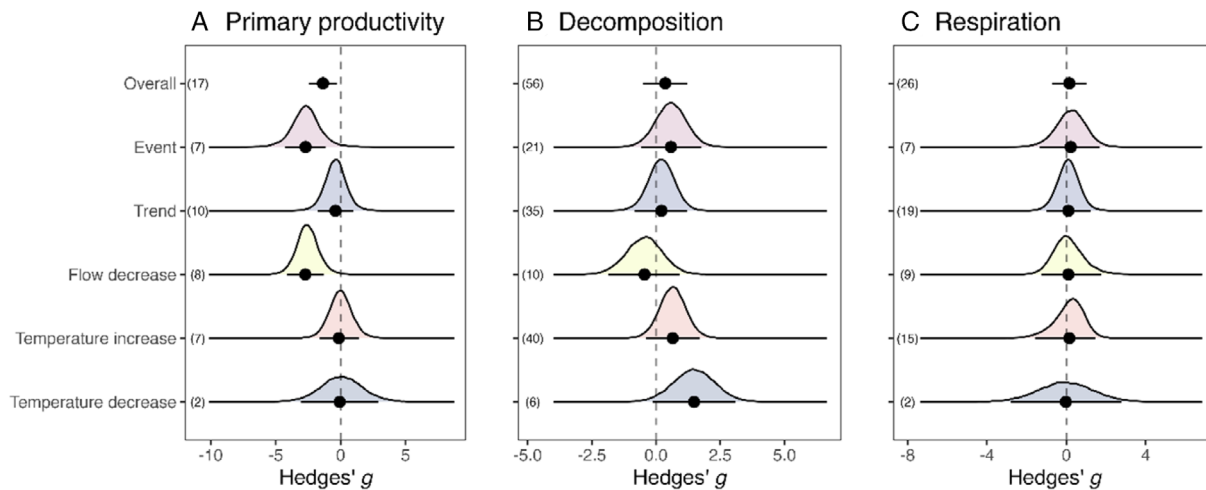


Fig. 4. Impacts of trend and event effects and anomaly type on ecosystem functions of rivers: (A) primary productivity, (B) decomposition, and (C) respiration. The distributions display the posterior probability of different effect sizes, with dots corresponding to posterior means, and their horizontal bars to 95% credible intervals. The dashed line corresponds to an effect size of zero. Numbers in parentheses represent the sample size (i.e. number of effect sizes) for each predictor variable. Only weather events, particularly flow decrease, had a significant effect, and only on primary productivity.

primary productivity was negatively affected by abrupt flow decreases (Fig. 4A, posterior mean: -2.73 , CI: -4.12 to -1.3). The between-study heterogeneity variance of these models (anomaly type) was estimated at $\tau = 1.05$ (95%CI: 0.05 – 2.73) for respiration; $\tau = 1.62$ (95%CI: 1.04 – 2.45) for decomposition; and $\tau = 0.88$ (95%CI: 0.04 – 2.46) for primary productivity.

IV. DISCUSSION

Ongoing changes in weather patterns may lead to transformative impacts on the biodiversity and ecosystem functions of river ecosystems across the globe. Here, we present a comprehensive meta-analysis showing that extreme weather events negatively affect the biodiversity of rivers, while of the ecosystem functions assessed, only primary productivity responded significantly, and only to weather events.

(1) Impacts on biodiversity of rivers

We found that extreme weather events had consistent, negative impacts on biodiversity (species richness and biomass) of river ecosystems. We determined that, on average, event effects on biodiversity were twice as strong as trend effects, which adheres to the definition of extreme event disturbances as localized, high-energy, rapid changes in environmental conditions (Peters *et al.*, 2011). Our results raise concerns about the future of riverine biodiversity since extreme events are increasingly frequent and will challenge the adaptation capacity of the biota (Ummerhofer & Meehl, 2017; Jentsch & White, 2019).

Event effects have driven considerable changes in a variety of ecosystems and biological compartments, spanning from soil microbiota (Fierer & Schimel, 2002), to meadow-dwelling insects (Piessens *et al.*, 2009), to fish foraging in coral reefs (Stuart-Smith *et al.*, 2021; Richardson *et al.*, 2018). In rivers, abrupt changes in water flow and temperature directly affect the habitat extent and suitability for organisms as they cause rapid variations in hydraulic and chemical conditions (Guse *et al.*, 2015; Petrovic *et al.*, 2011; Ponsati *et al.*, 2015). These variations challenge the adaptability of many species, with potential effects on the composition, diversity, and abundance of biological communities. Our results show that such effects differ for different biological compartments, with some being more vulnerable than others.

Our synthesis of the available evidence reveals that river biota do not exhibit consistent responses to extreme events. While the species richness and biomass of invertebrates were consistently negatively affected by water flow interruption, microbial communities showed inconsistent responses, ranging from non-significant effects for benthic algal (biofilm) biomass to decreases for fungal biomass. Rivers undergoing complete or abrupt flow interruptions experience dramatic declines in available habitat (Suren & Jowett, 2006; Pace, Bonada & Prat, 2013), leading to habitat fragmentation and to the prevalence of colonization–extinction processes. Only taxa with traits conferring resistance to low-flow conditions (usually associated with physical and chemical stressors, such as high temperatures, organic matter and fine sediment accumulations, and low dissolved oxygen levels) or prolonged droughts, will remain after an extreme event occurs (Townsend & Hildrew, 1994). The different responses obtained in our meta-analysis suggest that organisms with shorter life cycles (microbes) may resist and recover from

pulse disturbances (event effects) to a greater extent than organisms with longer lifespans. Shorter generation times, higher dispersal ability and greater heat, abrasion, and desiccation tolerance may confer microorganisms with a greater resistance to hydrological extremes (Sabater *et al.*, 2016; Chester & Robson, 2014).

By contrast with specific studies considered in our analysis (Gonçalves *et al.*, 2019; Romero *et al.*, 2019), we conclude that neither changes in water flow nor temperature affected biomass of microbes (except for fungi). The absence of detectable effects on microbial communities can be attributed to high heterogeneity among studies or perhaps to the inaccuracy of species richness as a measure of the impacts of environmental changes on river biodiversity (Hillebrand *et al.*, 2018). Losses of aquatic microbial species may favour the arrival of terrestrial species that are adapted to resist desiccation (Truchy *et al.*, 2020), which may alter the composition of the bacterial community, but not necessarily its richness (following a rather general pattern across ecosystems; Blowes *et al.*, 2019). Alternatively, the limited response of microbial biomass to hydrological disturbances suggests that other factors, such as the availability of resources or biological interactions, may enhance resistance (Krauss *et al.*, 2011). Water flow reduction, for example, does not reduce benthic algal biomass because lower flow primarily reduces grazing pressure (Truchy *et al.*, 2020).

Invertebrates are the biological group for which the most detailed evidence is available regarding responses to environmental effects. While several studies have determined that changes in the distribution, diversity and abundance of invertebrates are associated with long-term increases in water temperature or flow patterns (Durance & Ormerod, 2007; Domisch *et al.*, 2013), our analysis concludes that invertebrate richness and biomass are mostly sensitive to sudden (event) changes in water temperature and flow. Abrupt changes such as extreme droughts may induce effects on diversity (Bogan, Boersma & Lytle, 2015), mostly by affecting the most sensitive taxa (Piggot *et al.*, 2015a; Madji *et al.*, 2020). Ephemeroptera, Plecoptera and Trichoptera are the most affected groups of invertebrates, likely because they tend to be adapted to cold and highly oxygenated water, and they adapt poorly to warmer temperatures, lower dissolved oxygen levels, and shrinking waters (Céréghino, Boutet & Lavandier, 1997; Tierno de Figueroa *et al.*, 2010). It has been observed that unseasonal or suprasonal flow interruptions (Lake, 2003) can cause unpredictable effects on macroinvertebrate richness and biomass, especially in permanent systems (Hill *et al.*, 2019). Several studies included in our meta-analysis show that flow interruptions may result in extensive loss of individuals and species (Calapez *et al.*, 2014; Dewson, James & Death, 2007), thereby directly affecting species richness and biomass. Direct effects of water flow interruption not only challenge the resistance of invertebrate communities, but also their recovery because the colonization rate of drifting and flying invertebrates is a function of the distance to drought refuges (Vander Vorste, Malard & Datry, 2015).

In contrast to interruptions in water flow, floods did not show consistent impacts on either species richness or biomass. While flood events may lead to losses of algae and macroinvertebrates *via* physical disturbance and washout (the scouring effect; Feeley *et al.*, 2012) and cause important changes in the geomorphological structure of rivers, they do not necessarily affect all taxonomic groups similarly (Piniewski *et al.*, 2017). This variability may reflect the differential ability of organisms to find shelter and the differential capacity of populations to recover quickly after floods subside (response diversity; Hershkovitz & Gasith, 2013). Our meta-analysis included several studies describing the effects of catastrophic floods (Tsai *et al.*, 2014; Feeley *et al.*, 2012; Foord & Fouché, 2016), which indeed reported large changes in the biomass of algae or invertebrates. Species loss of macroinvertebrates is most likely related to substratum movement and associated drift, and taxa inhabiting riffle areas (e.g. blackflies) are the most affected (Milner *et al.*, 2013). However, with certain exceptions (e.g. Hynes, 1970; Woodward *et al.*, 2015), studies monitoring the responses of invertebrate communities after floods have shown rapid invertebrate recovery (Herbst *et al.*, 2019; Baillie *et al.*, 2020), with an initial decline in abundance usually followed by a rapid increase in both abundance and species richness. Moderate floods may even enhance the mobility of nutrients and sediment, and the complexity of the river habitat (Death, Fuller & Macklin, 2015). Floods may therefore confer a competitive advantage to invertebrates with rapid development of aerial stages, asynchronous egg hatching, and synchronized metamorphosis with flood timing (Lytle & Poff, 2004).

Compared to water flow, we found that temperature changes induced few direct and indirect effects on the biomass of stream biota. Moderate short-term warming has not been found to cause substantial effects on the biomass of biofilm communities (Romero *et al.*, 2019), but sustained warming may increase the functional richness and diversity of benthic microbial communities (Ylla, Canhoto & Román, 2014). Warming generally enhances microbial activity (Diaz Villanueva, Albariño & Canhoto, 2011) but may cause changes in resource acquisition (Romero *et al.*, 2019). In macro-organisms, warming may produce direct effects on the metabolism, leading to increased growth rates and smaller size at maturity. Indirect effects on macro-organism survival occur through changes in the availability and quality of basal resources (Piggot *et al.*, 2015b; Hogg & Williams, 1996), which may account for our observed decrease in invertebrate biomass in response to warming (Fig. 3D).

(2) Impacts on ecosystem functions of rivers

Contrasting with responses in biodiversity, the ecosystem functions of rivers did not exhibit consistent, negative responses to weather variability. Only primary productivity exhibited a negative response to event effects, largely due to a negative response to extreme water flow decreases. Neither

respiration nor organic matter decomposition were affected by trend or event effects.

This synthesis of available evidence reveals that extreme water flow reduction consistently reduces primary productivity. Low flow, particularly during certain periods (e.g. summer), consistently decreases stream width and water velocity, favours higher water temperature, and reduces nutrient uptake (Riis *et al.*, 2017). The physical constraints imposed by low water velocity (and associated higher thickness of the boundary layer over the stream bottom) have been found to lead to consistent decreases in net and gross primary production (Riis *et al.*, 2017; Arias-Font *et al.*, 2021), moving the balance from autotrophic to heterotrophic (Acuña *et al.*, 2015; Romero *et al.*, 2019). This shift towards heterotrophy is probably due to collapse of the photosynthetic capacity of primary producers under dry conditions (Colls *et al.*, 2021).

The lack of response of respiration and decomposition to trend or event effects in our meta-analysis does not support results of previous case studies showing that extreme events affect organic matter decomposition in river ecosystems. A recent study showed that the effects of drying on shredders did not affect leaf litter decomposition (Carey, Chester & Robson, 2021), highlighting the variable or uncertain outcomes of interactions among climate, water quality, and decomposers (Bernabé *et al.*, 2018). The response of microbial decomposition to changes in water stress is highly context dependent, reflecting differential responses of microbial communities to temperature, nutrient, and oxygen levels (Duarte *et al.*, 2017). Our meta-analysis indicates that extreme events can reduce fungal biomass, which is associated with decomposing substrates, while decomposition itself remained unaffected. Gonçalves *et al.* (2019) showed that fungal biomass and diversity decreased after experimentally reducing water flow by 74–88%, but that ecosystem functions were maintained, suggesting that fungal communities have high functional redundancy. Similarly, Arias-Real *et al.* (2022) found that a reduction in species richness did not alter decomposition rates in fungal communities with initial higher richness. Species-rich communities exhibit a wider range of ecological and functional responses to stressors than less-diverse communities, making them more resistant to disturbances (McLean *et al.*, 2019). Overall, the apparent discrepancy between biodiversity and functional responses of river ecosystems to hydrological and climate trends and events highlights the role that functional redundancy (Biggs *et al.*, 2020) may have on conserving the provisioning of ecological functions.

(3) Caveats of the analysis

While our meta-analysis revealed stronger effects from extreme weather events, we recognize that our results may reflect limitations associated with the distribution, type, and number of studies. We found few studies from Asia, Africa, and South America, whose river ecosystems show specific differences (e.g. Dudgeon, 2008; Petsch *et al.*, 2020; González-Trujillo *et al.*, 2021) compared with the temperate ecosystems

that comprise most effect sizes in our study. Secondly, only a small number of studies provided initial conditions to be compared with data after disturbances (Peters *et al.*, 2011). This is an essential requirement for quantifying effect sizes. Due to this constraint, we included studies from a variety of contexts, ranging from field observations, to manipulative field studies, to experimental studies in the laboratory. Including this variety of studies to enable sufficient statistical power may, however, restrict the transferability of our results to real-world ecosystems, as the magnitude of climate change treatments frequently exceeds model-based projections (Korell *et al.*, 2020). Thirdly, the data gaps for ecosystem functions, which are pervasive (von Schiller *et al.*, 2017), did not allow us to define the temporal frame or period under which trend or event effects are more (or less) damaging (Trisos, Merow & Pigot, 2020). It should be kept in mind that most studies conducted so far on ecosystem functions have been performed under controlled conditions, at relatively short spatial and temporal scales (Estes *et al.*, 2018) and exclude biotic components that may also contribute to ecosystem functions (e.g. detritivores in decomposition studies and grazers in primary production studies).

Finally, the low sample size also affected our ability to quantify precisely the impacts of weather anomalies, particularly for groups such as fish or bacteria. There is need for a larger number of studies to reduce between-studies heterogeneity (our measured τ) and provide more accurate estimates. We dealt with imperfect data availability by conducting a Bayesian meta-analysis, which allows direct modelling of the uncertainty of τ estimates and improves estimations of the pooled effects when the number of included studies is small (McNeish, 2016). Bayesian methods produce full posterior distributions that allow comparison of the whole spectrum of impact levels caused by trend or event effects.

Despite these caveats, our meta-analysis is the most comprehensive to date on the impacts of hydrology and climate trends and events on the biodiversity and ecosystem functions of river ecosystems. Future research should aim to expand how the impacts of trend and event effects on river ecosystems are quantified in terms of biodiversity or ecosystem functions in order to test the differential effects of extreme stressors and their consequences for the future of rivers. We call on future investigators to measure the impacts of statistically unusual events (i.e. above the 99th percentile) using standardized protocols.

V. CONCLUSIONS

- (1) Our study provides insights into the impacts of extreme weather events on the maintenance of biodiversity and ecosystem functions in river ecosystems.
- (2) We found evidence that substantial changes may occur at population and community levels, but mostly for larger organisms such as invertebrates.

- (3) Even though impacts on ecosystem functions are less evident, primary productivity was particularly impacted by extreme conditions.
- (4) Strong, negative impacts of certain types of anomalies, especially water flow interruption, cause effects that may shift biodiversity and (at least some) ecosystem functions irreversibly beyond their dynamic stable states (Trisos *et al.*, 2020).
- (5) Evidence that weather extremes may have long-lasting impacts on the biodiversity and ecosystem functioning of river ecosystems already exists. The Millennium drought in Australia (1997–2009) led to some rivers being unable to recover to pre-drought flow regimes (Peterson *et al.*, 2021), with these river ecosystems providing examples of ‘no turning back’ in response to weather extremes that cause irreversible effects.

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VII. AUTHOR CONTRIBUTIONS

S. S. and J. L.-D. designed the study. S. S., J. L.-D., A. F., L. J. and N. P. extracted data from the text, tables, figures, or supplementary information in the reviewed papers. J. D. G.-T. performed the statistical analyses. S. S. and J. D. G.-T. led the writing, and all other authors discussed and contributed to revisions.

VIII. REFERENCES

References used in the meta-analysis are identified with an asterisk (*).

- ACUÑA, V., CASELLAS, M., CORCOLL, N., TIMONER, X. & SABATER, S. (2015). Increasing extent of periods of no flow in intermittent waterways promotes heterotrophy. *Freshwater Biology* **60**(9), 1810–1823.
- *ARCHDEACON, T. P., DIVER-FRANSSSEN, T. A., BERTRAND, N. G. & GRANT, J. D. (2020). Drought results in recruitment failure of Rio Grande silvery minnow (*Hybognathus amarus*), an imperiled, pelagic broadcast-spawning minnow. *Environmental Biology of Fishes* **103**(9), 1033–1044.
- *ARIAS-FONT, R., KHAMIS, K., MILNER, A. M., SAMBROOK SMITH, G. H. & LEDGER, M. E. (2021). Low flow and heatwaves alter ecosystem functioning in a stream mesocosm experiment. *Science of the Total Environment* **777**, 146067.
- ARIAS-REAL, R., GUTIÉRREZ-CÁNOVAS, C., MUÑOZ, I., PASCOAL, C. & MENÉNDEZ, M. (2022). Fungal biodiversity mediates the effects of drying on freshwater ecosystem functioning. *Ecosystems* **25**, 780–794.
- ARNELL, N. W. & GOSLING, S. N. (2016). The impacts of climate change on river flood risk at the global scale. *Climate Change* **134**, 387–401.
- *ARROITA, M., FLORES, L., LARRAÑAGA, A., MARTÍNEZ, A., MARTÍNEZ-SANTOS, M., PEREDA, O., RUIZ-ROMERA, E., SOLAGAISTUA, L. & ELOSEGI, A. (2016). Water abstraction impacts stream ecosystem functioning via wetted-channel contraction. *Freshwater Biology* **62**(2), 243–257.
- *BAILLIE, B. R., EVANSON, A. W., KIMBERLEY, M. O. & BERGIN, D. O. (2020). Combined effects of an anthropogenic (forest harvesting) and natural (extreme rainfall event) disturbance on headwater streams in New Zealand. *Freshwater Biology* **65**(10), 1806–1823.
- *BATISTA, D., PASCOAL, C. & CÁSSIO, F. (2012). Impacts of warming on aquatic decomposers along a gradient of cadmium stress. *Environmental Pollution* **169**, 35–41.
- BENEDETTI-CECCHI, L., BERTOCCHI, I., VASELLI, S. & MAGGI, E. (2006). Temporal variance reverses the impact of high mean intensity of stress in climate change experiments. *Ecology* **87**(10), 2489–2499.
- BERNABÉ, T. N., DE OMEGA, P. M., DOS SANTOS, V. P., DE SIQUEIRA, V. M., DE OLIVEIRA, V. M. & ROMERO, G. Q. (2018). Warming weakens facilitative interactions between decomposers and detritivores, and modifies freshwater ecosystem functioning. *Global Change Biology* **24**(7), 3170–3186.
- BEST, J. & DARBY, S. E. (2020). The pace of human-induced change in large rivers: stresses, resilience, and vulnerability to extreme events. *One Earth* **2**(6), 510–514.
- BIGGS, C. R., YEAGER, L. A., BOLSER, D. G., BONSELL, C., DICHIERA, A. M., HOU, Z., KEYSER, S. R., KHURSIGARA, A. J., LU, K., MUTH, A. F., NEGRETE, B. JR. & ERISMAN, B. A. (2020). Does functional redundancy affect ecological stability and resilience? A review and meta-analysis. *Ecosphere* **11**(7), e03184.
- BLOWES, S. A., SUPP, S. R., ANTAO, L. H., BATES, A., BRUELHEIDE, H., CHASE, J. M., MOYES, F., MAGURRAN, A., MCGILL, B., MYERS-SMITH, I. H., WINTER, M., BJORKMAN, A. D., BOWLER, D. E., BYRNES, J. E. K., GONZALEZ, A., *ET AL.* (2019). The geography of biodiversity change in marine and terrestrial assemblages. *Science* **366**(6463), 339–345.
- *BOERSMA, K. S., BOGAN, M. T., HENRICH, B. A. & LYTLE, D. A. (2013). Invertebrate assemblages of pools in arid-land streams have high functional redundancy and are resistant to severe drying. *Freshwater Biology* **59**(3), 491–501.
- BOGAN, M. T., BOERSMA, K. S. & LYTLE, D. A. (2015). Resistance and resilience of invertebrate communities to seasonal and suprasedasonal drought in arid-land headwater streams. *Freshwater Biology* **60**(12), 2547–2558.
- *BOULÉTREAU, S., LYAUTEY, E., DUBOIS, S., COMPIN, A., DELATTRE, C., TOURON BODILIS, A., MASTRORILLO, S. & GARABETIAN, F. (2014). Warming-induced changes in denitrifier community structure modulate the ability of phototrophic river biofilms to denitrify. *Science of the Total Environment* **466–467**, 856–863.
- BOWLER, D. E., BJORKMAN, A. D., DORNELAS, M., MYERS-SMITH, I. H., NAVARRO, L. M., NIAMIR, A., SUPP, S. R., WALDOCK, C., WINTER, M., VELLEND, M., BLOWES, S. A., BÖHNING-GAESE, K., BRUELHEIDE, H., ELAHI, R., ANTAO, L. H., *ET AL.* (2020). Mapping human pressures on biodiversity across the planet uncovers anthropogenic threat complexes. *People and Nature* **2**, 380–394.
- BÜRKNER, P. C. (2017). brms: An R package for Bayesian multilevel models using Stan. *Journal of Statistical Software* **80**(1), 1–28.
- BÜRKNER, P. C. (2018). Advanced Bayesian multilevel modeling with the R package brms. *The R Journal* **10**(1), 395–411.
- *CALAPEZ, A. R., ELIAS, C. L., ALMEIDA, S. F. P. & FEIO, M. J. (2014). Extreme drought effects and recovery patterns in the benthic communities of temperate streams. *Limnetica* **33**(2), 281–296.
- CAREY, N., CHESTER, E. T. & ROBSON, B. J. (2021). Flow regime change alters shredder identity but not leaf litter decomposition in headwater streams affected by severe, permanent drying. *Freshwater Biology* **66**(9), 1813–1830.
- CEREGHINO, R., BOUTET, T. & LAVANDIER, P. (1997). Abundance, biomass, life history and growth of six Trichoptera species under natural and hydropeaking conditions with hypolimnetic releases in a Pyrenean stream. *Archiv für Hydrobiologie* **138**(3), 307–328.
- CHESTER, E. T. & ROBSON, B. J. (2014). Do recolonisation processes in intermittent streams have sustained effects on benthic algal density and assemblage composition? *Marine and Freshwater Research* **65**(9), 784–790.
- COLLS, M., TIMONER, X., FONT, C., ACUÑA, V. & SABATER, S. (2021). Biofilm pigments in temporary streams indicate duration and severity of drying. *Limnology and Oceanography* **66**(9), 3313–3326.
- *COVICH, A. P., CROWL, T. A. & SCATENA, F. N. (2003). Effects of extreme low flows on freshwater shrimps in a perennial tropical stream. *Freshwater Biology* **48**(7), 1199–1206.
- DEATH, R. G., FULLER, I. C. & MACKLIN, M. G. (2015). Resetting the river template: the potential for climate-related extreme floods to transform river geomorphology and ecology. *Freshwater Biology* **60**(12), 2477–2496.
- *DELGADO, C., ALMEIDA, S. F. P., ELIAS, C. L., FERREIRA, V. & CANHOTO, C. (2017). Response of biofilm growth to experimental warming in a temperate stream. *Ecology* **10**(6), e1868.

- *DEWSON, Z. S., JAMES, A. B. W. & DEATH, R. G. (2007). Invertebrate community responses to experimentally reduced discharge in small streams of different water quality. *Journal of the North American Benthological Society* **26**(4), 754–766.
- *DIAZ VILLANUEVA, V., ALBARIÑO, R. & CANHOTO, C. (2011). Detritivores feeding on poor quality food are more sensitive to increased temperatures. *Hydrobiologia* **678**(1), 155–165.
- DOHERTY, T. S., BALOUCH, S., BELL, K., BURNS, T. J., FELDMAN, A., FIST, C., GARVEY, T. F., JESSOP, T. S., MEIRI, S. & DRISCOLL, D. A. (2020). Reptile responses to anthropogenic habitat modification: a global meta-analysis. *Global Ecology and Biogeography* **29**(7), 1265–1279.
- DÖLL, P. & ZANG, J. (2010). Impact of climate change on freshwater ecosystems: a global-scale analysis of ecologically relevant river flow alterations. *Hydrology and Earth System Sciences* **14**(5), 783–799.
- DOMISCH, S., ARAÚJO, M. B., BONADA, N., PAULS, S. U. & JÄHNIG, S. C. (2013). Modelling distribution in European stream macroinvertebrates under future climates. *Global Change Biology* **19**(3), 752–762.
- DUARTE, S., MORA-GÓMEZ, J., ROMANÍ, A. M., CÁSSIO, F. & PASCOAL, C. (2017). Responses of microbial decomposers to drought in streams may depend on the environmental context. *Environmental Microbiology Reports* **9**(6), 756–765.
- DUDGEON, D. (2008). *Tropical Stream Ecology*. Academic Press, Elsevier, London.
- DURANCE, I. & ORMEROD, S. J. (2007). Climate change effects on upland stream macroinvertebrates over a 25-year period. *Global Change Biology* **13**(5), 942–957.
- EGGER, M., SMITH, G. D., SCHNEIDER, M. & MINDER, C. (1997). Bias in meta-analysis detected by a simple, graphical test. *British Medical Journal* **315**(7109), 629–634.
- ESPINOZA, J.-C., MARENGO, J. A., SCHONGART, J. & JIMÉNEZ, J. C. (2022). The new historical flood of 2021 in the Amazon River compared to major floods of the 21st century: atmospheric features in the context of the intensification of floods. *Weather and Climate Extremes* **35**, 100406.
- ESTES, L., ELSÉN, P. R., TREUER, T., AHMED, L., CAYLOR, K., CHANG, J., CHOI, J. J. & ELLIS, E. C. (2018). The spatial and temporal domains of modern ecology. *Nature Ecology and Evolution* **2**(5), 819–826.
- EVANS, J. P. & BOYER-SOUCHET, I. (2012). Local sea surface temperatures add to extreme precipitation in Northeast Australia during La Niña. *Geophysical Research Letters* **39**, L10803.
- *FEELEY, H. B., DAVIS, S., BRUEN, M., BLACKLOCKE, S. & KELLY-QUINN, M. (2012). The impact of a catastrophic storm event on benthic macroinvertebrate communities in upland headwater streams and potential implications for ecological diversity and assessment of ecological status. *Journal of Limnology* **71**(2), 309–318.
- *FENOGLIO, S., BO, T., CUCCO, M. & MALACARNE, G. (2007). Response of benthic invertebrate assemblages to varying drought conditions in the Po river (NW Italy). *Italian Journal of Zoology* **74**(2), 191–201.
- *FERNANDES, I., UZUN, B., PASCOAL, C. & CÁSSIO, F. (2009). Responses of aquatic fungal communities on leaf litter to temperature-change events. *International Review of Hydrobiology* **94**(4), 410–418.
- *FERREIRA, V. & CANHOTO, C. (2015). Future increase in temperature may stimulate litter decomposition in temperate mountain streams: evidence from a stream manipulation experiment. *Freshwater Biology* **60**(5), 881–892.
- *FERREIRA, V., CHAUVET, E. & CANHOTO, C. (2015). Effects of experimental warming, litter species, and presence of macroinvertebrates on litter decomposition and associated decomposers in a temperate mountain stream. *Canadian Journal of Fisheries and Aquatic Sciences* **72**(2), 206–216.
- FIERER, N. & SCHIMEL, J. P. (2002). Effects of drying–rewetting frequency on soil carbon and nitrogen transformations. *Soil Biology and Biochemistry* **34**(6), 777–787.
- *FOORD, S. H. & FOUCHÉ, P. S. O. (2016). Response of instream animal communities to a short-term extreme event and to longer-term cumulative impacts in a strategic water resource area, South Africa. *African Journal of Aquatic Science* **41**(1), 29–40.
- *FOUCREAU, N., PISCART, C., PUJALON, S. & HERVANT, F. (2016). Effects of rising temperature on a functional process: consumption and digestion of leaf litter by a freshwater shredder. *Fundamental and Applied Limnology* **187**(4), 295–306.
- GELMAN, A. & RUBIN, D. B. (1992). Inference from iterative simulation using multiple sequences. *Statistical Science* **7**(4), 457–472.
- *GERALDES, P., PASCOAL, C. & CÁSSIO, F. (2012). Effects of increased temperature and aquatic fungal diversity on litter decomposition. *Fungal Ecology* **5**(6), 734–740.
- *GIONCHETTA, G., OLIVA, F., MENÉNDEZ, M., LÓPEZ-LASERAS, P. & ROMANÍ, A. M. (2019). Key role of streambed moisture and flash storms for microbial resistance and resilience to long-term drought. *Freshwater Biology* **64**(2), 306–322.
- *GONÇALVES, A. L., SIMÕES, S., BÄRLOCHER, F. & CANHOTO, C. (2019). Leaf litter microbial decomposition in salinized streams under intermittency. *Science of the Total Environment* **653**(25), 1204–1212.
- GONZÁLEZ-TRUJILLO, J. D., SAITO, V. S., PETSCH, D. K., MUÑOZ, I. & SABATER, S. (2021). Historical legacies and contemporary processes shape beta diversity in Neotropical montane streams. *Journal of Biogeography* **48**(1), 101–117.
- *GOSSIAUX, A., JABIOL, J., POUPIN, P., CHAUVET, E. & GUÉROLD, F. (2019). Seasonal variations overwhelm temperature effects on microbial processes in headwater streams: insights from a temperate thermal spring. *Aquatic Sciences* **81**(2), 30.
- *GROSSMAN, G. D., SUNDIN, G. & RATAJCAK, R. E. JR. (2016). Long-term persistence, density dependence and effects of climate change on rosyside dace (Cyprinidae). *Freshwater Biology* **61**(6), 832–847.
- GUSE, B., KAIL, J., RADINGER, J., SCHRODER, M., KIESEL, J., HERING, D., WOLTER, C. & FOHRER, N. (2015). Eco-hydrologic model cascades: simulating land use and climate change impacts on hydrology, hydraulics and habitats for fish and macroinvertebrates. *Science of the Total Environment* **533**, 542–556.
- GUSENBAUER, M. & HADDAWAY, N. R. (2020). Which academic search systems are suitable for systematic reviews or meta-analyses? Evaluating retrieval qualities of Google scholar, PubMed, and 26 other resources. *Research Synthesis Methods* **11**(2), 181–217.
- *HAAG, W. R. & WARREN, M. L. JR. (2008). Effects of severe drought on freshwater mussel assemblages. *Transactions of the American Fisheries Society* **137**(4), 1165–1178.
- HAMMAN, E. A., PAPPALARDO, P., BENICE, J. R., PEACOR, S. D. & OSENBERG, C. W. (2018). Bias in meta-analyses using Hedges' d. *Ecosphere* **9**(9), e02419.
- HARRIS, R. M. B., BEAUMONT, L. J., VANCE, T. R., TOZER, C. R., REMENYI, T. A., PERKINS-KIRKPATRICK, S. E., MITCHELL, P. J., NICOTRA, A. B., MCGREGOR, S., ANDREW, N. R., LETNIC, M., KEARNEY, M. R., WERNBERG, T., HUTLEY, L. B., CHAMBERS, L. E., ET AL. (2018). Biological responses to the press and pulse of climate trends and extreme events. *Nature Climate Change* **8**, 579–587.
- HEINO, J., VIRKKALA, R. & TOIVONEN, H. (2009). Climate change and freshwater biodiversity: detected patterns, future trends and adaptations in northern regions. *Biological Reviews* **84**(1), 39–54.
- *HERBST, D. B. & COOPER, S. D. (2010). Before and after the deluge: rain-on-snow flooding effects on aquatic invertebrate communities of small streams in the Sierra Nevada, California. *Journal of the North American Benthological Society* **29**(4), 1354–1366.
- *HERBST, D. B., COOPER, S. D., MEDHURST, R. B., WISEMAN, S. W. & HUNSAKER, C. T. (2019). Drought ecophysiology alters the structure and function of benthic invertebrate communities in mountain streams. *Freshwater Biology* **64**(5), 886–902.
- HERSHKOVITZ, Y. & GASITH, A. (2013). Resistance, resilience, and community dynamics in mediterranean-climate streams. *Hydrobiologia* **719**(1), 59–75.
- HILL, M. J., MATHERS, K. L., LITTLE, S., WORRAL, T., GUNN, J. & WOOD, P. J. (2019). Ecological effects of a supra-seasonal drought on macroinvertebrate communities differ between near-perennial and ephemeral river reaches. *Aquatic Science* **81**(4), 62.
- HILLEBRAND, H., LANGENHEDER, S., LEBRET, K., LINDSTROM, E., OSTMAN, O. & STRIEBEL, M. (2018). Decomposing multiple dimensions of stability in global change experiments. *Ecology Letters* **21**(1), 21–30.
- HIRABAYASHI, Y., MAHENDRAN, R., KOIRALA, S., KONOSHIMA, L., YAMAZAKI, D., WATANABE, S., KIM, H. & KANAE, S. (2013). Global flood risk under climate change. *Nature Climate Change* **3**, 816–821.
- *HOGG, I. D. & WILLIAMS, D. D. (1996). Response of stream invertebrates to a global-warming thermal regime: an ecosystem-level manipulation. *Ecology* **77**(2), 395–407.
- *HOOD, J. M., BENSTEAD, J. P., CROSS, W. F., HURYN, A. D., JOHNSON, P. W., GÍSLASON, G. M., JUNKER, J. R., NELSON, D., ÓLAFSSON, J. S. & TRAN, C. (2017). Increased resource use efficiency amplifies positive response of aquatic primary production to experimental warming. *Global Change Biology* **24**(3), 1069–1084.
- HOOPER, D. U., ADAIR, E. C., CARDINALE, B. J., BYRNES, J. E., HUNGATE, B. A., MATULICH, K. L., GONZALEZ, A., DUFFY, J. E., GAMFELDT, L. & O'CONNOR, M. I. (2012). A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* **486**(7401), 105–108.
- HYNES, H. B. N. (1970). *The Ecology of Running Waters*. Toronto: U Toronto Press.
- INMAN, D. L. & JENKINS, S. A. (1999). Climate change and the episodicity of sediment flux of small California rivers. *The Journal of Geology* **107**(3), 251–270.
- ISELL, F., CRAVEN, D., CONNOLLY, J., LOREAU, M., SCHMID, B., BEIERKUHNLIN, C., MARTIJN BEZEMER, T., BONIN, C., BRUELHEIDE, H., DE LUCA, E., EBELING, A., GRIFFIN, J. N., GUO, Q., HAUTIER, Y., HECTOR, A., ET AL. (2015). Biodiversity increases the resistance of ecosystem productivity to climate extremes. *Nature* **526**, 574–577.
- JENTSCH, A., KREYLING, J. & BEJERKUHNLIN, C. (2007). A new generation of climate-change experiments: events, not trends. *Frontiers in Ecology and the Environment* **5**(7), 365–374.
- JENTSCH, A. & WHITE, P. (2019). A theory of pulse dynamics and disturbance in ecology. *Ecology* **100**(7), e02734.
- KAUSHAL, S. S., LIKENS, G. E., JAWORSKI, N. A., PACE, M. L., SIDES, A. M., SEEKELL, D., BELT, K. T., SECOR, D. H. & WINGATE, R. L. (2010). Rising stream and river temperatures in the United States. *Frontiers in Ecology and the Environment* **8**(9), 461–466.
- *KENDRICK, M. R., HERSHEY, A. E. & HURYN, A. D. (2019). Disturbance, nutrients, and antecedent flow conditions affect macroinvertebrate community structure and productivity in an Arctic river. *Limnology and Oceanography* **64**, S93–S104.

- *KIM, D. G., YOON, T. J., BAEK, M. J. & BAE, Y. J. (2018). Impact of rainfall intensity on benthic macroinvertebrate communities in a mountain stream under the east Asian monsoon climate. *Journal of Freshwater Ecology* **33**(1), 489–501.
- KORELL, L., AUGE, H., CHASE, J. M., HARPOLE, S. & KNIGHT, T. M. (2020). We need more realistic climate change experiments for understanding ecosystems of the future. *Global Change Biology* **26**(2), 325–327.
- KRAUSS, G.-J., SOLÉ, M., KRAUSS, G., SCHLOSSER, D., WESENBERG, D. & BÄRLOCHER, F. (2011). Fungi in freshwaters: ecology, physiology and biochemical potential. *FEMS Microbiology Reviews* **35**(4), 620–665.
- LAKE, P. S. (2000). Disturbance, patchiness, and diversity in streams. *Journal of the North American Benthological Society* **19**(4), 573–592.
- LAKE, P. S. (2003). Ecological effects of perturbation by drought in flowing waters. *Freshwater Biology* **48**(7), 1161–1172.
- *LANDEIRA-DABARCA, A., PÉREZ, J., GRAÇA, M. A. S. & BOYERO, L. (2019). Joint effects of temperature and litter quality on detritivore-mediated breakdown in streams. *Aquatic Sciences* **81**(1), 1.
- *LEBERFINGER, K., BOHMAN, I. & HERRMANN, J. (2010). Drought impact on stream detritivores: experimental effects on leaf litter breakdown and life cycles. *Hydrobiologia* **652**(1), 247–254.
- *LEDGER, M. E., BROWN, L. E., EDWARDS, F. K., HUDSON, L. N., MILNER, A. M. & WOODWARD, G. (2013). Extreme climatic events alter aquatic food webs: a synthesis of evidence from a mesocosm drought experiment. In *Global Change in Multispecies Systems: Part 3*, Advances in Ecological Research (Volume 48, eds G. WOODWARD and E. J. O'GORMAN), pp. 343–395. Cambridge, MA: Academic Press.
- LEDGER, M. E. & MILNER, A. M. (2015). Extreme events in running waters. *Freshwater Biology* **60**(12), 2455–2460.
- LYTLE, D. A. & POFF, N. L. (2004). Adaptation to natural flow regimes. *Trends in Ecology and Evolution* **19**(2), 94–100.
- *MADJI, N., UTHOFF, J., TRAUNSPURGER, W., LAFAILLE, P. & MAIRE, A. (2020). Effect of water warming on the structure of biofilm-dwelling communities. *Ecological Indicators* **117**, 106622.
- MANTUA, N., TOHVER, I. & HAMLET, A. (2010). Climate change impacts on streamflow extremes and summertime stream temperature and their possible consequences for freshwater salmon habitat in Washington state. *Climatic Change* **102**, 187–223.
- *MARCUS, H., WEY, J. K., NORF, H. & WEITERE, M. (2014). Disturbance alters the response of consumer communities towards warming: a mesocosm study with biofilm-dwelling ciliates. *Ecosphere* **5**(1), 1–15.
- *MARTÍNEZ, A., LARRAÑA, A., PÉREZ, J., DESCALS, E. & POZO, J. (2014). Temperature affects leaf litter decomposition in low-order forest streams: field and microcosm approaches. *FEMS Microbiology Ecology* **87**(1), 257–267.
- MCLEAN, M., AUBER, A., GRAHAM, N. A. J., HOUK, P., VILLÉGER, S., VIOLLE, C., THUILLER, W., WILSON, S. K. & MOUILLOT, D. (2019). Trait structure and redundancy determine sensitivity to disturbance in marine fish communities. *Global Change Biology* **25**(10), 3424–3437.
- MCNEISH, D. (2016). On using Bayesian methods to address small sample problems. *Structural Equation Modeling: A Multidisciplinary Journal* **23**(5), 750–773.
- MESSAGER, M. L., LEHNER, B., COCKBURN, C., LAMOUREUX, N., PELLA, H., SNELDER, T., TOCKNER, K., TRAUTMANN, T., WATT, C. & DATRY, T. (2021). Global prevalence of non-perennial rivers and streams. *Nature* **594**, 391–397.
- *MILNER, A. M., ROBERTSON, A. L., McDERMOTT, M. J., KLAAR, M. J. & BROWN, L. E. (2013). Major flood disturbance alters river ecosystem evolution. *Nature Climate Change* **3**, 137–141.
- *MOGHADAM, F. S. & ZIMMER, M. (2014). Effects of warming and nutrient enrichment on how grazing pressure affects leaf litter-colonizing bacteria. *Journal of Environmental Quality* **43**(3), 851–858.
- MORRILL, J. C., BALES, R. C. & CONKLIN, M. H. (2005). Estimating stream temperature from air temperature: implications for future water quality. *Journal of Environmental Engineering* **131**(1), 139–146.
- *MOUTHON, J. & DAUFRESNE, M. (2006). Effects of the 2003 heatwave and climatic warming on mollusc communities of the Saone: a large lowland river and of its two main tributaries (France). *Global Change Biology* **12**(3), 441–449.
- *MUÑOZ, I., ABRIL, M., CASA-RUIZ, P., CASELLAS, M., GÓMEZ-GENER, L., MARCÉ, R., MENÉNDEZ, M., OBRADOR, B., SABATER, S., VON SCHILLER, D. & ACUÑA, V. (2018). Does the severity of non-flow periods influence ecosystem structure and function of temporary streams? A mesocosm study. *Freshwater Biology* **63**(7), 613–625.
- *NAVARRO, F. K. S. P., REZENDE, R. & GONÇALVES, J. F. JR. (2013). Experimental assessment of temperature increase and presence of predator carcass changing the response of invertebrate shredders. *Biota Neotropica* **13**(4), 28–33.
- *NELSON, D., BENSTEAD, J. P., HURYN, A. D., CROSS, W. F., HOOD, J. M., JOHNSON, P. W., JUNKER, J. R., GÍSLASON, G. M. & ÓLAFSSON, J. S. (2017). Experimental whole-stream warming alters community size structure. *Global Change Biology* **23**(7), 2618–2628.
- *NIYOGI, D. K., HU, C. Y. & VESELL, B. P. (2020). Response of stream fungi on decomposing leaves to experimental drying. *International Review of Hydrobiology* **105**(1–2), 52–58.
- *NOGUEIRA, J. G., LOPES-LIMA, M., VARANDAS, S., TEIXEIRA, A. & SOUSA, R. (2019). Effects of an extreme drought on the endangered pearl mussel *Margaritifera margaritifera*: a before/after assessment. *Hydrobiologia* **848**, 3003–3013.
- *NORF, H., ARNDT, H. & WEITERE, M. (2007). Impact of local temperature increase on the early development of biofilm-associated ciliate communities. *Oecologia* **151**(2), 341–350.
- *NORF, H. & WEITERE, M. (2010). Resource quantity and seasonal background alter warming effects on communities of biofilm ciliates. *FEMS Microbiology Ecology* **74**(2), 361–370.
- *NORTHINGTON, R. M. & WEBSTER, J. R. (2017). Experimental reductions in stream flow alter litter processing and consumer subsidies in headwater streams. *Freshwater Biology* **62**(4), 737–750.
- *NUHFER, A. J., ZORN, T. G. & WILLS, T. C. (2015). Effects of reduced summer flows on the brook trout population and temperatures of a groundwater-influenced stream. *Ecology of Freshwater Fish* **26**(1), 108–119.
- O'DEA, R. E., LAGISZ, M., JENNIONS, M. D., KORICHEVA, J., NOBLE, D. W. A., PARKER, T. H., GUREVITCH, J., PAGE, M. J., STEWART, G., MOHER, D. & NAKAGAWA, S. (2021). Preferred reporting items for systematic reviews and meta-analyses in ecology and evolutionary biology: a PRISMA extension. *Biological Reviews* **96**(5), 1695–1722.
- *OPREI, A., ZLATANOVIC, S. & MUTZ, M. (2019). Grazers superimpose humidity effect on stream biofilm resistance and resilience to dry-rewet stress. *Science of the Total Environment* **659**, 841–850.
- PACE, G., BONADA, N. & PRAT, N. (2013). Long-term effects of climatic–hydrological drivers on macroinvertebrate richness and composition in two Mediterranean streams. *Freshwater Biology* **58**(7), 1313–1328.
- *PÉREZ, J., CORREA-ARANEDA, F., LÓPEZ-ROJO, N., BASAGUREN, A. & BOYERO, L. (2021). Extreme temperature events alter stream ecosystem functioning. *Ecological Indicators* **121**, 106984.
- *PÉREZ, J., MARTÍNEZ, A., DESCALS, E. & POZO, J. (2018). Responses of aquatic hyphomycetes to temperature and nutrient availability: a cross-transplantation experiment. *Microbial Ecology* **76**(2), 328–339.
- *PERNECKER, B., MAUCHART, P. & CSABAI, Z. (2020). What to do if streams go dry? Behaviour of Balkan Goldenring (*Cordulegaster heros*, Odonata) larvae in a simulated drought experiment in SW Hungary. *Ecological Entomology* **45**(6), 1457–1465.
- PETERS, D. P. C., LUGO, A. E., CHAPIN III, F. S., PICKETT, S. T. A., DUNIWAY, M., ROCHA, A. V., SWANSON, F. J., LANEY, C. & JONES, J. (2011). Cross-system comparisons elucidate disturbance complexities and generalities. *Ecosphere* **2**(7), 1–26.
- PETERSON, T. J., SAFT, M., PEEL, M. & JOHN, A. (2021). Watersheds may not recover from drought. *Science* **372**(6543), 745–749.
- PETROVIC, M., GINEBRED, A., ACUÑA, V., BATALLA, R. J., ELOSEGI, A., GUASCH, H., LÓPEZ DE ALDA, M., MARCÉ, R., MUÑOZ, I., NAVARRO-ORTEGA, A., NAVARRO, E., VERICAT, D., SABATER, S. & BARCELÓ, D. (2011). Combined scenarios of chemical and ecological quality under water scarcity in Mediterranean rivers. *Trends in Analytical Chemistry* **30**(8), 1269–1278.
- PETSCH, D. K., SAITO, V. S., LANDEIRO, V. L., SILVA, T. S., BINI, L. M., HEINO, J., SOININEN, J., TOLONEN, K. T., JYRKÄNKALLIO-MIKKOLA, J. & PAJUNEN, V. (2020). Beta diversity of stream insects differs between boreal and subtropical regions, but land use does not generally cause biotic homogenization. *Freshwater Science* **40**(1), 53–64.
- PIESSENS, K., ADRIAENS, D., JACQUEMYN, H. & HONNAY, O. (2009). Synergistic effects of an extreme weather event and habitat fragmentation on a specialised insect herbivore. *Oecologia* **159**(1), 117–126.
- *PIGGOT, J. J., NIYOGI, D. K., TOWNSEND, C. R. & MATTHAEI, C. D. (2015a). Multiple stressors and stream ecosystem functioning: climate warming and agricultural stressors interact to affect processing of organic matter. *Journal of Applied Ecology* **52**(5), 1126–1134.
- *PIGGOT, J. J., SALIS, R. K., LEAR, G., TOWNSEND, C. R. & MATTHAEI, C. D. (2015b). Climate warming and agricultural stressors interact to determine stream periphyton community composition. *Global Change Biology* **21**(1), 206–222.
- *PIGGOTT, J. J., TOWNSEND, C. R. & MATTHAEI, C. D. (2015). Climate warming and agricultural stressors interact to determine stream macroinvertebrate community dynamics. *Global Change Biology* **21**, 1887–1906.
- PINIEWSKI, M., SZCZESNIAK, M., KARDEL, I., BEREZOWSKI, T., OKRUSZKO, T., SRINIVASAN, R., VIKHAR, SCHULER, D. & KUNDZEWICZ, Z. W. (2017). Hydrological modelling of the Vistula and Odra river basins using SWAT. *Hydrological Science Journal* **62**(8), 1266–1289.
- *POHLON, E., OCHOA FANDINO, A. & MARXSEN, J. (2013). Bacterial community composition and extracellular enzyme activity in temperate streambed sediment during drying and rewetting. *PLoS One* **8**(12), e83365.
- PONSATÍ, L., ACUÑA, V., ARISTI, I., ARROITA, M., GARCÍA-BERTHOU, E., VON SCHILLER, D., ELOSEGI, A. & SABATER, S. (2015). Biofilm responses to flow

- regulation by dams in Mediterranean Rivers. *River Research and Applications* **31**(8), 1003–1016.
- R CORE TEAM (2020). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna.
- RICHARDSON, L. E., GRAHAM, N. A. J., PRATCHETT, M. S., EURICH, J. G. & HOEY, A. S. (2018). Mass coral bleaching causes biotic homogenization of reef fish assemblages. *Global Change Biology* **24**(7), 3117–3129.
- *RIIS, T., LEVI, P. S., BAATRUP-PEDERSEN, A., JEPPESEN, K. G. & LETH, S. R. (2017). Experimental drought changes ecosystem structure and function in a macrophyte-rich stream. *Aquatic Science* **79**, 841–853.
- RILLIG, M. C., RYO, M., LEHMANN, A., AGUILAR-TRIGUEROS, C. A., BUCHERT, S., WULF, A., IWASAKI, A., ROY, J. & YANG, G. (2019). The role of multiple global change factors in driving soil functions and microbial biodiversity. *Science* **366**, 886–890.
- *ROBERTSON, A. L., BROWN, L. E. & KLAAR, M. J. (2015). Stream ecosystem responses to an extreme rainfall event across multiple catchments in Southeast Alaska. *Freshwater Biology* **60**(12), 2523–2534.
- ROHATGI, A. (2015). WebPlotDigitizer, version: 3.4. September, 2015, ZENODO. <https://automeris.io/WebPlotDigitizer>.
- *ROMANÍ, A. M., BORREGO, C. M., DÍAZ-VILLANUEVA, V., FREIXA, A., GICH, F. & YLLA, I. (2014). Shifts in microbial community structure and function in light- and dark-grown biofilms driven by warming. *Environmental Microbiology* **16**(8), 2550–2567.
- *ROMERO, F., ACUÑA, V., FONT, C., FREIXA, A. & SABATER, S. (2019). Effects of multiple stressors on river biofilms depend on the time scale. *Scientific Reports* **9**, 15810.
- *ROSA, J., FERREIRA, V., CANHOTO, C. & GRAÇA, M. A. S. (2013). Combined effects of water temperature and nutrients concentration on periphyton respiration implications of global change. *International Review of Hydrobiology* **98**(1), 14–23.
- SABATER, S. (2008). Alterations of the global water cycle and their effects on river structure, function and services. *Freshwater Reviews* **1**(1), 75–88.
- SABATER, S., TIMONER, X., BORREGO, C. & ACUÑA, V. (2016). Stream biofilm responses to flow intermittency: from cells to ecosystems. *Frontiers in Environmental Science* **4**, 14.
- *SÁINZ-BARIÁIN, M., ZAMORA-MUÑOZ, C., SOLER, J. J., BONADA, N., SÁINZ-CANTERO, C. E. & ALBA-TERCEDOR, J. (2016). Changes in Mediterranean high mountain Trichoptera communities after a 20-year period. *Aquatic Sciences* **78**(4), 669–682.
- *SCHLIEF, J. & MUTZ, M. (2011). Leaf decay processes during and after a supra-seasonal hydrological drought in a temperate lowland stream. *International Review of Hydrobiology* **96**(6), 633–655.
- STUART-SMITH, R. D., MELLIN, C., BATES, A. E. & EDGAR, G. J. (2021). Habitat loss and range shifts contribute to ecological generalization among reef fishes. *Nature Ecology & Evolution* **5**(5), 656–662.
- SUREN, A. M. & JOWETT, I. G. (2006). Effects of floods versus low flows on invertebrates in a New Zealand gravel-bed river. *Freshwater Biology* **51**(12), 2207–2227.
- THORP, J. H., THOMS, M. C. & DELONG, M. D. (2006). The riverine ecosystem synthesis: biocomplexity in river networks across space and time. *River Research and Applications* **22**(2), 123–147.
- TIERNO DE FIGUEROA, J., LÓPEZ-RODRÍGUEZ, M. J., LORENZ, A., WOLFRAM, G., SCHMIDT-KLOIBER, A. & HERING, D. (2010). Vulnerable taxa of European Plecoptera (Insecta) in the context of climate change. *Biodiversity and Conservation* **19**, 1269–1277.
- *TIMONER, X., COLLS, M., SALOMÓN, S. M., OLIVA, F., ACUÑA, V. & SABATER, S. (2020). Does biofilm origin matter? Biofilm responses to non-flow period in permanent and temporary streams. *Freshwater Biology* **65**(3), 514–523.
- TOWNSEND, C. R. & HILDREW, A. G. (1994). Species traits in relation to a habitat template for river systems. *Freshwater Biology* **31**(3), 265–275.
- TRISOS, C. H., MEROW, C. & PIGOT, A. L. (2020). The projected timing of abrupt ecological disruption from climate change. *Nature* **580**(7804), 496–501.
- *TRUCHY, A., SARREMEJANE, R., MUOTKA, T., MYKRÁ, H., ANGELER, D. G., LEHOSMAA, K., HUUSKO, A., JOHNSON, R. K., SPONSELLER, R. A. & MCKIE, B. G. (2020). Habitat patchiness, ecological connectivity and the uneven recovery of boreal stream ecosystems from an experimental drought. *Global Change Biology* **26**(6), 3455–3472.
- *TSAI, J., CHUANG, Y., WU, Z., KUO, M. & LIN, H. (2014). The effects of storm-induced events on the seasonal dynamics of epilithic algal biomass in subtropical mountain streams. *Marine and Freshwater Research* **65**, 25–38.
- UMMENHOFER, C. C. & MEEHL, G. A. (2017). Extreme weather and climate events with ecological relevance: a review. *Philosophical Transactions of the Royal Society B: Biological Sciences* **372**(1723), 20160135.
- *VANDER VORSTE, R., CORTI, R., SAGOUIS, A. & DATRY, T. (2016). Invertebrate communities in gravel-bed, braided rivers are highly resilient to flow intermittence. *Freshwater Science* **35**(1), 164–177.
- *VANDER VORSTE, R., MALARD, F. & DATRY, T. (2015). Is drift the primary process promoting the resilience of river invertebrate communities? A manipulative field experiment in an intermittent alluvial river. *Freshwater Biology* **61**(8), 1276–1292.
- VEHTARI, A., GELMAN, A. & GABRY, J. (2017). Practical Bayesian model evaluation using leave-one out cross-validation and WAIC. *Statistics and Computing* **27**(5), 1413–1432.
- VIECHTBAUER, W. (2010). Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software* **36**(3), 1–48.
- VON SCHILLER, D., ACUÑA, V., ARISTI, I., ARROITA, M., BASAGUREN, A., BELLIN, A., BOYERO, L., BUTTURINI, A., GINEBREDI, A., KALOGIANNI, E., LARRAÑAGA, A., MAJONE, B., MARTÍNEZ, A., MONROY, S., MUÑOZ, I., ET AL. (2017). River ecosystem processes: a synthesis of approaches, criteria of use and sensitivity to environmental stressors. *Science of the Total Environment* **596–597**, 465–480.
- *WOODWARD, G., BONADA, N., FEELEY, H. B. & GILLER, P. S. (2015). Resilience of a stream community to extreme climatic events and long-term recovery from a catastrophic flood. *Freshwater Biology* **60**(12), 2497–2510.
- YLLA, I., CANHOTO, C. & ROMANÍ, A. M. (2014). Effects of warming on stream biofilm organic matter use capabilities. *Microbial Ecology* **68**(1), 132–145.
- *YLLA, I., ROMANÍ, A. M. & SABATER, S. (2012). Labile and recalcitrant organic matter utilization by river biofilm under increasing water temperature. *Microbial Ecology* **64**(3), 593–604.

IX. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Search terms used in the literature search for studies used in our meta-analysis.

Appendix S2. PRISMA diagram for the literature search.

Table S1. List of moderators used in statistical models.

Table S2. Identification of the most appropriate random effects structure by leave-one-out cross-validation.

Fig. S1. Funnel plots of effect sizes (Hedges' g) plotted against the inverse standard error of sampling variances.

Table S3. Results of the Egger's tests assessing publication bias.

Table S4. Mean effect sizes (Hedges' g and log response ratio) and 95% credible intervals for biodiversity and ecosystem function response variables.

Table S5. Completed PRISMA ECO-EVO checklist.

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