Received: 9 May 2016 | Revised: 19 July 2016 | Accepted: 14 September 2016
DOI 10.1002/eco.1793
WILEY

RESEARCH ARTICLE

Responses of fish and invertebrates to floods and droughts in Europe

M. Piniewski[1,2] | **C. Prudhomme**[3] | **M. C. Acreman**[3] | **L. Tylec**[1] | **P. Oglęcki**[1] | **T. Okruszko**[1]

[1]Warsaw University of Life Sciences, Warsaw, Poland
[2]Potsdam Institute for Climate Impact Research, Potsdam, Germany
[3]Centre for Ecology and Hydrology, UK

Correspondence
M. Piniewski, Warsaw University of Life Sciences, Warsaw, Poland.
Email: m.piniewski@levis.sggw.pl

Funding information
EU-project REFORM, Grant/Award Number: 282656; NERC-CEH Water Resources Science Area; NERC project Marius, Grant/Award Number: NE/L010208/1; Belmont Forum project DriVER, Grant/Award Number: G8MUREFU3FP-2200-108

Abstract

Floods and droughts, two opposite natural components of streamflow regimes, are known to regulate population size and species diversity. Quantifiable measures of these disturbances and their subsequent ecological responses are needed to synthesize the knowledge on flow–ecosystem relationships. This study for the first time combines the systematic review approach used to collect evidence on the ecological responses to floods and droughts in Europe with the statistical methods used to quantify the extreme events severity. Out of 854 publications identified in literature search, 54 papers were retained after screening and eligibility checks, providing in total 82 case studies with unique extreme event—ecological response associations for which data were extracted. In this way, a database with metadata of case studies that can be explored with respect to various factors was constructed. This study pinpointed the research gaps where little evidence could be synthesized, for example, drought event studies and fish studies. It was demonstrated that in many cases the studied metrics (abundance, density, richness, and diversity) showed statistically significant decreases after or during the event occurrence. The responses in invertebrate density and richness were in general more negative than the corresponding responses in fish. Biota resistance to floods was found to be lower than the resistance to droughts. The severity of extreme events was not found to be an important factor influencing ecological metrics, although this analysis was often hampered by insufficient number of case studies. Conceivably, other factors could mask any existing relationships between disturbance severity and biotic response.

KEYWORDS

abundance, disturbance, diversity, ecological response, extreme event, perturbation, resistance, streamflow variability

1 | INTRODUCTION

The natural flow of a river varies on a range of time scales, from hours to years and longer (Poff et al., 1997). Flow regimes vary regionally, and their properties are typically controlled by environmental factors such as climate, topography, land cover, soils and geology, and anthropogenic factors such as morphologic alteration, water abstraction, dams, or diversions. Extreme high and low flows are two opposite natural components of flow regimes of rivers worldwide. These excesses and deficits in water movement are often perceived by stream ecologists as disturbances (Lake, 2000) that regulate population size and species diversity across a range of spatial and temporal scales (Lytle & Poff, 2004) and that are “the dominant organizing factor in stream ecology” (Resh et al., 1988). For example, some consequences of developing droughts are (a) reduction and fragmentation of habitat space, (b) breaking longitudinal connectivity, (c) deterioration in water quality, and ultimately (d) loss of biota (Lake, 2000). Sequential drying of different habitats that act as refuges when connectivity is lost triggers a stepped response of the biota (Environment Agency, 2013). Floods, in contrast, lead to (a) a rapid movement and redistribution of bed materials, (b) plant removal, and (c) washing organisms downstream to the estuary or sea. However, hydrological extremes do not always have negative impacts: for example, floods may also open up new habitats on floodplains, and a wide variety of aquatic and riparian organisms have developed adaptations to floods and droughts involving life histories, behaviors, and morphologies of plants and animals (Lytle & Poff, 2004). The effects of single hydrological extreme events are highly context dependent, ranging from deleterious to beneficial, and reliant upon event magnitude, extent, and timing relative to life cycles of constituent species (Ledger & Milner, 2015). Much insight into the nature of extreme flow–biota relationships is offered by long-term hydroecological datasets comprising community metrics and streamflow time series, such as the one available for the Little Stour River in the UK (Wood & Petts, 1999; Wood & Armitage, 2004; Stubbington, Wood, & Boulton, 2009a; Stubbington, Boulton, Little, & Wood, 2015).

Hydrologists have developed a wide range of indices that quantify the severity of hydrological extreme events. These include, for example, flow duration curves, low-flow frequency curves, continuous low-flow events analyses, baseflow separation techniques and recession analysis for droughts, (Smakhtin, 2001; Keyantash & Dracup, 2002; Lake, 2011); and flood frequency or flood peak magnitude, duration above a threshold (high-flow pulses) for floods. Unfortunately, these indices are rarely used in ecological studies to characterize hydrological extremes under investigation, which hampers any comparisons between events across different studies (e.g., (Lake, 2011) for droughts). While there have been studies relating ecological scores to hydrological metrics, they are rarely targeted to extreme events. For example, Monk, Wood, Hannah, and Wilson (2008) used the Lotic Invertebrate Index for Flow Evaluation (LIFE) scores to study the interannual dynamics in instream macroinvertebrate community response in 83 sites across England and Wales. The results allowed to distinguish the responses between dry (1990–1992) and wet (1996–1997) years, but not between individual events. Quantifiable measures of the disturbances, of their effects on abiotic and biotic components, and of the subsequent responses by the biota would help to progress and usefully compare ecological studies in a systematic manner (Lake, 2000). There are flow thresholds where invertebrates and fish show a behavioral response to drought conditions (Environment Agency, 2013). Among 20 research priorities aimed at addressing knowledge gaps in the context of geomorphological and ecological role of floods, Death, Fuller, and Macklin (2015) specified a few directly related to the largely unknown role of extreme events severity, in particular, hydrological indices thresholds. In our view, lack of reported extreme event indicators in ecological studies can only be overcome by completing the hydrological analysis associated with the published material.

Against this background, the objective of this study is to identify evidence in quantitative response of freshwater biota to hydrological extremes in Europe. More specifically, three research questions were formulated: (1) Are freshwater biota significantly impacted by extreme hydrological events? (2) Do ecological responses to extreme events differ between different groups, such as fish and invertebrates or between flood and drought events? (3) Are ecological responses influenced by the severity of flood or drought events? In order to answer these questions, we gathered published evidence through a systematic review, enhanced by a consistent quantification of hydrological extreme events, and employed a robust statistical framework to quantify hydrological extremes–biota relationship in Europe.

We investigated the responses of fish and invertebrates only, as the published evidence is largest within these species (e.g. Garcia De Jalón et al., 2014; Edwards, Baker, Dunbar, & Laizé, 2012; Lake, 2011), selecting studies in Europe that reported biological sampling results (pre- and during- or post-event values) for at least one of the ecological metrics: abundance, density, taxon richness, or diversity (sensu Shannon diversity index or similar indices). Because we were seeking relationships between hydrological events and subsequent ecological responses, we excluded studies for which establishing such connections was impossible.

Even though there have been some previous explorative studies to develop flow–ecosystem relationships, their primary focus was either on the effects of flow alterations (Lloyd et al., 2003; Poff & Zimmerman, 2010; Webb et al. 2013) or of a whole array of natural and anthropogenic changes in different flow regime components, notably including droughts, floods, and high flows (McManamay, Orth, Kauffman, & Davis, 2013). Only Jones and Petreman (2013) focused clearly on the effects of extreme flows on fish populations, but in contrast to other studies (including ours), their methodology did not contain systematic evidence collection and had much more narrow geographical scope (Lake Ontario region). McManamay et al. (2013) reported predominantly negative responses of fish and invertebrates due to droughts and more variable, although predominantly positive, responses due to floods in the South Atlantic Region of the United States. Because their study was aimed to help local managers in developing environmental flow standards in the South Atlantic Region, it focused to a large extent on region-specific anthropogenic flow alterations, which makes a clear difference from our study aiming to better understand the ecological responses to floods and droughts in Europe.

In this paper, we follow the terminology introduced by Lake (2011), that is, whenever we refer to "disturbances," "responses," and "perturbations," we mean, respectively, the following: (a) "disturbances"—hydrological extreme events, that is, either floods or droughts, understood here as (natural) events, having a particular, defined time of occurrence; (b) "responses" (to the disturbance)—impacts of a certain event on biotic components of the ecosystem, here measured by the change in aforementioned ecological metrics; (c) "perturbations"—disturbances and responses considered together. In order to clearly distinguish between biota resistance (capacity of the biota to withstand the stresses of a disturbance) and resilience (capacity to recover from the disturbance; Lake, 2011), in this study, we focus only on the first property, trying to capture evidence of the direct, usually immediate and maximum response in selected metrics.

2 | DATA AND METHODS

2.1 | Evidence collection

We used systematic review methods in order to collect evidence required to address the aforementioned research questions, as they provide a methodological framework to reduce bias present in narrative reviews, allowing to perform a comprehensive literature search and critical appraisal of the individual studies. Here, we carried out all the important steps associated with the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) statement (Moher, Liberati, Tetzlaff, Altman, & Group, 2009), specifically, Identification, Screening, and Eligibility, as summarized in Figure 1 and described below.

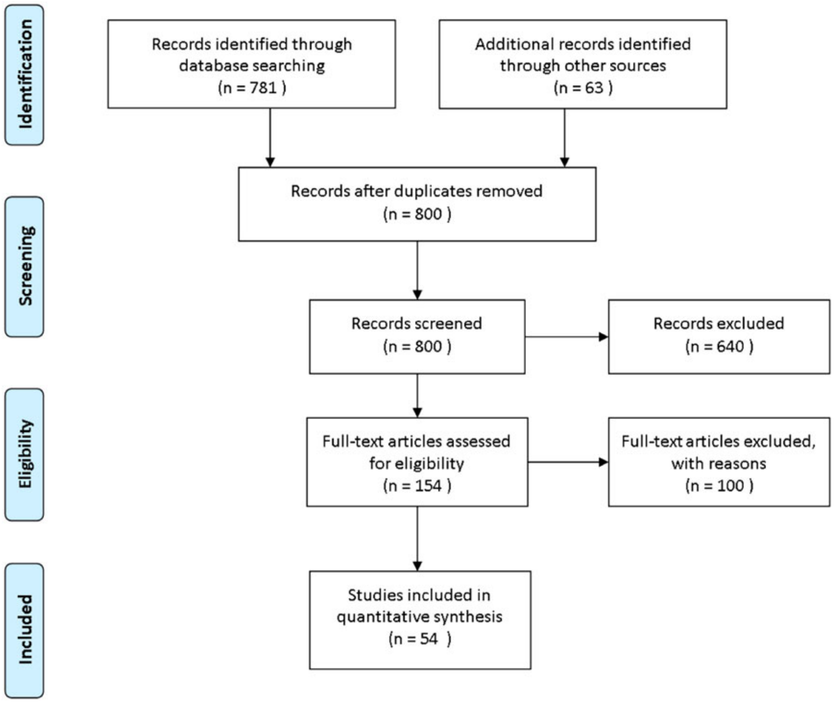


FIGURE 1 The flow of information through the different phases of a systematic review (modified after Moher et al., 2009)

2.2 | Identification

Literature search of scientific peer-reviewed studies (journal and conference proceedings articles) was performed using the Thomson Reuters Web of Science Core Collection in June 2014, assumed the main environmental publication electronic database source (see, e.g., Newman et al., 2015). The search terms design was focused on retrieving publications addressing the research questions (Table 1, cf. Table S1 in Supporting Information for the complete list). The search was restricted to 12 research categories related to Biology, Geography, or Environmental Sciences. No restrictions were applied regarding the year of publication. Seven hundred eighty-one papers were selected in the Web of Science search and exported to a Bibtex library for further evaluation.

As a complementary publication source, we took 63 papers identified upon an initial phase of this research related to the Restoring Rivers for Effective Catchment Management project (Garcia De Jalón et al., 2014). As a result of cross-checking two lists of records obtained from different sources, 44 duplicate records were eliminated and 800 records were kept for further evaluation.

2.3 | Screening and eligibility

Study inclusion (or exclusion) criteria were applied to consecutively narrow search results and derive only relevant articles (Table 2). Filtering was carried out at three levels: by title, by abstract, and finally by full text. A total of 198 records were maintained after title reading (which in dubious cases was followed by quick abstract screening), of which 179 came from the Web of Science search and 19 from the previous report. After abstract reading, 38 papers were excluded, with 160 papers (of which 147 from the Web of Science search) kept for full text filtering. The two most frequent exclusion reasons at this stage were (a) lack of hydrological extreme events (b) studies outside Europe. Full text retrieval was successful in 154 cases. All these cases underwent eligibility checks (cf. Figure 1). The full texts screening resulted in a further 74 publications to be excluded. Papers were then analyzed for their quantitative data on ecological responses in terms of abundance, density, richness, and diversity (cf. last two rows of Table 2), with 26 papers excluded mainly due to lack of quantitative pre-event sampling data. A total of 54 papers fulfilled all specified criteria and were included for data extraction. The bibliographic information related to this set of papers can be found in the Supporting Information (file Literature_systematic_review.bib).

2.4 | Data extraction

The full text of each of the retained articles was read for case study (i.e., perturbation) identification and data extraction. If a paper contained relevant data on two or more perturbations, each of them was treated as a separate case study; if it contained data on responses of different biota to the same event, each of them was treated as a separate case study. However, one case study could provide ecological response data for up to four analyzed ecological metrics. In total, 54 papers provided data on 82 case studies. Description of all fields included in the data extraction database can be found in Table S2. They can be grouped into three categories: (a) hydrological event, (b) ecological response, (c) geographical location (saved also in Geographic Information System software). For each location, an approximate upstream catchment area was calculated and classified according to the order of magnitude (e.g., 10–100 km^2). Several important assumptions had to be made upon data extraction in order to ensure the coherence of the undertaken approach:

1. If for a given case study sampling results were provided for different habitats or different sites on the same river or on nearby rivers, all results were averaged.
2. If a given case study contained data for different taxons, the results were averaged across taxons (except when the authors clearly

TABLE 1 Search terms used in the Web of Science search (see Table S1 for the full search expression used)

Group	Group 1	Group 2	Group 3	Group 4	Group 5	Group 6
Group name	Hydrological extreme event	Biota	Ecosystem	Ecological response	Location keywords	Exclusion keywords
Searched in Topic or Title field	Topic	Topic	Topic	Topic	Topic	Title
Terms				population	See Table S1 in Supporting Information for the complete list	See Table S1 in Supporting Information for the complete list
				structure		
				abundance		
				densit*		
				richness		
				migration		
				drift		
				spawn*		
	drought	fish*		reproduc*		
	flood	*invertebrate*		recruitment		
	high flow*	adult		forag*		
	high discharge*	fry	river	feed*		
	low flow*	larva*	stream	mortal*		
	low discharge*	juvenile	lotic	surviv*		
	extreme flow*	smolt		*diversity		
	extreme discharge*	parr		growth		
	spate	fauna		composition		
				*colonization		
				resistan*		
				resilien*		
				recover*		
				refug*		
				dispers*		
				movement		
				production		

Note: The asterisk (*) represents any group of characters, including no character.

TABLE 2 Publication inclusion and exclusion criteria

Category	Inclusion criteria	Exclusion criteria
Disturbance type	Natural flood/drought events	E.g., hydropeaking, experimental floods, etc.
Event occurrence time	Event occurrence dates specified at least on a monthly basis and falling within the period 1961–2011	Unspecified event occurrence dates (or outside the period of interest)
Ecosystem type	Lotic ecosystems	E.g., lakes, wetlands, estuaries, etc.
Biota type	Fish or invertebrates	Other biota (e.g., plants, algae, bacteria, etc.)
Study location	Well defined (allowing for approximate mapping in GIS) and inside Europe	Not specified or outside Europe
Event-response connection	Ecological responses can be attributed to single events	E.g., statistical approaches not permitting to link responses to single events
Response variables	Reporting values for at least one of the ecological metrics[a]	Lack of values for specified metrics
Sampling design	Including at least two samplings, one before and one after (or during) an even	Only one sampling or many sampling but without a separation by the event (e.g., only post-event values)

Note: [a] The following metrics were initially considered: abundance, density, richness, diversity (e.g., Shannon index and similar indices), biomass, mortality, reproduction/recruitment, and growth. GIS, Geographic Information System.

distinguished results between analyzed taxons), to achieve consistency with studies with averaged results.

3. If for a given case study sampling results were provided for multiple dates preceding the event, the last one was attributed as a reference sampling date for this event, except when there were premises in the paper to select another date (e.g., in the same season or month the preceding year).
4. If for a given case study sampling results were provided for multiple dates following the event, the date that produced the largest relative change with respect to the reference value

was attributed to the event except when the authors specified a date.

As most investigated papers did not report sufficient quantitative information on the severity of the hydrological extreme events, additional analysis was conducted to quantify consistently the severity of the disturbances to answer the research questions.

2.5 | Floods and droughts severity metrics

Drought and flood episodes have different generation processes, spatial and temporal scales, with floods persisting over days to months and across local (0.5 km^2) to regional (10,000 km^2) scales while droughts last for months to decades over areas of 50–1.5M km^2 (Garner, Van Loon, Prudhomme, & Hannah, 2015). As a result, methods for characterization and quantification of floods and droughts are also different. In particular, flood events are usually quantified at their peak and frequency of nonexceedance calculated using the extreme value theory (Madsen, Rasmussen, & Rosbjerg, 1997). In contrast, due to their slow onset, droughts are generally defined as periods when flow is lower than a threshold considered as representative of low-flow conditions, and duration and deficit volume are common metrics to quantify drought (Van Loon, 2015). In addition, because the cumulative impact of droughts on the terrestrial ecosystem increases with affected area, drought spatial extent has also been used as a measure of severity.

2.6 | Flood indices

The flood index metric applied here is the nonexceedance probability of the maximum daily streamflow recorded for each event of interest, expressed as return period T or average number of years between two events of the same magnitude or larger. The Peak-Over-Threshold (or partial-duration-series) method was selected because it selects all independent extreme flood events independently of their periodicity (Madsen et al., 1997). Following Bayliss and Jones (1993) a total of $3{\cdot}N$ (N = number of complete years of record) independent flood peaks were sampled from daily mean river flow, with a 7-day minimum duration between two selected peaks. A Generalized Pareto Distribution was fitted on each Peak-Over-Threshold sample based on the probability weighted moments technique (Madsen et al., 1997), giving a uniform relationship between a flood peak magnitude and its return period T.

For seven out of 57 flood case studies, the values of T were extracted from the papers. For the remaining 50 case studies, we searched for representative gauging stations in the proximity of 100 km, with sufficient daily flow record available to us (Figure 2a). This was successful for 44 out of 50 case studies. Of these, 39 representative gauges lay within less than 50 km of the investigated ecological sites. Once the relevant flow data series was identified, the return period associated with the flood event of the case study was derived from the Generalized Pareto Distribution.

The six case studies for which we were not able to identify a representative gauging station were located in Spain. For them we extracted precipitation time series from the high-resolution gridded precipitation dataset Spain02 (Herrera, Fernández, & Gutiérrez, 2016) and associated precipitation events severity with case study flood events.

2.7 | Drought indices

Following Parry, Hannaford, Lloyd-Hughes, and Prudhomme (2012); Stahl and Demuth (1999), the drought metric used is the maximum Regional Deficit Index (RDI), which gives the maximum proportion

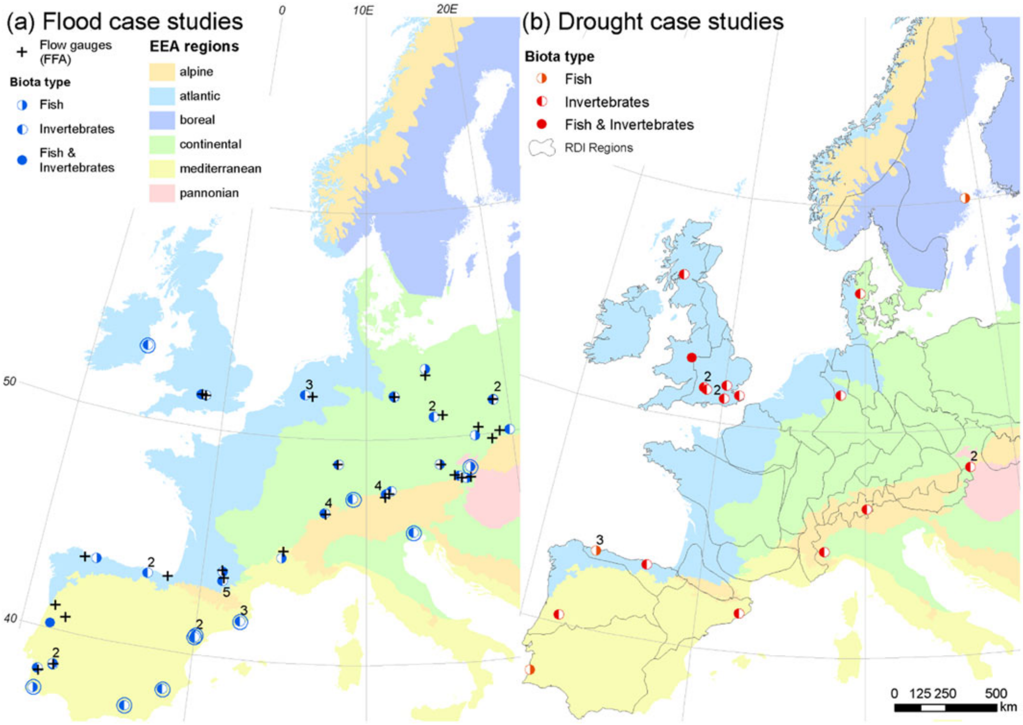


FIGURE 2 Location of flood (a) and drought (b) case studies, representative flow gauges used for flood frequency analysis, Regional Deficit Index (RDI) regions, and European Environment Agency (EEA) biogeographical regions. A blue circle around some of the flood case studies denotes the fact that no gauging station was assigned, either because the return periods were extracted from the paper, or because no suitable gauge was identified. Numbers next to symbols denote the number of case studies associated with a given symbol on a map

of a region under low flow conditions during a drought event. The higher the index, the more generalized flow deficits in rivers across the region, and the more extensive and severe the drought. The concept follows the well-established "threshold-level" concept (Zelenhasic & Salvai, 1987) where flows below a low flow threshold are termed deficit flows. To account for the natural variability of flow within the year, low flow thresholds were defined for each streamflow series as the 10th percentile flow (Q90) recorded over a 31-day window centered around the day of interest (Hannaford, Lloyd-Hughes, Keef, Parry, & Prudhomme, 2011).

The European Drought Catalogue (Parry et al., 2012) was used and extended to cover events post 2005, where possible using all original gauges. Additional regions were created to cover ecological sites outside the original drought catalogue using data from relevant measuring authorities across Europe. Each ecological site identified from the systematic review was assigned to a region either containing the site or whose boundary was closest to it (three cases).

3 | Methods to quantify disturbance-response relationships

3.1 | Flood and drought metrics categorization

To enable a rigorous comparative assessment of all levels of analysis to answer the research question, flood and drought indices were summarized in three classes of severity each: low, medium, and high. For flood events, categories were assigned based on the value of return period T with threshold values of 2 and 20 years (Table 3). For drought events categorization was based on two criteria: duration D and severity measured by RDI. For each event, daily RDI values were extracted from respective RDI regions and RDI_{90} value (90th percentile of the RDI time series) was calculated. To provide a more comprehensive integration of events across Europe we applied less stringent threshold levels (0.4 and 0.7) for RDI_{90} compared to those used by Parry et al. (2012). In order to distinguish between single season, multi-season and multi-annual droughts, thresholds for drought duration were set at 3 and 12 months. The full classification scheme is included in Table 3.

3.2 | Response ratios for ecological metrics

For each case study (perturbation), the values of at least one of four ecological metrics (Abundance, Density, Richness, and Diversity) were retrieved for two dates t_0 and t_1 (before and after/during an event). For each metric, log response ratios were calculated as

$$RR_{EM} = \log\frac{x_1}{x_0} \tag{1}$$

where RR_{EM} is a response ratio for ecological metric EM (where EM can be Abundance Ab, Density De, Richness Ri, and Diversity Di), and x_0, x_1 are the ecological metric values before and during or after an event, respectively. Positive values of RR indicate that values of a given metric increased between t_0 and t_1, and negative values indicate that they decreased. The use of response ratios facilitates comparisons and output data presentation and has been also used in other systematic reviews in ecology (Newman et al., 2015; McManamay et al., 2013).

3.3 | Statistical tests

Three types of statistical tests were distinguished to address three specified research questions.

To test whether biota are significantly impacted by extreme hydrological events, we applied the one-sample t-test. This test is applied for RR_{EM} (cf. Equation (1)): for the whole sample, and by sub-groups, for example, stratified by the event type (flood or drought), biota type (fish or invertebrates), event severity class (low, medium, and high), and so forth. The null hypothesis states that the population mean is equal to a specified value. Hence, in order to test whether the values of ecological metrics after an event are statistically different from the corresponding values before an event, RR_{EM} is compared to the value of zero in t test.

To test whether ecological responses to extreme events differ between subgroups (e.g., between floods and droughts, or between fish and invertebrates), we applied the independent-samples t test. The null hypotheses state that there is no difference between the mean of two samples. While the previous test compared the mean RR_{EM} to zero, this one compares two means of RR_{EM} between subgroups.

To test whether ecological responses to extreme events are influenced by their severity, we applied the one-way analysis of variance (one-way ANOVA), which is a generalization of the two-sample t test for more than two samples. The null hypothesis states that samples in specified groups are drawn from populations with the same mean values. Here, one-way ANOVA is applied for comparing response ratios between three classes of flood/drought severity metrics: low, medium, and high.

All statistical analyses were performed only if subgroup counts were higher or equal than three, following the recommendation from the systematic review of Newman et al. (2015).

4 | RESULTS

4.1 | Synthesis of case studies

The systematic review and hydrological analyses resulted in a database of hydrological extreme event—ecological response associations in Europe of 82 case studies (CS) originating from 54 papers satisfying the systematic review criteria (cf. Table 4 for list of all selected CS with their attributes and Table S3 for the whole database). Figure 2 shows all flood

TABLE 3 Flood and drought event severity classification scheme

Flood event classification scheme		Drought event classification scheme			
			$RDI_{90} < 0.4$	$0.4 \leqslant RDI_{90} < 0.7$	$RDI_{90} \geqslant 0.7$
$T < 2$	Low	$D < 3$	Low	Low	Medium
$2 \leqslant T < 20$	Medium	$3 \leqslant D < 12$	Low	Medium	High
$T \geqslant 20$	High	$D \geqslant 12$	Medium	High	High

Note: T stands for flood return period, D for drought duration, and RDI_{90} for the 90th percentile of the Regional Deficiency Index.

TABLE 4 Synthesis of case studies (the complete table with all attributes can be found in Table S3)

Reference	Code[a]	Location[b]	Year[c]	Severity[d]	Taxon	RR^e_{Ab}	RR^e_{De}	RR^e_{Ri}	RR^e_{Di}
Acuña et al. (2005)	Acuna2005_DI	ES\Me	2003	1	Benthic macroinvertebrates		0.29	– 0.32	– 0.32
Argerich (2004)	Argerich2004_FI1	ES\Me	1984	1	Benthic macroinvertebrates		– 0.60	– 0.17	
Argerich (2004)	Argerich2004_FI2	ES\Me	2000	3	Benthic macroinvertebrates		– 2.00	– 0.44	
Arscott, Tockner, and Ward (2003)	Arscott2003_FI	IT\Al	1998	2	Benthic macroinvertebrates		– 0.60	– 0.39	– 0.37
Baumgartner and Waringer (1997)	Baumgartner1997_FI	AU\Co	1991	3	Benthic macroinvertebrates		– 1.10		
Bischoff and Wolter (2001)	Bischoff2001_FF	DE\Co	1997	3	0+fish community	– 0.96	– 0.55	0.20	0.43
Cattaneo et al. (2001)	Cattaneo2001_FF	FR\Me	1993	3	Cyprinid fish	1.24		0.10	
Chaves et al. (2008)	Chaves2008_DI	PT\Me	2004	1	Benthic macroinvertebrates	– 0.28		0.12	
Cowx, Young, and Hellawell (1984)	Cowx1984_DF1	UK\At	1976	3	*Salmo trutta* L.		– 0.05		
Cowx et al. (1984)	Cowx1984_DF3	UK\At	1976	3	*Salmo salar* - parr		– 0.80		
Cowx et al. (1984)	Cowx1984_DI2	UK\At	1976	3	Benthic macroinvertebrates	– 0.22	– 0.29		
Effenberger et al. (2006)	Effenberger2006_FI1	DE\Co	2001	1	Benthic macroinvertebrates		0.33	0.10	
Effenberger et al. (2006)	Effenberger2006_FI2	DE\Co	2001	1	Benthic macroinvertebrates		0.14	0.09	
Effenberger et al. (2006)	Effenberger2006_FI3	DE\Co	2001	2	Benthic macroinvertebrates		– 0.23	– 0.08	
Effenberger et al. (2006)	Effenberger2006_FI4	DE\Co	2001	1	Benthic macroinvertebrates		– 0.34	– 0.24	
Extence (1981)	Extence1981_DI	UK\At	1976	3	Benthic macroinvertebrates		0.35		
Extence (1981)	Feeley2012_FI	IR\At	2011	3	Benthic macroinvertebrates		– 0.82	– 0.19	
Fellendorf, Mohra, and Paxton (2004)	Fellendorf2004_FI	DE\Co	1999	3	*Andrena vaga*	– 0.40			
Fenoglio, Bo, Cucco, and Malacarne (2007)	Fenoglio2007_DI	IT\Al	2004	2	Dytiscidae beetles		– 0.82	– 0.24	
Gaudes et al. (2010)	Gaudes2010_DI1	ES\Me	2003	2	Meiofaunal community		– 0.42		
Gaudes et al. (2010)	Gaudes2010_DI2	ES\Me	2003	1	Meiofaunal community		– 0.14		
Gaudes et al. (2010)	Gaudes2010_DI3	ES\Me	2004	2	Meiofaunal community		– 1.00		
Gerisch, Dziock, Schanowski, Ilg, and Henle (2012)	Gerisch2012_FI	DE\Co	2002	3	Ground beetles	– 0.72		– 0.33	– 0.39
Grzybkowska and Witczak (1990)	Grzybkowska1990_FI	PL\Co	1985	2	Chironomids		– 0.89	– 0.51	– 0.29
Grzybkowska, Temech, and Dukowska (1996)	Grzybkowska1996_FI	PL\Co	1985	2	Chironomids		– 0.40		
Hering, Gerhard, Manderbach, and Reich (2004)	Hering2004_FI1	DE\Al	1999	3	Benthic macroinvertebrates	0.30		0.10	
Hering et al. (2004)	Hering2004_FI2	DE\Al	1999	3	Carabidae and Bembidion	– 1.52		– 0.57	
Ilg et al. (2008)	Ilg2008_FI1	DE\Co	2002	3	Mollusks	0.36		0.08	0.33
Ilg et al. (2008)	Ilg2008_FI2	DE\Co	2002	3	Carabid beetles	– 0.20		– 0.12	– 0.21
Imbert, Gonzalez, Basaguren, and Pozo (2005)	Imbert2005_FI1	ES\Co	1997	1	Benthic macroinvertebrates		– 0.18		
Imbert et al. (2005)	Imbert2005_FI2	ES\Co	1997	1	Benthic macroinvertebrates		– 0.46		
Jurajda, Reichard, and Smith (2006)	Jurajda2006_FF	AU\Co	1997	3	Fish community	– 0.11		– 0.09	– 0.05
Kaendler and Seidler (2013)	Kaendler2013_FI1	DE\Co	2010	2	Benthic macroinvertebrates	– 0.36			

TABLE 4 Continued

Reference	Code[a]	Location[b]	Year[c]	Severity[d]	Taxon	RR^{e}_{Ab}	RR^{e}_{De}	RR^{e}_{Ri}	RR^{e}_{Di}
Kaendler and Seidler (2013)	Kaendler2013_FI2	DE\Co	2010	2	Benthic macroinvertebrates	– 0.77			
Kajzer-Bonk et al. (2013)	Kajzer-Bonk2013_FI1	PL\Co	2010	3	*Maculinea phengaris*	– 0.02			
Ledger and Hildrew (2001)	Ledger2001_DI2	UK\At	1995	3	Benthic macroinvertebrates		– 0.48	– 0.19	0.17
Lobon-Cervia (1996)	Lobon-Cervia1996_FF	ES\Co	1994	2	*Salmo trutta*, *Salmo salar*	– 0.10			
Lobon-Cervia (2009)	Lobon-Cervia2009_DF1	ES\Co	1990	3	*Salmo trutta*, *Salmo salar*		– 0.23		
Lobon-Cervia (2009)	Lobon-Cervia2009_DF2	ES\Co	2000	1	*Salmo trutta*, *Salmo salar*		– 0.35		
Lobon-Cervia (2009)	Lobon-Cervia2009_DF3	ES\Co	2007	1	Salmo trutta, Salmo salar		– 0.15		
Lojkásek, Lusk, Halačka, Lusková, and Drozd (2005)	Lojkasek2005_FF	CZ\Co	1997	3	Fish community	0.03	– 0.10	0.01	0.07
Lopez-Rodréguez et al. (2012)	LopezRodriguez2012_FI	ES\Me	2010	1	Benthic macroinvertebrates		– 1.30		– 0.74
Lusk, Halačka, Lusková, and Holub (2004)	Lusk2004_FF	CZ\Co	2002	3	Fish community	1.00	1.19	0.05	-0.13
Magalhães, Beja, Schlosser, and Collares-Pereira (2007)	Magalhaes2007_DF	PT\Me	1993	3	Fish community	-0.24			
Maier (2001)	Maier2001_FI1	CH\Al	1991	1	Benthic macroinvertebrates	– 0.22			
Maier (2001)	Maier2001_FI2	CH\Al	1992	1	Benthic macroinvertebrates		– 0.82		
Maier (2001)	Maier2001_FI3	CH\Al	1992	1	Benthic macroinvertebrates		0.02		
Maier (2001)	Maier2001_FI4	CH\Al	1992	1	Benthic macroinvertebrates		– 1.10		
Majdi et al. (2012)	Majdi2012_FI1	FR\Co	2004	2	Rotifers, nematodes		– 0.27		
Majdi et al. (2012)	Majdi2012_FI2	FR\Co	2004	1	Rotifers, nematodes		– 0.55		
Majdi et al. (2012)	Majdi2012_FI3	FR\Co	2009	1	Rotifers, nematodes		– 2.00		
Majdi et al. (2012)	Majdi2012_FI4	FR\Co	2009	1	Rotifers, nematodes		– 3.00		
Majdi et al. (2012)	Majdi2012_FI5	FR\Co	2009	1	Rotifers, nematodes		– 1.70		
Mastrorillo and Copp (2005)	Mastrorillo2005_FF	FR\Co	1998	1	Non-salmonid fish		0.30		
Matthaei, Uehlinger, and Frutiger (1997)	Matthaei1997_FI	CH\Al	1994	2	Benthic macroinvertebrates	– 1.00	– 1.15	– 0.17	
Meyer & Meyer (2000)	Meyer2000_DI	DE\At	1996	1	Benthic macroinvertebrates			0.17	
Morais, Pinto, Guilherme, Rosado, and Antunes (2004)	Morais2004_FI	PT\Me	2002	1	Benthic macroinvertebrates		– 0.26	– 0.09	0.03
Morrison (1990)	Morrison1990_DI	UK\At	1984	3	Benthic macroinvertebrates			– 0.04	
Moth Iversen, Wiberg-Larsen, Birkholm Hansen, and Hansen (1978)	Mothiversen1978_DI	DK\Co	1976	3	Benthic macroinvertebrates		– 0.19	– 0.07	0.10
Ortega, Suárez Alonso, Vidal-Abarca, and Ramírez-Díaz (1991)	Ortega1991_FI	ES\Me	1986	1	Benthic macroinvertebrates	– 1.70		– 0.35	– 0.12
Otermin, Basaguren, and Pozo (2002)	Otermin2002_DI	ES\Co	1995	2	Benthic macroinvertebrates			– 0.28	
Pires, Cowx, and Coelho (1999)	Pires1999_FF	ES\Me	1996	1	Fish community		– 0.77		0.07

TABLE 4 Continued

Reference	Code[a]	Location[b]	Year[c]	Severity[d]	Taxon	RR^{e}_{Ab}	RR^{e}_{De}	RR^{e}_{Ri}	RR^{e}_{Di}
Pires, Cowx, and Coelho (2000)	Pires2000_FI	ES\Me	1996	1	Benthic macroinvertebrates		0.20	– 0.10	– 0.31
Pires, Magalhães, Da Costa, Alves, and Coelho (2008)	Pires2008_FF	PT\Me	1997	3	Fish community	– 0.18		0.00	
Pupilli and Puig (2003)	Pupilli2003_FI	ES\Me	2000	3	Mayflies, stoneflies		– 1.40	– 0.25	
Řezničková et al. (2007)	Reznickova2007_DI1	CZ\Co	2002	1	Benthic macroinvertebrates	– 0.09		0.02	
Řezničková et al. (2007)	Reznickova2007_DI2	CZ\Co	2003	3	Benthic macroinvertebrates	– 0.42		0.00	
Ruegg and Robinson (2004)	Ruegg2004_DI	CH\Al	2003	2	Benthic macroinvertebrates			– 0.33	
Silva-Santos et al. (2004)	Silva-Santos2004_FF2	PT\Me	2001	2	Fish community	0.01		0.04	– 0.01
Silva-Santos et al. (2004)	Silva-Santos2004_FI1	PT\Me	2001	2	Benthic macroinvertebrates	– 0.34		– 0.15	0.18
Spindler (1995)	Spindler1995_FF	AU\Co	1985	2	*Blicca bjoerkna*		– 0.30		
Titus and Mosegaard (1992)	Titus1992_DF	SE\Bo	1990	1	*Salmo trutta*		– 0.89		
Wood, Boulton, Little, and Stubbington (2010)	Wood2010_DI	UK\At	2006	1	Benthic macroinvertebrates	– 0.35		– 0.16	
Wright (1992)	Wright1992_DI1	UK\At	1973	3	Benthic macroinvertebrates		0.28		
Wright (1992)	Wright1992_DI2	UK\At	1976	3	Benthic macroinvertebrates		0.33		
Wright and Symes (1999)	Wright1999_DI1	UK\At	1973	3	Benthic macroinvertebrates		– 0.16	– 0.04	
Wright and Symes (1999)	Wright1999_DI2	UK\At	1976	3	Benthic macroinvertebrates		0.21	– 0.06	
Wright et al. (2004)	Wright2004_FI1	UK\At	2000	2	Benthic macroinvertebrates		0.12	0.045	
Wright et al. (2004)	Wright2004_FI2	UK\At	2000	3	Benthic macroinvertebrates		0.24	0.08	
Zorn et al. (2005)	Zorn2005_FI1	NL\At	2001	2	Earthworms		– 0.34		
Zorn et al. (2005)	Zorn2005_FI2	NL\At	2002	2	Earthworms		– 0.11		
Zorn et al. (2005)	Zorn2005_FI3	NL\At	2002	1	Earthworms		– 0.42		

Note: [a]Code: AuthorNamePublicationYear_EventType_BiotaTypeNumber. EventType can be "D" for drought or "F" for flood. BiotaType can be "F" for fish" or "I" for invertebrates. Number is added only if it is required, that is, there is more than one case studies related to one paper. [b]Country\European Environment Agency Region. European country codes: AU—Austria, CH—Switzerland, CZ—Czech Republic, DE—Germany, DK—Denmark, ES—Spain, FR—France, IR—Ireland, IT—Italy, NL—Netherlands, PL—Poland, PT—Portugal, SE—Sweden, UK—United Kingdom; EEA biogeographical region codes: Al—Alpine, At—Atlantic, Bo—Boreal, Co—Continental, Me—Mediterranean. [c]Event occurrence year. [d]Event severity classes: 1—low, 2—medium, 3—high. [e]Response ratios related to Abundance (Ab), Density (De), Richness (Ri), or Diversity (Di) (cf. Equation (1)).

and drought CS locations, and Figure 3 summarizes the CS: (a) more flood CS than drought CS, (b) more invertebrate CS than fish CS, (c) flood CS more often in Germany and Spain, drought CS generally in UK, (d) flood CS mostly in the continental European Environment Agency (EEA) biogeographical region, whereas drought CS are generally in the Atlantic region, (e) large variability of upstream catchment areas (from 1–10 km^2 to more than 100,000 km^2) with medium size catchments (100–1,000 km^2) associated most frequently to both floods and droughts CS, (f) flood CS generally during the 1996–2005 period, while drought CS most frequently refer to the 1976–1980 period, (g) even distribution of severity classes in flood CS, while drought CS are generally referring to high severity class, (h) most CS on biota density, followed by richness, abundance, and diversity (Figure 4). The most frequently occurring combination were studies on the impacts of floods on invertebrate density (35 cases). In contrast, studies on the impacts of droughts on fish were the least frequent (seven cases), and none of them reported data on richness or diversity.

4.2 | Statistical analyses

In response to the first research question, Figure 4 shows the results of one-sample *t* tests verifying whether response ratios related to flood and drought events for the whole population and different subgroups (biota types, event severity classes, EEA biogeographical regions, and catchment sizes) and different ecological metrics are statistically different than 0. Note that all statistically significant tests show a decrease in given ecological metrics (i.e., negative response to hydrological extremes). Results were most often significant (50 % of cases) when the full sample was considered (no subgroups except flood and drought events). For tests at subgroup level, tests showed significant results in 16 (EEA regions) to 38 % (biota types) of the CS. Insufficient CS numbers were available to study the effect of EEA regions or catchment size. When analyzing biota types, the most robust findings (Figure 4) showed a decrease of invertebrate density and richness following flood events ($p < 0.01$ and $N > 20$) and a decrease of invertebrate abundance (richness) following flood (drought) events ($p < 0.05$ and $N > 10$). Lower significance results for much smaller samples were associated with decrease in invertebrate abundance (five CS and $p < 0.01$) and fish density (six CS and $p < 0.05$) following drought events. Not enough CS between drought and fish biota metrics were available, but fish response to flood events (quantified from 6 to 8 CS) was found to be not significant, with examples of increase and decrease.

To address the second question, two types of analyses were made. Firstly, a comparison of the ecological responses of one group, fish or invertebrates, between flood and drought events was possible for all invertebrate metrics and for the density of fish. Out of five conducted independent-sample *t* tests, only one test produced significant results at the level of 0.05: invertebrate density responded differently to floods than to droughts (Figure 5a). Mean RR_{De} values of -0.05 and -0.65 correspond to mean decreases in invertebrate density by 11% and 78% for droughts and floods, respectively. Secondly, a comparison of ecolog-

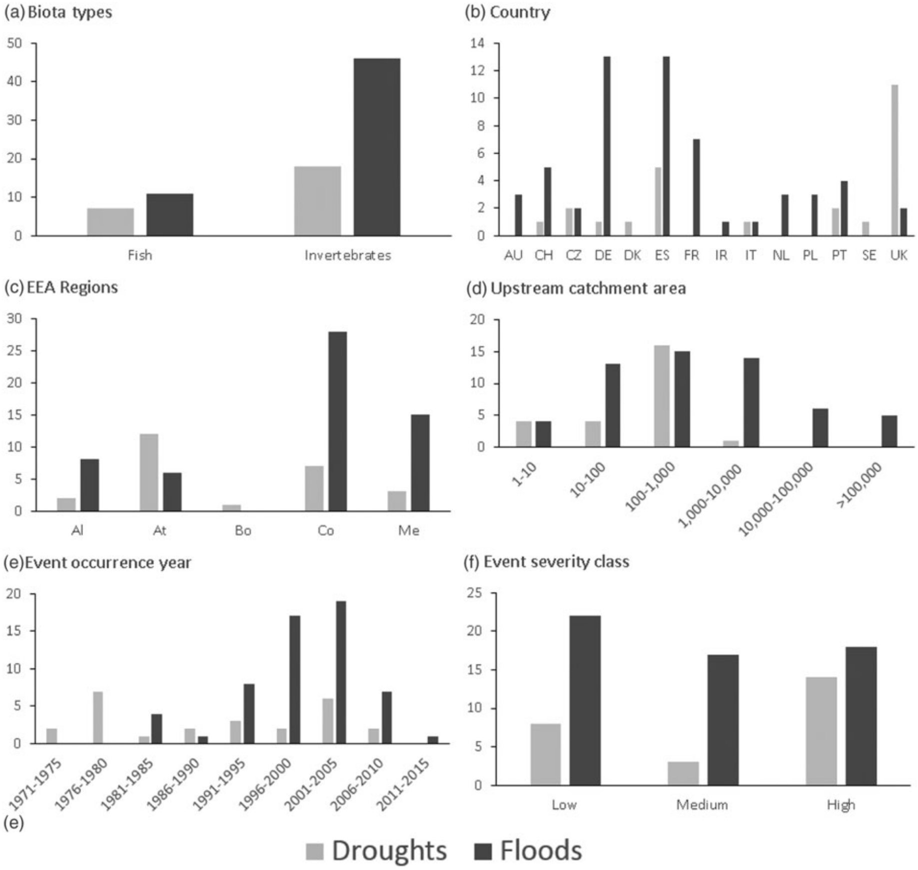
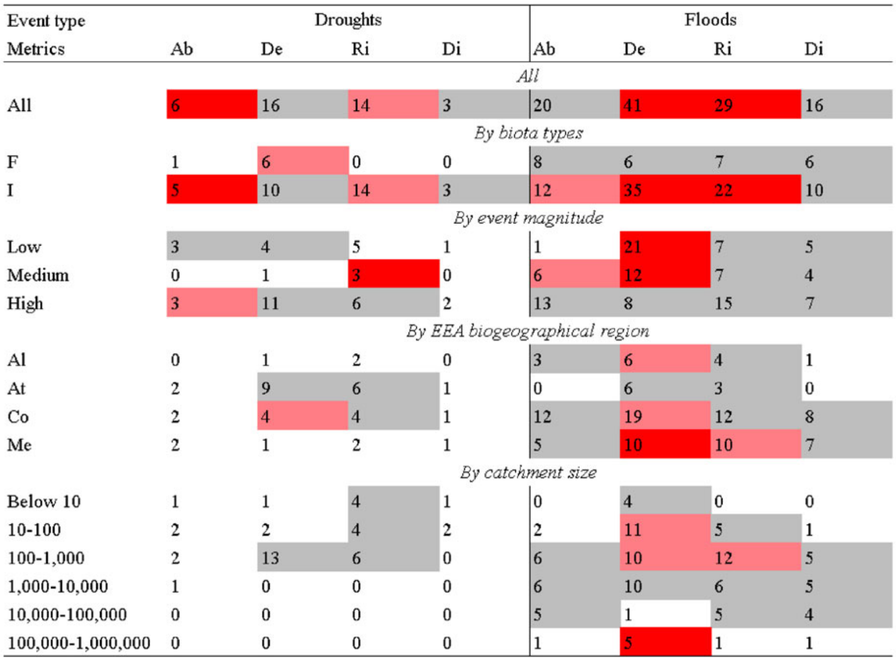


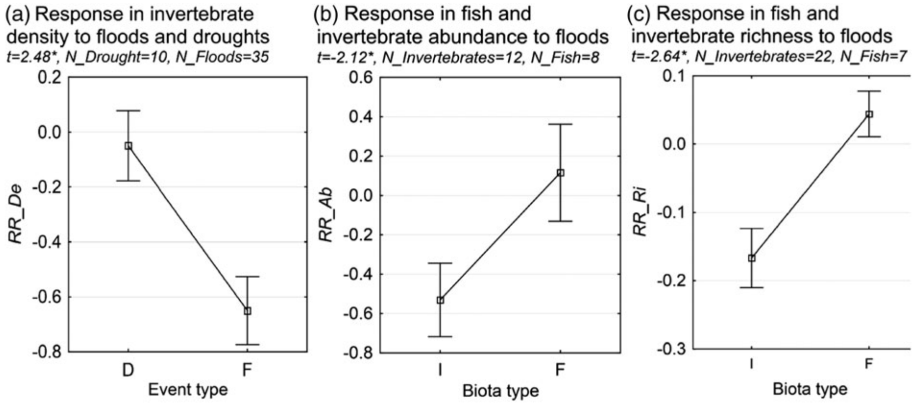
FIGURE 3 Histograms of flood (F) and drought (D) case studies categorized by biota types (a), countries (b), European Environment Agency (EEA) biogeographical regions (c), upstream catchment areas (km^2) (d), event occurrence dates (e), and event severity classes (f)



Event type	Droughts				Floods			
Metrics	Ab	De	Ri	Di	Ab	De	Ri	Di
					All			
All	6	16	14	3	20	41	29	16
					By biota types			
F	1	6	0	0	8	6	7	6
I	5	10	14	3	12	35	22	10
					By event magnitude			
Low	3	4	5	1	1	21	7	5
Medium	0	1	3	0	6	12	7	4
High	3	11	6	2	13	8	15	7
					By EEA biogeographical region			
Al	0	1	2	0	3	6	4	1
At	2	9	6	1	0	6	3	0
Co	2	4	4	1	12	19	12	8
Me	2	1	2	1	5	10	10	7
					By catchment size			
Below 10	1	1	4	1	0	4	0	0
10-100	2	2	4	2	2	11	5	1
100-1,000	2	13	6	0	6	10	12	5
1,000-10,000	1	0	0	0	6	10	6	5
10,000-100,000	0	0	0	0	5	1	5	4
100,000-1,000,000	0	0	0	0	1	5	1	1

Note: red colour denotes a statistically significant decrease at $p < 0.01$ level, pink colour denotes a statistically significant decrease at $p < 0.05$ level, grey colour denotes the lack of statistical significance, and white colour denotes the number of cases lower than 3. The numbers in respective cells denote the numbers of cases for different sub-groupings.

FIGURE 4 The results of one sample *t* tests verifying whether response ratios of ecological metrics for different subgroups (biota type, event magnitude, European Environment Agency (EEA) region, and catchment size) are statistically different than 0



(a) Response in invertebrate density to floods and droughts
t=2.48, N_Drought=10, N_Floods=35*

(b) Response in fish and invertebrate abundance to floods
t=-2.12, N_Invertebrates=12, N_Fish=8*

(c) Response in fish and invertebrate richness to floods
t=-2.64, N_Invertebrates=22, N_Fish=7*

FIGURE 5 Mean plots of response ratios for selected ecological metrics and sub-groups. All between-group differences are statistically significant at the 0.05 level. T-test statistics values are given in the sub-title

ical responses to one type of event, flood or drought, between fish and invertebrates was possible for all metrics in response to flood events and only for density in response to drought events. In this case, two out of five tests generated statistically significant results: abundance and richness differed between fish and invertebrates in response to flood events (Figure 5b,c). The results show that not only the magnitude but also the direction of response differed between biota types. While the invertebrate metrics were decreasing by 70% and 32% (mean values) for abundance and richness, respectively, the corresponding fish metrics were increasing by 31% and 11%, respectively.

In response to the third question, the one-way ANOVA was performed to test the effect of event severity class on ecological metrics for samples of at least three CS, but none gave statistical significance at 0.05 level. For illustrative purposes, Figure S1 in the Supporting Information shows the effect plot for RR_{De} of invertebrates to floods, indicating that the difference between classes is not significant.

To further investigate the effect of event severity on ecological responses (as our statistical analysis was limited due to too small sample size), we also looked at selected individual papers that included at least two case studies (i.e., either two different floods or two different droughts) with different severity classes. The rationale was that comparing different case studies (extreme events) within one paper is potentially more homogenous and does not introduce so much noise as in the case of comparing studies from different publications. There were, in total, eight publications meeting this criterion, of which none included three different severity classes (low, medium, and high). There was no clear pattern in these eight publications concerning the responses to events of different severity. For example, in Argerich (2004); Řezničková, Pařil, and Zahrádková (2007); Gaudes, Artigas, and Muñoz (2010), the changes in ecological variables were positively correlated with severity classes (the more severe class the more negative response). On the other hand, in Majdi et al. (2012); Zorn, Van Gestel, and Eijsackers (2005); Wright, Clarke, Gunn, Kneebone, and Davy-Bowker (2004) the relationship was the opposite. In Effenberger, Sailer, Townsend, and Matthaei (2006) and Lobon-Cervia (2009), there was no correlation.

5 | DISCUSSION

The objective of this paper was to identify evidence in quantitative response of fish and invertebrates to floods and droughts as a first step toward a better understanding of the nature of flow–ecosystem relationships in Europe. Specified research questions dealt with significant changes in ecological metrics following floods/droughts events, significant differences in ecological response between different groups, and the role of extreme event severity. To address these questions and facilitate exploratory data analyses, a database of extreme events and corresponding ecological responses was developed using a systematic review framework. The majority of assembled responses were direct, immediate responses that quantitatively characterized biota resistance to extreme events.

The synthesis of European case studies suggests that there exists an evidence gap related to studying the responses of biota to drought events and to the fish responses to extreme events. Notably, the effect of droughts on fish richness, diversity, and abundance remains the biggest gap, with only one case study identified (for abundance) and no case studies for richness and diversity. A relatively low number of perturbations (maximum eight) were identified also for the effects of floods on fish. Metadata analysis as undertaken here is, however, dependent on hypothesis, search terms, and inclusion criteria (cf. Table 2). A number of theoretically relevant studies could have been missed in literature search or excluded during screening/eligibility checks, and hence could not be systematically assessed within a rigorous and comparative framework such as implemented here. The most striking examples of studies that, despite being highly relevant, were either uncaptured or excluded are

1. A study was missed because the authors did not use any of the terms listed in Table 1 to describe investigated biota (Hastie, Boon, Young, & Way, 2001).
2. Some studies reporting mortalities of invertebrates (Sousa et al., 2012) or fish (Brooker & Morris, 1977) following very extreme events had to be excluded as mortality rates could not be translated into changes in population sizes and in consequence, the response ratios could not be calculated.
3. Several studies were excluded because of reporting values of ecological metrics that underwent a specific standardization and were thus not comparable to all other studies reporting the same metrics without standardization (Wood & Armitage, 2004; Stubbington et al., 2009a).
4. The most frequent exclusion reason for highly relevant studies was, however, the lack of pre-event sampling data that could be used for calculating the response ratios of ecological metrics. Examples include: studies on invertebrate responses following some major droughts in the UK: the 1989–1992 (Wood & Petts, 1999) and 1996–1997 (Wright et al., 2002) drought; a study on invertebrate responses to a severe flood that occurred in a karst river in the UK in 2007 (Stubbington et al., 2009b). Some studies in the Mediterranean regions (Bravo, Soriguer, Hernando, 2001; Langton & Casas, 1998) tended to compare sampling results between drought and wet periods, which also made it impossible to extract the appropriate data for our purposes.

Despite these methodological problems, it was possible to (a) compare ecological responses before and after hydrological extreme events (cf. Figure 4); (b) compare ecological responses between different groups such as fish and invertebrates, or droughts and floods (cf. Figure 5); and (c) compare ecological responses between three event severity classes. When considering all samples together, CS showed statistically significant decreases in ecological metrics after the peak of the event, most frequently for invertebrates; for example, invertebrate abundance, density, and richness were significantly lower after the flood than before the flood. This is consistent with the findings of Greenwood and Booker (2015), who showed an overtime increase in invertebrates taxa richness after a flood from 22 years of data over 66 sites in New Zealand, inferring lowest values occurred immediately after the flood.

When comparing subgroups, sample size was often insufficient to show statistically significant responses. However results highlighted (a) higher magnitude of decrease in invertebrate density for floods than for droughts, and (b) a large decrease in abundance and richness of invertebrates compared to a small increase for fish following flood events. Very few published studies explore the response of both floods and droughts for comparison with our conclusions, but Suren and Jowett (2006) found a decrease in invertebrate density was more common after floods than droughts based on five discrete flood and low-flow events in a New Zealand river, while Lake (2000,2003) suggested low biota resistance to floods, high resistance to seasonal droughts, and medium to low resistance for supraseasonal droughts. This is consistent with our conclusions of higher decreases of invertebrate density after floods than droughts, albeit from a much smaller drought sample (10 CS) compared with that of floods (35 CS). No statistically significant differences were found between fish and invertebrates' responses to natural (McManamay et al., 2013) and anthropogenic (McManamay et al., 2013; Poff & Zimmerman, 2010) flow variation, but Silva-Santos, Oliveira, Cortes, and Albuquerque (2004) and Meffe and Minckley (1987) reported sharp post-flood decreases in taxa richness and density/abundance for invertebrates and very little effects on fish. The results of the study of Nislow, Magilligan, Folt, and Kennedy (2002) show a more complex pattern, with benthic invertebrate densities generally decreasing following the flood and salmonid responses strongly depending on the age: habitat change-triggered positive effects on overyearling fish compared to greatly diminishing numbers of age-0 salmonids.

No statistically significant ecological response to extreme event severity class (low, medium, or high) was identified, but this might be caused by the very small sample size available for the analysis, except the effects of floods on invertebrates. Lack of robust quantitative relationships between flow and ecosystems had been reported in the past (Poff & Zimmerman, 2010; Jones & Petreman, 2013; McManamay et al., 2013; Nislow et al., 2002). Poff & Zimmerman (2010) found that the size of flow alteration was not correlated with subsequent ecological responses, which varied among the different taxonomic groups, and Jones and Petreman (2013) found weak correlations between high- and low-flow event severity (coupled with extreme air temperature) and fish responses in Ontario, Canada, the impact of hydrological extreme on fish possibly being reduced by factors such as the buffering ability of groundwater, habitat heterogeneity, or recovery period. The role of natural flow variation on ecological responses in the south Atlantic region of the United States was reviewed by McManamay et al. (2013), who concluded that the occurrence of floods and high-flow periods in an unconstrained coastal plain stream may have less negative consequences for river communities than in a floodplain constrained upland stream. Nislow et al. (2002) indicated that hydrologic and hydraulic measures of flood intensity were much less important than bed load movement to predict the magnitude of change in benthic invertebrate and salmonid densities after the flood. These studies were suggesting that hydromorphology is an important factor in modulating the hydrological extreme–ecological response relationships, but this had to be excluded from our study by lack of sufficient detail on hydromorphology of sampling sites in a part of the reviewed literature.

It is an inherent challenge of most ecological reviews that individual studies composing the analysis were not designed specifically to address the research questions posed in a review (Poff & Zimmerman, 2010). This could be due to a lack of common experimental methodology for investigating the ecological effects of floods or droughts that is approved and used by the majority of researchers. In consequence, empirical design of individual CS from our database was heterogeneous. For example, the time lags between event occurrence dates and pre-event or post-event sampling dates were highly variable across studies, ranging from days to years for pre-event samplings and from days to months for post-event sampling. We were often faced with necessity to select sampling dates based on expert judgment, for example, when there were many pre- or post-event samplings and none of them were clearly indicated by the authors as “reference” or “impact.” This heterogeneity can be partly explained by the stochastic nature of hydrological extreme events, which makes it difficult to plan field surveys in advance, with capturing of a series of extreme events within a long-term sampling data set sometimes fortuitous (Woodward, Bonada, Feeley, & Giller, 2015). In consequence, very few studies investigating ecological responses to floods and droughts follow the rigorous Before-After Control-Impact design (Edwards et al., 2012). Another point is that insufficient methodological detail in ecological papers hampers systematic reviews (Haddaway & Verhoeven, 2015). Failing to report sampling dates, extreme events occurrence dates, or quantitative indices of their severity are typical examples encountered in our review, increasing the uncertainty of our assessment.

Because floods and droughts are natural phenomena, part of the expected variation in the hydrological cycle (although they may be exacerbated by anthropogenic-driven climate change), one could question whether they are “harmful” to ecosystems. There is evidence that droughts eliminate weak individuals and prevent invasive species, and so can have a positive impact on the ecosystem (Everard, 1996). Both droughts and floods may also be favorable for fish reproduction and recruitment (Keaton, Haney, & Andersen, 2005; Cattaneo, Carrel, Lamouroux, & Breil, 2001), and floodplain inundation may also lead to short- and long-term increases in ecological metrics of invertebrate assemblages (Ballinger, Nally, & Lake, 2005). Furthermore, even when the effects are “harmful”, that is, biota and ecological processes have been greatly diminished after the disturbance, they often have sufficient capacity to recover (Lake, 2011). Many organisms, such as microbes, may return to a river within a few weeks of a drought terminating; the following year, higher plants (Wright et al., 2002) and macroinvertebrates (Wood & Petts, 1999) can recover, whereas reduction in fish numbers may persist for five or more years (Elliott, Hurley, & Elliott, 1997). So provided that another drought does not occur within this period, the ecosystem can normally recover, although Holmes (1999) found that some plant communities shifted permanently after drought, and never returned to predrought conditions. Death et al. (2015) stated that the recovery of the biota from extreme flood events can be quick provided that instream habitat is not dramatically affected (then recovery would be much slower, if at all). Woodward et al. (2015) reported that most invertebrate populations returned to their predisturbance state within 3 years after a catastrophic flood that triggered a 10-fold decrease in abundance, although for some it took up to 10 years. It should be noted that because our study focused on direct, immediate effects and responses (resistance), investigating resilience and recovery was beyond its scope.

Further steps building on the outcomes of this work could include a more in-depth analysis of case studies for which collected evidence was the most abundant, that is, the effect of floods on invertebrate density. This could even include a more formal meta-analysis, provided that the effect sizes were additionally estimated for each perturbation. In the case of fish and/or drought CS, where evidence was more modest, it should be considered to extend the geographical coverage of review to the global scale. Another direction is a focus on recovery/resilience rather than pure resistance of biota. Further progress in synthesizing evidence on the ecological role of floods and droughts in Europe can also be achieved in a different way: by carrying out comprehensive flume studies across a range of physiographic conditions using a multi-factorial design allowing to control other factors than solely the hydrological stress, such as it has been on the ecological role of floods and droughts can also be achieved in a different way: by carrying out comprehensive flume studies across a range of physiographic conditions using multi-factorial experiments planned in the MARS project (Hering et al., 2015).

6 | CONCLUSIONS

In this study, we synthesized knowledge on the direct responses of fish and invertebrates to flood and drought events in European rivers and streams. Systematic review methods were employed to collect evidence from existing ecological literature, and hydrological techniques used for extreme event estimation were used to classify the severity of floods and droughts from the identified papers. While the resulting database is a significant product in itself, this study pinpointed the research gaps where no or very little evidence can be synthesized at this stage (e.g., the effect of drought on fish), as well as the more widely researched areas that would benefit from more in-depth quantitative analyses (e.g., the effect of floods on invertebrates). It was demonstrated that the studied metrics (abundance, density, richness, and diversity) experienced statistically significant decreases following extreme events in a number of cases, particularly for invertebrate responses to flood (higher significance) and drought (lower significance) events. Lack of significance for the effect of floods on fish shows, on one hand, that the identified responses in studied metrics were both increasing and decreasing. On the other hand, this result should be treated with caution due to a relatively low number of case studies, compared to invertebrates. Furthermore, a comparison of ecological responses between different subgroups showed that (a) the responses in invertebrate abundance and richness were more negative than the corresponding responses in fish following flood events, and (b) invertebrate density decreased more after floods than after droughts. Finally, contrary to our expectations, the severity class of extreme events was either not found to be an important factor influencing ecological metrics, or the number of studies was too low to perform such analysis (in most cases for droughts and for fish). Conceivably, other factors such as hydromorphology, biogeographical region, river size, or inhomogeneity between studies could mask any existing relationships between severity and response. Thus, the call of Lake (2000) for quantification of disturbance–ecosystem relationships: "If we are to progress and usefully compare both disturbance impacts and the consequential biotic responses, we need quantifiable measures of the disturbances (…), of the effects on abiotic and biotic components (…), and of the subsequent responses by the biota." remains as valid and urgent as ever. Hopefully, this paper also provides useful insights for future ecological studies regarding the type of information that should preferably be reported so that future evidence-based reviews could benefit from a more consistent material.

ACKNOWLEDGMENTS

Mikołaj Piniewski, Pawel Oglecki, Luiza Tylec, and Tomasz Okruszko were supported by the EU-project REFORM (Restoring rivers for effective catchment management), contract no. 282656 under the 7th Framework Programme, in the initial phase of this study, and by the Department of Hydraulic Engineering statutory activity in its second phase. Mikołaj Piniewski is grateful for support to the Alexander von Humboldt Foundation and the Foundation for Polish Science (START programme). Christel Prudhomme was supported by CEH-NERC National Capability Water Resource Science Area. Mike Acreman acknowledges funding from NERC (Marius project NE/L010208/1) and Belmont Forum (Driver project G8MUREFU3FP-2200-108). The associate editor Paul Wood and two anonymous referees helped to improve the original manuscript. Many people provided useful guidance concerning getting access to streamflow data necessary to carry out the research. Notably, Jamie Hannaford (NERC-CEH Wallingford), Benjamin Renard (IRSTEA), Luis Mediero (UPM Madrid), Tobias Conradt (PIK Potsdam), Pedro Chambel-Leitão (IST Lisbon), Walter Bertoldi (University Trento), Jarkko Koskela (SYKE), and Niels Bering Ovesen (Aarhus University) were helpful. The authors are grateful to the following European flow data providers: (1) Global Runoff Data Centre (GRDC), Germany; (2) European Water Archive (EWA), Germany; (3) German Federal Institute of Hydrology (BfG), Germany (including data acquired from the water authorities of the German Federal States); (4) National River Flow Archive (NRFA), UK; (5) Centre for Hydrographic Studies (CEDEX), Spain; (6) National Information System for Water Resources (SNIRH), Portugal; (7) Institute of Meteorology and Water Management - National Research Institute (IMGW-PIB), Poland; Austrian Federal Ministry of Agriculture, Forestry, Environment and Water Management (BMLFUW), Austria; (8) Central Service of Hydrometeorology and Support for Flood Forecasting, Banque HYDRO, France; (9) Finish Environment Institute (SYKE), Finland; (10) Danish Centre for Environment and Energy (DCE), Denmark. The authors have no conflict of interest to declare.

REFERENCES

Acuña, V., Muñoz, I., Giorgi, A., Omella, M., Sabater, F., & Sabater, S. (2005). Drought and postdrought recovery cycles in an intermittent Mediterranean stream: Structural and functional aspects. *Journal of the North American Benthological Society*, *24*, 919–933. doi: 10.1899/04-078.1

Argerich, A. (2004). Effect of floods of different magnitude on the macroinvertebrate communities of Matarranya stream (Ebro river basin, NE Spain). *Limnetica*, *23*, 283–294.

Arscott, D., Tockner, K., & Ward, J. (2003). Spatio-temporal patterns of benthic invertebrates along the continuum of a braided Alpine river. *Archiv für Hydrobiologie*, *158*, 431–460. doi: 10.1127/0003-9136/2003/0158-0431

Ballinger, A., Nally, R. M., & Lake, P. S. (2005). Immediate and longer-term effects of managed flooding on floodplain invertebrate assemblages in south-eastern Australia: Generation and maintenance of a mosaic landscape. *Freshwater Biology*, *50*, 1190–1205. doi: 10.1111/j.1365-2427.2005.01391.x

Baumgartner, A., & Waringer, J. (1997). Longitudinal zonation and life cycles of macrozoobenthos in the Mauerbach near Vienna, Austria. *Internationale Revue der gesamten Hydrobiologie und Hydrographie*, *82*, 379–s394. doi: 10.1002/iroh.19970820311

Bayliss, A. C., & Jones, R. C. (1993). Peaks-over-threshold flood database: Summary statistics and seasonality. (*Tech. rep.*) Wallingford: Institute of Hydrology.

Bischoff, A., & Wolter, C. (2001). The flood of the century on the River Oder: Effects on the 0+ fish community and implications for floodplain restoration. *Regulated rivers - Research & Management*, *17*, 171–190. doi: 10.1002/rrr.612

Bravo, R., Soriguer, M. C., Villar, N., & Hernando, J. A. (2001). The dynamics of fish populations in the Palancar stream, a small tributary of the river Guadalquivir, Spain. *Acta Oecologica*, *22*, 9–20. http://dx.doi.org/doi: 10.1016/ S1146-609X(00)01098-5

Cattaneo, F., Carrel, G., Lamouroux, N., & Breil, P. (2001). Relationship between hydrology and cyprinid reproductive success in the Lower Rhone at Montelimar, France. *Archiv für Hydrobiologie*, *151*, 427–450.

Chaves, M., Rieradevall, M., Chainho, P., Costa, J. L., Costa, M. J., & Prat, N. (2008). Macroinvertebrate communities of non-glacial high altitude intermittent streams. *Freshwater Biology*, *53*, 55–76. doi: 10.1111/j.1365-2427.2007.01867.x

Cowx, I., Young, W., & Hellawell, J. (1984). The influence of drought on the fish and invertebrate populations of an upland stream in Wales. *Freshwater Biology*, *14*, 165–177. doi: 10.1111/j.1365-2427.1984.tb00030.x

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*, 2477–2496. doi: 10.1111/fwb.12639

Edwards, F. K., Baker, R., Dunbar, M., & Laizé, C. (2012). *A Review of the Processes and Effects of Droughts and Summer Floods in Rivers and Threats*

Due to Climate Change on Current Adaptive Strategies, Deliverable 2.14 of REFRESH. Wallingford: NERC Centre for Ecology and Hydrology.

Effenberger, M., Sailer, G., Townsend, C., & Matthaei, C. (2006). Local disturbance history and habitat parameters influence the microdistribution of stream invertebrates. *Freshwater Biology*, *51*, 312–332. doi: 10.1111/j. 1365. 2427.2005.01502.x

Elliott, J. M., Hurley, M. A., & Elliott, J. A. (1997). Variable effects of droughts on the density of a sea-trout Salmo trutta population over 30 Years. *Journal of Applied Ecology*, *34*, 1229–1238.

Environment Agency (2013). Monitoring and assessment of environmental impacts of droughts: Literature synthesis. SC120024/R1.

Everard, M. (1996). The importance of periodic droughts for maintaining diversity in the freshwater environment. *Freshwater Forum*, *7*, 33–50.

Extence, C. A. (1981). The effect of drought on benthic invertebrate communities in a lowland river. *Hydrobiologia*, *83*, 217–224.

Fellendorf, M., Mohra, C., & Paxton, R. J. (2004). Devasting effects of river flooding to the ground-nesting bee, Andrena vaga (Hymenoptera: Andrenidae), and its associated fauna. *Journal of Insect Conservation*, *8*, 311–322. doi: 10. 1007/s10841-004-0514-5

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*, 191–201. doi: 10.1080/11250000701286696

Garcia De Jalón, D., González Del Tánago, M., Oglecki, P., Wolter, C., Buijse, T., Parasiewcz, P., ..., & Okruszko, T. (2014). *Influence of Natural Hydromorphological Dynamics on Biota and Ecosystem Function. Part 2 (Chapters 4 to 6 of 6)*: Deliverable 2.2 Part 2 of REFORM.

Garner, G., Van Loon, A. F., Prudhomme, C., & Hannah, D. M. (2015). Hydroclimatology of extreme river flows. *Freshwater Biology*, *60*, 2461–2476. doi: 10. 1111/fwb.12667

Gaudes, A., Artigas, J., & Muñoz, I. (2010). Species traits and resilience of meiofauna to floods and drought in a Mediterranean stream. *Marine and Freshwater Research*, *61*, 1336–1347. doi: 10.1071/MF10044

Gerisch, M., Dziock, F., Schanowski, A., Ilg, C., & Henle, K. (2012). Community resilience following extreme disturbances: The response of ground beetles to a severe summer flood in a Central European lowland stream. *River Research and Applications*, *28*(81), 92. doi: 10.1002/rra.1438

Greenwood, M. J., & Booker, D. J. (2015). The influence of antecedent floods on aquatic invertebrate diversity, abundance and community composition. *Ecohydrology*, *8*(ECO-14-0018.R1), 188–203. doi: 10.1002/eco.1499

Grzybkowska, M., Temech, A., & Dukowska, M. (1996). *Impact of long-term alternations of discharge and spate on the chironomid community in the lowland Widawka River (Central Poland)*, Vol. *324*, pp. 107–115. doi: 10.1007/BF00018171

Grzybkowska, M., & Witczak, J. (1990). Distribution and production of Chironomidae (Diptera) in the lower course of the Grabia River (Central Poland). *Freshwater Biology*, *24*, 519–531. doi: 10.1111/j.1365-2427.1990.tb00729.x

Haddaway, N. R., & Verhoeven, J. T. (2015). Poor methodological detail precludes experimental repeatability and hampers synthesis in ecology. *Ecology and Evolution*, *5*, 4451–4454. doi: 10.1002/ece3.1722

Hannaford, J., Lloyd-Hughes, B., Keef, C., Parry, S., & Prudhomme, C. (2011). Examining the large-scale spatial coherence of European drought using regional indicators of precipitation and streamflow deficit. *Hydrological Processes*, *25*, 1146–1162. doi: 10.1002/hyp.7725

Hastie, L., Boon, P., Young, M., & Way, S. (2001). The effects of a major flood on an endangered freshwater mussel population. *Biological Conservation*, *98*, 107–115. http://dx.doi.org/ doi: 10.1016/S0006-3207(00)00152-X

Hering, D., Carvalho, L., Argillier, C., Beklioglu, M., Borja, A., Cardoso, A. C., ..., & Birk, S. (2015). Managing aquatic ecosystems and water resources under multiple stress. An introduction to the MARS project. *Science of The Total Environment*, *503–504*, 10–21. doi: 10.1016/ j.scitotenv.2014.06.106

Hering, D., Gerhard, M., Manderbach, R., & Reich, M. (2004). Impact of a 100-year flood on vegetation, benthic invertebrates, riparian fauna and large woody debris standing stock in an Alpine floodplain. *River Research and Applications*, *20*, 445–457. doi: 10.1002/rra.759

Herrera, S., Fernández, J., & Gutiérrez, J. M. (2016). Update of the Spain02 gridded observational dataset for EURO-CORDEX evaluation: Assessing the effect of the interpolation methodology. *International Journal of Climatology*, *36*, 900–908. doi: 10.1002/joc.4391

Holmes, N. T. H. (1999). Recovery of headwater stream flora following the 1989–1992 groundwater drought. *Hydrological Processes*, *13*, 341–354. doi: 10.1002/(SICI)1099-1085(19990228)13:3<341::AID-HYP742>3.0.CO;2-L

Ilg, C., Dziock, F., Foeckler, F., Follner, K., Gerisch, M., Glaeser, J., ..., & Henle, K. (2008). Long-term reactions of plants and macroinvertebrates to extreme floods in floodplain grasslands. *Ecology*, *89*, 2392–2398. doi: 10.1890/08-0528.1

Imbert, J., Gonzalez, J., Basaguren, A., & Pozo, J. (2005). Influence of inorganic substrata size, leaf litter and woody debris removal on benthic invertebrates resistance to floods in two contrasting headwater streams. *International Review of Hydrobiology*, *90*, 51–70. doi: 10.1002/iroh.200410739

Jones, N. E., & Petreman, I. C. (2013). Relating extremes of flow and air temperature to stream fish communities. *Ecohydrology*, *6*, 826–835. doi: 10.1002/eco.1305

Jurajda, P., Reichard, M., & Smith, C. (2006). Immediate impact of an extensive summer flood on the adult fish assemblage of a channelized lowland river. *Journal of Freshwater Ecology*, *21*, 493–501. doi: 10.1080/02705060.2006. 9665027

Kaendler, M., & Seidler, C. (2013). Influence of hydrological situations on benthic organisms in a small river in Saxony (Germany). *Journal of Hydrology and Hydromechanics*, *61*, 188–194. doi: 10.2478/johh-2013-0024

Kajzer-Bonk, J., Nowicki, P., Bonk, M., Skórka, P., Witek, M., & Woyciechowski, M. (2013). Local populations of endangered Maculinea (Phengaris) butterflies are flood resistant. *Journal of Insect Conservation*, *17*, 1105–1112. doi: 10.1007/s10841-013-9591-7

Keaton, M., Haney, D., & Andersen, C. B. (2005). Impact of drought upon fish assemblage structure in two South Carolina Piedmont streams. *Hydrobiologia*, *545*, 209–223. doi: 10.1007/s10750-005-2674-z

Keyantash, J., & Dracup, J. A. (2002). The quantification of drought: An evaluation of drought indices. *Bulletin of the American Meteorological Society*, *83*, 1167–1180. doi: 10.1175/1520-0477(2002)083<1191:TQODAE>2.3.CO;2

Lake, P. S. (2000). Disturbance, patchiness, and diversity in streams. *Journal of North American Benthological Society*, *19*, 573–592.

Lake, P. S. (2003). Ecological effects of perturbation by drought in flowing waters. *Freshwater Biology*, *48*, 1161–1172. doi: 10.1046/j.1365-2427.2003. 01086.x

Lake, P. S. (2011). *Drought and aquatic ecosystems: Effects and responses*. Oxford, UK: Wiley- Blackwell; 400.

Langton, P. H., & Casas, J. (1998). Changes in chironomid assemblage composition in two Mediterranean mountain streams over a period of extreme hydrological conditions. *Hydrobiologia*, *390*, 37–49. doi: 10.1023/A:1003589216389

Ledger, M. E., & Milner, A. M. (2015). Extreme events in running waters. *Freshwater Biology*, *60*, 2455–2460. doi: 10.1111/fwb.12673

Ledger, M., & Hildrew, A. (2001). Recolonization by the benthos of an acid stream following a drought. *Archiv für Hydrobiologie*, *152*, 1–17.

Lloyd, N., Quinn, G., Thoms, M., Arthington, A., Gawne, B., Humphries, P., & Walker, K. (2003). Does flow modification cause geomorphological and ecological response in rivers? A literature review from an Australian perspective. (*Technical Report 1 2004*): Canberra, Australia: CRC for Freshwater Ecology.

Lobon-Cervia, J. (1996). Response of a stream fish assemblage to a severe spate in northern Spain. *Transactions of the American Fisheries Society*, *125*, 913–919. 10.1577/1548-8659(1996)125<0913:ROASFA>2.3.CO;2.

Lobon-Cervia, J. (2009). Why, when and how do fish populations decline, collapse and recover? The example of brown trout (Salmo trutta) in Rio

Chaballos (northwestern Spain). *Freshwater Biology*, *54*, 1149–1162. doi: 10.1111/j. 1365-2427.2008.02159.x

Lojkásek, B., Lusk, S., Halačka, K., Lusková, W., & Drozd, P. (2005). The impact of the extreme floods in July 1997 on the ichthyocenosis of the Oder Catchment area (Czech Republic). *Hydrobiologia*, *548*, 11–22. doi: 10.1007/s-10750- 005-3644-1

Lopez-Rodréguez, M. J., Peralta-Maraver, I., Gaetani, B., Sainz-Cantero, C. E., Fochetti, R., & Manuel Tierno de Figueroa, J. (2012). Diversity patterns and food web structure in a Mediterranean intermittent stream. *International Review of Hydrobiology*, *97*, 485–496. doi: 10.1002/iroh.201201541

Lusk, S. P. H., Halačka, K., Lusková, V., & Holub, M. (2004). Impact of extreme flood on fishes in rivers and their floodplains. *Ecohydrology & Hydrobiology*, *4*, 173–181.

Lytle, D. A., & Poff, N. L. (2004). Adaptation to natural flow regimes. *Trends in Ecology and Evolution*, *19*, 94–100. j.tree.2003.10.002.

M. P. Brooker, D. L., & Morris R. J. H. (1977). Mass mortalities of adult salmon, Salmo salar, in the R. Wye, 1976. *Journal of Applied Ecology*, *14*, 409–417.

Madsen, H., Rasmussen, P. F., & Rosbjerg, D. (1997). Comparison of annual maximum series and partial duration series methods for modeling extreme hydrologic events: 1. At-site modeling. *Water Resources Research*, *33*, 747–757. doi: 10.1029/96WR03848.

Magalhães, M. F., Beja, P., Schlosser, I. J., & Collares-Pereira, M. J. (2007). Effects of multi-year droughts on fish assemblages of seasonally drying Mediterranean streams. *Freshwater Biology*, *52*, 1494–1510. doi: 10.1111/j.1365-2427. 2007.01781.x

Maier, K. (2001). The influence of floods on benthic insect populations in a Swiss mountain stream and their strategies of damage prevention. *Archiv für Hydrobiologie*, *150*, 227–247.

Majdi, N., Mialet, B., Boyer, S., Tackx, M., Leflaive, J., Boulêtreau, S., ..., & Buffan-Dubau, E. (2012). The relationship between epilithic biofilm stability and its associated meiofauna under two patterns of flood disturbance. *Freshwater Science*, *31*, 38–50. 10.1899/11-073.1.

Mastrorillo, S., & Copp, G. (2005). Diel dynamics of young and small fishes in a side-channel of the River Garonne, France, before and after a late-summer spate. *Annales de Limnologie*, *41*, 15–25. 10.1051/limn/2005001.

Matthaei, C., Uehlinger, U., & Frutiger, A. (1997). Response of benthic invertebrates to natural versus experimental disturbance in a Swiss prealpine river. *Freshwater Biology*, *37*, 61–77. doi: 10.1046/j.1365-2427.1997.00141.x

McManamay, R. A., Orth, D. J., Kauffman, J., & Davis, M. M. (2013). A database and meta-analysis of ecological responses to stream flow in the South Atlantic Region. *Southeastern Naturalist*, *12*, 1–36. doi: 10.1656/058.012.m501

Meffe, G. K., & Minckley, W. L. (1987). Persistence and stability of fish and invertebrate assemblages in a repeatedly disturbed Sonoran Desert stream. *The American Midland Naturalist*, *117*, 177–191.

Meyer, A., & Meyer, E. I. (2000). Discharge regime and the effect of drying on macroinvertebrate communities in a temporary karst stream in East Westphalia (Germany). *Aquatic Sciences*, *62*, 216–231. doi: 10.1007/PL00001333

Moher, D., Liberati, A., Tetzlaff, J., Altman, D. G., & Group, T. P. (2009). Preferred Reporting Items for Systematic Reviews and Meta-Analyses: The PRISMA Statement. *PLoS Med*, *6*, 1–6. doi: 10.1371/journal.pmed.1000097

Monk, W. A., Wood, P. J., Hannah, D. M., & Wilson, D. A. (2008). Macroinvertebrate community response to inter-annual and regional river flow regime dynamics. *River Research and Applications*, *24*, 988–1001. doi: 10.1002/rra.1120

Morais, M., Pinto, P., Guilherme, P., Rosado, J., & Antunes, I. (2004). Assessment of temporary streams: The robustness of metric and multimetric indices under different hydrological conditions. *Hydrobiologia*, *516*, 229–249. doi: 10.1023/B:HYDR.0000025268.66163.32

Morrison, B. (1990). Recolonisation of 4 small streams in Central Scotland following drought conditions in 1984. *Hydrobiologia*, *208*, 261–267. doi: 10.1007/ BF00007791

Moth Iversen, T., Wiberg-Larsen, P., Birkholm Hansen, S., & Hansen, F. (1978). The effect of partial and total drought on the macroinvertebrate communities of three small Danish streams. *Hydrobiologia*, *60*, 235–242.

Newman, J. R., Duenas-Lopez, M. A., Acreman, M. C., Palmer-Felgate, E. J., Verhoeven, J. T., Scholz, M., & Maltby, E. (2015). Do on-farm natural, restored, managed and constructed wetlands mitigate agricultural pollution in Great Britain and Ireland? A systematic review. (*Final report WT0989 DEFRA*) Wallingford, UK: Centre for Ecology & Hydrology.

Nislow, K. H., Magilligan, F. J., Folt, C. L., & Kennedy, B. P. (2002). Within-basin variation in the short-term effects of a major flood on stream fishes and invertebrates. *Journal of Freshwater Ecology*, *17*, 305–318. 10. doi: 1080/02705060.2002.9663899

Ortega, M., Suárez Alonso, M., Vidal-Abarca, M., & Ramírez-Díaz, L. (1991). Aspectos dinámicos de la composición y estructura de la comunidad de invertebrados acuáticos de la Rambla del Moro después de una riada (Cuenca del Río Segura: SE de España). *Limnetica*, *7*, 11–24.

Otermin, A., Basaguren, A., & Pozo, J. (2002). Recolonization by the macroinvertebrate community after a drought period in a first-order stream (Agüera basin, Northern Spain). *Limnetica*, *21*, 117–128.

Parry, S., Hannaford, J., Lloyd-Hughes, B., & Prudhomme, C. (2012). Multi-year droughts in Europe: Analysis of development and causes. *Hydrology Research*, *43*, 689–706. doi: 10.2166/nh.2012.024

Pires, A. M., Cowx, I. G., & Coelho, M. M. (1999). Seasonal changes in fish community structure of intermittent streams in the middle reaches of the Guadiana basin, Portugal. *Journal of Fish Biology*, *54*, 235–249.

Pires, A. M., Cowx, I. G., & Coelho, M. M. (2000). Benthic macroinvertebrate communities of intermittent streams in the middle reaches of the Guadiana Basin (Portugal). *Hydrobiologia*, *435*, 167–175. doi: 10.1023/A:1004003726283

Pires, A. M., Magalhães, M. F., Da Costa, L. M., Alves, M. J., & Coelho, M. M. (2008). Effects of an extreme flash flood on the native fish assemblages across a Mediterranean catchment. *Fisheries Management and Ecology*, *15*, 49–58. doi: 10.1111/j.1365-2400.2007.00570.x

Poff, N. L., Allan, J. D., Bain, M. B., Karr, J. R., Prestegaard, K. L., Richter, B. D., ..., & Stromberg, J. C. (1997). The natural flow regime. *Bioscience*, *47*, 769–784. doi: 10.2307/1313099

Poff, N. L., & Zimmerman, J. K. H. (2010). Ecological responses to altered flow regimes: A literature review to inform the science and management of environmental flows. *Freshwater Biology*, *55*, 194–205. doi: 10.1111/j.1365-2427.2009. 02272.x

Pupilli, E., & Puig, M. (2003). Effects of a major flood on the mayfly and stonefly populations in a Mediterranean stream (Matarranya Stream, Ebro River basin, North East of Spain). *Biogeography, Biodiversity & Ecology*, 381–389.

Resh, V. H., Brown, A. V., Covich, A. P., Gurtz, M. E., Li, H. W., Minshall, G. W., ..., & Wissmar, R. C. (1988). The role of disturbance in stream ecology. *Journal of the North American Benthological Society*, *7*, 433–455.

Řezníčková, P., Pařil, P., & Zahrádková, S. (2007). The ecological effect of drought on the macroinvertebrate fauna of a small intermittent stream - An example from the Czech Republic. *International Review of Hydrobiology*, *92*, 514–526. doi: 10.1002/iroh.200610997

Ruegg, J., & Robinson, C. (2004). Comparison of macroinvertebrate assemblages of permanent and temporary streams in an Alpine flood plain, Switzerland. *Archiv für Hydrobiologie*, *161*, 489–510. doi: 10.1127/0003-9136/2004/ 0161-0489

Silva-Santos, P., Oliveira, S., Cortes, R., & Albuquerque, A. (2004). Natural and anthropogenic variations in a channelized water course in Centre of Portugal. *Limnetica*, *23*, 257–270.

Smakhtin, V. (2001). Low flow hydrology: a review. *Journal of Hydrology*, *240*, 147–186. doi: 10.1016/S0022-1694(00)00340-1

Sousa, R., Varandas, S., Cortes, R., Teixeira, A., Lopes-Lima, M., Machado, J., & Guilhermino, L. (2012). Massive die-offs of freshwater bivalves as resource pulses. *Ann. Limnol. - Int. J. Lim*, *48*, 105–112. doi: 10.1051/limn/2012003

Spindler, T. (1995). The influence of high waters on stream fish populations in regulated water. *Hydrobiologia*, *303*, 159–161. doi: 10.1007/BF00034053

Stahl, K., & Demuth, S. (1999). Linking streamflow drought to the occurrence of atmospheric circulation patterns. *Hydrological Sciences Journal*, *44*, 467–482. doi: 10.1080/02626669909492240

Stubbington, R., Wood, P. J., & Boulton, A. J. (2009a). Low flow controls on benthic and hyporheic macroinvertebrate assemblages during supra-seasonal drought. *Hydrological Processes*, *23*, 2252–2263. doi: 10. 1002 / hyp. 7290

Stubbington, R., Boulton, A. J., Little, S., & Wood, P. J. (2015). Changes in invertebrate assemblage composition in benthic and hyporheic zones during a severe supraseasonal drought. *Freshwater Science*, *34*, 344–354.

Stubbington, R., Greenwood, A. M., Wood, P. J., Armitage, P. D., Gunn, J., & Robertson, A. L. (2009b). The response of perennial and temporary headwater stream invertebrate communities to hydrological extremes. *Hydrobiologia*, *630*, 299–312. doi: 10.1007/s10750-009-9823-8

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*, 2207–2227. doi: 10.1111/j.1365-2427.2006.01646.x

Titus, R., & Mosegaard, H. (1992). Fluctuating recruitment and variable life history of migratory brown trout, Salmo trutta L., in a small, unstable stream. *Journal of Fish Biology*, *41*, 239–255. doi: 10.1111/j.1095-8649.1992. tb02654.x

Van Loon, A. F. (2015). Hydrological drought explained. *Wiley Interdisciplinary Reviews: Water*, *2*, 359–392. doi: 10.1002/wat2.1085

Webb, A. J., Miller, K. A., King, E. L., de Little, S. C., Stewardson, M. J., Zimmerman, J. K. H., & LeRoy Poff, N. (2013). Squeezing the most out of existing literature: A systematic re-analysis of published evidence on ecological responses to altered flows. *Freshwater Biology*, *58*, 2439–2451. doi: 10.1111/fwb.12234

Wood, P. J., Boulton, A. J., Little, S., & Stubbington, R. (2010). Is the hyporheic zone a refugium for aquatic macroinvertebrates during severe low flow conditions. *Fundamental and Applied Limnology*, *176*, 377–390. doi: 10.1127/1863- 9135/2010/0176-0377

Wood, P. J., & Petts, G. E. (1999). The influence of drought on chalk stream macroinvertebrates. *Hydrological Processes*, *13*, 387–399. doi: 10. 1002 / (SICI) 1099-1085(19990228)13:3<387::AID-HYP745>3.0.CO;2-R

Wood, P., & Armitage (2004). The response of the macroinvertebrate community to low-flow variability and supra-seasonal drought within a groundwater dominated stream. *Archiv für Hydrobiologie - Hauptbände*, *161*, 1–20. doi: 10.1127/0003-9136/2004/0161-0001

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*, 2497–2510. doi: 10.1111/fwb.12592

Wright, J. F., Gunn, R. J. M., Winder, J. M., Wiggers, R., Vowles, K., Clarke, R. T., & Harris, I. (2002). A comparison of the macrophyte cover and macroinvertebrate fauna at three sites on the River Kennet in the mid 1970s and late 1990s. *Science of The Total Environment*, *282–283*, 121–142. doi: 10.1016/S0048-9697(01) 00948-2

Wright, J. (1992). Spatial and temporal occurrence of invertebrates in a chalk stream, Berkshire, England. *Hydrobiologia*, *248*, 11–30. doi: 10.1007/BF00008882

Wright, J., Clarke, R., Gunn, R., Kneebone, N., & Davy-Bowker, J. (2004). Impact of major changes in flow regime on the macroinvertebrate assemblages of four chalk stream sites, 1997-2001. *River Research and Applications*, *20*, 775–794. doi: 10.1002/rra.790

Wright, J., & Symes, K. (1999). A nine-year study of the macroinvertebrate fauna of a chalk stream. *Hydrological Processes*, *13*, 371–385. doi: 10.1002/(SICI) 1099-1085(19990228)13:3<371::AID-HYP744>3.0.CO;2-C

Zelenhasic, E., & Salvai, A. (1987). A method of streamflow drought analysis. *Water Resources Research*, *23*, 156–168. doi: 10.1029/WR023i001p00156

Zorn, M., Van Gestel, C., & Eijsackers, H. (2005). Species-specific earthworm population responses in relation to flooding dynamics in a Dutch floodplain soil. *Pedologia*, *49*, 189–198. doi: 10.1016/j.pedobi.2004.08.004

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Piniewski, M., Prudhomme, C., Acreman, MC., Tylec, L., Oglęcki, P., Okruszko, T. Responses of fish and invertebrates to floods and droughts in Europe. *Ecohydrol*. 2017;*10*:e1793. doi:10.1002/eco.1793.