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DOI:
10.1002/eco.2422

Received: 20 September 2021 | Revised: 13 March 2022 | Accepted: 22 March 2022

DOI: 10.1002/eco.2422

SPECIAL ISSUE PAPER

WILEY

Extreme low-flow effects on riverine fauna: A perspective on methodological assessments

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Abstract

River flow regimes face increasing pressure from human activities including water resource management operations and climate change. Consequently, extreme hydrological events are becoming more severe and commonplace, and there is a pressing need to understand and manage their ecological effects. Extreme low flows (ELFs)—those displaying significantly greater magnitudes and durations than typical low-flow conditions—are being increasingly experienced globally. Fish and macroinvertebrate responses to ELFs have been more widely researched relative to other organism groups in riverine environments, although such studies have employed variable methodological techniques. In this perspective piece, we identify field-based assessments and controlled experiments as two key research paradigms used to examine riverine faunal responses to ELFs. Field-based assessments are often explorative and can benefit from utilising large-scale and long-term datasets. Alternatively, controlled experiments typically employ more hypothesis-driven approaches and can establish strong cause and effect linkages through high replication and control over potentially confounding parameters. Each paradigm clearly possesses their respective strengths, which we highlight and discuss how these could be better harnessed to optimise scientific advancements. To date, studies examining faunal responses to ELFs in these two research paradigms have largely been undertaken in parallel. Here, we argue that future research should seek to develop closer synergies to optimise the quality and quantity of evidence to better understand riverine faunal responses to ELFs. Such scientific advances are of paramount importance given the vulnerability of riverine fauna, and the ecosystems they comprise, to a new era of ELFs in many global regions.

KEYWORDS

drought, fish, flow–ecology, low flow, macroinvertebrate, mesocosm

1 | INTRODUCTION

River flow regimes vary spatially and temporally in response to intra- and inter-annual climatic (precipitation and evaporation) variations and are mediated by catchment characteristics, including geology, soil type, land cover, topography and human activity (Blöschl et al., 2007; Carlisle et al., 2010; Poff, 2018). Riverine fauna (the focus of this perspective piece) have evolved to survive and exploit natural flow regime variations, including routine low-flow events, over evolutionary timeframes through a range of functional adaptions (Carey et al., 2021; Lytle & Poff, 2004). For low-flow periods that fall within the typical range of historic discharge variability (e.g. 'seasonal droughts'—sensu Lake, 2003), fauna can persist via a range of resistance (i.e. ability to withstand disturbances in situ) and resilience (i.e. capacity to recover following a disturbance) mechanisms (Crabot et al., 2021; De la Fuente et al., 2018; Mims & Olden, 2012). For instance, various species possess specialist respiratory systems, display substrate burrowing strategies or disperse to seek alternative refuges in response to low-flow events (Chessman, 2015; Lennox et al., 2019). However, low flows are increasing in their frequency, duration and severity globally as anthropogenic activities including flow regulation, irrigation and land cover modifications interact with a changing climate, as illustrated within the IPCC Sixth Assessment Report (IPCC, 2021). Many riverine fauna may lack the adaptations to persist within this new era of low-flow extremes (e.g. Archdeacon & Reale, 2020; Aspin, Hart, et al., 2019; Jourdan et al., 2018; Kennedy et al., 2016), and further research is required to provide the scientific evidence needed to safeguard freshwater ecosystems in the future.

This perspective paper discusses key approaches and techniques used to assess faunal responses to extreme low-flow (ELF) conditions in riverine environments. We define ELFs strictly from a hydrological perspective, while acknowledging that global perspectives and research on 'drought' have outlined that water deficits below normal conditions may be defined and characterised from other standpoints (e.g. meteorological, agricultural, socio-economic and ecological; Sarremejane, Messager, & Datry, 2021; Van Loon, 2015). Specifically, we define ELFs as low-flow events that exceed the severity or duration of those typically experienced at a particular location. Our definition is intentionally broad to account for studies adopting various hydrological criteria, such as between different climatic regions (Smakhtin, 2001), as well as those failing to define hydrological thresholds in ELF research (as with many ecological-focussed studies; see Sarremejane, Messager, & Datry, 2021). We also established our definition in accordance with the IPCC's definition of a 'hydrological drought' as 'a period of abnormally dry weather that persists for long enough to cause a serious hydrological imbalance … that propagate [s] over time into deficits in soil moisture, streamflow, and water storage' (IPCC, 2021, pp. 8–27). ELFs are driven by severe, broad-scale climatic patterns (e.g. El Niño–Southern Oscillation and North Atlantic Oscillation) and/or significant anthropogenic pressures (e.g. flow regulation, water abstraction and climate change). ELF events may include normally perennial sections of river exhibiting abnormal low-flow conditions or ceasing to flow, through to temporary rivers experiencing uncharacteristically severe or prolonged ponding or drying conditions. For the purpose of this perspective piece, we do not consider temporary rivers undergoing their naturally recurring dry or ponded phases that are in keeping with historic flow regime variations (i.e. not driven by direct human activities such as water abstraction) as an ELF event. However, we recognise how ecohydrological research on naturally recurring flow cessation events in temporary rivers has dramatically improved our scientific understanding on how riverine fauna respond to flow conditions that commonly occur during ELF events (Sarremejane, Messager, & Datry, 2021).

The characteristics of ELF events are contextually dependent across space (spanning multiple spatial scales—see following text) and time. As they are typically rare events, characterising ELF events at a given geographic location requires placing hydrological conditions in the context of its long-term variability. Hydroclimatologists routinely use a benchmark period of 30 years to assess deviations from average conditions and to identify extreme water deficits. This practice is founded on the notion that this time period is long enough to sample variability but not so long that it becomes susceptible to non-stationarities, such as those driven by climate or land use change (Slater et al., 2021). The same premise can be applied to hydrological data to help identify ELF events (Wilby et al., 2015). Based on similar principles, others advocate 30 years as a minimum hydrological time series length required to identify ELF events (Beyene et al., 2014), whereby such conditions can be characterised based on thresholds and anomalies within this timeframe (rather than relative to a 30-year benchmark period). Intuitively, longer hydrological time series increases the likelihood of encountering and detecting multiple ELF events. For example, Marsh et al. (2007) reported a chronology of hydrologically defined 'major droughts' (i.e. ELFs) in England and Wales based on ranked runoff deficiencies and listed nine events in a ∼200-year record, equating to approximately a 20-year recurrence interval. Here, the longest observed run of below average river flows since the 1950s lasted 5.5 years during 1988–1993 (Wilby et al., 2015) where accumulated gauged runoff levels dropped by up to 400 mm relative to the long-term average (Bryant et al., 1994; although lotic conditions were sustained throughout—UK Centre for Ecology and Hydrology, 2021). In comparison, the Murray–Darling Basin in Australia has experienced numerous long-term periods of well below average river flows, as in 1895–1902, 1937–1945 and 1997–2009 (Leblanc et al., 2012). During the latter 'Millennium' drought, the observed 39% reduction in mean runoff was estimated to have a recurrence interval of more than 300 years (Potter et al., 2010). This substantially increased flow cessation events across the Murray–Darling Basin, whereby lotic conditions were recorded just 43% of the time along one river, compared to 75% observed during other historic ELFs (Mallen-Cooper & Zampatti, 2020).

Statistically quantifying and generalising ELFs using river discharge series is not straightforward. Such data are sensitive to various catchment characteristics that can limit spatial transferability (Chen & Olden, 2018; Verdon-Kidd & Kiem, 2009). For this reason, most drought severity and aridity indices that are globally applicable tend to rely on combinations of precipitation and temperature (or evaporation) anomalies (see Ekström et al., 2018). However, carefully screening data sources to ensure discharge time series are derived from environments with comparable catchment properties provides greater certainty when identifying ELF events (e.g. Mathers, White, et al., 2020). Hydrological metrics selected to characterise ELFs vary considerably worldwide and between studies due to data availability (e.g. length and quality of records), study region (e.g. arid vs. temperate climate regimes; perennial vs. temporary rivers) and scientific discipline (e.g. ecology- vs. hydrology-driven perspectives). How such considerations have governed the use of different hydrological metrics has been summarised in other review papers (e.g. AghaKouchak et al., 2021; Beyene et al., 2014; Parry et al., 2016; Sarremejane, Messager, & Datry, 2021; Smakhtin, 2001). Ultimately inconsistent usage of hydrological metrics when characterising ELF events between studies and regions limits our scientific ability to understand and generalise their spatial and temporal variability, as well as their impacts on riverine fauna.

In this perspective piece, we highlight different scientific approaches used to advance knowledge on how riverine fauna respond to ELFs, along with opportunities for further research. We focus on macroinvertebrate and fish responses to ELF conditions, since they represent the most widely studied groups of organisms within this field of research (Piniewski et al., 2017). Research on riverine faunal responses to ELFs has gained momentum during recent decades. For instance, an examination of the Scopus database (using search terms 'drought' or 'low-flow' or 'low flow' and 'river' or 'riverine' and 'fauna' or 'macroinvertebrate' or 'invertebrate' or 'fish') indicates a 15-fold increase in the number of peer-reviewed publications from 1990 ($n = 15$) to 2020 ($n = 224$; see Figure 1). This partly reflects an improved understanding of the threats to faunal communities posed by ELF events (e.g. loss of keystone and/or native species, partial collapse of food webs and spread of non-native fauna), as well as our scientific and societal awareness surrounding the ongoing shift to a warmer, and in many places a drier, climate (IPCC, 2021; Jarić et al., 2020).

For the first time, this paper provides a novel synthesis of literature examining riverine faunal responses to ELFs and appraises the range of scientific techniques employed to do so. The paper comprises four sections. First, we draw on case studies from across the world to summarise our current scientific understanding of key hydrological controls shaping ELFs and their effects on riverine faunal communities. Second, we outline two research paradigms that have been fundamental to our current scientific understanding of riverine faunal responses to ELFs: (i) field-based assessments—whereby ecological properties derived from riverine environments exhibiting flow regimes that have not been manipulated for research purposes are statistically examined in association with hydrological parameters, and (ii) controlled experiments—where different biota and faunal communities are examined within controlled environments subjected to specific flow conditions (i.e. river discharge, flow velocities or water volumes) that are designed to reflect ELF conditions. We consider the historic development of both research paradigms along with their typical scope and study design. Third, we identify six key criteria that are integral to advancing our scientific understanding of riverine faunal responses to ELFs and outline how effectively these have been addressed and incorporated within the two research paradigms. Finally, we consider how future research can advance our scientific understanding of riverine faunal responses to ELFs. We do so by highlighting approaches and technologies that may be incorporated within each research paradigm and how these can be better synergised to provide a more holistic ecohydrological framework.

2 | EXISTING SCIENTIFIC KNOWLEDGE ON ELFS AND THEIR INFLUENCES ON RIVERINE FAUNA

In the following two subsections, we consider the key natural and anthropogenic hydrological drivers shaping ELFs and summarise their documented impacts on riverine fauna. In each of these subsections, we adopt a global perspective and draw on examples reporting different hydrological and ecological responses to ELFs, but for more detailed syntheses on these topics, we refer readers to historic reviews focusing on hydrology (see preceding text) and ecology (Dewson et al., 2007; Lake, 2003; Lennox et al., 2019; Sarremejane, Messager, & Datry, 2021).

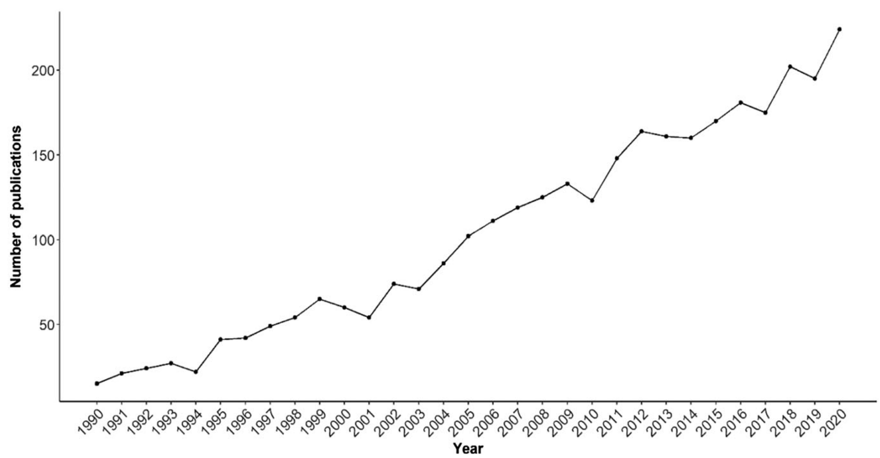

FIGURE 1 Annual number of peer-reviewed publications within the Scopus database examining riverine faunal responses to extreme low flows between 1990 and 2020

TABLE 1 Examples of research reporting the effects of hydrological controls on the severity, duration or spatial distribution of extreme low flow (ELF) events

	Hydrological control	Relative effect on flow	Study location	Description	Source
Natural	Tributaries	Increase	Amazon River, Amazonia, Brazil	Tributaries mitigated the severity of an ELF event along the mainstem river during the 1996–1997 El Niño event, whereas the 2004–2005 ELF event lasted longer as the flow regimes of tributaries were more severely affected	Tomasella et al. (2011)
	Groundwater spring inputs	Increase	River Lathkill Derbyshire, UK	A groundwater spring approx. 4 km downstream of the source maintained perennial flows during an ELF event in 2011, whereas the entire river upstream of the spring remained dry for *c.* 11 months	Stubbington et al. (2016)
	Evaporation	Decrease	Clare Valley, Australia	Up to 50% of the water volume within instream pools was lost to evaporation during an ELF event in 2008–2009	Bestland et al. (2017)
	Riverbed sediment infiltration/ groundwater percolation	Decrease	Rio Grande, New Mexico, USA	Multiple ELF events changed the study reach from a gaining to a losing system between 2011 and 2016, with up to 0.03 km^3 of water being lost to the underlying aquifer during a major ELF event in 2014	Fuchs et al. (2019)
Anthropogenic	Effluent water returns	Increase	Santa Cruz River, Arizona, USA	Groundwater levels were approx. 80 m below the streambed of this temporary river, but two sections of river approx. 5 and 30 km in length were perennial due to effluent water returns and have flowed continuously during region-wide ELF events, including 2018	Eppehimer et al. (2020)
	Low-flow alleviation schemes	Increase	River Lambourn, Berkshire, UK	A low-flow alleviation scheme, where groundwater was pumped directly into the river channel, was introduced to mitigate the effects of a major ELF event during 1975–1976. Discharges increased from 0 to 0.2 m^3, and the perennial source shifted approx. 2 km upstream after the scheme was initiated	Wright and Berrie (1987)

TABLE 1 (Continued)

Hydrological control	Relative effect on flow	Study location	Description	Source
Water withdrawals (e.g. abstraction and irrigation)	Decrease	River cox, New South Wales, Australia	Significant groundwater abstraction for irrigation purposes aggravated ELF conditions by over 200% during a period that included the 1997–2009 millennium drought	Van Loon et al. (2019)
Flow regulation	Mixed (rivers may experience discharges below or above natural levels depending on dam operations)	Ardabil Province, Iran	Yamchi Dam exacerbated ELF events along the Balikhli River, while the Sabalan Dam had the opposite effect on the Garesou river	Amini et al. (2019)
		River Darling, multiple states (New South Wales, Queensland, Victoria and South Australia), Australia	Inadequate damflow releases led to unnaturally extensive lentic conditions during ELF events in 1997–2009 (millennium drought) and 2013–2019, although sustained flows in some reaches (e.g. downstream of Menindee Lakes) led to the opposite effect	Mallen-Cooper and Zampatti (2020)
Inter-basin transfer scheme	Mixed (donor and receiving basins gain and lose water, respectively – alleviation of ELF events associated with the latter are most commonly reported)	Chelmer River, Essex, UK	An inter-basin water transfer scheme was introduced to alleviate hydrological losses from increasing human populations in Essex. This reduced the long-term ELF severity by 76% over a period that included a major ELF event during 1976	Van Loon et al. (2019)
		The Bridge River, British Columbia, Canada	Water transferred to the neighbouring Sedon catchment resulted in a complete dewatering of the river for 3 km below the reservoir (in response to this, dam operations were subsequently altered from 2000)	Bradford et al. (2011)

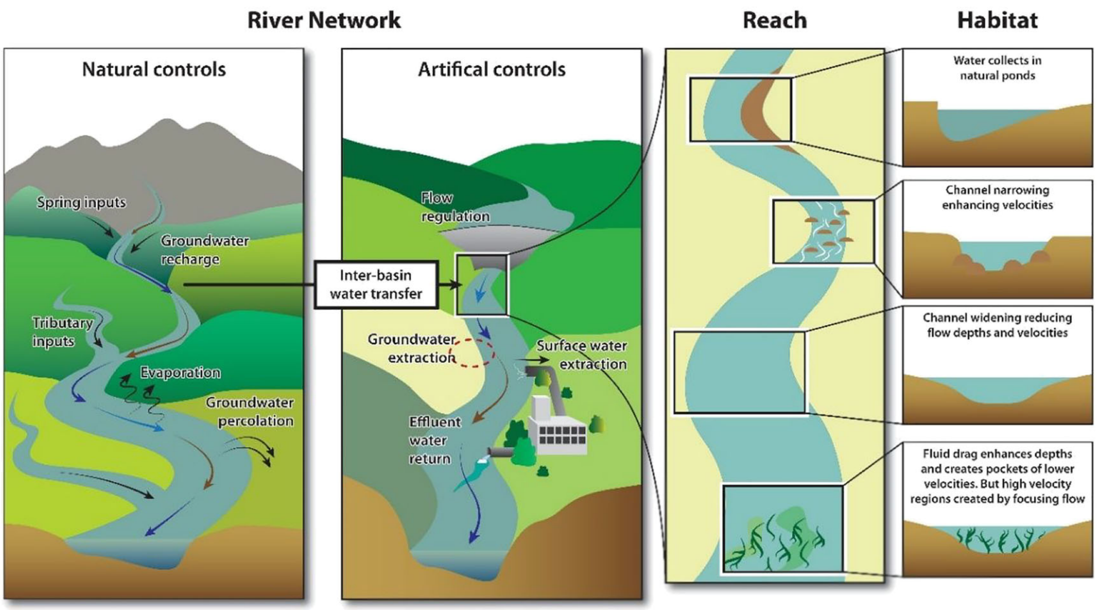

FIGURE 2 A schematic diagram illustrating how extreme low-flow conditions may vary spatially across different scales due to natural and anthropogenic controls. Brown, light blue and dark blue arrows represent low, intermediate and high discharges, respectively

2.1 | The spatial variability of ELFs

Across river networks, ELFs vary spatially due to different catchment properties (both natural and artificial—see Table 1 and Figure 2; see preceding text and Van Loon, 2015 for a detailed review on how ELFs vary temporally). As such, characterising ELF events at a particular geographical location requires consideration of the contextual dependence of flow conditions relative to historic region-wide spatial variations in river discharges. Determining how natural and anthropogenic factors that increase (e.g. tributaries and groundwater spring inputs) and decrease (e.g. surface water losses to unsaturated groundwater regions and evaporation) river discharges interact to determine the severity, duration and spatial variability of ELFs remains a challenge within hydrological modelling (AghaKouchak et al., 2021). This complexity is confounded by the spatially discrete nature of river flow gauge data, which may offer insights into long-term trends at high temporal resolutions (e.g. sub-hourly), but do not always accurately measure low-flow discharges or capture spatial variations in ELFs across wider riverine networks and habitats (Wilby et al., 2017). Despite this, some studies have sought to understand how different natural and anthropogenic controls collectively shape ELFs. For instance, Laaha and Blöschl (2006) examined the relative effects of different climatic (e.g. annual precipitation) and catchment-scale (e.g. geology, topography and land use) controls in shaping ELFs across 325 catchments in Austria. The authors found that catchment topography, precipitation and geology (in decreasing order) were the most important environmental characteristics governing the severity of ELFs. Similarly, Roodari et al. (2021) reported that the downstream intensification of ELFs along the Helmand River, Afghanistan, was largely attributable to precipitation deficits, while flow regulation and irrigation abstraction practices yielded limited effects. Such large-scale studies are challenging to undertake as they require extensive data collation, quality assurance and analysis of environmental information from multiple data sources (e.g. geological and land use maps and hydrological models) that cover long-term timeframes. However, more fundamental studies like these are required to predict and model the spatial variability of ELFs across riverine networks and to identify where anthropogenic water resource management operations can be modified to mitigate these potential damaging effects on freshwater ecosystems.

The morphological properties of rivers can moderate the hydrological and hydraulic characteristics of ELFs within individual reaches supporting different habitat conditions. For instance, narrower channels arising from natural (e.g. valley confinement and marginal vegetation encroachment) or anthropogenic controls (e.g. artificially gentle bank profiles and channelisation) may elevate flow velocities during ELF conditions. Channel widening may have the opposite effects on flow, such as in an unconfined valley along Sycamore Creek (Arizona, USA) which facilitated a complete dewatering of the channel during 1989, while adjacent confined reaches largely maintained surface flows (Stanley et al., 1997).

The deepest pool habitats are typically the last part of the channel to become hydrologically disconnected during flow cessation events (Boulton, 2003) and may thus hold the only surface water during ELF events. For instance, in the historically perennial French Joe Canyon River (Arizona, USA), only two pools retained water during a major ELF event in 2003–2004, while the wider riverbed dried completely (Bogan & Lytle, 2011). The variability of within-reach hydrological conditions during ELFs due to physical habitat heterogeneity has been widely recognised within many environmental flow ‘habitat simulation' methodologies (sensu Poff et al., 2017). This includes MesoHABSIM, where the area of specific habitat conditions required by different ecological assets (primarily fish species at different life stages) is characterised across varying discharges and can be specifically tailored to examine ELF conditions (Parasiewicz et al., 2018).

An additional key habitat-level influence affecting the spatial variability of ELFs is the presence of macrophytes. These can mitigate the severity of ELFs due to fluid drag around plant stands holding back flow and enhancing water levels (Verschoren et al., 2016). This can help support the functionality of riverine ecosystems during ELFs as water levels are maintained and macrophytes create areas of elevated flow velocities between stands that support important rheophilic taxa (White, Krajenbrink, et al., 2019). However, the water retention effects of macrophytes can exacerbate local flood risk under high-flow conditions, prompting many landowners or river managers to undertake weed cutting. For instance, Baattrup-Pedersen et al. (2018) reported 3086 weed cutting events across 126 small to medium-sized rivers in Denmark and found that these reduced flow depths by up to 16 cm, although limited research has explored how such management interventions affect hydraulic conditions during ELF events.

2.2 | Global evidence characterising riverine faunal responses to ELFs

A range of studies worldwide utilising field-based assessments and controlled experiments have examined riverine faunal responses to ELFs. These have primarily been conducted in economically developed nations (Figure 3). A Scopus literature review (see previous text for search terms) yielded 4388 publications, of which 1285, 349 and 286 were led by a corresponding author based in the United States, Australia or the United Kingdom, respectively.

A recurrent theme of global research is that riverine faunal responses to ELFs depend on hydromorphological conditions and the tolerance of communities or species present. However, ELFs consistently trigger reductions in taxonomic richness, particularly vulnerable fauna such as Ephemeroptera, Plecoptera and Trichoptera (EPT) riverflies (Herbst et al., 2019) and salmonid species (Lennox et al., 2019). Importantly, some studies have demonstrated that ELFs have more severe negative effects on the diversity of riverine fauna compared to typical low-flow conditions (Benejam et al., 2010; Crabot et al., 2021).

Studies examining macroinvertebrate community responses to ELFs often use compositional data or derivative metrics (e.g. taxonomic and functional diversity indices—e.g. Belmar et al., 2013) and place less emphasis on individual species. There has been little research into how ELFs promote the spread and successful establishment of non-native macroinvertebrate species (Mathers, White, et al., 2020 being a rare example). Research examining ELF effects on fish more routinely explore the responses of individual species and native versus non-native taxa (e.g. Ruhí et al., 2015). Studies of fish responses to ELFs also tend to analyse behavioural (e.g. species movements) or physical attributes (e.g. animal length and weight; Hopper et al., 2020) more often than macroinvertebrate studies.

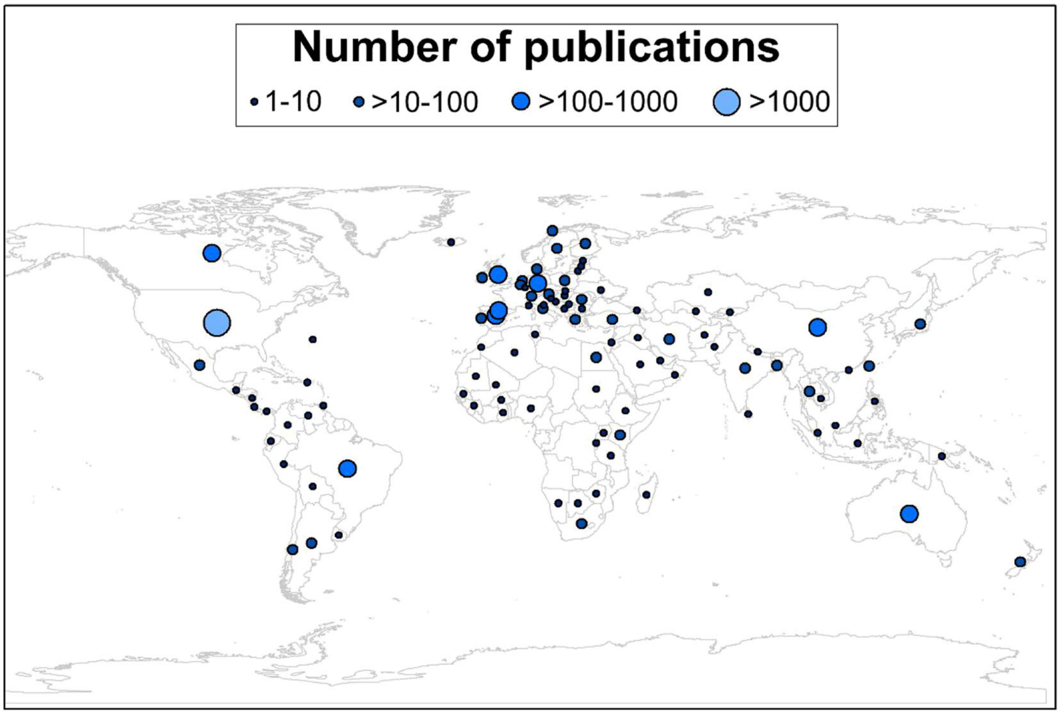

FIGURE 3 Number of peer reviewed publications addressing riverine faunal responses to extreme low-flows by the country of the corresponding authors' affiliation

3 | RESEARCH PARADIGMS USED TO EXAMINE RIVERINE FAUNAL RESPONSES TO ELFS

In this section, we explore field-based assessments and experimental approaches as the two primary research paradigms that have been fundamental to our scientific understanding of riverine faunal responses to ELFs. We specifically consider the historic development and scope of these research paradigms by drawing on a range of examples worldwide.

3.1 | Constructing flow–ecology associations from field-based assessments

Most research examining riverine faunal responses to ELFs has involved field-based collection of ecological samples from systems experiencing flow regimes that have not been manipulated for the purposes of the study. Such studies can encompass large spatial scales and long-term time periods through data collection initiatives like biomonitoring programmes (e.g. for environmental policy) and flow gauging networks (e.g. for water management and compliance purposes). These may capture ELF events and thus incidentally reveal its effects on riverine fauna (e.g. Bruckerhoff et al., 2019; Fornaroli, Muñoz-Mas, & Martínez-Capel, 2020). Such field-based assessments statistically relate community metrics (e.g. community abundances and taxonomic or functional diversity responses) to hydrological indices characterising various elements of the natural flow regime (sensu Poff et al., 1997; e.g. averaged monthly discharge and number of low- or high-flow events). Such 'flow–ecology' relationships evolved with the introduction of environmental flows over the course of the 20th century, with early interest in the minimum discharge required to sustain iconic fish populations, usually salmonids (Poff et al., 2017). As such, examining ecological responses to ELFs has been fundamental to scientific advances made in flow–ecology relationships, with the majority of such studies adopting some form of ELF proxy or metric when long-term flow records are available (e.g. averaged summer discharge and the discharge exceeded 95% of the time, Q95; White et al., 2021), with exceptions being research exclusively examining ecological responses to high-flow or flooding events (e.g. Greenwood & Booker, 2015). Since the start of the 21st century, the focus of environmental flows has evolved from considering individual iconic fish species to the wider needs of the ecosystem (Poff et al., 2017). Consequently, in recent years, flow–ecology studies examining riverine fauna responses to ELF events have incorporated an increasingly wide array of ecological data and information to better capture whole community responses, including functional trait databases (e.g. Bruckerhoff et al., 2019; Chessman, 2015) and metacommunity dynamics (Driver & Hoeinghaus, 2016; Sarremejane, Stubbington, et al., 2021).

Flow–ecology relationships have been derived at a range of spatial scales, from individual habitat patches (White, Krajenbrink, et al., 2019) to the global river network (Xenopoulos et al., 2005) and can be established from targeted sampling dates covering short timescales (Perkin et al., 2019) through to multi-decadal datasets (White et al., 2021). Generally, flow–ecology relationships are derived from datasets at the catchment or regional scale, the latter being defined as discrete management units characterised by scientists or practitioners encompassing relevant natural (e.g. climate and geology) and anthropogenic (e.g. water management operational boundaries) factors (Poff et al., 2010; White, 2018). Regional-scale flow–ecology relationships have been widely advocated in environmental flow strategies as the pace of hydrological alterations is exceeding our scientific capacity to construct flow–ecology relationships on a river-by-river basis (Poff et al., 2010). Moreover, there is a robust scientific basis for constructing region-wide flow–ecology relationships given that river discharges typically respond congruently to climatic controls at this scale (unless dramatically altered by anthropogenic activities such as river impoundment) and result in broadly comparable hydraulic conditions between watercourses and neighbouring river basins (Hannaford et al., 2011; Rosenfeld, 2017). Flow–ecology studies typically use datasets spanning multiple years to account for inter-annual flow variability, although few have conducted such analyses across multiple decades (i.e. ≥30- ears; Le et al., 2020 being a rare example).

Many flow–ecology studies are explorative rather than hypothesis driven, incorporating multiple response metrics and hydrological indices. For instance, Fornaroli, Muñoz-Mas, and Martínez-Capel (2020) used biomonitoring data from the Mediterranean Júcar River (Spain) to quantify the responses of 25 fish-based metrics to 33 hydrological descriptors (11 of which characterised low-flow conditions). The authors found that opportunistic, non-native species populations expanded during more severe ELFs as their early maturation allowed greater juvenile survivorship. Although less common, some flow–ecology studies employ more targeted sampling strategies and construct more explicit hypotheses centred on ELFs. For instance, Perkin et al. (2019) hypothesised that pelagic-broadcast spawners would experience less successful recruitment than fish species adopting other spawning modes, so sampled Cyprinidae fish species 20 times during an ELF period between 2011 and 2012 in south-central Kansas, USA.

3.2 | Controlled experiments testing riverine faunal responses to ELFs

Controlled experiments considered in this perspective piece include those where flow conditions (e.g. water volume, river discharge or flow velocities) are manipulated to represent ELFs either in isolation (e.g. Patel et al., 2021; Riis et al., 2017) or alongside other controlled parameters that covary with flow during ELFs, including dissolved oxygen (e.g. Calapez et al., 2018), fine sediment depositions (e.g. Blöcher et al., 2020) and water temperature (e.g. Nelson et al., 2021). Such experiments are less common than field-based assessments, but started to gain momentum towards the end of the 20th century as researchers sought to better understand the risk of fish stranding during ELF events by placing target species in artificial

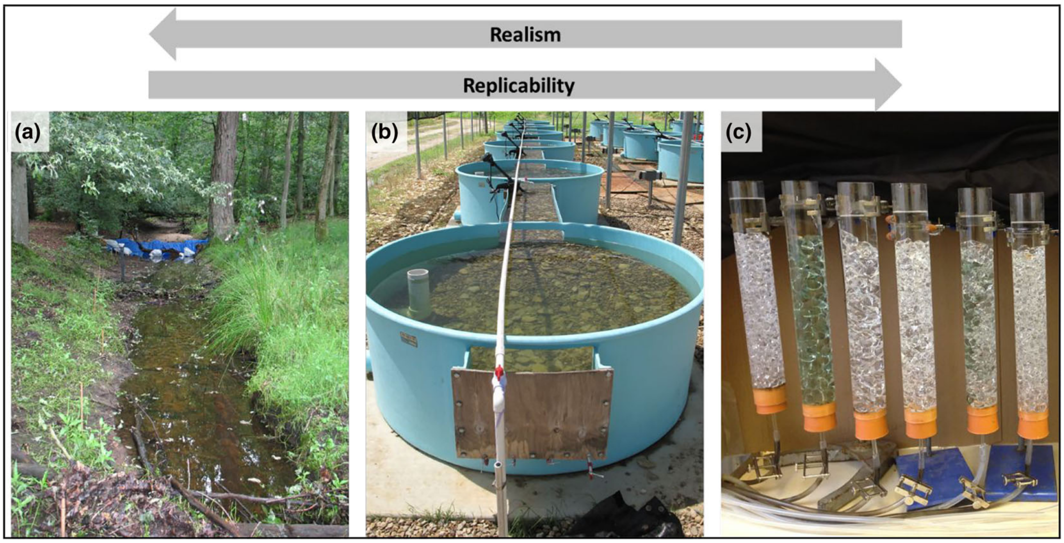

FIGURE 4 Examples of different controlled experiments used to study riverine faunal responses to ELFs showing the trade-off between realism and replicability. (a) An instream flow manipulation experiment used by Verdonschot et al. (2015) to divert flows from the studied reach and study macroinvertebrate community responses (photo credit: Dr Ralf Verdonschot). (b) Mesocosms with dimensions 10.98 (length) × 1.83 m (diameter of 'instream pools') used by Driver and Hoeinghaus (2016) to examine fish metacommunity responses to experimental ELF events across pool-riffle sequences (photo credit: Dr Lucas Driver). (c) Mesocosms with dimensions 0.35 × 0.05 m used by Vadher et al. (2017) to examine selected macroinvertebrate taxa responses to dewatering (photo credit: Dr Atish Vadher)

enclosures (e.g. Dale Becker et al., 1982). However, there is a longer history of scientists using controlled experiments to examine riverine faunal responses to manipulated physico-chemical conditions associated with ELFs (e.g. low dissolved oxygen levels or high water temperatures; Downing & Merkens, 1957), but in the absence of flow manipulation, such studies are beyond the scope of this perspective.

We focus on three types of controlled experiments (Figure 4): (i) 'instream flow manipulations', where flows from a natural river system are diverted away from the experimental reach (reducing the flow volume) and the responses of existing riverine fauna are monitored; (ii) 'community composition' experiments, where communities representative of natural systems are exposed to manipulated ELF events in experimental enclosures (or 'mesocosms') and their responses are monitored; and (iii) 'target-taxa' experiments, where the responses of selected taxa to ELF conditions are monitored within mesocosms. Experimental designs vary in their realism with respect to both their hydromorphological properties (such as channel dimensions and habitat variability) and biocomplexity (spanning individual species to whole communities), typically in decreasing order from (i) to (iii). However, there is a trade-off between achieving greater realism in controlled experiments and replicability, since larger enclosures tend to be fewer in number. For more detailed discussions on different experimental typologies within freshwater research, see Stewart et al. (2013) and Menczelesz et al. (2020).

The biocomplexity of instream flow manipulation studies is greater than any other controlled experiments because established freshwater ecosystems are subjected to discharge reductions. The realism of faunal assemblages within community composition mesocosms can vary depending on the colonisation pathways open to riverine fauna before and during the experiment. For instance, some offline experiments (e.g. recirculating containers and groundwater-fed systems) may create realistically complex faunal assemblages by seeding mesocosms with communities sourced from the field prior to the experiment, but then only allowing the aerial colonisation of invertebrates displaying adult oviposition mechanisms after flow conditions have been manipulated (e.g. Aspin, Khamis, et al., 2019; Driver & Hoeinghaus, 2016). Alternatively, community composition experiments fed directly by surface waters (i.e. online systems) can allow drifting macroinvertebrates to colonise mesocosms before and potentially during the experiment depending on the study design. For instance, Ledger et al. (2012) closed inlet valves on experimental streams at different frequencies to simulate different ELF conditions, and macroinvertebrates could colonise via aquatic dispersal mechanisms between treatments. Alternatively, Blöcher et al. (2020) simulated different flow conditions in mesocosms by altering velocities, and macroinvertebrates could colonise throughout the experiment via drift and adult oviposition. Generally, community composition experiments using fish communities are likely to yield lower degrees of biocomplexity due to limited space available to support natural fish densities and population size structures within experimental enclosures (Petersen & Englund, 2005). Target-taxa mesocosms often focus on larger-bodied species and are therefore more widely used to study fish than macroinvertebrates, although individual crayfish species responses to ELFs have been well explored in controlled experiments (e.g. Magoulick, 2014). Such studies may analyse the response of a single species, such as Dale Becker et al. (1982) who examined the response of Chinook salmon (*Oncorhynchus tshawytscha*) eggs and alevins to dewatering in experimental tanks (dimensions:

0.68 × 0.16 × 0.30 m). Other target-taxa mesocosms have been used to study inter-species interactions. For example, Stradmeyer et al. (2008) examined the competitive behaviours of brown trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*) during ELF events in an experimental stream (dimensions: 60 × 1.5 × 0.46 m), reporting an initial increase and subsequent decrease in aggression following dewatering.

The physical dimensions of instream flow manipulations depend on the study environment but are typically implemented on small river channels (<5 m wide) where flow diversions can be more easily managed, such as headwaters (James et al., 2008; Nuhfer et al., 2017) or side channels (Riley et al., 2009; Verdonschot et al., 2015). The shape and size of mesocosms used in ELF research (both community composition and target-taxa experiments) vary significantly based on the scientific research question(s) and target fauna (Menczelesz et al., 2020; Stewart et al., 2013). Community composition and target-taxa experiments incorporating fish require relatively large enclosures, comparable in size to some headwater streams (e.g. Driver & Hoeinghaus, 2016; Stradmeyer et al., 2008). However, target-taxa mesocosms are more likely to comprise smaller enclosures containing lower water volumes, in which individual taxa can be more efficiently monitored. For example, Vadher et al. (2017) used transparent, acrylic pipes with dimensions 0.35 (depth) × 0.05 m (internal diameter) to monitor the response of individual macroinvertebrate specimens to dewatering using transparent sediments.

4 | KEY CRITERIA WITHIN ELF RESEARCH

We identify six key criteria that govern how effectively studies have advanced our fundamental scientific understanding of riverine faunal responses to ELFs, as well as their ability to inform effective river conservation and management decisions:

i. Large-scale spatial transferability
ii. Replicability of ecohydrological conditions
iii. Control over extraneous environmental factors
iv. Scope for analyses of long-term ecohydrological trends
v. Attribution of causal mechanisms
vi. Predictive capability for future hydroclimatic conditions

These attributes are not mutually exclusive. In particular, large-scale assessments of faunal responses to ELFs are rarely compatible with high replicability of ecohydrological conditions or control over extraneous environmental factors, given that greater spatial coverage translates to greater ecological and environmental heterogeneity (Fornaroli, White, et al., 2020; Mota-Ferreira et al., 2021). The extent to which these key criteria have been addressed varies between the two research paradigms and experimental techniques. For instance, flow–ecology relationships can yield high degrees of transferability across large spatial scales (Chen & Olden, 2018), but this has been explored in far less detail within controlled experiments. Instead, the latter have been found to yield greater replicability (Harris et al., 2007) and control over confounding factors (Harris et al., 2020). Table 2 highlights our perspective on the relative degree to which studies from each of the research paradigms have addressed these key criteria. We recognise that there will be exceptions to our interpretations and have included examples within Table 2 to highlight this, with further elaboration in the following sub-sections.

4.1 | Large-scale coverage versus replicability and control

As outlined above, studies that aim to derive transferable ecohydrological patterns across large spatial scales often sacrifice replicability and control over extraneous factors, which may potentially confound ecological responses to ELFs. This is due to riverine environments observed across greater spatial scales displaying greater environmental variability (including differences in flow regimes, physico-chemical properties and habitat conditions), as well as ecological heterogeneity (e.g. biogeographical controls and metacommunity dynamics). Balancing these key criteria remains a challenge within contemporary ecohydrological studies. As such, we highlight the importance of these criteria together and outline how they have been incorporated within different research paradigms.

Characterising how riverine fauna respond to ELFs across coarse spatial scales is critical for guiding region-wide environmental flow strategies (Chen & Olden, 2018; Poff et al., 2010). Moreover, studies undertaken at broad spatial scales can help overcome limitations encountered in local assessments, including spatial autocorrelation effects; anomalous sites exhibiting unique local environmental conditions (e.g. severely polluted systems); and small site or sample numbers not capturing a comprehensive range of ecohydrological conditions, thus restricting the construction of robust statistical trends (Bruckerhoff et al., 2019). In contrast, achieving a high degree of ecohydrological replicability between sites or samples is critical to understanding riverine faunal responses to ELFs and being able to reliably isolate and quantify cause-and-effect associations (Brown et al., 2011; Harris et al., 2007). Controlling the influence of extraneous factors (or at least reliably accounting for their effects via statistical techniques) is also fundamental to understanding faunal responses to ELFs. For instance, Chen and Olden (2018) highlighted that the spatial transferability of region-wide flow-ecology relationships was constrained by river impoundments driving changes in both environmental and ecological conditions (Mims & Olden, 2013; Aspin, House, et al., 2020 reported comparable findings).

Large-scale (i.e. catchment-scale or beyond) examinations of riverine faunal responses to ELFs have almost exclusively been conducted through field-based assessments. To help overcome lower replicability and control over potentially confounding factors, most assessments of this type adopt stringent site selection and classification procedures to maximise the geographical coverage of ecohydrological data (and the number of samples analysed) while minimising environmental variability. For instance, Bruckerhoff et al. (2019) collated fish survey data from 3700 watercourses across

TABLE 2 Our perspective on the degree (high, medium or low) to which the two primary research paradigms used to study faunal responses to extreme low flows (ELFs) have addressed different key criteria

Key criteria	Research paradigm 1: Field-based assessments	Research paradigm 2: Controlled experiments
Large-scale spatial transferability	**High**—Riverine fauna can respond congruently to ELFs at regional scales when community compositions, hydrological regimes and other extraneous environmental controls (e.g. physico-chemical parameters) are comparable (Bruckerhoff et al., 2019; Chen & Olden, 2018)	**Low**—Experimental studies can achieve high degrees of realism relative to natural systems from both environmental (e.g. hydromorphological and physico-chemical parameters) and ecological perspectives (e.g. community compositions and biotic interactions). However, few studies have compared experimental and field data (but see Harris et al., 2020; Vadher et al., 2018a) and even less have demonstrated the transferability of experimental data to large-scale ecohydrological trends during ELFs
Replicability of ecohydrological conditions	**Medium**—Achieving highly replicable ecohydrological conditions using large-scale and long-term data is challenging due to high environmental heterogeneity across river catchments (Fornaroli, White, et al., 2020; Mota-Ferreira et al., 2021). But congruent ELF conditions can be observed at the regional scale (see above) and structured sampling designs (e.g. comparable geologies and land covers) and/or statistical techniques (e.g. standardising hydrological controls) can create comparable ecohydrological conditions (White et al., 2021)	**High**—Controlling flow conditions and target species or community compositions provides high replication among mesocosms (Brown et al., 2011, Harris et al., 2007)
Control over extraneous environmental factors	**Medium**—Ecological stressors not directly attributed to ELFs can confound scientific findings (Harris et al., 2020). Structured sampling designs (e.g. hydrologically pristine rivers; Bruckerhoff et al., 2019) and/or statistical techniques (e.g. those reducing unexplained variability in models; Webb et al., 2010) can account for such influences to a certain degree	**High**—Some experiments maintain stable abiotic conditions, such as Vander Vorste et al. (2016) who mimicked dewatering events while maintaining temperature and oxygen levels. Others may allow abiotic conditions to vary with changing flow or might deliberately manipulate multiple abiotic parameters alongside flow to examine interactive effects. This includes Blöcher et al. (2020), who manipulated flow velocities and fine sediment concentrations, but did not alter physico-chemical properties
Scope for analyses of long-term ecohydrological trends	**High**—Continuous hydrological measurements and long-standing field-based sampling campaigns provide long-term ecohydrological data (Le et al., 2020; White et al., 2021)	**Low**—Studies typically last short durations (hours to months) due to logistical constraints (typically funding), but some have been run for multiple years (Leigh et al., 2019; Nuhfer et al., 2017)
Attribution of causal mechanisms	**Low**—Empirically linking ecohydrological responses to ELF events has to overcome certain challenges that controlled experiments do not (see preceding rows). However, specific sampling strategies can strengthen a causal understanding (e.g. Durkota et al., 2019 undertook benthic, hyporheic and phreatic samples to examine macroinvertebrate responses to ELFs), as can specific ecological responses like functional trait analyses (Chessman, 2015)	**High**—Greater replication and control provides greater certainty when empirically relating riverine fauna responses to flow manipulations. As such, linking cause and effect is most robust in target-taxa designs undertaken at smaller scales (Patel et al., 2021) compared to larger flow manipulations and community composition experiments, where greater system complexity and biotic interactions may obscure responses

(Continues)

TABLE 2 (Continued)

Key criteria	Research paradigm 1: Field-based assessments	Research paradigm 2: Controlled experiments
Predictive capability for future hydroclimatic conditions	**Medium**—Long-term field-based assessments can provide a detailed understanding of the effects of hydroclimatic changes, including more severe or prolonged ELF events, that could inform ecological responses to future flow conditions (Hain et al., 2018; Pyne & Poff, 2017). However, predictions of faunal responses to hypothetical future ELF events are likely to require extrapolation beyond the range of data observations found in historic flow regime variations	**Medium**—Controlled experiments can simulate flow conditions that are expected to occur under future hydroclimatic scenarios (e.g. increased drying frequencies, Ledger et al., 2012 or durations, Vadher et al., 2018b). However, such flow conditions are often hypothetical and are rarely manipulated in accordance with projected hydrological information (such as under different IPCC scenarios)

Arkansas (USA), but restricted their analyses to 302 least-disturbed streams. This allowed flow–ecology relationships to be subcategorised within distinct flow regime classification typologies that improved intraregional transferability.

Although various controlled experiments exhibit a high degree of replicability and control over extraneous environmental factors (e.g. Aspin, Hart, et al., 2019; Harris et al., 2007; Stewart et al., 2013), how riverine faunal responses to ELFs observed in such conditions translate to natural systems has been less widely explored. Experiments typically aim to mimic the ecohydrological conditions of the river environments they are sourced from or are proximal to, which some studies have empirically demonstrated (e.g. Brown et al., 2011; Driver & Hoeinghaus, 2016; Ledger et al., 2009). However, such findings are often based on localised ecohydrological data rather than information spanning catchments or larger spatial scales. Furthermore, few studies have directly compared faunal responses to ELFs detected from field-based assessments with controlled experiments. Harris et al. (2020) represents a rare exception, reporting comparable emergence rates of lamprey species (*Entosphenus tridentatus* and *Lampetra richardsoni*) in response to ELF events observed under both field and laboratory conditions. However, the authors did report some discrepancies in measured body size versus survival relationship during an ELF and attributed this to factors including avian predation in the field that was not possible to account for in the controlled experiment.

The extent to which riverine faunal responses to ELFs observed in controlled experiments represent those found in nature largely depends on their environmental and ecological realism. Most instream flow manipulations display high degrees of realism and are therefore likely to represent ecohydrological processes occurring within the source river (and potentially comparable watercourses regionally) during ELFs. However, the realism of mesocosm experiments may vary considerably, not only from a biocomplexity perspective (as discussed above) but also through the hydromorphological characteristics within the mesocosms. The physical dimensions of the enclosure will strongly govern ecological processes including population dynamics and biotic interactions through the influence of 'edge effects' (sensu Englund & Cooper, 2003) and increasing faunal densities in response to reduced flow conditions mimicking ELF events (Lancaster & Ledger, 2015). Some authors have advocated controlled experiments that can optimise the realism of stream mesocosms, including larger, once-through outdoor channels which are proximal to and fed by the source stream (allowing colonisation via aquatic and aerial dispersal mechanisms; Blöcher et al., 2020; Ledger et al., 2009; Piggott et al., 2015). Others advocate techniques to create more realistic hydraulic and morphological conditions, including riverbed casting techniques (Rice et al., 2010).

4.2 | Analyses of long-term ecohydrological trends

Examining long-term ecohydrological patterns is critical for understanding the impacts of ELFs on riverine fauna, whereby such responses can be assessed within the context of historic hydrological conditions. Long-term studies also allow faunal responses to sustained or recurring ELF events to be assessed. For example, Vander Vorste et al. (2020) studied fish community responses to receding flows across California, USA, between 2011 and 2017, where a major drought between 2012 and 2016 resulted in ELF events during the summer months (when sampling took place) that reduced fish survival rates. Another benefit of long-term studies is their potential to assess long-term faunal recovery patterns following ELF events. For example, Wood and Armitage (2004) estimated that macroinvertebrate community recovery from an ELF event took over 2 years.

Although the datasets used in field-based assessments lend themselves to long-term ecohydrological assessments (e.g. inter-annual biomonitoring and continuous flow gauge observations; see previous text), controlled experiments rarely operate across such timescales due to logistical issues. These include obtaining long-term funding and maintaining infrastructure that can sustain ELF conditions for prolonged time periods, including when high-flow conditions occur in the source river that may overwhelm flow manipulation or diversion structures (e.g. Walters & Post, 2011). Conversely, long-term datasets used within field-based assessments may overlook short-term ecohydrological processes critical to understanding riverine faunal responses to ELFs. For instance, Bogan et al. (2015) reported that tolerant invertebrate taxa can recolonise arid streams in Arizona, USA, within 2–3 days and that community densities can recover within 8–10 weeks. Findings like these highlight the need for studies to account for faunal responses to ELFs spanning short- to long-term timescales. Examples that address this need include big data approaches that quantify the time elapsed since an ELF event within long-term data time series (e.g. White, 2018; Sarremejane et al., 2019 conducted similar analyses for seasonally recurring low-flow events). Studies collecting high-frequency ecological samples (e.g. weekly to monthly) across multiple years in both field-based assessments (e.g. Perkin et al., 2019; White, Armitage, et al., 2019) and experimental studies (e.g. Leigh et al., 2019) can also explore both short- and long-term responses of riverine fauna to ELF events.

4.3 | Attribution of mechanisms underpinning ecohydrological trends

The need to fully understand the causal mechanisms underpinning ecohydrological (or 'ecohydraulic') observations has been widely debated (e.g. Lamouroux et al., 2010; Lancaster & Downes, 2010a, 2010b). Notwithstanding, understanding the causal mechanisms underpinning faunal responses to ELFs can provide information on whether such conditions facilitate or hinder particular life-cycle strategies of specific organisms. Such information may be particularly valuable in the development of environmental flow strategies intended to conserve riverine faunal assemblages vulnerable to changing river flow regimes driven by pressures including water abstraction and climate change. This includes demographic models aiming to characterise how specific river flow regime elements (including ELFs) are required to support key ecological assets (Tonkin et al., 2019).

Field-based assessments may often overlook or be unable to identify causal mechanisms underpinning ecohydrological patterns due to many of the reasons identified above (e.g. the influences of extraneous effects). One widely reported criticism of such studies is their potential to overlook demographic changes driven by dispersal mechanisms and biotic interactions (Lancaster & Downes, 2010a; Sarremejane, Truchy, et al., 2021). However, field-based assessments based on high-frequency sampling of an individual river (or a small number of watercourses within a specific region) undergoing a single ELF event provide a greater opportunity to detect and attribute the causal mechanisms associated with faunal responses (e.g. Perkin et al., 2019; White, Armitage, et al., 2019) relative to larger-scale or longer-term studies.

Many of the constraints in identifying causal mechanisms underpinning faunal responses to ELFs are easier to overcome within controlled experiments given the high degree of control over key variables of interest (e.g. fauna present and flow variability), which allows greater intuitive linkage between flow conditions and ecological responses. This is most evident within target-taxa experiments operating at small spatial scales, where both the number and density of species can be carefully controlled alongside environmental conditions, and observations can be more reliably measured. For instance, Patel et al. (2021) used clear substrates and mesocosms (0.35 m depth, 0.05 m internal diameter) to directly observe the behavioural responses of two amphipods (*Gammarus pulex* and *Dikerogammarus villosus*) under different water drawdown rates. Such empirical observations are more difficult to obtain in larger-scale instream flow manipulations and community composition experiments due to a lack of technology or equipment, as well as other factors such as biotic interactions.

4.4 | Predictive capability for future hydroclimatic conditions

Long-term field-based assessments can provide a detailed understanding of how future hydroclimatic changes, including more severe or longer ELF events, may affect riverine fauna. For instance, Pyne and Poff (2017) used long-term biomonitoring data to examine the responses of 88 freshwater insects to a hydrological metric derived from precipitation and surface runoff projections from global circulation models. The authors subsequently altered these hydrological values in accordance with climate change projections to quantify the future vulnerability of these taxa. Statistical predictions beyond the observed data range (i.e. predicting faunal responses to future ELFs under hydroclimatic scenarios based on historic discharge variations) are uncertain (Rosenfeld, 2017), which may be further exacerbated by uncertainties associated with climate change projections (Poff et al., 2016) and any changes in low-flow management (Wilby et al., 2011). However, field-based assessments remain a fundamental tool for understanding the vulnerability of fish and macroinvertebrates (alongside all freshwater biota) to ongoing climate change and recognising such uncertainties will be critical for such predictions (Tonkin et al., 2019).

Controlled experiments testing faunal responses to ELFs can simulate flow conditions that are expected to occur under future hydroclimatic scenarios. For instance, Verdonschot et al. (2015) created three flow states widely recognised within temporary river research (Sarremejane, Messager, & Datry, 2021) within an instream flow manipulation experiment by creating flowing, ponded and dry reaches. This has implications for ELF research as many normally perennial reaches globally are expected to experience flow cessation events under future hydroclimatic scenarios (Döll & Schmied, 2012). Alternatively, Aspin, Hart, et al. (2019) and Aspin, Khamis, et al. (2019) used experimental streams subjected to various flow depths (by manipulating discharges) that imitated key habitat losses associated with drying events outlined by Boulton (2003). However, no controlled experiments to our knowledge have directly manipulated flow conditions in accordance with future hydroclimatic projections. In this regard, experimental ELF studies lag behind those investigating other climate-related stressors such as warming (e.g. Nelson et al., 2017; Piggott et al., 2015), reflecting the greater uncertainty and context dependency associated with future changes to river flows and the technical challenges of simulation at small scales.

5 | FUTURE RESEARCH OPPORTUNITIES

The respective strengths of field-based assessments and controlled experiments have been pivotal in advancing our scientific understanding of faunal responses to ELFs. In this section, we highlight different scientific advances that could be explored more widely to collectively advance both research paradigms. Some of the advances we propose entail drawing on currently underutilised approaches within each individual research paradigm; others depend on greater synergy between field-based assessments and controlled experiments. For this, we draw on a key case study of how these research paradigms could be synergised based on the authors' perspectives and regional expertise. Figure 5 summarises some of the key research themes outlined below.

5.1 | Field-based assessments

Field-based assessments could incorporate underutilised sampling approaches and techniques to help pinpoint the causal mechanisms driving faunal responses to ELFs. There is also a pressing need for such studies to explore different forms of ecological information beyond traditional taxonomic-based responses (e.g. abundance and richness) during ELF events, especially for macroinvertebrate studies given that fish research more routinely examines features like demographical responses and biological measurements. For instance, macroinvertebrate body length or head size measurements often conducted within controlled experiments (Aspin, Khamis, et al., 2019; Patel et al., 2021) could be incorporated more widely in field-based assessments (Taylor, 1983). Low-cost sampling equipment could be more widely utilised in field-based assessments to better understand macroinvertebrate tolerance mechanisms (e.g. paired benthic and hyporheic sampling, Durkota et al., 2019; seedbank compositions, Stubbington et al., 2016); and demographic responses (e.g. drift nets, Caldwell et al., 2018; emergence traps, Drummond et al., 2015; colonisation cylinders, Mathers et al., 2017). However, it is recognised that these techniques can be time consuming and labour intensive and thus may result in higher labour costs.

We advocate the collection of a more diverse range of hydrological information within field-based assessments. For instance, incorporating hydrological models in such studies can enhance the number of ecological sampling points by providing data that span entire river networks, rather than relying exclusively on those proximal to spatially discrete flow gauges (Wilby et al., 2017). Moreover, some hydrological models can provide empirical evidence on how flow regimes have been altered by different water resource management operations (e.g. flow regulation, groundwater abstraction and effluent water returns; Streetly et al., 2014; White et al., 2021; Wilby et al., 2011). We also call for the more widespread use of field-based hydromorphological information and habitat conditions, including reach-scale flow velocities (e.g. Monk et al., 2018) or changes in flow 'states' (i.e. flowing, ponded or dry) associated with channel drying that may occur during ELF events (e.g. Sarremejane, Stubbington, et al., 2021). In addition, we call for more field-based assessments that model faunal responses to projected hydroclimatic changes (e.g. IPCC scenarios, Hain et al., 2018; Visser et al., 2019).

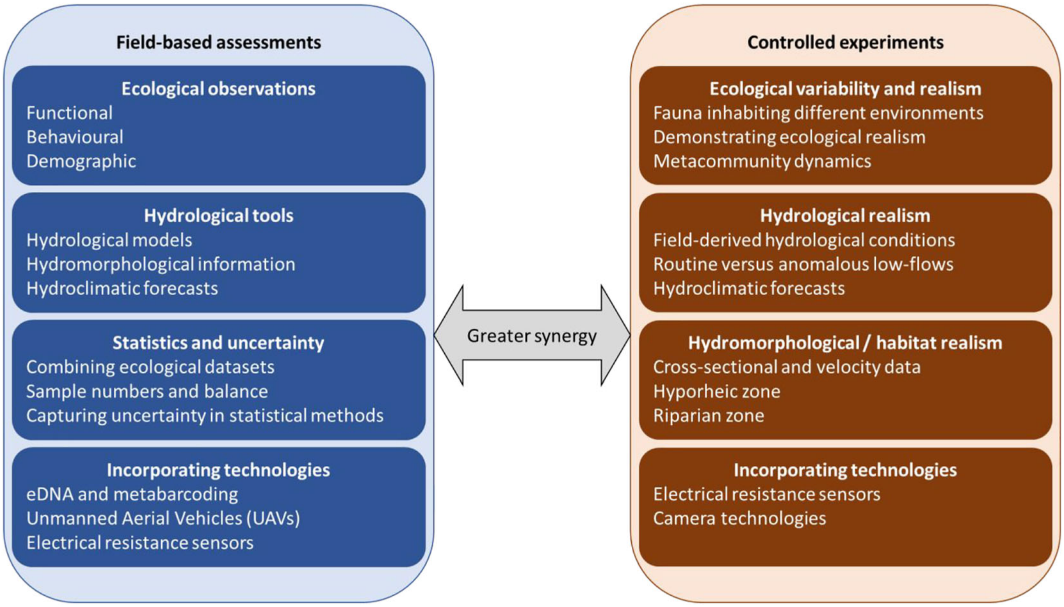

FIGURE 5 Research themes that could be explored and developed in future field-based assessments and controlled experiments to help provide a better scientific understanding of faunal responses to ELFs

Recognising and clearly documenting uncertainties via statistical evidence in field-based assessments is also critical for advancing our scientific understanding and informing river management initiatives (Tonkin et al., 2019). Scientific uncertainties may originate from various sources in ecological and hydrological data, and we focus on a select few here. First, amalgamating faunal datasets from different sources may cause uncertainty when taxonomic resolutions are not harmonised between samples and datasets. Statistically testing or screening for this potential influence could be more widely adopted (Cuffney & Kennen, 2018). Second, we advocate wider testing and reporting of the statistical effects of sampling balance and bias of both ecological and hydrological datasets utilised within field-based assessments (Hain et al., 2018). Lastly, there remains a need for demographic changes associated with faunal assemblages to be accounted for more routinely through measures of community stochasticity and temporal autocorrelation (e.g. Ruhí et al., 2015; Sarremejane, Truchy, et al., 2021) and spatial autocorrelation effects (e.g. Bruckerhoff et al., 2019; Larsen et al., 2021).

Technological advancements could also improve the robustness of field-based assessments. For instance, environmental DNA and metabarcoding techniques can better capture community biodiversity during ELFs as tolerant species are often difficult to identify in morphology-based taxonomical approaches (Stubbington et al., 2018). 'Passive Integrated Transponders' or radiotelemetry systems could be more widely utilise to detect faunal movements, particularly for macroinvertebrate communities where such technologies are currently lacking (but see Gherardi et al., 2002). Hydrological information during ELF events may be better characterised by utilising unmanned aerial vehicles (UAVs), including capturing channel cross-sectional data and habitat conditions capable of supporting target fauna (Zhao et al., 2017), as well as the use of thermal imagery to detect river network expansion and contraction (Micieli et al., 2020). Improved hydrological data can also be obtained from electrical resistance sensors, which provide information on hydrological and habitat conditions (e.g. depth and velocity) at high temporal resolutions, thus distinguishing between key flow states (i.e. zero flow from ponded and dry conditions) that traditional flow gauge information cannot normally achieve (Jaeger & Olden, 2012). In addition, electrical resistance sensors can provide hydrological information alongside other abiotic conditions affected during ELF events, including stream temperatures and electrical conductivity (Chapin et al., 2014).

5.2 | Controlled experiments

We emphasise the need for scientists to experimentally test how faunal communities inhabiting different riverine environments respond to ELFs and in more ecologically realistic settings. For instance, fauna inhabiting adjacent perennial and temporary river systems could be exposed to ELF conditions to better understand resistance and resilience capabilities (see Crabot et al., 2021 for a comparable field-based campaign). Similarly, the effects of ELF events on fauna sourced from contrasting riverine environments (e.g. groundwater vs. surface water dominated and temperate vs. arid) may help to elucidate the ecological mechanisms underpinning responses of communities or species adapted to varying environmental conditions.

Demonstrating ecological realism is fundamental to understanding how such findings translate to natural systems and has typically been achieved by comparing taxonomic identities and community structures. Efforts to recreate different metacommunity components have been less widely explored but could be addressed by comparing migratory or dispersal mechanisms (e.g. James et al., 2008) and biotic interaction types and strengths (e.g. Brown et al., 2011) between controlled experiments versus natural systems. We recognise that achieving true metacommunity realism may be challenging in controlled experiments, but further controls could be introduced to manipulate community assemblage dynamics alongside changes in flow conditions to pinpoint the ecological importance of different colonisation mechanisms. For example, dispersal pathways could be controlled, with macroinvertebrate responses to ELFs in online and offline experiments being compared to infer the importance of drift as a resilience mechanism. Similarly, outdoor mesocosm experiments could use artificial coverings (e.g. Boersma et al., 2014) to control aerial colonisation routes and improve our understanding of the effects of habitat isolation during ELF conditions. While such designs are not feasible within target-taxa experiments (and are clearly not a primary objective of such studies), recognising or capturing potential influences of metacommunity dynamics can help better place results within the context of natural systems (e.g. Driver & Hoeinghaus, 2016).

We advocate the design of controlled experiments replicating ELF conditions congruent with those experienced by natural systems and/or projected under future hydroclimatic conditions. This requires drawing on hydrological data from natural systems (i.e. long-term time series) from which specific ELF conditions can be identified and mimicked in controlled experiments. Such studies may require greater use of longer-term experiments that can replicate conditions like varying transition rates (days to months) between normal flow and ELF conditions (e.g. Nuhfer et al., 2017); mimic inter-seasonal variability or inter-annual drought (Leigh et al., 2019); and capture long-term ecological recovery patterns (i.e. return to ecological conditions exhibited prior to the ELF event—which has not been explored to our knowledge). We specifically advocate experimental studies that recreate and test the effects of routine low-flow periods versus ELFs (or seasonal vs. supra-seasonal droughts—sensu Lake, 2003) based on long-term hydrological data, models or hydroclimatic forecasts.

We also recognise the need for experimental studies to better capture hydromorphological (e.g. channel dimensions and flow velocity) and habitat conditions (e.g. substrate characteristics and floral assemblages) in systems that reflect the changes experienced in natural channels subject to ELF events. Many controlled experiments provide limited habitat complexity relative to natural systems due to the enclosure designs. For instance, experimental enclosures often lack substantial (or any) hyporheic zones, which could be more widely incorporated in enclosure-like experimental streams. However, instream flow manipulations benefit from realistically extensive hyporheic zones in which ecological responses to ELFs could be examined (Maazouzi et al., 2017), as do various target-taxa experiments using 'column-style' designs to understand how specific macroinvertebrate taxa migrate vertically in response to dewatering (Vander Vorste et al., 2016; Patel et al., 2021). In addition, the effects of riparian habitat structure on ecological responses to ELF events need to be better incorporated into experimental approaches to reflect the importance of key processes, including early loss of critical habitat (Chadd et al., 2017), shifts in terrestrial-aquatic subsidies (Boucek et al., 2016) and buffering of impacts due to microclimatology (Bond et al., 2008). Next-generation ELF mesocosm experiments able to incorporate some degree of riparian habitat complexity are thus likely to be particularly informative.

Many of the technological advancements that we outlined for field-based assessments could be applied within controlled experiments, and there is indeed a significant need for data loggers that can better characterise abiotic variations that occur during ELF conditions. For instance, Kurz et al. (2017) monitored continuous dissolved oxygen and stream temperature variations within experimental channels exposed to ELF conditions to measure whole ecosystem respiration. Sensors and ultrasonic flow meters could be more widely utilised to derive continuous hydrological measurements and help ensure true replication of flow conditions between controlled experiments. Target-taxa experiments in particular could more widely utilise novel technologies to characterise the behavioural responses of fauna to ELF conditions. For instance, video footage from high-resolution cameras could be used to track faunal movement responses to ELFs (Rice et al., 2010), and Mathers, Michalec, et al. (2020) recently highlighted how such technologies could be used alongside transparent substrates to track subsurface movements of the freshwater amphipod *Gammarus fossarum* during controlled low-flow conditions, which could be extended to ELF studies.

5.3 | Synergies between research paradigms

By highlighting the relative advantages of both research paradigms discussed within this perspective piece, we hope to encourage scientists to seek opportunities for greater synergy. We recognise that field-based assessments and controlled experiments have benefitted (directly or indirectly) and drawn upon evidence from each other. In addition, we acknowledge that some field-based assessments and controlled experiments may be inherently linked, but the results published separately (e.g. Vadher et al., 2018a, 2018b) and/or may be interwoven within larger research projects like PhD theses (e.g. Dewson, 2007; Picken, 2021). There are also instances of various field-based assessments and controlled experiments drawing heavily on information derived from the alternative research paradigm based on regionally contextual studies, and we welcome the further publication of such studies. For instance, DuBose et al. (2019) scrutinised reports of freshwater mussel losses in field-based assessments across the southern USA and used this to guide the density of freshwater mussels and a fish predator (largemouth bass, *Micropterus salmoides*) seeded at different ELF stages within their experiment.

Nevertheless, there remain a limited number of studies that have employed a dual approach. Notable exceptions include Harris et al. (2020) (see Section 4.1). Avery-Gomm et al. (2014) supplemented field-based measurements highlighting declines in Nooksack dace (*Rhinichthys cataractae*) abundances with evidence from an experimental setup highlighting the effects of ELFs on their growth rates. Han et al. (2013) examined the flow preferences of the cyprinid *Spinibarbus hollandi* in the laboratory and applied this to a fish dynamics model used in the field to demonstrate that refuge habitat was not available during anthropogenically driven ELFs within a regulated river. Beyond ELF research specifically, Gruppuso et al. (2021) highlighted that the leaf litter decomposition rates of freshwater macroinvertebrate communities were comparable between drying events observed in intermittent streams versus those fashioned in the flume. We advocate the wider implementation of such dual approaches as they provide greater evidence and certainty in results by harnessing the relative strengths of each research paradigm.

5.4 | The case study of English chalk rivers

We conclude by highlighting how field-based assessments and controlled experiments could be more widely examined and better synergised in 'chalk' (a fine-grained limestone) streams and rivers situated in southern and eastern England (UK) as a case study. Chalk rivers are considered nationally iconic systems due to their aesthetic (e.g. clear waters and dense macrophyte coverages) and ecological qualities (e.g. salmonid populations and EPT riverflies as their primary food source; Mainstone et al., 1999). Chalk rivers are groundwater-dominated systems and display highly buffered hydrological responses to individual rainfall events that provides seasonally stable flow regimes. However, such environments are being subjected to increasing ELF frequencies due to groundwater abstraction (chalk supports more abstraction than any other aquifer in the United Kingdom) and hydroclimatic changes (Visser et al., 2019; White et al., 2021; Wilby et al., 2006). While freshwater ecosystems and riverine fauna have adapted to seasonally typical low-flows during the summer and autumn, including periodic drying in the headwaters and some mid-reaches (Sarremejane, Stubbington, et al., 2021; White et al., 2018), many taxa lack adaptations to survive ELF events in such environments (Aspin, Hart, et al., 2019; Ledger et al., 2011, 2012; Wood & Armitage, 2004). As such, there is a pressing need to better understand the vulnerability of chalk river ecosystems, and specifically supported faunal assemblages, from a national conservation perspective. Moreover, biotic adaptations to (and dependencies on) seasonally predictable flow regimes in chalk rivers make them ideal sentinel ecosystems to study the ecological effects of ELF events given that impacts on riverine fauna (and all biota) may be more significant compared to communities naturally subjected to more hydrologically dynamic environments. While a significant body of ecohydrological studies has been undertaken on chalk rivers, there remains a pressing need to establish a more cohesive research agenda that can better inform the vulnerability of riverine fauna to ELF events in such environments. We highlight three key areas where scientific advancements within and between research paradigms could be made in the context of chalk rivers and other comparable groundwater-dominated systems (e.g. many karstic environments; Bonacci et al., 2009).

5.4.1 | Hydrological characterisation of present and future ELF events

Flow regimes can vary significantly in chalk headwater environments where a gradient of flow permanence from temporary systems dry for >9 months of the year to perennial environments can occur within small spatial scales (e.g. <7 km; White et al., 2018). Recurring monitoring (Sarremejane, Stubbington, et al., 2021; White et al., 2018) and modelling (Eastman et al., 2021) of flow conditions or states can provide spatially continuous hydrological data over longer time periods, which could be more widely used to better characterise ELF thresholds within chalk river networks. Such information could be more routinely combined with information including groundwater models, human population growth estimates and water demands, and hydroclimatic change projections (e.g. the UK Climate Projections 2018, UKCP18; Lowe et al., 2019) to model the potential hydro(morpho)logical effects of future ELF events. Such information could also help target sampling sites within field-based assessments, including deep pools where salmonid species (brown trout [*S. trutta*] and Atlantic salmon [*S. salar*]) congregate during ELF events to better understand population collapse risks from stranding and habitat size thresholds associated with this. Improved hydrological characterisations of current and future ELF conditions could also help directly inform flow conditions within controlled experiments, which could explore the vulnerability of different communities seeded from sites yielding different degrees of flow permanence to respective ELF conditions (e.g. perennial communities subjected to slow-flow conditions; temporary communities exposed to prolonged drying).

5.4.2 | Metacommunity dynamics

Some field-based assessments have explored faunal assemblage metacommunity dynamics during ELF conditions within chalk rivers (e.g. Sarremejane, Stubbington, et al., 2021). However, there remains a limited understanding of how demographic (e.g. biotic interactions and aerial and aquatic dispersal rates) and environmental filters interact to shape the tolerance of faunal assemblages during ELF conditions. For instance, more field-based assessments are required to understand the emigration (e.g. upstream, downstream or vertical movements and emergence as winged adults for riverfly species) of fauna during ELF events. For fauna residing in situ during ELF events, a detailed understanding of the temporal trajectory of individual populations associated with changing environmental conditions and biotic interactions would dramatically improve our scientific ability to predict ecological changes and thresholds. Specifically for chalk rivers, it is unclear how rare temporary water specialists such as *Paraleptophlebia werneri* (Order: Ephemeroptera) and *Nemoura lacustris* (Order: Plecoptera) respond to ELFs (as opposed to routine drying) as their hydrological requirements are not known, nor is the cause of their suggested vulnerability to competitively superior taxa that precludes their establishment in perennial systems (Armitage & Bass, 2013). As such, flow–ecology relationships examining how such taxa respond to ELFs as well as exploring their co-occurrence alongside other species could address critical research gaps. Such field-based assessments could again help inform controlled experiments, such as targeting early emigrants exiting hydrologically impacted regions at the early onset of ELF events. Such taxa could also be experimentally exposed to different flow conditions (and potentially other abiotic parameters including temperature; see following text) to identify environmental cues triggering refugia-seeking behaviours. In addition, co-occurrence patterns examined during ELF events in the field could be used to inform controlled experiments to explore the causal mechanisms explaining why some taxa are outcompeting *P. werneri* and *N. lacustris* during ELF conditions or subsequently during flow recovery.

5.4.3 | Examining multi-stressor interactions

In addition to reductions in discharge, chalk river environments are exposed to other pressures that exacerbate the ecological effects of ELF events, including hydromorphological alterations (Dunbar et al., 2010); fine sediment concentrations and elevated nutrient levels due to agricultural practices (e.g. watercress farms on chalk rivers; Casey & Smith, 1994); invasive species (Mathers, White, et al., 2020) and climate-induced warming (Durance & Ormerod, 2009). The dense amount of information from secondary datasets along chalk rivers (e.g. Environment Agency, 2022a, 2022b; Naura, 2022; UK Centre for Ecology and Hydrology, 2021) could be more widely used in field-based assessments to better understand the interactive effects of abiotic stressors operating during ELF events. For instance, riverine faunal responses to the magnitude, frequency, duration, timing and rate of change of different abiotic regimes (e.g. flow, temperature and nutrient levels) could be assessed using such secondary datasets. Key ecological findings from such research could inform future experimental studies to help identify whether specific abiotic stressors or combinations of stressors at different levels associated with ELF events exert additive, subtractive, synergistic or antagonistic effects on riverine fauna. Such information would be highly valuable to help target specific management interventions required to effectively mitigate the ecological effects of ELF events. In addition, there is a better need to understand how different management actions are likely to affect riverine faunal responses to ELF events. For instance, field-based assessments could test the ecohydrological outcomes of management interventions such as increased riparian shade, nutrient control, reduced groundwater abstraction and the introduction of environmental flows during ELF events, which could be statistically modelled to forecast riverine faunal responses under different contemporary and future scenarios (Whitehead et al., 2006; Wilby et al., 2010, 2011).

6 | CONCLUSIONS

ELF events are becoming more prevalent globally as river flow regimes face increasing pressures from water resource management operations and climate change. Consequently, there is a pressing need to better diagnose and predict riverine faunal responses to ELFs in order to safeguard freshwater ecosystems. We identify field-based assessments and controlled experiments as two dominant research paradigms that have, and continue to, advance our scientific understanding in this field. To date, these research paradigms have largely been undertaken in parallel, with ELF research grants typically invested in one or other approach, reflecting different research objectives and contrasting scales of study. We have highlighted how the respective strengths of both paradigms could be better harnessed and how future research could more readily look for areas of synergy. A more integrated and holistic approach would optimise the quality and amount of scientific evidence examining faunal responses to ELF events, which can better inform riverine management decisions now and in the future.

ACKNOWLEDGEMENT

The authors would like to extend their gratitude to Dr Jonathan Wheatland for designing Figure 2.

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REFERENCES

AghaKouchak, A., Mirchi, A., Madani, K., Baldassarre, G. D., Nazemi, A., Alborzi, A., Anjileli, H., Azarderakhsh, M., Chiang, F., Hassanzadeh, E., Huning, L. S., Mallakpour, I., Martinez, A., Mazdiyasni, O., Moftakhari, H., Norouzi, H., Sadegh, M., Sadeqi, D., Loon, A. F. V., & Wanders, N. (2021). Anthropogenic drought: Definition, challenges, and opportunities. *Reviews of Geophysics*, *59*(2), e2019RG000683. https://doi.org/10.1029/2019RG000683

Amini, H., Esmali-Ouri, A., Mostafazadeh, R., Sharari, M., & Zabihi, M. (2019). Hydrological drought response of regulated river flow under the influence of dam reservoir in Ardabil Province. *Journal of the Earth and Space Physics*, *45*(2), 473–486. https://doi.org/10.22059/JESPHYS.2019.272671.1007078

Archdeacon, T. P., & Reale, J. K. (2020). No quarter: Lack of refuge during flow intermittency results in catastrophic mortality of an imperiled minnow. *Freshwater Biology*, *65*(12), 2108–2123.

Armitage, P. D., & Bass, J. (2013). Long-term resilience and short-term vulnerability of south winterbourne macroinvertebrates. *Proceedings of the Dorset Natural History and Archaeology Society*, *134*, 43–55.

Aspin, T., House, A., Martin, A., & White, J. (2020). Reservoir trophic state confounds flow-ecology relationships in regulated streams. *The Science of the Total Environment*, *748*, 748141304. https://doi.org/10.1016/j.scitotenv.2020.141304

Aspin, T. W. H., Hart, K., Khamis, K., Milner, A. M., O'Callaghan, M. J., Trimmer, M., Wang, Z., Williams, G. M. D., Woodward, G., & Ledger, M. E. (2019). Drought intensification alters the composition, body size, and trophic structure of invertebrate assemblages in a stream mesocosm experiment. *Freshwater Biology*, *64*(4), 750–760. https://doi.org/10.1111/fwb.13259

Aspin, T. W. H., Khamis, K., Matthews, T. J., Milner, A. M., O'Callaghan, M. J., Trimmer, M., Woodward, G., & Ledger, M. E. (2019). Extreme drought pushes stream invertebrate communities over functional thresholds. *Global Change Biology*, *25*(1), 230–244. https://doi.org/10.1111/gcb.14495

Avery-Gomm, S., Rosenfeld, J. S., Richardson, J. S., & Pearson, M. (2014). Hydrological drought and the role of refugia in an endangered riffle-dwelling fish, Nooksack dace (*Rhinichthys cataractae* ssp.). *Canadian Journal of Fisheries and Aquatic Sciences*, *71*(11), 1625–1634. https://doi.org/10.1139/cjfas-2013-0585

Baattrup-Pedersen, A., Ovesen, N. B., Larsen, S. E., Andersen, D. K., Riis, T., Kronvang, B., & Rasmussen, J. J. (2018). Evaluating effects of weed cutting on water level and ecological status in Danish lowland streams. *Freshwater Biology*, *63*(7), 652–661. https://doi.org/10.1111/fwb.13101

Becker, C. D., Neitzel, D. A., & Fickeisen, D. H. (1982). Effects of dewatering on Chinook salmon redds: Tolerance of four developmental phases to daily dewaterings. *Transactions of the American Fisheries Society*, *111*(5), 624–637. https://doi.org/10.1577/1548-8659(1982)111<624:EODOCS>2.0.CO;2

Belmar, O., Velasco, J., Gutiérrez-Cánovas, C., Mellado-Díaz, A., Millán, A., & Wood, P. J. (2013). The influence of natural flow regimes on macroinvertebrate assemblages in a semiarid Mediterranean basin. *Ecohydrology*, *6*(3), 363–379. https://doi.org/10.1002/eco.1274

Benejam, L., Angermeier, P. L., Munné, A., & García-Berthou, E. (2010). Assessing effects of water abstraction on fish assemblages in Mediterranean streams. *Freshwater Biology*, *55*(3), 628–642. https://doi.org/10.1111/j.1365-2427.2009.02299.x

Bestland, E., George, A., Green, G., Olifent, V., Mackay, D., & Whalen, M. (2017). Groundwater dependent pools in seasonal and permanent streams in the Clare Valley of South Australia. *Journal of Hydrology: Regional Studies*, *9*, 216–235. https://doi.org/10.1016/j.ejrh.2016.12.087

Beyene, B. S., Van Loon, A. F., Van Lanen, H. A. J., & Torfs, P. J. J. F. (2014). Investigation of variable threshold level approaches for hydrological drought identification. *Hydrology and Earth System Sciences Discussions*, *11*(11), 12765–12797. https://doi.org/10.5194/hessd-11-12765-2014

Blöcher, J. R., Ward, M. R., Matthaei, C. D., & Piggott, J. J. (2020). Multiple stressors and stream macroinvertebrate community dynamics: Interactions between fine sediment grain size and flow velocity. *The Science of the Total Environment*, *717*, 717137070. https://doi.org/10.1016/j.scitotenv.2020.137070

Blöschl, G., Ardoin-Bardin, S., Bonell, M., Dorninger, M., Goodrich, D., Gutknecht, D., Matamoros, D., Merz, B., Shand, P., & and Szolgay, J. (2007). At what scales do climate variability and land cover change impact on flooding and low flows? *Hydrological Processes*, *21*(9), 1241–1247. https://doi.org/10.1002/hyp.6669

Boersma, K. S., Bogan, M. T., Henrichs, B. A., & Lytle, D. A. (2014). Invertebrate assemblages of pools in arid-land streams have high functional redundancy and are resistant to severe drying. *Freshwater Biology*, *59*(3), 491–501. https://doi.org/10.1111/fwb.12280

Bogan, M. T., Boersma, K. S., & Lytle, D. A. (2015). Resistance and resilience of invertebrate communities to seasonal and supraseasonal drought in arid-land headwater streams. *Freshwater Biology*, *60*(12), 2547–2558. https://doi.org/10.1111/fwb.12522

Bogan, M. T., & Lytle, D. A. (2011). Severe drought drives novel community trajectories in desert stream pools. *Freshwater Biology*, *56*(10), 2070–2081. https://doi.org/10.1111/j.1365-2427.2011.02638.x

Bonacci, O., Pipan, T., & Culver, D. C. (2009). A framework for karst ecohydrology. *Environmental Geology*, *56*(5), 891–900. https://doi.org/10.1007/s00254-008-1189-0

Bond, N. R., Lake, P. S., & Arthington, A. H. (2008). The impacts of drought on freshwater ecosystems: An Australian perspective. *Hydrobiologia*, *600*(1), 3–16. https://doi.org/10.1007/s10750-008-9326-z

Boucek, R. E., Soula, M., Tamayo, F., & Rehage, J. S. (2016). A once in 10 year drought alters the magnitude and quality of a floodplain prey subsidy to coastal river fishes. *Canadian Journal of Fisheries and Aquatic Sciences*, *73*(11), 1672–1678. https://doi.org/10.1139/cjfas-2015-0507

Boulton, A. J. (2003). Parallels and contrasts in the effects of drought on stream macroinvertebrate assemblages. *Freshwater Biology*, *48*(7), 1173–1185. https://doi.org/10.1046/j.1365-2427.2003.01084.x

Bradford, M. J., Higgins, P. S., Korman, J., & Sneep, J. (2011). Test of an environmental flow release in a British Columbia river: Does more water mean more fish? *Freshwater Biology*, *56*(10), 2119–2134. https://doi.org/10.1111/j.1365-2427.2011.02633.x

Brown, L. E., Edwards, F. K., Milner, A. M., Woodward, G., & Ledger, M. E. (2011). Food web complexity and allometric scaling relationships in stream mesocosms: Implications for experimentation. *The Journal of Animal Ecology*, *80*(4), 884–895. https://doi.org/10.1111/j.1365-2656.2011.01814.x

Bruckerhoff, L. A., Leasure, D. R., & Magoulick, D. D. (2019). Flow–ecology relationships are spatially structured and differ among flow regimes. *Journal of Applied Ecology*, *56*(2), 398–412. https://doi.org/10.1111/1365-2664.13297

Bryant, S. J., Arnell, N. W., & Law, F. M. (1994). The 1988–92 drought in its historical perspective. *Water Environment Journal*, *8*(1), 39–51. https://doi.org/10.1111/j.1747-6593.1994.tb01091.x

Calapez, A. R., Serra, S. R. Q., Santos, J. M., Branco, P., Ferreira, T., Hein, T., Brito, A. G., & Feio, M. J. (2018). The effect of hypoxia and flow decrease in macroinvertebrate functional responses: A trait-based approach to multiple-stressors in mesocosms. *The Science of the Total Environment*, *637-638*, 647–656. https://doi.org/10.1016/j.scitotenv.2018.05.071

Caldwell, T. J., Rossi, G. J., Henery, R. E., & Chandra, S. (2018). Decreased streamflow impacts fish movement and energetics through reductions to invertebrate drift body size and abundance. *River Research and Applications*, *34*(8), 965–976. https://doi.org/10.1002/rra.3340

Carey, N., Chester, E. T., & Robson, B. J. (2021). Life-history traits are poor predictors of species responses to flow regime change in headwater streams. *Global Change Biology*, *27*(15), 3547–3564. https://doi.org/10.1111/gcb.15673

Carlisle, D. M., Falcone, J., Wolock, D. M., Meador, M. R., & Norris, R. H. (2010). Predicting the natural flow regime: Models for assessing hydrological alteration in streams. *River Research and Applications*, *26*(2), 118–136. https://doi.org/10.1002/rra.1247

Casey, H., & Smith, S. M. (1994). The effects of watercress growing on chalk headwater streams in Dorset and Hampshire. *Environmental Pollution*, *85*(2), 217–228. https://doi.org/10.1016/0269-7491(94)90088-4

Chadd, R. P., England, J. A., Constable, D., Dunbar, M. J., Extence, C. A., Leeming, D. J., Murray-Bligh, J. A., & Wood, P. J. (2017). An index to track the ecological effects of drought development and recovery on riverine invertebrate communities. *Ecological Indicators*, *82*, 344–356. https://doi.org/10.1016/j.ecolind.2017.06.058

Chapin, T. P., Todd, A. S., & Zeigler, M. P. (2014). Robust, low-cost data loggers for stream temperature, flow intermittency, and relative conductivity monitoring. *Water Resources Research*, *50*(8), 6542–6548. https://doi.org/10.1002/2013WR015158

Chen, W., & Olden, J. D. (2018). Evaluating transferability of flow–ecology relationships across space, time and taxonomy. *Freshwater Biology*, *63*(8), 817–830. https://doi.org/10.1111/fwb.13041

Chessman, B. C. (2015). Relationships between lotic macroinvertebrate traits and responses to extreme drought. *Freshwater Biology*, *60*(1), 50–63. https://doi.org/10.1111/fwb.12466

Crabot, J., Polášek, M., Launay, B., Pařil, P., & Datry, T. (2021). Drying in newly intermittent rivers leads to higher variability of invertebrate communities. *Freshwater Biology*, *66*(4), 730–744. https://doi.org/10.1111/fwb.13673

Cuffney, T. F., & Kennen, J. G. (2018). Potential pitfalls of aggregating aquatic invertebrate data from multiple agency sources: Implications for detecting aquatic assemblage change across alteration gradients. *Freshwater Biology*, *63*(8), 738–751. https://doi.org/10.1111/fwb.13031

De la Fuente, M., Bonada, N., Bêche, L., Dahm, C. N., Mendez, P. K., Tockner, K., Uehlinger, U., & Acuña, V. (2018). Evolutionary responses of aquatic macroinvertebrates to two contrasting flow regimes. *Hydrobiologia*, *808*(1), 353–370. https://doi.org/10.1007/s10750-017-3437-3

Dewson, Z. S. (2007). Small stream ecosystems and irrigation: An ecological assessment of water abstraction impacts. PhD thesis, Massey University, Palmerston North, New Zealand.

Dewson, Z. S., James, A. B. W., & Death, R. G. (2007). A review of the consequences of decreased flow for instream habitat and macroinvertebrates. *Journal of the North American Benthological Society*, *26*(3), 401–415. https://doi.org/10.1899/06-110.1

Döll, P., & Schmied, H. M. (2012). How is the impact of climate change on river flow regimes related to the impact on mean annual runoff? A global-scale analysis. *Environmental Research Letters*, *7*(1), e014037. https://doi.org/10.1088/1748-9326/7/1/014037

Downing, K. M., & Merkens, J. C. (1957). The influence of temperature on the survival of several species of fish in low tensions of dissolved oxygen. *The Annals of Applied Biology*, *45*(2), 261–267. https://doi.org/10.1111/j.1744-7348.1957.tb00465.x

Driver, L. J., & Hoeinghaus, D. J. (2016). Fish metacommunity responses to experimental drought are determined by habitat heterogeneity and connectivity. *Freshwater Biology*, *61*(4), 533–548. https://doi.org/10.1111/fwb.12726

Drummond, L. R., McIntosh, A. R., & Larned, S. T. (2015). Invertebrate community dynamics and insect emergence in response to pool drying in a temporary river. *Freshwater Biology*, *60*(8), 1596–1612. https://doi.org/10.1111/fwb.12591

DuBose, T. P., Atkinson, C. L., Vaughn, C. C., & Golladay, S. W. (2019). Drought-induced, punctuated loss of freshwater mussels alters ecosystem function across temporal scales. *Frontiers in Ecology and Evolution*, *7*, 274. https://doi.org/10.3389/fevo.2019.00274

Dunbar, M. J., Pedersen, M. L., Cadman, D. A. N., Extence, C., Waddingham, J., Chadd, R., & Larsen, S. E. (2010). River discharge and local-scale physical habitat influence macroinvertebrate LIFE scores. *Freshwater Biology*, *55*(1), 226–242. https://doi.org/10.1111/j.1365-2427.2009.02306.x

Durance, I., & Ormerod, S. J. (2009). Trends in water quality and discharge confound long-term warming effects on river macroinvertebrates. *Freshwater Biology*, *54*(2), 388–405. https://doi.org/10.1111/j.1365-2427.2008.02112.x

Durkota, J. M., Wood, P. J., Johns, T., Thompson, J. R., & Flower, R. J. (2019). Distribution of macroinvertebrate communities across surface and groundwater habitats in response to hydrological variability. *Fundamental and Applied Limnology*, *193*, 79–92. https://doi.org/10.1127/fal/2019/1156

Eastman, M., Parry, S., Sefton, C., Park, J., & England, J. (2021). Reconstructing spatiotemporal dynamics in hydrological state along intermittent rivers. *Water*, *13*(4), 493. https://doi.org/10.3390/w13040493

Ekström, M., Gutmann, E. D., Wilby, R. L., Tye, M. R., & Kirono, D. G. (2018). Robustness of hydroclimate metrics for climate change impact research. *Wiley Interdisciplinary Reviews Water*, *5*(4), e1288. https://doi.org/10.1002/wat2.1288

Englund, G., & Cooper, S. D. (2003). Scale effects and extrapolation in ecological experiments. *Advances in Ecological Research*, *33*, 161–213. https://doi.org/10.1016/S0065-2504(03)33011-9

Environment Agency. (2022a). Ecology and fish data explorer. https://environment.data.gov.uk/ecology/explorer/. [Accessed 08/01/2022]

Environment Agency. (2022b). Water quality data archive. https://environment.data.gov.uk/water-quality. [Accessed 08/01/2022]

Eppehimer, D. E., Hamdhani, H., Hollien, K. D., & Bogan, M. T. (2020). Evaluating the potential of treated effluent as novel habitats for aquatic invertebrates in arid regions. *Hydrobiologia*, *847*(16), 3381–3396. https://doi.org/10.1007/s10750-020-04343-6

Fornaroli, R., Muñoz-Mas, R., & Martínez-Capel, F. (2020). Fish community responses to antecedent hydrological conditions based on long-term data in Mediterranean river basins (Iberian peninsula). *The Science of the Total Environment*, *728*, 138052. https://doi.org/10.1016/j.scitotenv.2020.138052

Fornaroli, R., White, J. C., Boggero, A., & Laini, A. (2020). Spatial and temporal patterns of macroinvertebrate assemblages in the river Po catchment (northern Italy). *Water*, *12*(9), 2452. https://doi.org/10.3390/w12092452

Fuchs, E. H., King, J. P., & Carroll, K. C. (2019). Quantifying disconnection of groundwater from managed-ephemeral surface water during drought and conjunctive agricultural use. *Water Resources Research*, *55*(7), 5871–5890. https://doi.org/10.1029/2019WR024941

Gherardi, F., Tricarico, E., & Ilhéu, M. (2002). Movement patterns of an invasive crayfish, *Procambarus clarkii*, in a temporary stream of southern Portugal. *Ethology Ecology and Evolution*, *14*(3), 183–197. https://doi.org/10.1080/08927014.2002.9522739

Greenwood, M. J., & Booker, D. J. (2015). The influence of antecedent floods on aquatic invertebrate diversity, abundance and community composition. *Ecohydrology*, *8*(2), 188–203.

Gruppuso, L., Doretto, A., Piano, E., Falasco, E., Bruno, M. C., Bona, F., & Fenoglio, S. (2021). Effects of flow intermittence on ecosystem processes in mountain streams: Are artificial and field experiments comparable? *Fundamental and Applied Limnology*, *195*(1), 39–59. https://doi.org/10.1127/fal/2021/1367

Hain, E. F., Kennen, J. G., Caldwell, P. V., Nelson, S. A., Sun, G., & McNulty, S. G. (2018). Using regional scale flow–ecology modeling to identify catchments where fish assemblages are most vulnerable to changes in water availability. *Freshwater Biology*, *63*(8), 928–945.

Han, R., Chen, Q., Blanckaert, K., Li, W., & Li, R. (2013). Fish (*Spinibarbus hollandi*) dynamics in relation to changing hydrological conditions: Physical modelling, individual-based numerical modelling, and case study. *Ecohydrology*, *6*(4), 586–597. https://doi.org/10.1002/eco.1388

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*(7), 1146–1162. https://doi.org/10.1002/hyp.7725

Harris, J. E., Skalicky, J. J., Liedtke, T. L., Weiland, L. K., Clemens, B. J., & Gray, A. E. (2020). Effects of dewatering on behavior, distribution, and abundance of larval lampreys. *River Research and Applications*, *36*(10), 2001–2012. https://doi.org/10.1002/rra.3730

Harris, R. M. L., Armitage, P. D., Milner, A. M., & Ledger, M. E. (2007). Replicability of physicochemistry and macroinvertebrate assemblages in stream mesocosms: Implications for experimental research. *Freshwater Biology*, *52*(12), 2434–2443. https://doi.org/10.1111/j.1365-2427.2007.01839.x

Herbst, D. B., Cooper, S. D., Medhurst, R. B., Wiseman, S. W., & Hunsaker, C. T. (2019). Drought ecohydrology alters the structure and function of benthic invertebrate communities in mountain streams. *Freshwater Biology*, *64*(5), 886–902. https://doi.org/10.1111/fwb.13270

Hopper, G. W., Gido, K. B., Pennock, C. A., Hedden, S. C., Guinnip, J. P., Fisher, M. A., Tobler, C. M., Hedden, C. K., & Bruckerhoff, L. A. (2020). Biomass loss and change in species dominance shift stream community excretion stoichiometry during severe drought. *Freshwater Biology*, *65*(3), 403–416. https://doi.org/10.1111/fwb.13433

IPCC. (2021). In V. Masson-Delmotte, P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M. I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J. B. R. Matthews, T. K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, & B. Zhou (Eds.), *Climate change 2021: The physical science basis. Contribution of working group I to the sixth assessment report of the intergovernmental panel on climate change*. Cambridge University Press. In Press

Jaeger, K. L., & Olden, J. D. (2012). Electrical resistance sensor arrays as a means to quantify longitudinal connectivity of Rivers. *River Research and Applications*, *28*(10), 1843–1852. https://doi.org/10.1002/rra.1554

James, A. B. W., Dewson, Z. S., & Death, R. G. (2008). The effect of experimental flow reductions on macroinvertebrate drift in natural and streamside channels. *River Research and Applications*, *24*(1), 22–35. https://doi.org/10.1002/rra.1052

Jarić, I., Bellard, C., Courchamp, F., Kalinkat, G., Meinard, Y., Roberts, D. L., & Correia, R. A. (2020). Societal attention toward extinction threats: A comparison between climate change and biological invasions. *Scientific Reports*, *10*(1), 11085. https://doi.org/10.1038/s41598-020-67931-5

Jourdan, J., OHara, R. B., Bottarin, R., Huttunen, K.-L., Kuemmerlen, M., Monteith, D., Muotka, T., Ozoliņš, D., Paavola, R., Pilotto, F., Springe, G., Skuja, A., Sundermann, A., Tonkin, J. D., & Haase, P. (2018). Effects of changing climate on European stream invertebrate communities: A long-term data analysis. *The Science of the Total Environment*, *621*, 621588–621599. https://doi.org/10.1016/j.scitotenv.2017.11.242

Kennedy, T. A., Muehlbauer, J. D., Yackulic, C. B., Lytle, D. A., Miller, S. W., Dibble, K. L., Kortenhoeven, E. W., Metcalfe, A. N., & Baxter, C. V. (2016). Flow management for hydropower extirpates aquatic insects, undermining river food webs. *Bioscience*, *66*(7), 561–575. https://doi.org/10.1093/biosci/biw059

Kurz, M. J., Drummond, J. D., Martí, E., Zarnetske, J. P., Lee-Cullin, J., Klaar, M. J., Folegot, S., Keller, T., Ward, A. S., Fleckenstein, J. H., Datry, T., Hannah, D. M., & Krause, S. (2017). Impacts of water level on metabolism and transient storage in vegetated lowland rivers: Insights from a mesocosm study. *Journal of Geophysical Research – Biogeosciences*, *122*(3), 628–644. https://doi.org/10.1002/2016JG003695

Laaha, G., & Blöschl, G. (2006). Seasonality indices for regionalizing low flows. *Hydrological Processes*, *20*(18), 3851–3878. https://doi.org/10.1002/hyp.6161

Lake, P. S. (2003). Ecological effects of perturbation by drought in flowing waters. *Freshwater Biology*, *48*(7), 1161–1172. https://doi.org/10.1046/j.1365-2427.2003.01086.x

Lamouroux, N., Mérigoux, S., Capra, H., Dolédec, S., Jowett, I. G., & Statzner, B. (2010). The generality of abundance-environment relationships in microhabitats: A comment on Lancaster and Downes (2009). *River Research and Applications*, *26*(7), 915–920. https://doi.org/10.1002/rra.1366

Lancaster, J., & Downes, B. J. (2010a). Ecohydraulics needs to embrace ecology and sound science, and to avoid mathematical artefacts. *River Research and Applications*, *26*(7), 921–929. https://doi.org/10.1002/rra.1425

Lancaster, J., & Downes, B. J. (2010b). Linking the hydraulic world of individual organisms to ecological processes: Putting ecology into ecohydraulics. *River Research and Applications*, *26*(4), 385–403. https://doi.org/10.1002/rra.1274

Lancaster, J., & Ledger, M. E. (2015). Population-level responses of stream macroinvertebrates to drying can be density-independent or density-dependent. *Freshwater Biology*, *60*(12), 2559–2570. https://doi.org/10.1111/fwb.12643

Larsen, S., Majone, B., Zulian, P., Stella, E., Bellin, A., Bruno, M. C., & Zolezzi, G. (2021). Combining hydrologic simulations and stream-network models to reveal flow-ecology relationships in a large alpine catchment. *Water Resources Research*, *57*(4), e2020WR028496. https://doi.org/10.1029/2020WR028496

Le, C. T. U., Paul, W. L., Gawne, B., & Suter, P. J. (2020). Quantitative flow-ecology relationships using distributed lag nonlinear models: Large floods in the Murray river could have delayed effects on aquatic macroinvertebrates lasting more than three decades. *Water Resources Research*, *56*(8), e2019WR025896. https://doi.org/10.1029/2019WR025896

Leblanc, M., Tweed, S., Van Dijk, A., & Timbal, B. (2012). A review of historic and future hydrological changes in the Murray-Darling basin. *Global and Planetary Change*, *80*, 226–246. https://doi.org/10.1016/j.gloplacha.2011.10.012

Ledger, M. E., Edwards, F. K., Brown, L. E., Milner, A. M., & Woodward, G. (2011). Impact of simulated drought on ecosystem biomass production: An experimental test in stream mesocosms. *Global Change Biology*, *17*(7), 2288–2297. https://doi.org/10.1111/j.1365-2486.2011.02420.x

Ledger, M. E., Harris, R. M. L., Armitage, P. D., & Milner, A. M. (2009). Realism of model ecosystems: An evaluation of physicochemistry and macroinvertebrate assemblages in artificial streams. *Hydrobiologia*, *617*(1), 91–99. https://doi.org/10.1007/s10750-008-9530-x

Ledger, M. E., Harris, R. M. L., Armitage, P. D., & Milner, A. M. (2012). Climate change impacts on community resilience: Evidence from a drought disturbance experiment. In U. Jacob & G. Woodward (Eds.), *Global change in multispecies systems part 1*. Advances in Ecological Research. (pp. 211–258). Academic Press.

Leigh, C., Aspin, T. W. H., Matthews, T. J., Rolls, R. J., & Ledger, M. E. (2019). Drought alters the functional stability of stream invertebrate communities through time. *Journal of Biogeography*, *46*(9), 1988–2000. https://doi.org/10.1111/jbi.13638

Lennox, R. J., Crook, D. A., Moyle, P. B., Struthers, D. P., & Cooke, S. J. (2019). Toward a better understanding of freshwater fish responses to an increasingly drought-stricken world. *Reviews in Fish Biology and Fisheries*, *29*(1), 71–92. https://doi.org/10.1007/s11160-018-09545-9

Lowe, J. A., Bernie, D., Bett, P., Bricheno, L., Brown, S., Calvert, D., Clark, R., Eagle, K., Edwards, T., Fosser, G., & Fung, F. (2019). UKCP18 science overview report. Met Office Hadley Centre: Exeter, UK.

Lytle, D. A., & Poff, N. L. (2004). Adaptation to natural flow regimes. *Trends in Ecology & Evolution*, *19*(2), 94–100. https://doi.org/10.1016/j.tree.2003.10.002

Maazouzi, C., Galassi, D., Claret, C., Cellot, B., Fiers, F., Martin, D., Marmonier, P., & Dole-Olivier, M.-J. (2017). Do benthic invertebrates use hyporheic refuges during streambed drying? A manipulative field experiment in nested hyporheic flowpaths. *Ecohydrology*, *10*(6), e1865. https://doi.org/10.1002/eco.1865

Magoulick, D. D. (2014). Impacts of drought and crayfish invasion on stream ecosystem structure and function. *River Research and Applications*, *30*(10), 1309–1317. https://doi.org/10.1002/rra.2747

Mainstone, C. P., Holmes, N. T., Armitage, P. D., Wilson, A. M., Marchant, J. H., Evans, K., & Solomon, D. (1999). Chalk Rivers – Nature conservation and management. WRc Report to English Nature and the Environment Agency, Medmenham.

Mallen-Cooper, M., & Zampatti, B. P. (2020). Restoring the ecological integrity of a dryland river: Why low flows in the Barwon–Darling River must flow. *Ecological Management & Restoration*, *21*(3), 218–228. https://doi.org/10.1111/emr.12428

Marsh, T., Cole, G., & Wilby, R. (2007). Major droughts in England and Wales, 1800–2006. *Weather*, *62*, 87–93. https://doi.org/10.1002/wea.67

Mathers, K. L., Michalec, F.-G., Holzner, M., & Weber, C. (2020). Beneath the surface: Application of transparent super absorbent polymer substrates to track faunal activity within the sediment layer. *Freshwater Biology*, *65*(11), 1923–1935. https://doi.org/10.1111/fwb.13588

Mathers, K. L., Rice, S. P., & Wood, P. J. (2017). Temporal effects of enhanced fine sediment loading on macroinvertebrate community structure and functional traits. *The Science of the Total Environment*, *599-600*, 513–522. https://doi.org/10.1016/j.scitotenv.2017.04.096

Mathers, K. L., White, J. C., Fornaroli, R., & Chadd, R. (2020). Flow regimes control the establishment of invasive crayfish and alter their effects on lotic macroinvertebrate communities. *Journal of Applied Ecology*, *57*(5), 886–902. https://doi.org/10.1111/1365-2664.13584

Menczelesz, N., Szivák, I., & Schmera, D. (2020). How do we construct and operate experimental streams? An overview of facilities, protocols, and studied questions. *Hydrobiologia*, *847*(1), 1–10. https://doi.org/10.1007/s10750-019-04093-0

Micieli, M., Botter, G., Mendicino, G., & Senatore, A. (2020) UAV thermal images to support the study of the expansion and contraction dynamics of river networks: a preliminary methodological approach. 22nd EGU general assembly. 13166. https://doi.org/10.5194/egusphere-egu2020-13166

Mims, M. C., & Olden, J. D. (2012). Life history theory predicts fish assemblage response to hydrologic regimes. *Ecology*, *93*(1), 35–45. https://doi.org/10.1890/11-0370.1

Mims, M. C., & Olden, J. D. (2013). Fish assemblages respond to altered flow regimes via ecological filtering of life history strategies. *Freshwater Biology*, *58*(1), 50–62. https://doi.org/10.1111/fwb.12037

Monk, W. A., Compson, Z. G., Armanini, D. G., Orlofske, J. M., Curry, C. J., Peters, D. L., Crocker, J. B., & Baird, D. J. (2018). Flow velocity–ecology thresholds in Canadian rivers: A comparison of trait and taxonomy-based approaches. *Freshwater Biology*, *63*(8), 891–905. https://doi.org/10.1111/fwb.13030

Mota-Ferreira, M., Filipe, A. F., Magalhães, M. F., Carona, S., & Beja, P. (2021). Spatial modelling of temporal dynamics in stream fish communities under anthropogenic change. *Diversity and Distributions*, *27*(2), 313–326. https://doi.org/10.1111/ddi.13189

Naura, M. J. (2022). River habitat survey. https://www.riverhabitatsurvey.org/. [Accessed 08/01/2022]

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). Shifts in community size structure drive temperature invariance of secondary production in a stream-warming experiment. *Ecology*, *98*(7), 1797–1806. https://doi.org/10.1002/ecy.1857

Nelson, D., Busch, M. H., Kopp, D. A., & Allen, D. C. (2021). Energy pathways modulate the resilience of stream invertebrate communities to drought. *The Journal of Animal Ecology*, *90*(9), 2053–2064. https://doi.org/10.1111/1365-2656.13490

Nuhfer, A. J., Zorn, T. G., & Wills, T. C. (2017). 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. https://doi.org/10.1111/eff.12259

Parasiewicz, P., Prus, P., Suska, K., & Marcinkowski, P. (2018). E = mc2 of environmental flows: A conceptual framework for establishing a fish-biological foundation for a regionally applicable environmental low-flow formula. *Water*, *10*(11), 1501. https://doi.org/10.3390/w10111501

Parry, S., Prudhomme, C., Wilby, R. L., & Wood, P. (2016). Drought termination: Concept and characterisation. *Progress in Physical Geography*, *40*, 768–793. https://doi.org/10.1177/0309133316652801

Patel, C., Vadher, A. N., Mathers, K. L., Dwyer, C., & Wood, P. J. (2021). Body size affects the vertical movement of benthic amphipods through subsurface sediments in response to drying. *Hydrobiologia*, *848*(5), 1015–1025. https://doi.org/10.1007/s10750-020-04500-x

Perkin, J. S., Starks, T. A., Pennock, C. A., Gido, K. B., Hopper, G. W., & Hedden, S. C. (2019). Extreme drought causes fish recruitment failure in a fragmented Great Plains riverscape. *Ecohydrology*, *12*(6), e2120. https://doi.org/10.1002/eco.2120

Petersen, J. E., & Englund, G. (2005). Dimensional approaches to designing better experimental ecosystems: A practitioners guide with examples. *Oecologia*, *145*(2), 215–223.

Picken, J. L. (2021). The effects of low summer discharge on salmonid ecosystems. Queen Mary University, London, UK.

Piggott, J. J., Niyogi, D. K., Townsend, C. R., & Matthaei, C. D. (2015). 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. https://doi.org/10.1111/1365-2664.12480

Piniewski, M., Prudhomme, C., Acreman, M. C., Tylec, L., Oglęcki, P., & Okruszko, T. (2017). Responses of fish and invertebrates to floods and droughts in Europe. *Ecohydrology*, *10*(1), e1793. https://doi.org/10.1002/eco.1793

Poff, N. L. (2018). Beyond the natural flow regime? Broadening the hydro-ecological foundation to meet environmental flows challenges in a non-stationary world. *Freshwater Biology*, *63*(8), 1011–1021. https://doi.org/10.1111/fwb.13038

Poff, N. L., Allan, J. D., Bain, M. B., Karr, J. R., Prestegaard, K. L., Richter, B. D., Sparks, R. E., & Stromberg, J. C. (1997). The natural flow regime. *Bioscience*, *47*(11), 769–784. https://doi.org/10.2307/1313099

Poff, N. L., Brown, C. M., Grantham, T. E., Matthews, J. H., Palmer, M. A., Spence, C. M., Wilby, R. L., Haasnoot, M., Mendoza, G. F., Dominique, K. C., & Baeza, A. (2016). Sustainable water management under future uncertainty with eco-engineering decision scaling. *Nature Climate Change*, *6*(1), 25–34. https://doi.org/10.1038/nclimate2765

Poff, N. L., Richter, B. D., Arthington, A. H., Bunn, S. E., Naiman, R. J., Kendy, E., Acreman, M., Apse, C., Bledsoe, B. P., Freeman, M. C., Henriksen, J., Jacobson, R. B., Kennen, J. G., Merritt, D. M., Okeeffe, J. H., Olden, J. D., Rogers, K., Tharme, R. E., & Warner, A. (2010). The ecological limits of hydrologic alteration (ELOHA): A new framework for developing regional environmental flow standards. *Freshwater Biology*, *55*(1), 147–170. https://doi.org/10.1111/j.1365-2427.2009.02204.x

Poff, N. L., Tharme, R. E., & Arthington, A. H. (2017). Evolution of environmental flows assessment science, principles, and methodologies. In A. C. Horne, J. A. Webb, M. J. Stewardson, B. Richter, & M. Acreman (Eds.), *Water for the environment* (pp. 203–236). Academic Press.

Potter, N. J., Chiew, F. H. S., & Frost, A. J. (2010). An assessment of the severity of recent reductions in rainfall and runoff in the Murray–Darling basin. *Journal of Hydrology*, *381*(1–2), 52–64. https://doi.org/10.1016/j.jhydrol.2009.11.025

Pyne, M. I., & Poff, N. L. (2017). Vulnerability of stream community composition and function to projected thermal warming and hydrologic change across ecoregions in the western United States. *Global Change Biology*, *23*(1), 77–93. https://doi.org/10.1111/gcb.13437

Rice, S. P., Lancaster, J., & Kemp, P. (2010). Experimentation at the interface of fluvial geomorphology, stream ecology and hydraulic engineering and the development of an effective, interdisciplinary river science. *Earth Surface Processes and Landforms*, *35*(1), 64–77. https://doi.org/10.1002/esp.1838

Riis, T., Levi, P. S., Baattrup-Pedersen, A., Jeppesen, K. G., & Rosenhøj Leth, S. (2017). Experimental drought changes ecosystem structure and function in a macrophyte-rich stream. *Aquatic Sciences*, *79*(4), 841–853. https://doi.org/10.1007/s00027-017-0536-1

Riley, W. D., Maxwell, D. L., Pawson, M. G., & Ives, M. J. (2009). The effects of low summer flow on wild salmon (Salmo salar), trout (Salmo trutta) and grayling (*Thymallus thymallus*) in a small stream. *Freshwater Biology*, *54*(12), 2581–2599. https://doi.org/10.1111/j.1365-2427.2009.02268.x

Roodari, A., Hrachowitz, M., Hassanpour, F., & Yaghoobzadeh, M. (2021). Signatures of human intervention – or not? Downstream intensification of hydrological drought along a large central Asian river: The individual roles of climate variability and land use change. *Hydrology and Earth System Sciences*, *25*(4), 1943–1967. https://doi.org/10.5194/hess-25-1943-2021

Rosenfeld, J. S. (2017). Developing flow–ecology relationships: Implications of nonlinear biological responses for water management. *Freshwater Biology*, *62*(8), 1305–1324. https://doi.org/10.1111/fwb.12948

Ruhí, A., Holmes, E. E., Rinne, J. N., & Sabo, J. L. (2015). Anomalous droughts, not invasion, decrease persistence of native fishes in a desert river. *Global Change Biology*, *21*(4), 1482–1496. https://doi.org/10.1111/gcb.12780

Sarremejane, R., Messager, M. L., & Datry, T. (2021). Drought in intermittent river and ephemeral stream networks. *Ecohydrology*, e2390. https://doi.org/10.1002/eco.2390

Sarremejane, R., Stubbington, R., Dunbar, M. J., Westwood, C. G., & England, J. (2019). Biological indices to characterize community responses to drying in streams with contrasting flow permanence regimes. *Ecological Indicators*, *107*, 105620. https://doi.org/10.1016/j.ecolind.2019.105620

Sarremejane, R., Stubbington, R., England, J., Sefton, C. E. M., Eastman, M., Parry, S., & Ruhi, A. (2021). Drought effects on invertebrate metapopulation dynamics and quasi-extinction risk in an intermittent river network. *Global Change Biology*, *27*(17), 4024–4039. https://doi.org/10.1111/gcb.15720

Sarremejane, R., Truchy, A., McKie, B. G., Mykrä, H., Johnson, R. K., Huusko, A., Sponseller, R. A., & Muotka, T. (2021). Stochastic processes and ecological connectivity drive stream invertebrate community responses to short-term drought. *The Journal of Animal Ecology*, *90*(4), 886–898. https://doi.org/10.1111/1365-2656.13417

Slater, L. J., Anderson, B., Buechel, M., Dadson, S., Han, S., Harrigan, S., Kelder, T., Kowal, K., Lees, T., Matthews, T., Murphy, C., & Wilby, R. L. (2021). Nonstationary weather and water extremes: A review of methods for their detection, attribution, and management. *Hydrology and Earth System Sciences*, *25*, 3897–3935. https://doi.org/10.5194/hess-25-3897-2021

Smakhtin, V. U. (2001). Low flow hydrology: A review. *Journal of Hydrology*, *240*(3), 147–186. https://doi.org/10.1016/S0022-1694(00)00340-1

Stanley, E. H., Fisher, S. G., & Grimm, N. B. (1997). Ecosystem expansion and contraction in streams. *BioScience*, *47*(7), 427–435.

Stewart, R. I. A., Dossena, M., Bohan, D. A., Jeppesen, E., Kordas, R. L., Ledger, M. E., Meerhoff, M., Moss, B., Mulder, C., Shurin, J. B., Suttle, B., Thompson, R., Trimmer, M., & Woodward, G. (2013). Mesocosm experiments as a tool for ecological climate-change research. In G. Woodward & E. J. OGorman (Eds.), *Global change in multispecies systems: Part 3*. Advances in Ecological Research. (pp. 71–181). Academic Press.

Stradmeyer, L., Höjesjö, J., Griffiths, S. W., Gilvear, D. J., & Armstrong, J. D. (2008). Competition between brown trout and Atlantic salmon parr over pool refuges during rapid dewatering. *Journal of Fish Biology*, *72*(4), 848–860. https://doi.org/10.1111/j.1095-8649.2007.01767.x

Streetly, M. J., Bradley, D. C., Streetly, H. R., Young, C., Cadman, D., & Banham, A. (2014). Bringing groundwater models to LIFE: A new way to assess water resource management options. *Hydrological Sciences Journal*, *59*(3–4), 578–593. https://doi.org/10.1080/02626667.2013.853122

Stubbington, R., Chadd, R., Cid, N., Csabai, Z., Miliša, M., Morais, M., Munné, A., Pařil, P., Pešić, V., Tziortzis, I., Verdonschot, R. C. M., & Datry, T. (2018). Biomonitoring of intermittent rivers and ephemeral streams in Europe: Current practice and priorities to enhance ecological status assessments. *The Science of the Total Environment*, *618*, 1096–1113. https://doi.org/10.1016/j.scitotenv.2017.09.137

Stubbington, R., Gunn, J., Little, S., Worrall, T. P., & Wood, P. J. (2016). Macroinvertebrate seedbank composition in relation to antecedent duration of drying and multiple wet-dry cycles in a temporary stream. *Freshwater Biology*, *61*(8), 1293–1307. https://doi.org/10.1111/fwb.12770

Taylor, R. C. (1983). Drought-induced changes in crayfish populations along a stream continuum. *The American Midland Naturalist*, *110*(2), 286–298. https://doi.org/10.2307/2425270

Tomasella, J., Borma, L. S., Marengo, J. A., Rodriguez, D. A., Cuartas, L. A., Nobre, C. A., & Prado, M. C. R. (2011). The droughts of 1996–1997 and 2004–2005 in Amazonia: Hydrological response in the river main-stem. *Hydrological Processes*, *25*(8), 1228–1242. https://doi.org/10.1002/hyp.7889

Tonkin, J. D., Poff, N. L., Bond, N. R., Horne, A., Merritt, D. M., Reynolds, L. V., Olden, J. D., Ruhi, A., & Lytle, D. A. (2019). Prepare river ecosystems for an uncertain future. *Nature*, *570*(7761), 301–303. https://doi.org/10.1038/d41586-019-01877-1

UK Centre for Ecology and Hydrology. (2021). National river flow archive. https://nrfa.ceh.ac.uk. [Accessed 29/11/2021]

Vadher, A. N., Leigh, C., Millett, J., Stubbington, R., & Wood, P. J. (2017). Vertical movements through subsurface stream sediments by benthic macroinvertebrates during experimental drying are influenced by sediment characteristics and species traits. *Freshwater Biology*, *62*(10), 1730–1740. https://doi.org/10.1111/fwb.12983

Vadher, A. N., Millett, J., Stubbington, R., & Wood, P. J. (2018a). Drying duration and stream characteristics influence macroinvertebrate survivorship within the sediments of a temporary channel and exposed gravel bars of a connected perennial stream. *Hydrobiologia*, *814*(1), 121–132. https://doi.org/10.1007/s10750-018-3544-9

Vadher, A. N., Millett, J., Stubbington, R., & Wood, P. J. (2018b). The duration of channel drying affects survival of *Gammarus pulex* (Amphipoda: Gammaridae) within subsurface sediments: An experimental flume study. *Hydrobiologia*, *820*(1), 165–173. https://doi.org/10.1007/s10750-018-3652-6

Van Loon, A. F. (2015). Hydrological drought explained. *Wiley Interdisciplinary Reviews Water*, *2*(4), 359–392. https://doi.org/10.1002/wat2.1085

Van Loon, A. F., Rangecroft, S., Coxon, G., Breña Naranjo, J. A., Van Ogtrop, F., & Van Lanen, H. A. J. (2019). Using paired catchments to quantify the human influence on hydrological droughts. *Hydrology and Earth System Sciences*, *23*(3), 1725–1739. https://doi.org/10.5194/hess-23-1725-2019

Vander Vorste, R., Malard, F., & Datry, T. (2016). 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.

Vander Vorste, R., Obedzinski, M., Pierce, S. N., Carlson, S. M., & Grantham, T. E. (2020). Refuges and ecological traps: Extreme drought threatens persistence of an endangered fish in intermittent streams. *Global Change Biology*, *26*(7), 3834–3845. https://doi.org/10.1111/gcb.15116

Verdon-Kidd, D. C., & Kiem, A. S. (2009). Nature and causes of protracted droughts in southeast Australia: Comparison between the Federation, WWII, and big dry droughts. *Geophysical Research Letters*, *36*(22). https://doi.org/10.1029/2009GL041067

Verdonschot, R. C. M., Oosten-Siedlecka, A. M. v., ter Braak, C. J. F., & Verdonschot, P. F. M. (2015). Macroinvertebrate survival during cessation of flow and streambed drying in a lowland stream. *Freshwater Biology*, *60*(2), 282–296. https://doi.org/10.1111/fwb.12479

Verschoren, V., Meire, D., Schoelynck, J., Buis, K., Bal, K. D., Troch, P., Meire, P., & Temmerman, S. (2016). Resistance and reconfiguration of natural flexible submerged vegetation in hydrodynamic river modelling. *Environmental Fluid Mechanics*, *1*(16), 245–265. https://doi.org/10.1007/s10652-015-9432-1

Visser, A., Beevers, L., & Patidar, S. (2019). The impact of climate change on hydroecological response in chalk streams. *Water*, *11*(3), 596. https://doi.org/10.3390/w11030596

Walters, A. W., & Post, D. M. (2011). How low can you go? Impacts of a low-flow disturbance on aquatic insect communities. *Ecological Applications*, *21*(1), 163–174.

Webb, J. A., Stewardson, M. J., & Koster, W. M. (2010). Detecting ecological responses to flow variation using Bayesian hierarchical models. *Freshwater Biology*, *55*(1), 108–126. https://doi.org/10.1111/j.1365-2427.2009.02205.x

White, J. C. (2018). Quantifying riverine macroinvertebrate community responses to water resource management operations. PhD thesis, Loughborough University, Leicestershire, UK.

White, J. C., Armitage, P. D., Bass, J. A. B., Chadd, R. P., Hill, M. J., Mathers, K. L., Little, S., & Wood, P. J. (2019). How freshwater biomonitoring tools vary sub-seasonally reflects temporary river flow regimes. *River Research and Applications*, *35*(8), 1325–1337. https://doi.org/10.1002/rra.3501

White, J. C., Fornaroli, R., Hill, M. J., Hannah, D. M., House, A., Colley, I., Perkins, M., & Wood, P. J. (2021). Long-term river invertebrate community responses to groundwater and surface water management operations. *Water Research*, *189*, 116651. https://doi.org/10.1016/j.watres.2020.116651

White, J. C., House, A., Punchard, N., Hannah, D. M., Wilding, N. A., & Wood, P. J. (2018). Macroinvertebrate community responses to hydrological controls and groundwater abstraction effects across intermittent and perennial headwater streams. *The Science of the Total Environment*, *610-611*, 1514–1526. https://doi.org/10.1016/j.scitotenv.2017.06.081

White, J. C., Krajenbrink, H. J., Hill, M. J., Hannah, D. M., House, A., & Wood, P. J. (2019). Habitat-specific invertebrate responses to hydrological variability, anthropogenic flow alterations, and hydraulic conditions. *Freshwater Biology*, *64*(3), 555–576. https://doi.org/10.1111/fwb.13242

Whitehead, P. G., Wilby, R. L., Butterfield, D., & Wade, A. J. (2006). Impacts of climate change on in-stream nitrogen in a lowland chalk stream: An appraisal of adaptation strategies. *Science of the Total Environment*, *365*, 260–273. https://doi.org/10.1016/j.scitotenv.2006.02.040

Wilby, R. L., Clifford, N. J., Luca, P. D., Harrigan, S., Hillier, J. K., Hodgkins, R., Johnson, M. F., Matthews, T. K. R., Murphy, C., Noone, S. J., Parry, S., Prudhomme, C., Rice, S. P., Slater, L. J., Smith, K. A., & Wood, P. J. (2017). The 'dirty dozen' of freshwater science: Detecting then reconciling hydrological data biases and errors. *WIREs Water*, *4*(3), e1209. https://doi.org/10.1002/wat2.1209

Wilby, R. L., Fenn, C. R., Wood, P. J., Timlett, R., & LeQuesne, T. (2011). Smart licensing and environmental flows: Modeling framework and sensitivity testing. *Water Resources Research*, *47*(12). https://doi.org/10.1029/2011WR011194

Wilby, R. L., Orr, H., Watts, G., Battarbee, R. W., Berry, P. M., Chadd, R., Dugdale, S. J., Dunbar, M. J., Elliott, J. A., Extence, C., & Hannah, D. M. (2010). Evidence needed to manage freshwater ecosystems in a changing climate: Turning adaptation principles into practice. *Science of the Total Environment*, *408*, 4150–4164. https://doi.org/10.1016/j.scitotenv.2010.05.014

Wilby, R. L., Prudhomme, C., Parry, S., & Muchan, K. G. L. (2015). Persistence of hydrometeorological droughts in the United Kingdom: A regional analysis of multi-season rainfall and river flow anomalies. *Journal of Extreme Events*, *2*(02), 1550006. https://doi.org/10.1142/S2345737615500062

Wilby, R. L., Whitehead, P. G., Wade, A. J., Butterfield, D., Davis, R. J., & Watts, G. (2006). Integrated modelling of climate change impacts on water resources and quality in a lowland catchment: River Kennet, UK. *Journal of Hydrology*, *330*(1), 204–220. https://doi.org/10.1016/j.jhydrol.2006.04.033

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

Wright, J. F., & Berrie, A. D. (1987). Ecological effects of groundwater pumping and a natural drought on the upper reaches of a chalk stream. *Regulated Rivers: Research & Management*, *1*(2), 145–160. https://doi.org/10.1002/rrr.3450010205

Xenopoulos, M. A., Lodge, D. M., Alcamo, J., Märker, M., Schulze, K., & Vuuren, D. P. V. (2005). Scenarios of freshwater fish extinctions from climate change and water withdrawal. *Global Change Biology*, *11*(10), 1557–1564. https://doi.org/10.1111/j.1365-2486.2005.001008.x

Zhao, C. S., Zhang, C. B., Yang, S. T., Liu, C. M., Xiang, H., Sun, Y., Yang, Z. Y., Zhang, Y., Yu, X. Y., Shao, N. F., & Yu, Q. (2017). Calculating e-flow using UAV and ground monitoring. *Journal of Hydrology*, *552*, 552351–552365. https://doi.org/10.1016/j.jhydrol.2017.06.047

How to cite this article: White, J. C., Aspin, T. W. H., Picken, J. L., Ledger, M. E., Wilby, R. L., & Wood, P. J. (2022). Extreme low-flow effects on riverine fauna: A perspective on methodological assessments. *Ecohydrology*, e2422. https://doi.org/10.1002/eco.2422