Received: 30 August 2023 | Revised: 28 May 2024 | Accepted: 18 June 2024
DOI: 10.1002/wat2.1745

FOCUS ARTICLE

WIREs WATER WILEY

# The effects of drought on biodiversity in UK river ecosystems: Drying rivers in a wet country

**Rachel Stubbington**[1] | **Judy England**[2] | **Romain Sarremejane**[1] | **Glenn Watts**[2] | **Paul J. Wood**[3]

[1]School of Science and Technology, Nottingham Trent University, Nottingham, UK
[2]Environment Agency, UK
[3]Loughborough University, UK

**Correspondence**
Rachel Stubbington, School of Science and Technology, Nottingham Trent University, Nottingham, UK.
Email: rachel.stubbington@ntu.ac.uk

**Edited by:** Sonja Jähnig, Senior Editor and Jan Seibert, Co-Editor-in-Chief

## Abstract

Climate change is interacting with water resource pressures to alter the frequency, severity and spatial extent of drought, which can thus no longer be considered a purely natural hazard. Although particularly severe ecological impacts of drought have occurred in drylands, its effects on temperate ecosystems, including rivers, are also considerable. Extensive research spanning a diverse range of UK rivers offers an opportunity to place the effects of past drought in the context of intensifying climate change and to examine the likely effects of future drought in a typically cool, wet country. Here, drought manifests instream as deficits in surface water, modified flow velocities, and—increasingly—partial or complete drying of previously perennial and naturally non-perennial reaches. As a result, drought causes declines in the taxonomic and functional biodiversity of freshwater communities including microorganisms, algae, plants, invertebrates and fish, altering ecological processes and associated benefits to people. Although freshwater communities have typically recovered quickly after previous UK droughts, an increase in drought extremity may compromise recovery following future events. The risk of droughts that push ecosystems beyond thresholds to persistent, species-poor, functionally simplified states is increasing. Research and monitoring are needed to enable timely identification of rivers approaching such thresholds and thus to inform interventions that pull these ecosystems back from the brink. Management actions that support natural flow regimes and promote natural processes that diversify instream habitats, including drought refuges, are also crucial to support biodiversity within functional river ecosystems as they adapt to a changing world.

This article is categorized under:
Water and Life > Nature of Freshwater Ecosystems
Water and Life > Stresses and Pressures on Ecosystems
Water and Life > Conservation, Management, and Awareness

**KEYWORDS**
climate change, drought, ecological drought, ecological resilience, river ecosystem

## 1 | INTRODUCTION

Drought is defined by or originates from an unusually large and typically prolonged deficit in water compared to the long-term average, and this deficit causes a sufficient hydrological imbalance (Seneviratne et al., 2012; Van Loon, 2015; WMO, 1992) to alter ecosystems and their capacity to benefit people (Crausbay et al., 2017). As such, despite previous conceptualization of predictable annual dry periods as *seasonal droughts* (e.g., by Lake, 2003; also see Boulton, 2003; Kovach et al., 2019; Sarremejane et al., 2022), droughts are inherently unpredictable events and thus are disturbances sensu Resh et al. (1988). Drought can be conceptualized from multiple perspectives from meteorological to socioeconomic (Haile et al., 2020; Van Loon, 2015). Hydrological droughts are events defined by a deficit in surface water and/or groundwater (Fleig et al., 2006) which manifest as prolonged periods of abnormally low water levels in rivers and aquifers (i.e., streamflow drought and groundwater drought, respectively; Van Loon, 2015). Similarly, soil moisture drought indicates a water deficit within soil, and thus arguably also within unsaturated sediments including those associated with river channels (DelVecchia et al., 2022; Fleig et al., 2006). These water deficits have ecological impacts, but ecological drought has proven hard to define, particularly in river ecosystems (Box 1).

Droughts have typically been conceptualized as natural events, making hydrological drought part of the environmental variability that supports biodiverse freshwater ecosystems (Bickerton, 1995; Parasiewicz et al., 2019; Sarremejane et al., 2018). However, in ecosystems of the Anthropocene, drought increasingly interacts with other human pressures relating to natural resource use, land use and pollution (Crausbay et al., 2020; Van Loon et al., 2016; Wada et al., 2013). In particular, in river ecosystems, biodiversity and ecosystem functioning are limited by multiple

### BOX 1 The challenges of applying "ecological drought" definitions to river ecosystems

Defining ecological drought has proven problematic (Bachmair et al., 2016; IPCC, 2022; Slette et al., 2019), but recent attempts—in particular Crausbay et al.'s (2017) widely adopted definition (Kovach et al., 2019; NIDIS, 2023; Sarremejane et al., 2022; Vicente-Serrano et al., 2020)—emphasize the persistent impacts of a deficit in water on organism-to-ecosystem-scale structure and function, and thus on the ecosystem services available to people (Table S1). But in river ecosystems, despite sometimes severe short-term impacts, recovery from drought is typically rapid (Table S2). This lack of ecological footprint excludes river ecosystems from Crausbay et al.'s (2017) definition of transformational ecological drought as well as Esfahanian et al.'s (2016) definition of stream health drought (Figure 1b; Table S1). Equally, ecological drought sensu Munson et al. (2021) and Met Office (2023), which encompasses non-extreme ecological effects (Figure 1a; Table S1), may be difficult to detect or attribute to a single driver (e.g., streamflow drought; Van Loon, 2015) due to concurrent ecological responses to wider environmental variability. In short, no existing definition of ecological drought effectively represents river ecosystems. However, midway between these ecological drought definitions, Smith (2011) defines extreme climatic events including severe droughts based in part on their considerable but not necessarily long-term or even permanent impacts on ecosystem structure and function (Table S1). This "Goldilocks" definition effectively summarizes how drought typically alters river ecosystems (Figure 1c).

Should we develop Smith's (2011) definition of an extreme climatic event into a river-specific definition of ecological drought? Perhaps not. Such a definition would essentially seek to describe complex, diverse continua of biological community responses to easier-to-define, easier-to-quantify deficits in water—in particular surface water, as well as groundwater and sediment moisture. We therefore suggest that river ecologists focus on quantification of spatial and temporal variability in these responses (McMahon & Finlayson, 2003), which can be conceptualized as drought impacts (sensu Downes et al., 2002). This suggestion comes with a caveat: definition of ecological drought *is* warranted if it can be used to leverage management actions that mitigate the ecological impacts of drought (see Section 5).

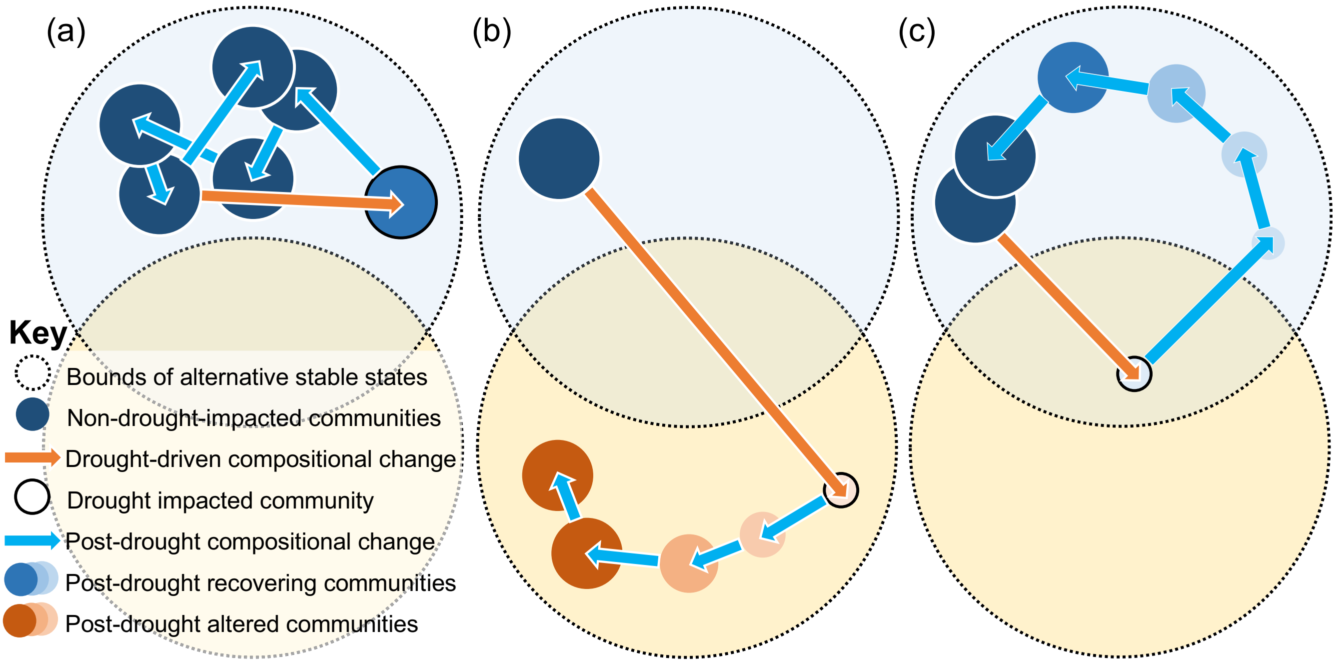


**FIGURE 1** Contrasting definitions of ecological drought based on (a) an unquantified and potentially minor reduction in performance (sensu Munson et al., 2021); (b) a persistent ecosystem shift to an alternative stable state, that is, drought that leaves an ecological footprint (sensu Crausbay et al., 2017); and (c) a non-permanent shift to outside the bounds of normal variability (sensu Smith, 2011; also see Table S1). Circle size and color intensity are proportional to ecological "health" (i.e., biodiversity and ecosystem functioning) and represent points along continua.

persistent and emerging pressures including surface water and groundwater abstraction, physical habitat modification and water pollution (Dudgeon et al., 2006; Haase et al., 2023; Whelan et al., 2022). In addition, climate change is altering drought characteristics including its frequency, magnitude, duration, rate of onset and termination, and spatial extent and coherence, with an increasing risk of rapid-onset flash droughts (Pendergrass et al., 2020; Tanguy et al., 2023; Yuan et al., 2023) and multiyear megadroughts (sensu Woodhouse & Overpeck, 1998; Williams et al., 2020). Drought is also increasingly likely to coincide with other anthropogenically driven climatic extremes, including heatwaves (Mazdiyasni & AghaKouchak, 2015; Sutanto et al., 2020; Tassone et al., 2023) and sporadic heavy rainfall events (Jones et al., 2013; Spinoni et al., 2018; Watts et al., 2015). Drought can thus no longer be conceptualized as purely natural (AghaKouchak et al., 2015; Van Loon et al., 2016).

Within river ecosystems, drought has highly variable effects on in-channel conditions, which collectively disrupt all levels of ecological organization, from the genes expressed by an organism (Robinson et al., 1992) to the connectivity of network-scale metacommunities (Robson et al., 2011; Sarremejane, Stubbington, et al., 2021) and meta-ecosystems (Cid et al., 2022). All biological groups within a river ecosystem are affected, from microorganisms to fish, as well as species in connected riparian and terrestrial habitats (Garssen et al., 2014; Ledger et al., 2013). Taxonomic effects include changes in the abundance and distribution of individual species, including temporary and long-term, local and regional losses that reduce community richness and diversity (Sarremejane, Stubbington, et al., 2021). These taxonomic changes have consequences for ecosystem functioning, for example altering energy transfer through food webs (Ledger et al., 2013; Lu et al., 2016). But as dynamic, disturbance-prone ecosystems, rivers typically recover from drought more quickly than terrestrial ecosystems (Häder & Barnes, 2019).

The ecological effects of drought have been well-characterized in typically cool, wet countries, in particular the United Kingdom (UK; Table S2), but these insights have not been synthesized nor set in the context of ongoing global change (but see Dollar et al., 2013). Our aim is thus to synthesize research investigating how drought shapes river ecosystems and their biodiversity in the UK's temperate (*Cfb* in the Köppen classification) climate. We review evidence documenting the impacts of past droughts, and consider the predicted effects of future droughts shaped by intensifying climate change. We discuss the effects of drought on riverine habitats, then consider ecological responses to changing habitat characteristics, focusing on the potential for future droughts to shift ecosystems to alternative stable states. We then explore post-drought ecological recovery, and explain variability in documented trajectories before suggesting how recovery may unfold after future droughts. We conclude by recommending management strategies and research priorities to promote ecological resilience to drought, where resilience is defined as the capacity to cope with drought and recover after it ends (Gunderson, 2000).

## 2 | FROM LOW FLOWS TO DRYING: HOW DROUGHT UNFOLDS IN UK RIVERS

Reflecting the five core components of the natural flow regime, droughts can be described by their frequency, magnitude, duration, timing and rate of change in flow conditions (Poff et al., 1997), with magnitude (i.e., intensity) and duration collectively determining drought severity (Boulton, 2003; Sarremejane et al., 2022), and with rate of change encompassing both drought onset and termination phases (Parry, Prudhomme, et al., 2016). Drought can also be described by its spatial extent, which is often regional (e.g., within part of an island nation such as the UK; see the UK Water Resources Portal https://eip.ceh.ac.uk/hydrology/water-resources) but can also be national (Marsh, 2014; UK CEH, 2023) or continental (Burke & Brown, 2010; Hannaford et al., 2011). Within the UK, hydrological drought manifests differently depending on the underlying geology. For example, in parts of the north and west, rivers underlain by impermeable geologies are vulnerable to even short rainfall deficits due to their limited baseflow, whereas groundwater-fed rivers (such as chalk streams in south and east England) are susceptible to successive dry winters that provide limited groundwater recharge (Environment Agency, 2017). However, the ecological impacts of drought are typically experienced at the smaller (habitat patch to catchment) spatial scales at which organisms interact with their environment (Aspin, Hart, et al., 2019; Aspin, Khamis, et al., 2019; Sarremejane et al., 2020).

### 2.1 | Variability in drought-driven habitat conditions within UK river networks

Within a river network, the effects of drought on the habitats within river channels can vary considerably in both space and time (Figure 2; Sefton et al., 2019). In large, lowland rivers with perennial flow, drought effects may be limited because flow velocities may already be slow, sediments may already be fine-grained, and water depths may remain high enough to avoid exposing in-channel sediments (Figure 2a; Wood & Petts, 1994; McMahon & Finlayson, 2003). In perennial mid-reaches with natural channel shapes, drought-driven low flows can manifest as declines in depth and wetted width that expose marginal and elevated mid-channel sediments, and/or reductions in flow velocity (Figure 2b; Boulton, 2003; Chadd et al., 2017; Stubbington, Wood, & Boulton, 2009). In the headwaters, drought may cause usually perennial reaches to dry out (Barker et al., 2024; Bass et al., 2023; Westwood et al., 2006).

None of these in-channel habitat states is unique to drought, but drought affects where in a network a particular state (e.g., discharge below a certain threshold) occurs and the duration for which a state persists (Sarremejane, Stubbington, et al., 2021; Sefton et al., 2019). At any one location, drought-driven changes to in-channel habitats unfold gradually over days to months, generally increasing in magnitude (and thus severity) to a maximum until drought conditions end, sometimes with the rapid return of normal or high flows (e.g., Kendon et al., 2013; Parry, Wilby, et al., 2016). Collectively, site-scale effects cause gradual network-scale contraction, fragmentation and sometimes terrestrialization of aquatic habitats (Fuller et al., 2015; Sarremejane et al., 2020), although entire river networks do not dry in the cool, wet UK climate (cf. dryland systems, e.g., Bogan et al., 2015).

As water volumes decline so too does solute dilution, potentially increasing salinity and concentrations of point source pollutants including the organic matter, inorganic nutrients, microplastics, pharmaceuticals and other toxins in sewage effluent (Extence, 1981; Graham et al., 2024; Parr & Mason, 2003). Conversely, drought reduces surface runoff, limiting diffuse inputs of anthropogenic and natural solutes including inorganic nutrients, which can reduce river nutrient loads (Graham et al., 2024; Mosley, 2015; Vicente-Serrano et al., 2020). Slow flow velocities promote deposition of suspended fine sediment and organic matter, which can smother coarse sediments including gravels and thus reduce habitat diversity (Figure 2b; Ledger & Hildrew, 2001; Wood & Petts, 1994; Wood & Petts, 1999; Wright & Berrie, 1987) as well as increasing residence times and associated algal blooms (Mosley, 2015; Turner et al., 2021). Deposited fine material can clog interstitial spaces, reducing connectivity between the surface stream and the subsurface sediments of the hyporheic zone (Beschta & Jackson, 1979; Schälchli, 1992; Vadher et al., 2018).

The reduced thermal inertia of low water volumes increases the influence of solar radiation, causing water temperature to increase and become more variable (van Vliet et al., 2011; White et al., 2023), especially in unshaded reaches

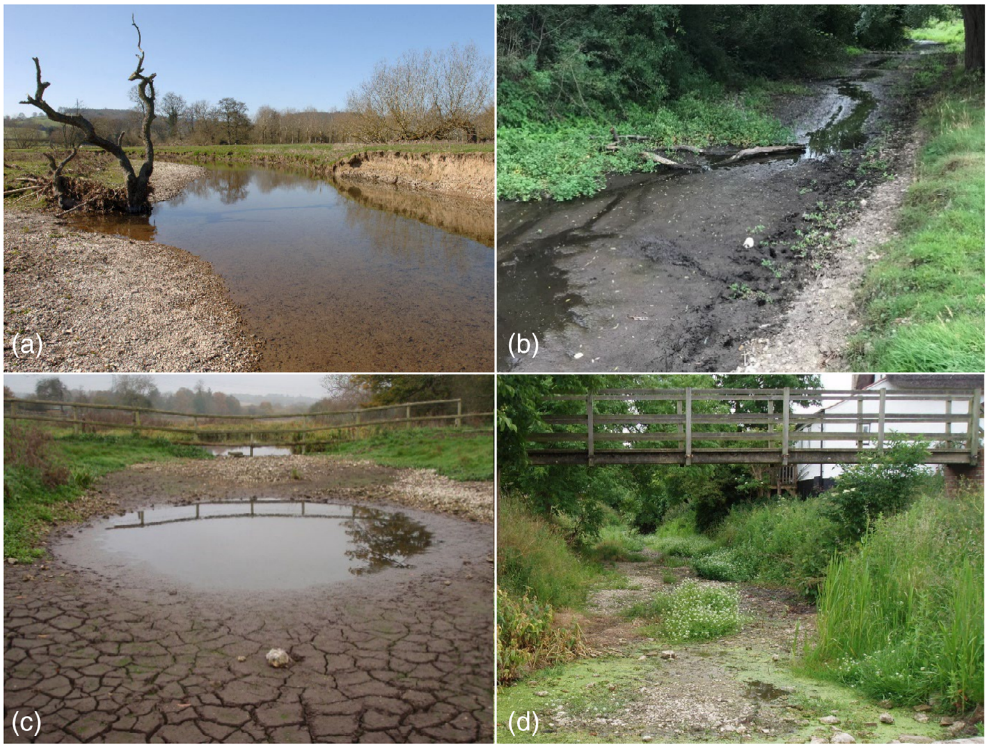


**FIGURE 2** In-channel conditions during drought in UK rivers: (a) a ponded reach; (b) extreme low flows; (c) isolated pools; and (d) a dry reach. (Photo credits: Environment Agency).

(Bowler et al., 2012; Dugdale et al., 2018) and surface-fed systems (Johnson et al., 2014), including both small streams (Aspin, Hart, et al., 2019; Aspin, Khamis, et al., 2019) and larger lowland rivers (Brooker et al., 1977). Thermal peaks are most likely during periods of hot weather including heatwaves, and in warmer regions (Whitehead et al., 2009)—even in groundwater-fed rivers (Stubbington, Wood, & Boulton, 2009). Oxygen solubility declines with increasing water temperatures, potentially culminating in severe deoxygenation, in particular when biological oxygen demand is high (e.g., due to decomposition of sewage-derived organic matter or plants killed by drought-related stress) and at night, when oxygen uptake by respiring primary producers is not balanced by its release during photosynthesis (Brooker et al., 1977; Parr & Mason, 2003).

Non-perennial rivers, which typically lose most or all surface water either seasonally or periodically, dominate global river networks (Messager et al., 2021) and are common and diverse in cool, wet countries such as the UK (Stubbington et al., 2017). Near-perennial reaches dry only during drought, and these rare dry phases represent a profound change in in-channel habitat characteristics (Sarremejane et al., 2022). In the UK (Hill et al., 2019; Wood & Armitage, 2004), alpine, continental and temperate Europe (Crabot et al., 2021; Piano et al., 2019) and other global regions (Carey et al., 2023), recent droughts have caused previously perennial systems to dry for the first time on record (Hammond et al., 2022; Zipper et al., 2021). Drought also alters in-channel conditions in seasonally non-perennial reaches: dry phases may start earlier and more abruptly, dry-phase durations may become unusually long (Bass et al., 2023) and drying magnitude may be particularly high (Boulton, 2003; Coulson et al., 2021).

## 2.2 | How might future droughts unfold in UK river ecosystems?

Across continents including Europe, drought is increasing (Bednar-Friedl et al., 2022); in the UK, a quick succession of streamflow droughts has occurred, in years including 2018–19 and 2022 (Barker et al., 2024; Kendon et al., 2023; Turner et al., 2021); and in England, long-term, temperature-driven increases in soil moisture drought have been modeled (Briffa et al., 2009; Wigley & Atkinson, 1977). Despite such observations, Watts et al. (2015) concluded that "no apparent trend in summer flows, low flows or [hydrological] drought" has been detected in UK rivers (also see Barker et al., 2019; Hannaford, 2015; Hannaford & Buys, 2012). This conclusion remains current, and despite notable dry periods, the UK was wetter in the decade to 2022 compared to the 1961–1990 average (Kendon et al., 2023). However, the UK's climatic variability hampers detection of trends in low flows (New et al., 2007; Watts et al., 2015), and evidence that climate change has altered the characteristics of UK droughts remains equivocal (Spinoni et al., 2015).

In contrast, there is greater confidence in predicted future increases in the magnitude, duration, severity, and spatial extent and coherence of UK hydrological droughts (Kay et al., 2023; Parry et al., 2024; Rudd et al., 2019; Tanguy et al., 2023). UK-wide reductions in streamflow are predicted to be greatest in south-east England and least pronounced in north-west Scotland (Parry et al., 2024). However, whereas in other global regions the specter of megadroughts looms large (Cook et al., 2022), at northern latitudes including the UK, it is unclear if the frequency of multiyear events will change (Chan et al., 2023). Drought onset and termination characteristics may also be changing (Parry, Prudhomme, et al., 2016). In particular, the risk of flash droughts, which are defined by their rapid onset and intensification, is increasing globally (Pendergrass et al., 2020; Trenberth et al., 2014; Walker & Van Loon, 2023), including in humid regions of Europe (Yuan et al., 2023). Flash droughts may have particular effects in surface-fed rivers, whereas groundwater-dominated systems may be buffered against rapid change (Sear et al., 1999; Stoelzle et al., 2014). The characteristics of future drought termination phases are unclear, but in places including the UK, observed and predicted wetter weather (Kendon et al., 2023; Watts et al., 2015) and the increasing occurrence of heavy rainfall events (Jones et al., 2013; Watts et al., 2015) suggest that droughts may become more likely to end more abruptly (Parry, Prudhomme, et al., 2016; Parry, Wilby, et al., 2016), including an increase in drought-breaking flood events (Arnell & Gosling, 2016).

Interactions with other environmental factors influence how drought unfolds in river ecosystems. Future droughts will occur in a warming climate (Arnell & Freeman, 2022; Kendon et al., 2023), resulting in hotter droughts (sensu Allen et al., 2015). Higher temperatures promote evapotranspiration (and reduce snowpack accumulation in upland areas; Harpold et al., 2017) and thus exacerbate drought-driven low flows by reducing the proportion of precipitation that becomes streamflow either directly or via aquifer recharge, as well as increasing evaporation of remaining surface water and elevating water temperatures (Gómez et al., 2017; Van Loon, 2015). The risk of heatwaves and thus of compound events (i.e., heatwaves occurring during droughts) is also increasing in the UK, across much of Europe and more widely, intensifying peaks in water temperature (AghaKouchak et al., 2020; Sutanto et al., 2020). In addition, heavy rainfall events are increasingly likely to occur during UK droughts (Jones et al., 2013; Kendon et al., 2023), potentially triggering runoff pulses that deliver fine sediment and solutes (including anthropogenic contaminants) to rivers, rapid changes in water temperature (Arnell et al., 2015; Burt et al., 2016), and/or short-duration flow resumptions (i.e., "false starts") in non-perennial reaches (Boulton et al., 2017).

Collectively, these predictions indicate an increasing risk that future UK droughts will be moextreme events (sensu Smith, 2011), with their rapid onset and high magnitude fueled by greater concurrence with heatwaves (Mazdiyasni & AghaKouchak, 2015; Sutanto et al., 2020; Tassone et al., 2023).

## 3 | ECOLOGICAL RESPONSES TO DROUGHT IN UK RIVERS

Considerable research has characterized ecological responses to drought in river ecosystems (Bond et al., 2008; Boulton, 2003; Lake, 2003; Lake, 2011; Lennox et al., 2019; Parasiewicz et al., 2019; Yang et al., 2023), including numerous UK studies conducted over >60 years. The responses documented by key UK studies are summarized in the "peak biotic impact of drought" column of Table S2. In short, across freshwater communities including fish, macroinvertebrates and macrophytes, these responses comprise compositional shifts typified by reductions in taxonomic richness and abundance, with drying of near-perennial reaches causing total loss of some species (Table S2). However, we argue below that changing drought characteristics mean that ecological responses to past events may not represent responses to future drought.

Any increase in drought magnitude and/or duration and thus severity could impair the extent and quality of refuges (places in which drought effects are reduced and thus survival is enhanced; Carey et al., 2023; Lancaster & Belyea, 1997), reducing the persistence of even drought-tolerant taxa, as taxon-specific tolerances of drought-related conditions (e.g., rising temperatures and associated declines in dissolved oxygen concentrations; Johnson et al., 2024) are surpassed. Any increase in drought frequency will make individual events increasingly likely to occur in ecosystems that have yet to recover from a preceding drought (or other disturbance), prolonging ecological impacts (Harris et al., 2018). Any increase in flash droughts and thus the acceleration of flow recession and, in non-perennial rivers, wet-to-dry transitions (Yuan et al., 2023) will give organisms less time to react—physiologically and/or behaviorally, for example by entering a desiccation-tolerant dormant state (Strachan et al., 2015) or by swimming to nearby refuges

(Hwan & Carlson, 2016; James et al., 2008)—stranding organisms in drought-impacted reaches (Archdeacon & Reale, 2020; Wright & Berrie, 1987). Taxon-specific responses to flash droughts could be particularly pronounced if organisms have less time to complete seasonal lifecycle events such as fish migration and insect emergence (Elliott et al., 1997; Harper & Peckarsky, 2006; Parmesan, 2006).

Collectively, responses to changing drought characteristics including severity, frequency and the rate and timing of onset could push ecosystem structure and function beyond the bounds of normal variability (Smith, 2011), with the potential for ecologically transformational droughts (sensu Crausbay et al., 2017, 2020) that shift ecosystems beyond tipping points to persistent, species-poor and functionally simplified states (Ledger et al., 2013; Scheffer et al., 2001; van Nes et al., 2016).

### 3.1 | Could future droughts push UK river ecosystems to new stable states?

As naturally dynamic, disturbance-prone ecosystems, rivers may be less likely to shift to alternative stable states than other ecosystem types (Figure 3a,b; Capon et al., 2015; Scheffer et al., 2001). As such, drought-driven state shifts are rare in river ecosystems, and have not, to our knowledge, occurred in cool, wet countries; Figure 3c illustrates a shift in macroinvertebrate community composition, but not necessarily in ecosystem state. Nonetheless, looking beyond such temperate regions, state shifts have occurred in river ecosystems during multiyear droughts, due to persistent changes to in-channel aquatic habitat availability. For example, a 5-year drought in a hot, summer-dry region enabled long-term establishment of an invasive fish population, concurrent with persistent changes to invertebrate communities (Bêche et al., 2009); and a high-magnitude, 5-year drought in an arid region caused unprecedented drying of isolated pools, eliminating large-bodied top predators, which were replaced by smaller predatory taxa (Bogan & Lytle, 2011). Drought-driven shifts to alternative states could thus occur in UK river ecosystems—*if* drought effects are persistent, which could result from altered flow regimes, or from loss and replacement of key species.

Alteration of flow regimes by climatic drying, for example to near-perennial flow at previously perennial sites, to higher dry-phase frequencies at near-perennial sites, and to longer dry-phase durations at seasonally non-perennial sites, are occurring globally and are expected to continue (Tramblay et al., 2021; Zipper et al., 2021). In the UK, temperature-driven reductions in low flows are predicted in most catchments, and in particular in south-east England (Kay et al., 2023; Parry et al., 2024), leading to greater drying of warming freshwaters (Johnson et al., 2024), especially in summer. Such hydrological regime shifts (sensu Zipper et al., 2022) represent high-potential triggers of drought-driven shifts in ecosystem state (Bogan & Lytle, 2011), but these may be localized and incremental. For example, in space, a shift from perennial to near-perennial flow may eliminate organisms over only a short distance (Hill

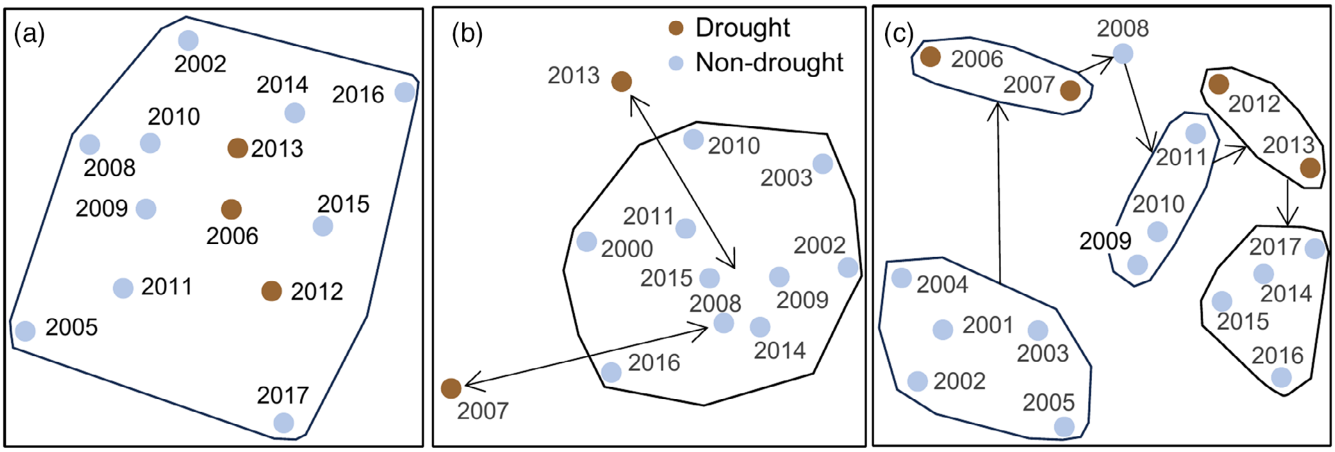


FIGURE 3 Macroinvertebrate community composition (represented by circles, as ordinated by nonmetric multidimensional scaling) in spring 2000–2017, indicating response to and recovery after two streamflow droughts (2006–2007 and 2012–2013) that affected three chalk stream tributaries of the River Colne, Hertfordshire, UK: (a) no response of a stress-tolerant community in a human-impacted stream; (b) response and rapid recovery to the pre-drought composition in a seasonally non-perennial stream; and (c) response and shift to an alternative post-drought composition in a relatively natural perennial stream. Drought years were identified using local hydrological data (Appendix S1). Missing years are those in which macroinvertebrates were not sampled.

et al., 2019), and in time, average dry-phase durations could increase by a few days (Jaeger et al., 2014). Nonetheless, such localized, incremental shifts collectively represent a large-scale drought-driven decline in the extent and diversity of aquatic habitats, including those acting as drought refuges, which could compromise the biodiversity and resilience of network-wide metacommunities (Jaeger et al., 2014; Sarremejane et al., 2020).

Both stochastic and deterministic local-scale species losses occur during drought (Table S2; Bogan & Lytle, 2011; Sarremejane, Truchy, et al., 2021), and can include permanent local extinctions, such as the loss of the internationally Endangered white-clawed crayfish *Austropotamobius pallipes* (IUCN, 2023) from a UK chalk stream (Perrow et al., 2007). The loss of an individual species typically has limited impact on ecosystem functioning due to community-level functional redundancy (sensu Rosenfeld, 2002). Nonetheless, each single drought-driven species loss contributes to an incremental decline in functional redundancy, increasing the risk that the next species loss will eliminate a unique trait or trait combination, reducing ecosystem functioning (Aspin, Khamis, et al., 2019; Fonseca & Ganade, 2001). In addition, drought-driven declines in the population densities of functionally important species such as shredder macroinvertebrates (which decompose leaf litter, fueling detritus-based food webs) and top predators can also impair ecosystem functioning (Datry et al., 2011; Stubbington, Wood, & Boulton, 2009). Moreover, if key species are lost—be that an abundant, dominant species, a habitat-forming plant species, or an ecosystem engineer or other true keystone species (sensu Power et al., 1996)—ecosystems may shift to new stable states. Below, we evaluate the evidence for three scenarios in which drought could drive species losses that lead to persistent state shifts in UK river ecosystems, in particular if droughts become more severe and frequent.

### 3.1.1 | Loss of habitat-forming plants

Submerged macrophytes can provide extensive habitats for microorganisms, invertebrates and fishes, and act as ecosystem engineers by trapping and stabilizing sediments, thus increasing variability in flow velocities and altering channel morphology (Gurnell et al., 2012). For example, rheophilic species of water crowfoot (genus *Ranunculus*) form a fundamental component of habitat structure in lowland UK rivers including England's chalk streams (Gurnell et al., 2006; Wilby et al., 1998) and support high densities of aquatic insects (Armitage & Cannan, 2000; Wright & Berrie, 1987). During drought, as flow velocities decline, deposited fine sediment may be colonized by slow-flow-loving filamentous algae and emergent macrophytes (Wright et al., 2004). Emergent macrophytes shade *Ranunculus* (Ladle & Bass, 1981; Wade et al., 2002) while a lack of scouring flows allows biofilms to accumulate on its leaves and stems, reducing its capacity to photosynthesize (Franklin et al., 2008; Wilby et al., 1998; Wright & Symes, 1999). As a result, established stands of submerged plants including *Ranunculus* decline in health and abundance during drought (Ladle & Bass, 1981; Westwood et al., 2006). Moreover, rheophilic plants such as most *Ranunculus* species may not establish populations in drought years if flows fail to meet their growing-season requirements (Wright et al., 2002).

The loss of habitat-forming plants such as *Ranunculus* creates niche space, which may be filled by the colonizing filamentous algae and emergent macrophytes (Ladle & Bass, 1981). A bottom-up trophic cascade may ensue, including the loss and replacement of previously abundant macroinvertebrates (e.g., Baetidae and Simuliidae by Chironomidae; Wright & Berrie, 1987) which in turn alters populations of their predators, including fishes (Mann et al., 1989), aquatic and riparian invertebrates, and riparian birds (Jenkins & Ormerod, 1996). In addition, a change from dominance of *Ranunculus*, a submerged macrophyte, to filamentous algae would alter flow patterns, and thus sediment transport and deposition, potentially culminating in altered river planforms (Cotton et al., 2006; Gurnell et al., 2006). To date, *Ranunculus* populations have re-established within 2 years of flow recovering after droughts (Holmes, 1999), but any increase in drought frequency and severity could interrupt their recovery, shifting producer communities toward long-term algal dominance. Downstream reaches with limited riparian shading (and thus high light availability) and elevated water temperatures could be at particular risk of such shifts (Hosen et al., 2019).

### 3.1.2 | Loss of riparian vegetation

Riparian vegetation is sensitive to both soil moisture and groundwater levels and thus to drought (Garssen et al., 2014). Although drought-driven loss of riparian vegetation has not been reported in the UK (Dobel et al., 2020), droughts have killed a high proportion of trees in other riparian zones (Giling et al., 2009; Portela et al., 2023; Reich et al., 2023) as well as in UK and other (non-riparian) temperate woodlands (Kirby et al., 1998; Peterken & Jones, 1987). Headwater and other small streams are at particular risk of ecological impacts resulting from reduced riparian canopies, due to the increased in-channel light levels and water temperatures and resultant increase in primary production and reduction in leaf litter inputs (Bowes et al., 2012; Giling et al., 2009). Multiple drought-related and other factors will interact to influence the outcomes of competitive interactions between the producers that colonize newly illuminated channels (Wilby et al., 1998). The consequences of altered basal resources will have bottom-up effects that extend through food webs as well as influencing the growth and reproductive success of individual species, potentially including ecosystem engineers such as crayfish (Giling et al., 2009, 2012).

Even if supported by management actions, riparian vegetation takes years to recover from drought (Portela et al., 2023), which could exacerbate the risk of a long-term shift to an alternative stable state with elevated primary production, reduced inputs of habitat-forming woody material and an altered river planform, in particular if increasingly frequent droughts (or other disturbances; Beniston et al., 2007; Guerreiro et al., 2018) repeatedly interrupt recovery. Over longer timescales, shifts in the composition of riparian plant communities toward drought-tolerant woody species could re-establish a detrital base to riverine food webs, albeit one with altered characteristics (O'Hare et al., 2016).

### 3.1.3 | Loss of a top predator

Droughts are likely to eliminate top predators such as fishes or large-bodied macroinvertebrates from riverine food webs (Bogan & Lytle, 2011; Ledger et al., 2013; Perkin et al., 2017), because typical predator traits (e.g., long life span, large body size) can increase drought sensitivity (Aspin, Khamis, et al., 2019; Sarremejane et al., 2020). In particular, sensitivity to low dissolved oxygen concentrations may reduce or eliminate populations of predatory fishes (Brooker et al., 1977; Cowx et al., 1984). Such losses could alter food webs via top-down trophic cascades by releasing prey from predator control (Lennox et al., 2019). For example, *Gammarus* amphipods and (non-native, invasive) *Potamopyrgus* mud snails can be more abundant when *Cottus gobio* bullhead fish are absent, potentially increasing both leaf litter decomposition (by shredder amphipods) and biofilm consumption (by grazing snails; Woodward et al., 2008). As a result, food-web structure and function could be simplified (Ledger et al., 2013; Lu et al., 2016). However, such state shifts may not occur if predators recolonize and re-establish their pre-drought population densities (Hynes, 1958; Matthews & Marsh-Matthews, 2003), with recolonization rates reflecting taxon-specific resilience traits as well as the distance and connectivity between drought-impacted sites and refuges. Subsequent population re-establishment by recolonists will then depend on the availability of sufficient food resources (Hakala & Hartman, 2004; Sarremejane, Truchy, et al., 2021).

### 3.1.4 | What is the most likely drought-driven state shift in UK rivers?

Of the three scenarios outlined above, drought-driven state shifts in UK river ecosystems may be most likely if riparian vegetation is lost, due to the long timescales required to reverse its loss and the increasing likelihood that its recovery will be interrupted by another drought. The risk of state shifts could then be exacerbated by synergistic interactions among drought-driven hydrological and thermal changes. For example, drought could be particularly likely to favor the establishment of filamentous algae rather than macrophytes as the dominant habitat-forming producers in newly illuminated channels, initiating unpredictable trophic cascades that lead to structurally and functionally simplified river ecosystems. Such changes are particularly likely in rivers in which multiple pressures including physical habitat modification, flow regulation and water pollution compromise natural ecological resilience (Dunbar, Pedersen, et al., 2010; Dunbar, Warren, et al., 2010; Wilby et al., 1998) and where drought allows invasive species gain a foothold (Wood & Petts, 1999), exacerbating drought impacts (Crook et al., 2010).

## 4 | LIFE AFTER DROUGHT: ECOLOGICAL RECOVERY OF UK RIVERS

Ecosystem recovery from drought is typically defined as the return to a stable pre-drought state (Müller & Bahn, 2022; Schwalm et al., 2017), but this conceptualization is difficult to reconcile with the everchanging, disturbance-prone nature of rivers, in which non-equilibrium conditions can dominate (Ryo et al., 2019; Thoms, 2006). Intensifying climatic extremity is compounding these conceptual difficulties (Rohde, 2023), and increasingly undermines the notion that ecosystems fluctuate within unchanging boundaries (Milly et al., 2008). Nonetheless, the post-drought recovery of taxonomic communities has been well-documented in the UK, largely for macroinvertebrates—which are a unique community in that overland flight of adult insects as well as aquatic dispersal contributes to their recovery—and also for microbial biofilms, macrophytes and fish (Table S2).

## 4.1 | Variability in documented post-drought recovery in UK rivers

Across upland and lowland areas, perennial and non-perennial reaches, surface and groundwater-fed systems, and across biotic groups, research suggests that biological communities in UK rivers have typically recovered from drought within 1–3 years (Table S2), as also observed in other freshwaters globally (Niemi et al., 1990). Although these recovery periods are short and consistent compared to terrestrial ecosystems (Peterken & Mountford, 1996), they are highly variable considering the annual or subannual lifecycles of most freshwater species (except fishes; Blanck & Lamouroux, 2007; Tachet et al., 2010). This variability reflects differences in drought characteristics, differences among and within biotic groups, and the environmental context in which drought unfolds, as well as the design of a drought investigation. Understanding this variability in the rates, trajectories and ultimate extent of post-drought recovery could inform management actions that support resilience to future drought and prevent ecosystems from tipping to alternative states in which their biodiversity and functioning are impaired.

### 4.1.1 | Recovery varies depending on drought characteristics

The rate and extent of post-drought community recovery may reflect drought characteristics including its magnitude and duration (and thus severity) and spatial extent (Figure 4a). In particular, although drought onset is typically gradual (Lake, 2000, 2003), its effects on local habitats (and thus biological communities) may or may not pass critical thresholds, from isolation of marginal vegetation through to drying of subsurface sediments in non-perennial rivers (Aspin, Hart, et al., 2019; Boulton, 2003; Chadd et al., 2017). As such, as drought severity increases, habitat and refuge availability and quality decline, reducing the in situ survival of viable organisms with the potential to act as post-drought recolonists, and thus potentially slowing post-drought recovery rates (Magoulick & Kobza, 2003). Increasing drought severity is likely to increase the spatial extent of ponded and dry in-channel conditions (Sefton et al., 2019), extending distances between refuges and drought-impacted sites and thus slowing post-drought recovery. As a result, the diversity of biological communities including macroinvertebrates declines with both the local-scale duration of dry or ponded in-channel conditions and the river-scale spatial extent of such conditions (Sarremejane et al., 2020).

Drought frequency may also influence community recovery, with higher frequencies repeatedly resetting recovery trajectories to earlier successional stages and preventing the return of taxa with weak dispersal abilities, thus reducing their distribution—potentially to the point of local then wider extinction (Hill et al., 2019; Sarremejane, Stubbington, et al., 2021). To date, such interruptions may only have compromised populations of taxa which lack drought resistance or resilience traits (Sarremejane, Stubbington, et al., 2021), whereas bet-hedging strategies (Lytle & Poff, 2004) and life-history diversity have supported the recovery of other taxa and whole communities (Greene et al., 2010; Stubbington et al., 2016). Drought timing may also explain variability among documented recovery trajectories. For example, recovery may be slower after summer droughts due to the greater likelihood that river drying will eliminate sensitive taxa (Sarremejane et al., 2020). Equally, winter droughts reduce sediment scouring by high flows, with persistent silt deposits compromising re-establishment of populations of macrophytes such as *Ranunculus* the following year (Holmes, 1999).

### 4.1.2 | Recovery varies among and within biotic groups

Variability in recovery rates can be explained in part by the contrasting traits of different biotic groups, for example a high proportion of taxa in microbial biofilms can be desiccation-tolerant, persisting on even “dry” sediments and thus recovering more rapidly than drought-sensitive macroinvertebrates and fishes (Calapez et al., 2014). However, even within groups, recovery times vary from weeks to years (Table S2), depending in part on taxon-specific adaptations to

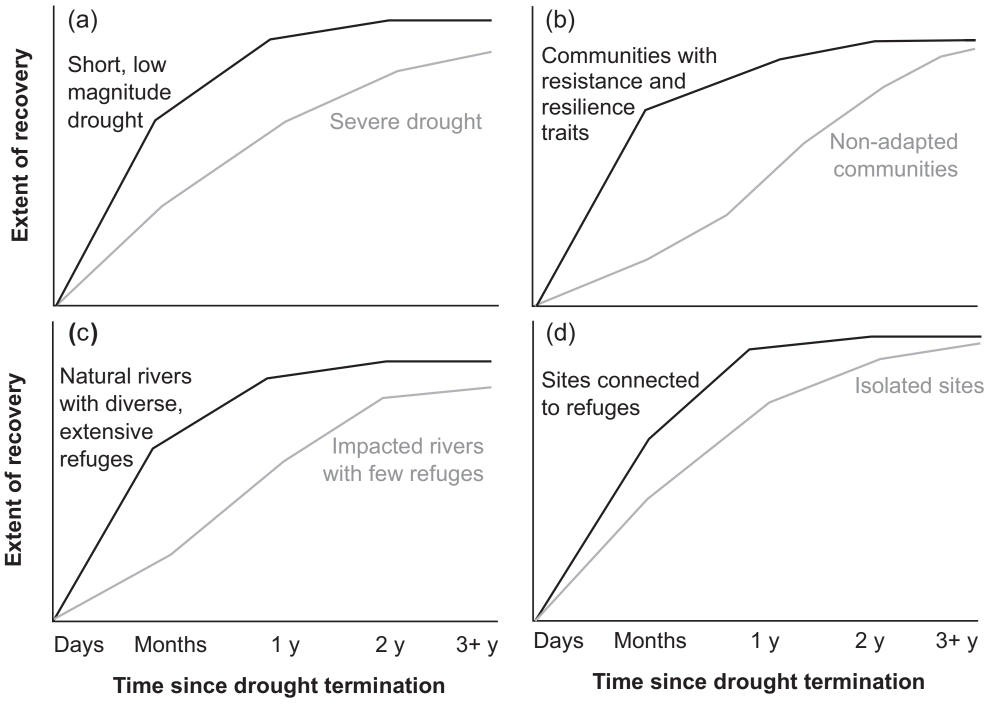


**FIGURE 4** Variability in post-drought recovery rates is explained by differences in (a) drought characteristics including severity; (b) the drought resistance and resilience traits of the taxa in recovering communities; (c) levels of river naturalness or anthropogenic modification, and thus the extent and diversity of refuges; and (d) connectivity between drought-impacted sites and refuges (i.e., sources of post-drought recolonists). *Extent of recovery* is relative to the pre-drought state and thus differs between scenarios (i.e., between black and gray lines).

the prevailing disturbance regime. Frequently disturbed and/or stress-adapted communities, which are typically species-poor, can recover particularly quickly (Figure 4b; also see Figure 3a,b). For example, after a rare, 9-week, near-complete summer dry phase in a flashy, oligotrophic, near-perennial river in south England, drought-driven taxonomic changes in macroinvertebrate communities persisted only until high winter flows restored pre-drought community composition (Ledger & Hildrew, 2001). In contrast, in hydrologically stable, mesotrophic, near-perennial systems such as England's chalk streams (Sear et al., 1999), communities may take 3 years to completely recover from a rare dry phase (Wood & Petts, 1999), with some eliminated k-selected insect taxa requiring up to 10 years to recolonize (Ledger et al., 2011; Sarremejane et al., 2019; Wright & Symes, 1999).

### 4.1.3 | Recovery reflects local to catchment-scale environmental context

Drought impacts and subsequent community recovery are context dependent (Ledger & Milner, 2015), reflecting local-to-network-scale environmental characteristics. At local scales, channel naturalness and thus the availability of drought refuges determine the extent to which organisms can persist in situ and thus rapidly re-establish populations, with these pioneer taxa representing the initial stages of community recovery during the drought (Figure 4c; Hynes, 1958; Cowx et al., 1984; Robson & Matthews, 2004). Refuge extent, diversity and quality can all be reduced by anthropogenic modification of channel shapes, and community recovery can therefore be faster in relatively natural rivers (Dunbar, Pedersen, et al., 2010; Dunbar, Warren, et al., 2010). For example, post-drought recovery trajectories of macrophyte communities in headwater streams include slow, partial recovery of species-poor communities in modified channels but complete, rapid recovery of species-rich communities at more natural sites (Westwood et al., 2006). Similarly, Wright et al. (2003) attributed rapid post-drought recovery of macroinvertebrate communities in a chalk river to its natural habitat characteristics.

River-scale and catchment-wide environmental variability can promote asynchronous fluctuations in local-scale species-specific population densities during drought, limiting concurrent population declines and promoting long-term, network-wide metapopulation persistence (Sarremejane, Stubbington, et al., 2021). Then, when a drought termination phase begins, local post-drought recovery rates and trajectories (in particular at stages beyond the initial pioneer assemblage) are influenced by the distance and direction to drought-impacted sites from catchment-wide refuges (including both hydrologically connected river reaches and other, unconnected waterbodies such as ponds) that represent potential recolonist sources, as well as connectivity between these sites and sources (Figure 4d; Driver & Hoeinghaus, 2016; Fournier et al., 2023; Robson et al., 2011). River-scale recovery thus relates positively to the spatial extent of flowing reaches that persist during drought (Sarremejane et al., 2020). However, widespread anthropogenic fragmentation of UK and global river networks by artificial barriers routinely reduces connectivity, blocking aquatic recolonization pathways (Grill et al., 2015; Jones et al., 2019). As such, motile aquatic organisms including fishes and many macroinvertebrates may be unable to reach impacted sites from catchment-wide refuges after drought termination, slowing recovery rates and reducing its ultimate extent (Perkin et al., 2013, 2015; Perrow et al., 2007).

The river-scale spatial arrangement of reaches exposed to different drought intensities influences recovery. Where drought-impacted reaches occur downstream of hydrologically connected refuges, drifting organisms may supply copious recolonists that contribute to community recovery soon after flow increases (Fournier et al., 2023; Pařil et al., 2019; Wood & Petts, 1994, 1999). Isolation from recolonist sources increases with progression upstream, and communities in near-perennial headwater streams may take longer to recover from drought (Tornwall et al., 2017) due to the lack of upstream perennial reaches that supply drifting recolonists (Aspin & House, 2022; Berrie, 1992 but see Stubbington & Wood, 2013).

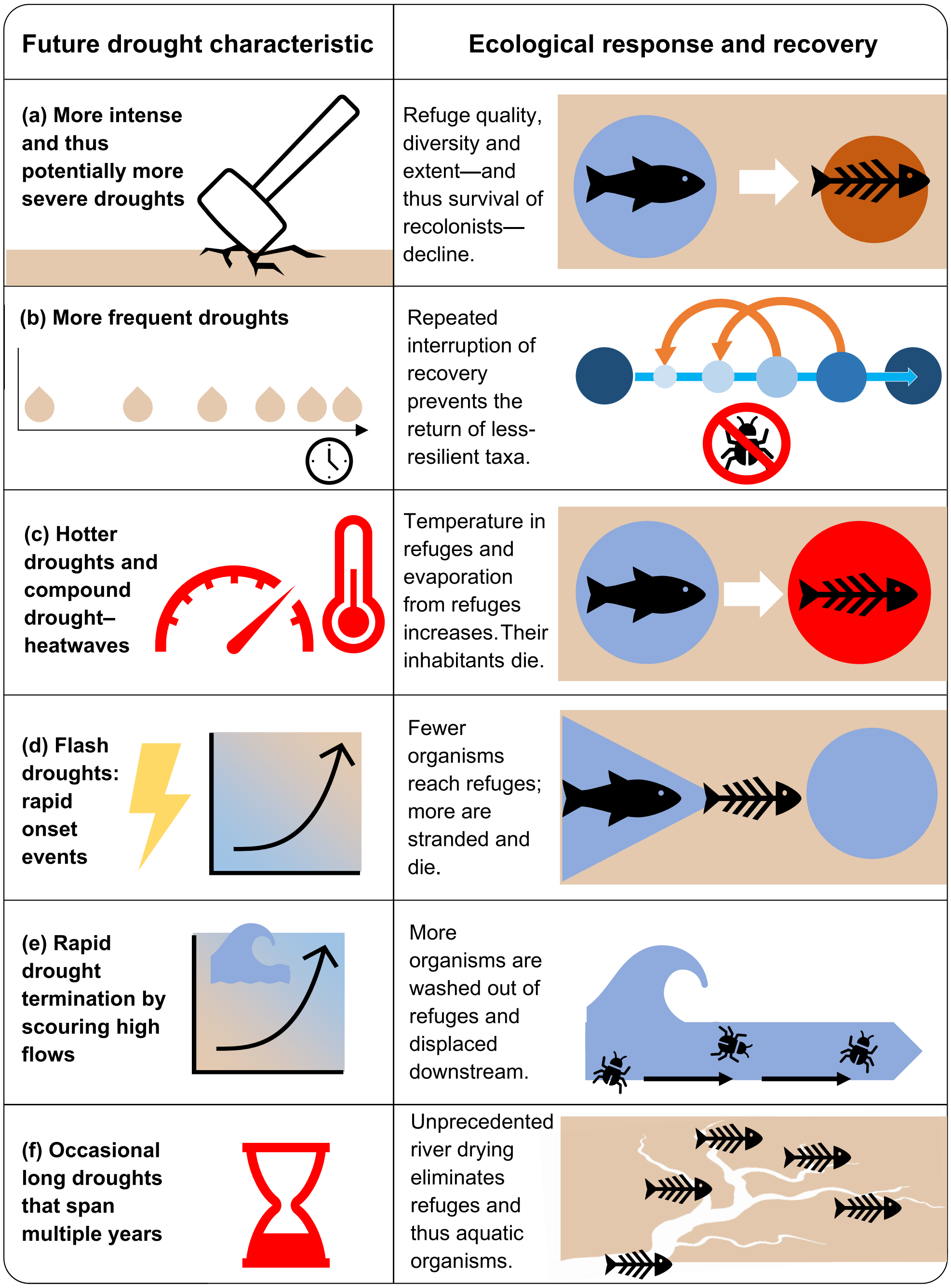
### 4.1.4 | Variability in characterized recovery reflects study design

Apparent variability in documented recovery rates and trajectories may also reflect study design. Studies of post-drought recovery routinely lack pre-drought data, or have insufficient data to adequately represent interannual variability in pre-drought conditions (Table S2; Bêche et al., 2009). In addition, characterization of recovery is typically limited by study duration; few studies report post-drought patterns over multiple years, and these few studies are typified by a coarse temporal resolution, that is, collection of 1–2 biological samples per year (Table S2). Such studies may describe considerable but not necessarily complete recovery (Hillebrand & Kunze, 2020). Coupled with the conceptual difficulties of characterizing stable, recovered states in disturbance-prone river ecosystems (Ryo et al., 2019; Thoms, 2006), this lack of data only allows documentation of post-drought changes (typically increases) in metrics such as abundance, biomass, diversity, richness and biotic index scores, and cannot indicate whether stabilization of such metrics represents the pre-drought state. For example, abundance and population densities (but not necessarily biomass) can increase rapidly after drought due to recolonization by pioneer taxa, with high densities thus indicative of an interim stage during the recovery trajectory (Ledger & Hildrew, 2001). Moreover, univariate metrics such as taxonomic richness routinely overlook drought-driven changes in community composition (e.g., Bêche et al., 2009; Wright & Symes, 1999).

## 4.2 | Recovery after future drought in UK rivers

The concepts of ecological memory and drought legacies acknowledge the persistent effects of past droughts and their capacity to influence ecological responses to and recovery after future events (Johnstone et al., 2016; Müller & Bahn, 2022), including alteration of vulnerability to persistent state shifts (see Section 3.1). As dynamic, disturbance-prone ecosystems, rivers appear to have poor memories, being less susceptible to drought legacies than terrestrial ecosystems (Müller & Bahn, 2022). Nonetheless, predicted increases in drought severity, frequency, spatial extent, cooccurrence with heatwaves, rate of onset and termination by flooding in UK rivers could collectively alter the rates, trajectories and ultimate extent of community recovery, thus increasing legacy effects. For example, increasing drought frequencies inherently shorten intervening recovery durations, preventing populations or whole ecosystems from "forgetting" a preceding event and thus compromising their resilience (Morris & Ball, 2021; Szejner et al., 2020). The consequences of predicted increases in drought severity, frequency and spatial extent for community recovery are logical extensions of patterns described in Section 4.1.1 and are not repeated here (Figure 5a,b).

Alongside any increase in drought severity, the increasing occurrence of compound drought–heatwave events and hotter droughts (Figure 5c; Table S1) is likely to reduce refuge quality, reducing persistence of potential recolonists and thus limiting post-drought recovery (see Section 4.1.1; Archdeacon & Reale, 2020; Moidu et al., 2023). In addition, any increase in flash droughts could mean that fewer organisms manage to move into refuges, also limiting the



| Future drought characteristic | Ecological response and recovery |
|---|---|
| **(a) More intense and thus potentially more severe droughts** | Refuge quality, diversity and extent—and thus survival of recolonists—decline. |
| **(b) More frequent droughts** | Repeated interruption of recovery prevents the return of less-resilient taxa. |
| **(c) Hotter droughts and compound drought–heatwaves** | Temperature in refuges and evaporation from refuges increases. Their inhabitants die. |
| **(d) Flash droughts: rapid onset events** | Fewer organisms reach refuges; more are stranded and die. |
| **(e) Rapid drought termination by scouring high flows** | More organisms are washed out of refuges and displaced downstream. |
| **(f) Occasional long droughts that span multiple years** | Unprecedented river drying eliminates refuges and thus aquatic organisms. |

FIGURE 5 Possible ecological responses to and thus recovery from future UK droughts with altered characteristics. Each response has the potential to limit post-drought recovery. Fish and beetle icons illustrate representative aquatic organisms.

densities and diversity of potential subsequent recolonists (Figure 5d; Archdeacon & Reale, 2020; Magoulick & Kobza, 2003). Any increase in drought-breaking high-flow events could limit local recovery by washing organisms from refuges including subsurface sediments, especially if sediments are mobilized (Figure 5e; Stubbington, Greenwood, et al., 2009), slowing community recovery. Subsequent high flows during the drought termination phase could displace more individuals, reducing local population densities and interrupting recovery trajectories (Leigh et al., 2015). In non-perennial reaches, redrying after false starts in flow could cause mass mortality of organisms that hatched during the short wet phase, depleting egg and seedbanks (Strachan et al., 2015). Although future changes to the frequency of multiyear droughts in the UK are uncertain, occasional long-duration events may be increasingly extreme (Chan et al., 2023), which could cause unprecedented loss of freshwater biodiversity (Figure 5f).

## 5 | MANAGEMENT TO SUPPORT ECOLOGICAL RESILIENCE TO DROUGHT

Despite short-term, high-profile ecological impacts such as mass mortality of prized Atlantic salmon *Salmo salar* driven by decaying masses of the iconic macrophyte *Ranunculus* (Brooker et al., 1977; Turner et al., 2021), river ecosystems in the cool, wet UK have, to date, proven resilient to drought, recovering within weeks to a few years (Table S2). However, in rivers of the Anthropocene, drought is no longer entirely natural. Driven by climate change, drought is becoming more extreme (Chan et al., 2023); as human populations rise, drought increasingly reflects water resource use alongside climatic drivers (Van Loon et al., 2016); and in interaction with multiple stressors, drought now compromises environmental quality (e.g., Turner et al., 2021; van Vliet & Zwolsman, 2008). These anthropogenic game-changers are creating droughts with greater potential to drive ecosystems beyond thresholds at which they shift to persistent, species-poor, functionally simplified states (Crook et al., 2010). As such, proactive management strategies are needed to limit future drought-driven biodiversity loss, and thus to maintain and enhance the resilience of UK river ecosystems (Figure 6; Kreibich et al., 2022), as summarized in Table S3.

Key management actions, implementation of which will depend on the relative contributions of groundwater and surface water to streamflow as well as water resource use, include reducing abstraction to maintain sufficient flow to support biodiversity and ecosystem functioning (i.e., environmental flows sensu Acreman, 2016), where "sufficient" balances ecological priorities (e.g., a species of conservation concern) with societal needs (Aldous et al., 2011; Erős et al., 2023; Kreibich et al., 2022). Catchment-specific management and restoration plans should also routinely incorporate wider measures to promote drought resilience, including actions that enhance water quality (Durance & Ormerod, 2009; Huml et al., 2020) and maintain or create a diverse range of high-quality drought refuges (Figure 6). Long-term actions should also seek to promote connectivity between refuges and drought-prone sites (Bond et al., 2008), including barrier removals that enable fishes to move to and from refuges (Gido et al., 2016) and creation of terrestrial habitat corridors that support insect flight between waterbodies (Robson et al., 2011). In the shorter term,

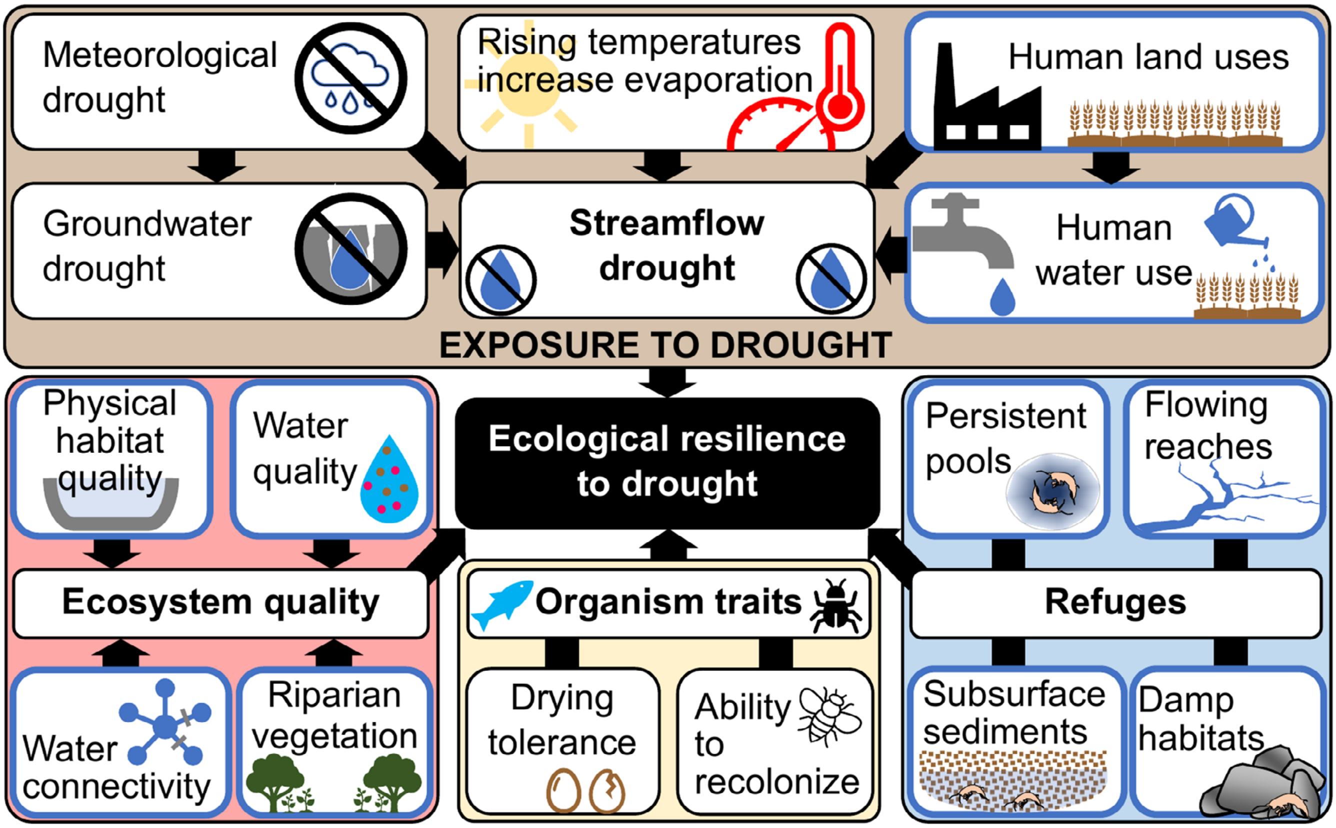


FIGURE 6 Factors affecting ecological resilience to drought. *Exposure* panel adapted from Crausbay et al. (2017; also see Kovach et al., 2019); *Refuges* icons (including *Gammarus*, as a representative macroinvertebrate) adapted from Stubbington (2012). Blue borders indicate factors that can be influenced by policy and practice.

**FIGURE 7** Large wood accumulation in a headwater stream in the New Forest, England (Photo credit: Angela Gurnell).

where such barriers remain, fish rescue and restocking may be needed to support populations that cannot naturally reach and recolonize from refuges (Axford, 2000; Jones et al., 2019), in particular to minimize the risk of shifts in ecosystem state following elimination of predatory fish with keystone roles in food webs (see Section 3.1.3). In addition, where drought-driven reductions in dissolved oxygen concentrations threaten notable fish populations, managers may respond with rapid deployment of chemical or mechanical aeration (Boys et al., 2022; Environment Agency, 2022).

We suggest *natural drought management* as a complementary approach to natural flood management (Harvey & Henshaw, 2023; Lane, 2017) within holistic natural water management strategies. Such strategies aim to support natural processes that enable catchments to store water and release it slowly into rivers, both during periods of water deficit and water excess, thus maintaining flows and mitigating drought impacts (Wohl et al., 2018) as well as flood risk. For example, allowing large wood to accumulate in the channel can hold up water in headwaters, providing drought refuges for species including salmonids and supporting stable downstream flows (Figure 7; Vehanen et al., 2010). Similarly, beaver dams (and thus beaver reintroductions, which are becoming more common in countries including the UK) promote storage and slow release of water, thus maintaining baseflows during drought (Brazier et al., 2021; Harvey et al., 2024). Although enhancing drought resilience using such natural processes is desirable, it takes years for riparian vegetation to establish, and for large wood to then accumulate and create persistent scour pools that act as high-quality refuges (Figure 6; Beechie et al., 2010). Given the urgency of future-proofing ecosystems against increasing climatic extremity (Henriques et al., 2015), natural water management actions that promote catchment-scale resilience to both droughts and floods may be needed at a larger scale, for example by introducing large wood across networks of headwater streams. In the longer term, riparian tree planting can provide future sources of large wood that promote natural hydrological variability and increase shading, moderating water temperatures (Grabowski et al., 2019; Johnson et al., 2024) and thus keeping coldwater species including salmonid fish within a tolerable thermal environment during summer droughts and compound drought–heatwave events (Broadmeadow et al., 2011).

## 5.1 | Concluding remarks: Priorities for future research and monitoring

Widespread, long-term hydrological monitoring data are translated into real-time reporting of daily flows and associated drought indices for mainstem UK rivers (via the UK Water Resources Portal; Barker et al., 2022), providing early warning of drought and thus enabling timely action to mitigate its impacts. Nonetheless, both research progress and management actions are hampered by the spatial and temporal limitations of these flow monitoring networks, in particular their poor representation of headwater sites, at which drought-driven changes in habitat conditions may be particularly pronounced (Krabbenhoft et al., 2022). Biological monitoring is even more limited (e.g., Environment Agency, 2017), which may allow gradually intensifying drought impacts to unfold largely undocumented, limiting interventions designed to support ecosystems facing profound change. As such, expanded monitoring networks that couple hydrological and biological data from both headwaters and mainstems are needed to generate data that enable timely drought detection and documentation, and thus to inform actions that mitigate its ecological impacts (Kovach et al., 2019). Citizen science projects and wider public observations could also contribute to the detection then monitoring of drought as it unfolds, as well as documenting post-drought recovery trajectories (Bachmair et al., 2016; Environment Agency, 2022; Smith et al., 2020). Earth observation technologies may also have the potential to enable large-scale, near-real-time drought monitoring (AghaKouchak et al., 2023).

Regulatory agencies may lack the resources to implement spatially extensive drought monitoring networks, but their rigorous, long-term, albeit limited data can be complemented by targeted surveys to identify at-risk sites as well as those acting as key drought refuges, and to evaluate the effectiveness of actions taken to enhance drought resilience. These long-term data also require analysis to develop resilience indicators: metrics that identify ecosystems on the approach to tipping points (van der Bolt et al., 2021; see Box 1), thus enabling timely action to prevent drought-driven shifts to alternative, simplified stable states (Dakos et al., 2015). In addition, characterizing responses to and recovery from drought in interaction with other anthropogenic pressures could identify non-hydrological parameters that managers can manipulate to maximize drought resilience (White et al., 2023). As the prospect of unprecedented, extreme drought increases even in cool, wet countries such as the UK, insights from research and monitoring require urgent application to inform actions designed to support the ecological resilience of river ecosystems as they adapt to droughts in the Anthropocene.

## AUTHOR CONTRIBUTIONS

**Rachel Stubbington:** Conceptualization (lead); investigation (lead); project administration (lead); visualization (lead); writing – original draft (lead); writing – review and editing (lead). **Judy England:** Conceptualization (equal); visualization (equal); writing – review and editing (equal). **Romain Sarremejane:** Conceptualization (supporting); visualization (equal); writing – review and editing (equal). **Glenn Watts:** Conceptualization (equal); visualization (supporting); writing – review and editing (equal). **Paul J. Wood:** Conceptualization (equal); visualization (supporting); writing – review and editing (equal).

## ACKNOWLEDGMENTS

This manuscript is based on an essay written for the Environment Agency (award SC220024). In turn, the essay was informed by work done by Jake Dimon during a Research Fellowship funded by the Nottingham Trent University Innovative Knowledge Exchange Pilot scheme, the outcomes of which were published by Stubbington et al. (2022). Thanks to Tom Aspin and Tim Sykes for useful discussions which informed the development of initial ideas, and to Stuart Allen, Mike Bowes and two anonymous reviewers for feedback that improved the manuscript. The views expressed are those of the authors and not necessarily those of their respective employers.

## FUNDING INFORMATION

None.

## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

## ORCID

*Rachel Stubbington* https://orcid.org/0000-0001-8475-5109
*Judy England* https://orcid.org/0000-0001-5247-4812
*Romain Sarremejane* https://orcid.org/0000-0002-4943-1173

*Glenn Watts* https://orcid.org/0009-0005-6789-8550
*Paul J. Wood* https://orcid.org/0000-0003-4629-3163

## RELATED WIREs ARTICLES

Hydrological drought explained
Drought indicators revisited: The need for a wider consideration of environment and society
People need freshwater biodiversity
Leading the path toward sustainable freshwater management

## REFERENCES

Acreman, M. (2016). Environmental flows—Basics for novices. *WIREs Water*, *3*(5), 622–628. https://doi.org/10.1002/wat2.1160

AghaKouchak, A., Chiang, F., Huning, L. S., Love, C. A., Mallakpour, I., Mazdiyasni, O., Moftakhari, H., Papalexiou, S. M., Ragno, E. and Sadegh, M. (2020). Climate extremes and compound hazards in a warming world. *Annual Review of Earth and Planetary Sciences*, *48*, 519–548. https://doi.org/10.1146/annurev-earth-071719-055228

AghaKouchak, A., Feldman, D., Hoerling, M., Huxman, T., & Lund, J. (2015). Water and climate: Recognize anthropogenic drought. *Nature*, *524*(7566), 409–411. https://doi.org/10.1038/524409a

AghaKouchak, A., Huning, L. S., Sadegh, M., Qin, Y., Markonis, Y., Vahedifard, F., Love, C. A., Mishra, A., Mehran, A., Obringer, R., Hjelmstad, A., Pallickara, S., Jiwa, S., Hanel, M., Zhao, Y., Pendergrass, A. G., Arabi, M., Davis, S. J., Ward, P. J., … Kreibich, H. (2023). Toward impact-based monitoring of drought and its cascading hazards. *Nature Reviews Earth & Environment*, *4*, 582–595. https://doi.org/10.1038/s43017-023-00457-2

Aldous, A., Fitzsimons, J., Richter, B., & Bach, L. (2011). Droughts, floods and freshwater ecosystems: Evaluating climate change impacts and developing adaptation strategies. *Marine and Freshwater Research*, *62*(3), 223–231. https://doi.org/10.1071/MF09285

Allen, C. D., Breshears, D. D., & McDowell, N. G. (2015). On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere*, *6*(8), 129–155. https://doi.org/10.1890/ES15-00203.1

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. https://doi.org/10.1111/fwb.13607

Armitage, P. D., & Cannan, C. E. (2000). Annual changes in summer patterns of mesohabitat distribution and associated macroinvertebrate assemblages. *Hydrological Processes*, *14*(16–17), 3161–3179. https://doi.org/10.1002/1099-1085(200011/12)14:16/17<3161::AID-HYP140>3.0.CO;2-8

Arnell, N. W., & Freeman, A. (2022). The impact of climate change on policy-relevant indicators of temperature extremes in the United Kingdom. *Climate Resilience and Sustainability*, *1*(2), e12. https://doi.org/10.1002/cli2.12

Arnell, N. W., & Gosling, S. N. (2016). The impacts of climate change on river flood risk at the global scale. *Climatic Change*, *134*, 387–401. https://doi.org/10.1007/s10584-014-1084-5

Arnell, N. W., Halliday, S. J., Battarbee, R. W., Skeffington, R. A., & Wade, A. J. (2015). The implications of climate change for the water environment in England. *Progress in Physical Geography*, *39*(1), 93–120. https://doi.org/10.1177/0309133314560369

Aspin, T., & House, A. (2022). Alpha and beta diversity and species co-occurrence patterns in headwaters supporting rare intermittent-stream specialists. *Freshwater Biology*, *67*(7), 1188–1202. https://doi.org/10.1111/fwb.13910

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

Axford, S. (2000). Management of fisheries in rivers used for potable abstractions in drought conditions: Public health versus ecology. In I. G. Cowx (Ed.), *Management and ecology of river fisheries* (pp. 218–231). Blackwell Science.

Bachmair, S., Stahl, K., Collins, K., Hannaford, J., Acreman, M., Svoboda, M., Knutson, C., Smith, K. H., Wall, N., Fuchs, B., Crossman, N. D., & Overton, I. C. (2016). Drought indicators revisited: The need for a wider consideration of environment and society. *WIREs Water*, *3*(4), 516–536. https://doi.org/10.1002/wat2.1154

Barker, L. J., Fry, M., Hannaford, J., Nash, G., Tanguy, M., & Swain, O. (2022). Dynamic high resolution hydrological status monitoring in real-time: The UK Water Resources Portal. *Frontiers in Environmental Science*, *10*, 752201. https://doi.org/10.3389/fenvs.2022.752201

Barker, L. J., Hannaford, J., Magee, E., Turner, S., Sefton, C., Parry, S., Evans, J., Szczykulska, M., & Haxton, T. (2024). An appraisal of the severity of the 2022 drought and its impacts. *Weather*, *79*, 208–219. https://doi.org/10.1002/wea.4531

Barker, L. J., Hannaford, J., Parry, S., Smith, K. A., Tanguy, M., & Prudhomme, C. (2019). Historic hydrological droughts 1891–2015: Systematic characterisation for a diverse set of catchments across the UK. *Hydrology and Earth System Sciences*, *23*(11), 4583–4602. https://doi.org/10.5194/hess-23-4583-2019

Bass, J. A., Armitage, P. D., & Tapia, G. (2023). Aquatic invertebrates of Dorset winterbournes: A comparison with the small perennial chalk streams. *Proceedings of the Dorset Natural History and Archaeological Society*, *143*, 41–50.

Bêche, L. A., Connors, P. G., Resh, V. H., & Merenlender, A. M. (2009). Resilience of fishes and invertebrates to prolonged drought in two California streams. *Ecography*, *32*(5), 778–788. https://doi.org/10.1111/j.1600-0587.2009.05612.x

Bednar-Friedl, B., Biesbroek, R., Schmidt, D. N., Alexander, P., Børsheim, K. Y., Carnicer, J., Georgopoulou, E., Haasnoot, M., Le Cozannet, G., Lionello, P., Lipka, O., Möllmann, C., Muccione, V., Mustonen, T., Piepenburg, D., & Whitmarsh, L. (2022). Europe. In H.-O. Pörtner, D. C. Roberts, M. Tignor, E. S. Poloczanska, K. Mintenbeck, A. Alegría, M. Craig, S. Langsdorf, S. Löschke, V. Möller, A. Okem, & B. Rama (Eds.), *Climate change 2022: Impacts, adaptation and vulnerability. Contribution of working group II to the sixth assessment report of the intergovernmental panel on climate change* (pp. 1817–1927). Cambridge University Press. https://doi.org/10.1017/9781009325844.015

Beechie, T. J., Sear, D. A., Olden, J. D., Pess, G. R., Buffington, J. M., Moir, H., Roni, P., & Pollock, M. M. (2010). Process-based principles for restoring river ecosystems. *Bioscience*, *60*(3), 209–222. https://doi.org/10.1525/bio.2010.60.3.7

Beniston, M., Stephenson, D. B., Christensen, O. B., Ferro, C. A. T., Frei, C., Goyette, S., Halsnaes, K., Holt, T., Jylhä, K., Koffi, B., Palutikof, J., Schöll, R., Semmler, T., & Woth, K. (2007). Future extreme events in European climate: An exploration of regional climate model projections. *Climatic Change*, *81*, 71–95. https://doi.org/10.1007/s10584-006-9226-z

Berrie, A. D. (1992). The chalk-stream environment. *Hydrobiologia*, *248*, 3–9. https://doi.org/10.1007/BF00008881

Beschta, R. L., & Jackson, W. L. (1979). The intrusion of fine sediments into a stable gravel bed. *Journal of the Fisheries Board of Canada*, *36*(2), 204–210. https://doi.org/10.1139/f79-030

Bickerton, M. A. (1995). Long-term changes of macroinvertebrate communities in relation to flow variations: The river Glen, Lincolnshire, England. *Regulated Rivers: Research & Management*, *10*(2–4), 81–92. https://doi.org/10.1002/rrr.3450100204

Blanck, A., & Lamouroux, N. (2007). Large-scale intraspecific variation in life-history traits of European freshwater fish. *Journal of Biogeography*, *34*(5), 862–875. https://doi.org/10.1111/j.1365-2699.2006.01654.x

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

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

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

Boulton, A. J., Rolls, R. J., Jaeger, K. L., & Datry, T. (2017). Hydrological connectivity in intermittent rivers and ephemeral streams. In T. Datry, N. Bonada, & A. Boulton (Eds.), *Intermittent rivers and ephemeral streams: Ecology and management* (pp. 79–108). Academic Press. https://doi.org/10.1016/B978-0-12-803835-2.00004-8

Bowes, M. J., Ings, N. L., McCall, S. J., Warwick, A., Barrett, C., Wickham, H. D., Harman, S. A., Armstrong, L. K., Scarlett, P. M., Roberts, C., Lehmann, K., & Singer, A. C. (2012). Nutrient and light limitation of periphyton in the river Thames: Implications for catchment management. *Science of the Total Environment*, *434*, 201–212. https://doi.org/10.1016/j.scitotenv.2011.09.082

Bowler, D. E., Mant, R., Orr, H., Hannah, D. M., & Pullin, A. S. (2012). What are the effects of wooded riparian zones on stream temperature? *Environmental Evidence*, *1*, 3. https://doi.org/10.1186/2047-2382-1-3

Boys, C. A., Baldwin, D. S., Ellis, I., Pera, J., & Cheshire, K. (2022). Review of options for creating and maintaining oxygen refuges for fish during destratification-driven hypoxia in rivers. *Marine and Freshwater Research*, *73*(2), 200–210. https://doi.org/10.1071/MF20364

Brazier, R. E., Puttock, A., Graham, H. A., Auster, R. E., Davies, K. H., & Brown, C. M. (2021). Beaver: Nature's ecosystem engineers. *WIREs Water*, *8*(1), e1494. https://doi.org/10.1002/wat2.1494

Briffa, K. R., van der Schrier, G., & Jones, P. D. (2009). Wet and dry summers in Europe since 1750: Evidence of increasing drought. *International Journal of Climatology: A Journal of the Royal Meteorological Society*, *29*(13), 1894–1905. https://doi.org/10.1002/joc.1836

Broadmeadow, S. B., Jones, J. G., Langford, T. E. L., Shaw, P. J., & Nisbet, T. R. (2011). The influence of riparian shade on lowland stream water temperatures in southern England and their viability for brown trout. *River Research and Applications*, *27*(2), 226–237. https://doi.org/10.1002/rra.1354

Brooker, M. P., Morris, D. L., & Hemsworth, R. J. (1977). Mass mortalities of adult salmon, *Salmo salar*, in the R. Wye, 1976. *Journal of Applied Ecology*, *14*(2), 409–417. https://doi.org/10.2307/2402554

Burke, E. J., & Brown, S. J. (2010). Regional drought over the UK and changes in the future. *Journal of Hydrology*, *394*(3–4), 471–485. https://doi.org/10.1016/j.jhydrol.2010.10.003

Burt, T., Boardman, J., Foster, I., & Howden, N. (2016). More rain, less soil: Long-term changes in rainfall intensity with climate change. *Earth Surface Processes and Landforms*, *41*(4), 563–566. https://doi.org/10.1002/esp.3868

Calapez, A. R., Elias, C. L., Almeida, S. F., & Feio, M. J. (2014). Extreme drought effects and recovery patterns in the benthic communities of temperate streams. *Limnetica*, *33*(2), 281–296. https://doi.org/10.23818/limn.33.22

Capon, S. J., Lynch, A. J. J., Bond, N., Chessman, B. C., Davis, J., Davidson, N., Finlayson, M., Gell, P. A., Hohnberg, D., Humphrey, C., Kingsford, R. T., Nielsen, D., Thomson, J. R., Ward, K., & Mac Nally, R. (2015). Regime shifts, thresholds and multiple stable states in freshwater ecosystems; a critical appraisal of the evidence. *Science of the Total Environment*, *534*, 122–130. https://doi.org/10.1016/j.scitotenv.2015.02.045

Carey, N., Chester, E. T., & Robson, B. J. (2023). Loss of functionally important and regionally endemic species from streams forced into intermittency by global warming. *Global Change Biology*, *29*(11), 3019–3038. https://doi.org/10.1111/gcb.16650

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

Chan, W. C., Arnell, N. W., Darch, G., Facer-Childs, K., Shepherd, T. G., Tanguy, M., & van der Wiel, K. (2023). Current and future risk of unprecedented hydrological droughts in Great Britain. *Journal of Hydrology*, *625*, 130074. https://doi.org/10.1016/j.jhydrol.2023.130074

Cid, N., Erős, T., Heino, J., Singer, G., Jähnig, S. C., Cañedo-Argüelles, M., Bonada, N., Sarremejane, R., Mykrä, H., Sandin, L., Paloniemi, R., Varumo, L., & Datry, T. (2022). From meta-system theory to the sustainable management of rivers in the Anthropocene. *Frontiers in Ecology and the Environment*, *20*(1), 49–57. https://doi.org/10.1002/fee.2417

Cook, B. I., Smerdon, J. E., Cook, E. R., Williams, A. P., Anchukaitis, K. J., Mankin, J. S., Allen, K., Andreu-Hayles, L., Ault, T. R., Belmecheri, S., Coats, S., Coulthard, B., Fosu, B., Grierson, P., Griffin, D., Herrera, D. A., Ionita, M., Lehner, F., Leland, C., … Wise, E. K. (2022). Megadroughts in the common era and the Anthropocene. *Nature Reviews Earth & Environment*, *3*(11), 741–757. https://doi.org/10.1038/s43017-022-00329-1

Cotton, J. A., Wharton, G., Bass, J. A. B., Heppell, C. M., & Wotton, R. S. (2006). The effects of seasonal changes to in-stream vegetation cover on patterns of flow and accumulation of sediment. *Geomorphology*, *77*(3–4), 320–334. https://doi.org/10.1016/j.geomorph.2006.01.010

Coulson, L. E., Schelker, J., Attermeyer, K., Griebler, C., Hein, T., & Weigelhofer, G. (2021). Experimental desiccation indicates high moisture content maintains hyporheic biofilm processes during drought in temperate intermittent streams. *Aquatic Sciences*, *83*(3), 46. https://doi.org/10.1007/s00027-021-00799-3

Cowx, I. G., Young, W. O., & Hellawell, J. M. (1984). The influence of drought on the fish and invertebrate populations of an upland stream in Wales. *Freshwater Biology*, *14*(2), 165–177. https://doi.org/10.1111/j.1365-2427.1984.tb00030.x

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

Crausbay, S. D., Betancourt, J., Bradford, J., Cartwright, J., Dennison, W. C., Dunham, J., Enquist, C. A. F., Frazier, A. G., Hall, K. R., Littell, J. S., Luce, C. H., Palmer, R., Ramirez, A. R., Rangwala, I., Thompson, L., Walsh, B. M., & Carter, S. (2020). Unfamiliar territory: Emerging themes for ecological drought research and management. *One Earth*, *3*(18), 337–353. https://doi.org/10.1016/j.oneear.2020.08.019

Crausbay, S. D., Ramirez, A. R., Carter, S. L., Cross, M. S., Hall, K. R., Bathke, D. J., Betancourt, J. L., Colt, S., Cravens, A. E., Dalton, M. S., Dunham, J. B., Hay, L. E., Hayes, M. J., McEvoy, J., McNutt, C. A., Moritz, M. A., Nislow, K. H., Raheem, N., & Sanford, T. (2017). Defining ecological drought for the twenty-first century. *Bulletin of the American Meteorological Society*, *98*(12), 2543–2550. https://doi.org/10.1175/BAMS-D-16-0292.1

Crook, D. A., Reich, P., Bond, N. R., McMaster, D., Koehn, J. D., & Lake, P. S. (2010). Using biological information to support proactive strategies for managing freshwater fish during drought. *Marine and Freshwater Research*, *61*(3), 379–387. https://doi.org/10.1071/MF09209

Dakos, V., Carpenter, S. R., van Nes, E. H., & Scheffer, M. (2015). Resilience indicators: Prospects and limitations for early warnings of regime shifts. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *370*(1659), 20130263. https://doi.org/10.1098/rstb.2013.0263

Datry, T., Corti, R., Claret, C., & Philippe, M. (2011). Flow intermittence controls leaf litter breakdown in a French temporary alluvial river: The "drying memory". *Aquatic Sciences*, *73*, 471–483. https://doi.org/10.1007/s00027-011-0193-8

DelVecchia, A. G., Shanafield, M., Zimmer, M. A., Busch, M. H., Krabbenhoft, C. A., Stubbington, R., Kaiser, K. E., Burrows, R. M., Hosen, J., Datry, T., Kampf, S. K., Zipper, S. C., Fritz, K., Costigan, K., & Allen, D. C. (2022). Reconceptualizing the hyporheic zone for non-perennial rivers and streams. *Freshwater Science*, *41*(2), 167–182. https://doi.org/10.1086/720071

Dobel, A. J., O'Hare, M., Gunn, I., & Edwards, F. (2020). *Streams and rivers: Report card 2020*. About Drought. https://aboutdrought.info/wp-content/uploads/2020/07/AboutDrought-ReportCard-Rivers-Streams-Final.pdf

Dollar, E., Edwards, F., Stratford, C., May, L., Biggs, J., Laize, C., Acreman, M., Blake, J., Carvalho, L., Elliott, A., Gunn, I., Hinsley, S., Mountford, O., Nunn, M., Preston, C., Sayer, E., Schonrogge, K., Spears, B., Spurgeon, D., … Wood, P. (2013). *Monitoring and assessment of environmental impacts of droughts: Literature synthesis: Report SC120024/R1*. Environment Agency. https://assets.publishing.service.gov.uk/government/uploads/system/uploads/attachment_data/file/291497/LIT_8569_b765dd.pdf

Downes, B. J., Barmuta, L. A., Fairweather, P. G., Faith, D. P., Keough, M. J., Lake, P. S., Mapstone, B. D., & Quinn, G. P. (2002). *Monitoring ecological impacts: Concepts and practice in flowing waters*. Cambridge University Press.

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

Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z. I., Knowler, D. J., Lévêque, C., Naiman, R. J., Prieur-Richard, A. H., Soto, D., Stiassny, M. L. J., & Sullivan, C. A. (2006). Freshwater biodiversity: Importance, threats, status and conservation challenges. *Biological Reviews*, *81*(2), 163–182. https://doi.org/10.1017/S1464793105006950

Dugdale, S. J., Malcolm, I. A., Kantola, K., & Hannah, D. M. (2018). Stream temperature under contrasting riparian forest cover: Understanding thermal dynamics and heat exchange processes. *Science of the Total Environment*, *610*, 1375–1389. https://doi.org/10.1016/j.scitotenv.2017.08.198

Dunbar, M. J., Pedersen, M. L., Cadman, D., 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

Dunbar, M. J., Warren, M., Extence, C., Baker, L., Cadman, D., Mould, D. J., Hall, J., & Chadd, R. (2010). Interaction between macroinvertebrates, discharge and physical habitat in upland rivers. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *20*(S1), S31–S44. https://doi.org/10.1002/aqc.1089

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

Elliott, J. M., Hurley, M. A., & Elliott, J. A. (1997). Variable effects of droughts on the density of a sea-trout *Salmo trutta* population over 30 years. *Journal of Applied Ecology*, *34*(5), 1229–1238. https://doi.org/10.2307/2405234

Environment Agency. (2017). *Drought response: Our framework for England*. Environment Agency. https://assets.publishing.service.gov.uk/government/uploads/system/uploads/attachment_data/file/625006/LIT_10104.pdf

Environment Agency. (2022). *Environment agency takes action to rescue fish during dry weather* [Online]. UK Government. https://environmentagency.blog.gov.uk/2022/08/11/environment-agency-takes-action-to-rescue-fish-during-dry-weather/

Erős, T., Hermoso, V., & Langhans, S. D. (2023). Leading the path toward sustainable freshwater management: Reconciling challenges and opportunities in historical, hybrid, and novel ecosystem types. *WIREs Water*, *10*(3), e1645. https://doi.org/10.1002/wat2.1645

Esfahanian, E., Nejadhashemi, A. P., Abouali, M., Daneshvar, F., Alireza, A. R., Herman, M. R., & Tang, Y. (2016). Defining drought in the context of stream health. *Ecological Engineering*, *94*, 668–681. https://doi.org/10.1016/j.ecoleng.2016.06.110

Extence, C. A. (1981). The effect of drought on benthic invertebrate communities in a lowland river. *Hydrobiologia*, *83*, 217–224. https://doi.org/10.1007/BF00008269

Fleig, A. K., Tallaksen, L. M., Hisdal, H., & Demuth, S. (2006). A global evaluation of streamflow drought characteristics. *Hydrology and Earth System Sciences*, *10*(4), 535–552. https://doi.org/10.5194/hess-10-535-2006

Fonseca, C. R., & Ganade, G. (2001). Species functional redundancy, random extinctions and the stability of ecosystems. *Journal of Ecology*, *89*(1), 118–125. https://doi.org/10.1046/j.1365-2745.2001.00528.x

Fournier, R. J., de Mendoza, G., Sarremejane, R., & Ruhi, A. (2023). Isolation controls reestablishment mechanisms and post-drying community structure in an intermittent stream. *Ecology*, *104*(2), e3911. https://doi.org/10.1002/ecy.3911

Franklin, P., Dunbar, M., & Whitehead, P. (2008). Flow controls on lowland river macrophytes: A review. *Science of the Total Environment*, *400*(1–3), 369–378. https://doi.org/10.1016/j.scitotenv.2008.06.018

Fuller, M. R., Doyle, M. W., & Strayer, D. L. (2015). Causes and consequences of habitat fragmentation in river networks. *Annals of the New York Academy of Sciences*, *1355*(1), 31–51. https://doi.org/10.1111/nyas.12853

Garssen, A. G., Verhoeven, J. T., & Soons, M. B. (2014). Effects of climate-induced increases in summer drought on riparian plant species: A meta-analysis. *Freshwater Biology*, *59*(5), 1052–1063. https://doi.org/10.1111/fwb.12328

Gido, K. B., Whitney, J. E., Perkin, J. S., & Turner, T. F. (2016). Fragmentation, connectivity and fish species persistence in freshwater ecosystems. In G. P. Closs, M. Krkosek, & J. D. Olden (Eds.), *Conservation of freshwater fishes* (pp. 292–323). Cambridge University Press.

Giling, D., Reich, P., & Thompson, R. M. (2009). Loss of riparian vegetation alters the ecosystem role of a freshwater crayfish (*Cherax destructor*) in an Australian intermittent lowland stream. *Journal of the North American Benthological Society*, *28*(3), 626–637. https://doi.org/10.1899/09-015.1

Giling, D. P., Reich, P., & Thompson, R. M. (2012). Riparian vegetation removal alters consumer–resource stoichiometry in an Australian lowland stream. *Marine and Freshwater Research*, *63*(1), 1–8. https://doi.org/10.1071/MF11092

Gómez, R., Arce, M. I., Baldwin, D. S., & Dahm, C. N. (2017). Water physicochemistry in intermittent rivers and ephemeral streams. In T. Datry, N. Bonada, & A. Boulton (Eds.), *Intermittent rivers and ephemeral streams: Ecology and management* (pp. 109–134). Academic Press. https://doi.org/10.1016/B978-0-12-803835-2.00005-X

Grabowski, R. C., Gurnell, A. M., Burgess-Gamble, L., England, J., Holland, D., Klaar, M. J., Morrissey, I., Uttley, C., & Wharton, G. (2019). The current state of the use of large wood in river restoration and management. *Water and Environment Journal*, *33*(3), 366–377. https://doi.org/10.1111/wej.12465

Graham, D. J., Bierkens, M. F., & van Vliet, M. T. (2024). Impacts of droughts and heatwaves on river water quality worldwide. *Journal of Hydrology*, *629*, 130590. https://doi.org/10.1016/j.jhydrol.2023.130590

Greene, C. M., Hall, J. E., Guilbault, K. R., & Quinn, T. P. (2010). Improved viability of populations with diverse life-history portfolios. *Biology Letters*, *6*(3), 382–386. https://doi.org/10.1098/rsbl.2009.0780

Grill, G., Lehner, B., Lumsdon, A. E., MacDonald, G. K., Zarfl, C., & Liermann, C. R. (2015). An index-based framework for assessing patterns and trends in river fragmentation and flow regulation by global dams at multiple scales. *Environmental Research Letters*, *10*(1), 015001. https://doi.org/10.1088/1748-9326/10/1/015001

Guerreiro, S. B., Dawson, R. J., Kilsby, C., Lewis, E., & Ford, A. (2018). Future heat-waves, droughts and floods in 571 European cities. *Environmental Research Letters*, *13*(3), 034009. https://doi.org/10.1088/1748-9326/aaaad3

Gunderson, L. H. (2000). Ecological resilience—In theory and application. *Annual Review of Ecology and Systematics*, *31*(1), 425–439. https://doi.org/10.1146/annurev.ecolsys.31.1.425

Gurnell, A. M., Bertoldi, W., & Corenblit, D. (2012). Changing river channels: The roles of hydrological processes, plants and pioneer fluvial landforms in humid temperate, mixed load, gravel bed rivers. *Earth-Science Reviews*, *111*(1–2), 129–141. https://doi.org/10.1016/j.earscirev.2011.11.005

Gurnell, A. M., Van Oosterhout, M. P., De Vlieger, B., & Goodson, J. M. (2006). Reach-scale interactions between aquatic plants and physical habitat: River Frome, Dorset. *River Research and Applications*, *22*(6), 667–680. https://doi.org/10.1002/rra.929

Haase, P., Bowler, D. E., Baker, N. J., Bonada, N., Domisch, S., Garcia Marquez, J. R., Heino, J., Hering, D., Jähnig, S. C., Schmidt-Kloiber, A., Stubbington, R., Altermatt, F., Álvarez-Cabria, M., Amatulli, G., Angeler, D. G., Archambaud-Suard, G., Jorrín, I. A., Aspin, T., … Welti, E. A. R. (2023). The recovery of European freshwater biodiversity has come to a halt. *Nature*, *620*, 582–588. https://doi.org/10.1038/s41586-023-06400-1

Häder, D. P., & Barnes, P. W. (2019). Comparing the impacts of climate change on the responses and linkages between terrestrial and aquatic ecosystems. *Science of the Total Environment*, *682*, 239–246. https://doi.org/10.1016/j.scitotenv.2019.05.024

Haile, G. G., Tang, Q., Li, W., Liu, X., & Zhang, X. (2020). Drought: Progress in broadening its understanding. *WIREs Water*, *7*(2), e1407. https://doi.org/10.1002/wat2.1407

Hakala, J. P., & Hartman, K. J. (2004). Drought effect on stream morphology and brook trout (*Salvelinus fontinalis*) populations in forested headwater streams. *Hydrobiologia*, *515*, 203–213. https://doi.org/10.1023/B:HYDR.0000027330.12182.24

Hammond, J. C., Simeone, C., Hecht, J. S., Hodgkins, G. A., Lombard, M., McCabe, G., Wolock, D., Wieczorek, M., Olson, C., Caldwell, T., Dudley, R., & Price, A. N. (2022). Going beyond low flows: Streamflow drought deficit and duration illuminate distinct spatiotemporal drought patterns and trends in the US during the last century. *Water Resources Research*, *58*(9), e2022WR031930. https://doi.org/10.1029/2022WR031930

Hannaford, J. (2015). Climate-driven changes in UK river flows: A review of the evidence. *Progress in Physical Geography*, *39*(1), 29–48. https://doi.org/10.1177/0309133314536755

Hannaford, J., & Buys, G. (2012). Seasonal trends in river flow regimes and extremes in the UK. *Journal of Hydrology*, *475*, 158–174. https://doi.org/10.1016/j.jhydrol.2012.09.044

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

Harper, M. P., & Peckarsky, B. L. (2006). Emergence cues of a mayfly in a high-altitude stream ecosystem: Potential response to climate change. *Ecological Applications*, *16*(2), 612–621. https://doi.org/10.1890/1051-0761(2006)016[0612:ECOAMI]2.0.CO;2

Harpold, A. A., Dettinger, M., & Rajagopal, S. (2017). Defining snow drought and why it matters. *Eos*, *98*, 15–17. https://doi.org/10.1029/2017EO068775

Harris, R. M., Beaumont, L. J., Vance, T. R., Tozer, C. R., Remenyi, T. A., Perkins-Kirkpatrick, S. E., Mitchell, P. J., Nicotra, A. B., McGregor, S., Andrew, N. R., Letnic, M., Kearney, M. R., Wernberg, T., Hutley, L. B., Chambers, L. E., Fletcher, M.-S., Keatley, M. R., Woodward, C. A., Williamson, G., … Bowman, D. M. J. S. (2018). Biological responses to the press and pulse of climate trends and extreme events. *Nature Climate Change*, *8*(7), 579–587. https://doi.org/10.1038/s41558-018-0187-9

Harvey, G. L., & Henshaw, A. J. (2023). Rewilding and the water cycle. *WIREs Water*, *10*(6), e1686. https://doi.org/10.1002/wat2.1686

Harvey, G. L., Henshaw, A. T., Henshaw, A. J., Zhan, Z., Clarke, S. J., Sandom, C. J., England, J., King, S., & Venn, O. (2024). The role of rewilding in mitigating hydrological extremes: State of the evidence. *WIREs Water*, *11*, e1710. https://doi.org/10.1002/wat2.1710

Henriques, C., Garnett, K., Weatherhead, E. K., Lickorish, F. A., Forrow, D., & Delgado, J. (2015). The future water environment—Using scenarios to explore the significant water management challenges in England and Wales to 2050. *Science of the Total Environment*, *512*, 381–396. https://doi.org/10.1016/j.scitotenv.2014.12.047

Hill, M. J., Mathers, K. L., Little, S., Worrall, T., Gunn, J., & Wood, P. J. (2019). Ecological effects of a supra-seasonal drought on macroinvertebrate communities differ between near-perennial and ephemeral river reaches. *Aquatic Sciences*, *81*, 62. https://doi.org/10.1007/s00027-019-0659-7

Hillebrand, H., & Kunze, C. (2020). Meta-analysis on pulse disturbances reveals differences in functional and compositional recovery across ecosystems. *Ecology Letters*, *23*(3), 575–585. https://doi.org/10.1111/ele.13457

Holmes, N. T. H. (1999). Recovery of headwater stream flora following the 1989–1992 groundwater drought. *Hydrological Processes*, *13*(3), 341–354. https://doi.org/10.1002/(SICI)1099-1085(19990228)13:3%3C341::AID-HYP742%3E3.0.CO;2-L

Hosen, J. D., Aho, K. S., Appling, A. P., Creech, E. C., Fair, J. H., Hall, R. O., Jr., Kyzivat, E. D., Lowenthal, R. S., Matt, S., Morrison, J., Saiers, J. E., Shanley, J. B., Weber, L. C., Yoon, B., & Raymond, P. A. (2019). Enhancement of primary production during drought in a temperate watershed is greater in larger rivers than headwater streams. *Limnology and Oceanography*, *64*(4), 1458–1472. https://doi.org/10.1002/lno.11127

Huml, J. V., Harris, W. E., Taylor, M. I., Sen, R., Prudhomme, C., & Ellis, J. S. (2020). Pollution control can help mitigate future climate change impact on European grayling in the UK. *Diversity and Distributions*, *26*(4), 17–532. https://doi.org/10.1111/ddi.13039

Hwan, J. L., & Carlson, S. M. (2016). Fragmentation of an intermittent stream during seasonal drought: Intra-annual and interannual patterns and biological consequences. *River Research and Applications*, *32*(5), 856–870. https://doi.org/10.1002/rra.2907

Hynes, H. B. N. (1958). The effect of drought on the fauna of a small mountain stream in Wales. *Internationale Vereinigung für Theoretische und Angewandte Limnologie: Verhandlungen*, *13*(2), 826–833. https://doi.org/10.1080/03680770.1956.11895473

IPCC (Intergovernmental Panel on Climate Change). (2022). Climate change 2022: Impacts, adaptation and vulnerability. In *Contribution of working group II to the sixth assessment report of the intergovernmental panel on climate change* (p. 3056). Cambridge University Press. https://doi.org/10.1017/9781009325844

IUCN (International Union for Conservation of Nature). (2023). *White-clawed crayfish*[Online]. IUCN. https://www.iucnredlist.org/species/2430/9438817

Jaeger, K. L., Olden, J. D., & Pelland, N. A. (2014). Climate change poised to threaten hydrologic connectivity and endemic fishes in dryland streams. *Proceedings of the National Academy of Sciences*, *111*(38), 13894–13899. https://doi.org/10.1073/pnas.1320890111

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

Jenkins, R. K. B., & Ormerod, S. J. (1996). The influence of a river bird, the dipper (*Cinclus cinclus*), on the behaviour and drift of its invertebrate prey. *Freshwater Biology*, *35*(1), 45–56. https://doi.org/10.1046/j.1365-2427.1996.d01-442.x

Johnson, M. F., Albertson, L. K., Algar, A. C., Dugdale, S. J., Edwards, P., England, J., Gibbins, C., Kazama, S., Komori, D., MacColl, A. D. C., Scholl, E. A., Wilby, R. L., de Oliveira Roque, F., & Wood, P. J. (2024). Rising water temperature in rivers: Ecological impacts and future resilience. *WIREs Water*, e1724. https://doi.org/10.1002/wat2.1724

Johnson, M. F., Wilby, R. L., & Toone, J. A. (2014). Inferring air–water temperature relationships from river and catchment properties. *Hydrological Processes*, *28*(6), 2912–2928. https://doi.org/10.1002/hyp.9842

Johnstone, J. F., Allen, C. D., Franklin, J. F., Frelich, L. E., Harvey, B. J., Higuera, P. E., Mack, M. C., Meentemeyer, R. K., Metz, M. R., Perry, G. L. W., Schoennagel, T., & Turner, M. G. (2016). Changing disturbance regimes, ecological memory, and forest resilience. *Frontiers in Ecology and the Environment*, *14*(7), 369–378. https://doi.org/10.1002/fee.1311

Jones, J., Börger, L., Tummers, J., Jones, P., Lucas, M., Kerr, J., Kemp, P., Bizzi, S., Conseuegra, S., Marcello, L., Vowles, A., Belletti, B., Verspoor, E., Van de Bund, W., Gough, P., & Garcia de Leaniz, C. (2019). A comprehensive assessment of stream fragmentation in Great Britain. *Science of the Total Environment*, *673*, 756–762. https://doi.org/10.1016/j.scitotenv.2019.04.125

Jones, M. R., Fowler, H. J., Kilsby, C. G., & Blenkinsop, S. (2013). An assessment of changes in seasonal and annual extreme rainfall in the UK between 1961 and 2009. *International Journal of Climatology*, *33*(5), 1178–1194. https://doi.org/10.1002/joc.3503

Kay, A. L., Bell, V. A., Davies, H. N., Lane, R. A., & Rudd, A. C. (2023). The UKSCAPE-G2G river flow and soil moisture datasets: Grid-to-grid model estimates for the UK for historical and potential future climates. *Earth System Science Data Discussions*, *15*(6), 2533–2546. https://doi.org/10.5194/essd-2022-439

Kendon, M., Marsh, T., & Parry, S. (2013). The 2010–2012 drought in England and Wales. *Weather*, *68*(4), 88–95. https://doi.org/10.1002/wea.2101

Kendon, M., McCarthy, M., Jevrejeva, S., Matthews, A., Williams, J., Sparks, T., & West, F. (2023). State of the UK climate 2022. *International Journal of Climatology*, *43*(S1), 1–82. https://doi.org/10.1002/joc.8167

Kirby, K. J., Reid, C. M., Thomas, R. C., & Goldsmith, F. B. (1998). Preliminary estimates of fallen dead wood and standing dead trees in managed and unmanaged forests in Britain. *Journal of Applied Ecology*, *35*(1), 148–155. https://doi.org/10.1046/j.1365-2664.1998.00276.x

Kovach, R. P., Dunham, J. B., Al-Chokhachy, R., Snyder, C. D., Letcher, B. H., Young, J. A., Beever, E. A., Pederson, G. T., Lynch, A. J., Hitt, N. P., Konrad, C. P., Jaeger, K. L., Rea, A. H., Sepulveda, A. J., Lambert, P. M., Stoker, J., Giersch, J. J., & Muhlfeld, C. C. (2019). An integrated framework for ecological drought across riverscapes of North America. *Bioscience*, *69*(6), 418–431. https://doi.org/10.1093/biosci/biz040

Krabbenhoft, C. A., Allen, G. H., Lin, P., Godsey, S. E., Allen, D. C., Burrows, R. M., DelVecchia, A. G., Fritz, K. M., Shanafield, M., Burgin, A. J., Zimmer, M. A., Datry, T., Dodds, W. K., Jones, C. N., Mims, M. C., Franklin, C., Hammond, J. C., Zipper, S., Ward, A. S., … Olden, J. D. (2022). Assessing placement bias of the global river gauge network. *Nature Sustainability*, *5*, 586–592. https://doi.org/10.1038/s41893-022-00873-0

Kreibich, H., Van Loon, A. F., Schröter, K., Ward, P. J., Mazzoleni, M., Sairam, N., Abeshu, G. W., Agafonova, S., AghaKouchak, A., Aksoy, H., Alvarez-Garreton, C., Aznar, B., Balkhi, L., Barendrecht, M. H., Biancamaria, S., Bos-Burgering, L., Bradley, C., Budiyono, Y., Buytaert, W., … Di Baldassarre, G. (2022). The challenge of unprecedented floods and droughts in risk management. *Nature*, *608*(7921), 80–86. https://doi.org/10.1038/s41586-022-04917-5

Ladle, M., & Bass, J. A. B. (1981). The ecology of a small chalk stream and its responses to drying during drought conditions. *Archiv für Hydrobiologie*, *90*(4), 448–466.

Lake, P. S. (2000). Disturbance, patchiness, and diversity in streams. *Journal of the North American Benthological Society*, *19*(4), 573–592. https://doi.org/10.2307/1468118

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

Lake, P. S. (2011). *Drought and aquatic ecosystems: Effects and responses*. John Wiley & Sons.

Lancaster, J., & Belyea, L. R. (1997). Nested hierarchies and scale-dependence of mechanisms of flow refugium use. *Journal of the North American Benthological Society*, *16*(1), 221–238. https://doi.org/10.2307/1468253

Lane, S. N. (2017). Natural flood management. *WIREs Water*, *4*(3), e1211. https://doi.org/10.1002/wat2.1211

Ledger, M. E., Brown, L. E., Edwards, F. K., Milner, A. M., & Woodward, G. (2013). Drought alters the structure and functioning of complex food webs. *Nature Climate Change*, *3*, 223–227. https://doi.org/10.1038/nclimate1684

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., & Hildrew, A. G. (2001). Recolonization by the benthos of an acid stream following a drought. *Archiv für Hydrobiologie*, *152*(1), 1–17. https://doi.org/10.1127/archiv-hydrobiol/152/2001/1

Ledger, M. E., & Milner, A. M. (2015). Extreme events in running waters. *Freshwater Biology*, *60*(12), 2455–2460. https://doi.org/10.1111/fwb.12673

Leigh, C., Bush, A., Harrison, E. T., Ho, S. S., Luke, L., Rolls, R. J., & Ledger, M. E. (2015). Ecological effects of extreme climatic events on riverine ecosystems: Insights from Australia. *Freshwater Biology*, *60*(12), 2620–2638. https://doi.org/10.1111/fwb.12515

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*, 71–92. https://doi.org/10.1007/s11160-018-09545-9

Lu, X., Gray, C., Brown, L. E., Ledger, M. E., Milner, A. M., Mondragón, R. J., Woodward, G., & Ma, A. (2016). Drought rewires the cores of food webs. *Nature Climate Change*, *6*, 875–878. https://doi.org/10.1038/nclimate3002

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

Magoulick, D. D., & Kobza, R. M. (2003). The role of refugia for fishes during drought: A review and synthesis. *Freshwater Biology*, *48*(7), 1186–1198. https://doi.org/10.1046/j.1365-2427.2003.01089.x

Mann, R. H. K., Blackburn, J. H., & Beaumont, W. R. C. (1989). The ecology of brown trout *Salmo trutta* in English chalk streams. *Freshwater Biology*, *21*(1), 57–70. https://doi.org/10.1111/j.1365-2427.1989.tb01348.x

Marsh, T. (2014). *The UK drought of 2003: An overview*. Centre for Ecology & Hydrology; British Geological Survey. https://nora.nerc.ac.uk/id/eprint/510184/1/N510184CR.pdf

Matthews, W. J., & Marsh-Matthews, E. (2003). Effects of drought on fish across axes of space, time and ecological complexity. *Freshwater Biology*, *48*(7), 1232–1253. https://doi.org/10.1046/j.1365-2427.2003.01087.x

Mazdiyasni, O., & AghaKouchak, A. (2015). Substantial increase in concurrent droughts and heatwaves in the United States. *Proceedings of the National Academy of Sciences*, *112*(37), 11484–11489. https://doi.org/10.1073/pnas.1422945112

McMahon, T. A., & Finlayson, B. L. (2003). Droughts and anti-droughts: The low flow hydrology of Australian rivers. *Freshwater Biology*, *48*(7), 1147–1160. https://doi.org/10.1046/j.1365-2427.2003.01098.x

Messager, M. L., Lehner, B., Cockburn, C., Lamouroux, N., Pella, H., Snelder, T., Tockner, K., Trautmann, T., Watt, C., & Datry, T. (2021). Global prevalence of non-perennial rivers and streams. *Nature*, *594*, 391–397. https://doi.org/10.1038/s41586-021-03565-5

Met Office. (2023). *UK and global extreme events—Drought*[Online]. Met Office. https://www.metoffice.gov.uk/research/climate/understanding-climate/uk-and-global-extreme-events-drought

Milly, P. C., Betancourt, J., Falkenmark, M., Hirsch, R. M., Kundzewicz, Z. W., Lettenmaier, D. P., & Stouffer, R. J. (2008). Stationarity is dead: Whither water management? *Science*, *319*(5863), 573–574. https://doi.org/10.1126/science.1151915

Moidu, H., Rodríguez-Lozano, P., Leidy, R. A., Bogan, M. T., Grantham, T. E., & Carlson, S. M. (2023). Ecological consequences of shifting habitat mosaics within and across years in an intermittent stream. *Freshwater Biology*, *68*(7), 1161–1175. https://doi.org/10.1111/fwb.14094

Morris, R. K. A., & Ball, S. G. (2021). Death by one hundred droughts: Is climate change already driving biodiversity declines in Britain? *British Wildlife*, *33*(1), 13–20.

Mosley, L. M. (2015). Drought impacts on the water quality of freshwater systems; review and integration. *Earth-Science Reviews*, *140*, 203–214. https://doi.org/10.1016/j.earscirev.2014.11.010

Müller, L. M., & Bahn, M. (2022). Drought legacies and ecosystem responses to subsequent drought. *Global Change Biology*, *28*(17), 5086–5103. https://doi.org/10.1111/gcb.16270

Munson, S. M., Bradford, J. B., & Hultine, K. R. (2021). An integrative ecological drought framework to span plant stress to ecosystem transformation. *Ecosystems*, *24*, 739–754. https://doi.org/10.1007/s10021-020-00555-y

New, M., Lopez, A., Dessai, S., & Wilby, R. (2007). Challenges in using probabilistic climate change information for impact assessments: An example from the water sector. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, *365*(1857), 2117–2131. https://doi.org/10.1098/rsta.2007.2080

NIDIS (National Integrated Drought Information System). (2023). *What is drought: Ecological drought* [Online]. NIDIS. https://www.drought.gov/what-is-drought/ecological-drought

Niemi, G. J., DeVore, P., Detenbeck, N., Taylor, D., Lima, A., Pastor, J., Yount, J. D., & Naiman, R. J. (1990). Overview of case studies on recovery of aquatic systems from disturbance. *Environmental Management*, *14*, 571–587. https://doi.org/10.1007/BF02394710

O'Hare, M. T., Mountford, J. O., Maroto, J., & Gunn, I. D. M. (2016). Plant traits relevant to fluvial geomorphology and hydrological interactions. *River Research and Applications*, *32*(2), 179–189. https://doi.org/10.1002/rra.2940

Parasiewicz, P., King, E. L., Webb, J. A., Piniewski, M., Comoglio, C., Wolter, C., Buijse, A., Bjerklie, D., Vezza, P., Melcher, A., & Suska, K. (2019). The role of floods and droughts on riverine ecosystems under a changing climate. *Fisheries Management and Ecology*, *26*(6), 461–473. https://doi.org/10.1111/fme.12388

Pařil, P., Leigh, C., Polášek, M., Sarremejane, R., Řezníčková, P., Dostálová, A., & Stubbington, R. (2019). Short-term streambed drying events alter amphipod population structure in a central European stream. *Fundamental and Applied Limnology*, *193*(1), 51–64. https://doi.org/10.1127/fal/2019/1164

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, *37*, 637–669. https://doi.org/10.1146/annurev.ecolsys.37.091305.110100

Parr, L. B., & Mason, C. F. (2003). Long-term trends in water quality and their impact on macroinvertebrate assemblages in eutrophic lowland rivers. *Water Research*, *37*(12), 2969–2979. https://doi.org/10.1016/S0043-1354(03)00115-5

Parry, S., Mackay, J. D., Chitson, T., Hannaford, J., Bell, V. A., Facer-Childs, K., Kay, A., Lane, R., Moore, R. J., Turner, S., & Wallbank, J. (2024). Divergent future drought projections in UK river flows and groundwater levels. *Hydrology and Earth System Sciences Discussions*, *28*, 417–440. https://doi.org/10.5194/hess-28-417-2024

Parry, S., Prudhomme, C., Wilby, R. L., & Wood, P. J. (2016). Drought termination: Concept and characterisation. *Progress in Physical Geography*, *40*(6), 743–767. https://doi.org/10.1177/0309133316652801

Parry, S., Wilby, R. L., Prudhomme, C., & Wood, P. J. (2016). A systematic assessment of drought termination in the United Kingdom. *Hydrology and Earth System Sciences*, *20*(10), 4265–4281. https://doi.org/10.5194/hess-20-4265-2016

Pendergrass, A. G., Meehl, G. A., Pulwarty, R., Hobbins, M., Hoell, A., AghaKouchak, A., Bonfils, C. J. W., Gallant, A. J. E., Hoerling, M., Hoffmann, D., Kaatz, L., Lehner, F., Llewellyn, D., Mote, P., Neale, R. B., Overpeck, J. T., Sheffield, A., Stahl, K., Svoboda, M., …

Woodhouse, C. A. (2020). Flash droughts present a new challenge for subseasonal-to-seasonal prediction. *Nature Climate Change*, *10*(3), 191–199. https://doi.org/10.1038/s41558-020-0709-0

Perkin, J. S., Gido, K. B., Costigan, K. H., Daniels, M. D., & Johnson, E. R. (2015). Fragmentation and drying ratchet down Great Plains stream fish diversity. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *25*(5), 639–655. https://doi.org/10.1002/aqc.2501

Perkin, J. S., Gido, K. B., Falke, J. A., Fausch, K. D., Crockett, H., Johnson, E. R., & Sanderson, J. (2017). Groundwater declines are linked to changes in Great Plains stream fish assemblages. *Proceedings of the National Academy of Sciences*, *114*(28), 7373–7378. https://doi.org/10.1073/pnas.1618936114

Perkin, J. S., Shattuck, Z. R., Gerken, J. E., & Bonner, T. H. (2013). Fragmentation and drought legacy correlate with distribution of burrhead chub in subtropical streams of North America. *Transactions of the American Fisheries Society*, *142*(5), 1287–1298. https://doi.org/10.1080/00028487.2013.806352

Perrow, M., Leeming, D., England, J., & Tomlinson, M. (2007). Life after low flow—Ecological recovery of the river Misbourne. *British Wildlife*, *18*(5), 335–346.

Peterken, G. F., & Jones, E. W. (1987). Forty years of change in Lady Park Wood: The old-growth stands. *Journal of Ecology*, *75*(2), 477–512. https://doi.org/10.2307/2260429

Peterken, G. F., & Mountford, E. P. (1996). Effects of drought on beech in Lady Park Wood, an unmanaged mixed deciduous woodland. *Forestry: An International Journal of Forest Research*, *69*(2), 125–136. https://doi.org/10.1093/forestry/69.2.125

Piano, E., Doretto, A., Falasco, E., Gruppuso, L., Fenoglio, S., & Bona, F. (2019). The role of recurrent dewatering events in shaping ecological niches of scrapers in intermittent alpine streams. *Hydrbiologia*, *841*, 177–189. https://doi.org/10.1007/s10750-019-04021-2

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

Portela, A. P., Gonçalves, J., Durance, I., Vieira, C., & Honrado, J. (2023). Riparian forest response to extreme drought is influenced by climatic context and canopy structure. *Science of the Total Environment*, *881*, 163128. https://doi.org/10.1016/j.scitotenv.2023.163128

Power, M. E., Tilman, D., Estes, J. A., Menge, B. A., Bond, W. J., Mills, L. S., Daily, G., Castilla, J. C., Lubchenco, J., & Paine, R. T. (1996). Challenges in the quest for keystones: Identifying keystone species is difficult—but essential to understanding how loss of species will affect ecosystems. *Bioscience*, *46*(8), 609–620. https://doi.org/10.2307/1312990

Reich, P., Lake, P. S., Thomson, J. R., Daniel, T., Johnson, M., Metzeling, L., Boulton, A. J., & Hale, R. (2023). Aquatic invertebrate responses to riparian restoration and flow extremes in three degraded intermittent streams: An eight-year field experiment. *Freshwater Biology*, *68*(2), 325–339. https://doi.org/10.1111/fwb.14028

Resh, V. H., Brown, A. V., Covich, A. P., Gurtz, M. E., Li, H. W., Minshall, G. W., Reice, S. R., Sheldon, A. L., Wallace, B., & Wissmar, R. C. (1988). The role of disturbance in stream ecology. *Journal of the North American Benthological Society*, *7*(4), 433–455. https://doi.org/10.2307/1467300

Robinson, C. T., Reed, L. M., & Minshall, G. W. (1992). Influence of flow regime on life history, production and genetic structure of *Baetis tricaudatus* (Ephemeroptera) and *Hesperoperla pacifica* (Plecoptera). *Journal of the North American Benthological Society*, *11*(3), 278–289. https://doi.org/10.2307/1467648

Robson, B. J., Chester, E. T., & Austin, C. M. (2011). Why life history information matters: Drought refuges and macroinvertebrate persistence in non-perennial streams subject to a drier climate. *Marine and Freshwater Research*, *62*(7), 801–810. https://doi.org/10.1071/MF10062

Robson, B. J., & Matthews, T. G. (2004). Drought refuges affect algal recolonization in intermittent streams. *River Research and Applications*, *20*(7), 753–763. https://doi.org/10.1002/rra.789

Rohde, M. M. (2023). Floods and droughts are intensifying globally. *Nature Water*, *1*, 226–227. https://doi.org/10.1038/s44221-023-00047-y

Rosenfeld, J. S. (2002). Functional redundancy in ecology and conservation. *Oikos*, *98*(1), 156–162. https://doi.org/10.1034/j.1600-0706.2002.980116.x

Rudd, A. C., Kay, A. L., & Bell, V. A. (2019). National-scale analysis of future river flow and soil moisture droughts: Potential changes in drought characteristics. *Climatic Change*, *156*(3), 323–340. https://doi.org/10.1007/s10584-019-02528-0

Ryo, M., Aguilar-Trigueros, C. A., Pinek, L., Muller, L. A., & Rillig, M. C. (2019). Basic principles of temporal dynamics. *Trends in Ecology & Evolution*, *34*(8), 723–733. https://doi.org/10.1016/j.tree.2019.03.007

Sarremejane, R., England, J., Sefton, C. E., Parry, S., Eastman, M., & Stubbington, R. (2020). Local and regional drivers influence how aquatic community diversity, resistance and resilience vary in response to drying. *Oikos*, *129*(12), 1877–1890. https://doi.org/10.1111/oik.07645

Sarremejane, R., Messager, M. L., & Datry, T. (2022). Drought in intermittent river and ephemeral stream networks. *Ecohydrology*, *15*(5), e2390. https://doi.org/10.1002/eco.2390

Sarremejane, R., Mykrä, H., Huttunen, K. L., Mustonen, K. R., Marttila, H., Paavola, R., Veijalainen, N., & Muotka, T. (2018). Climate-driven hydrological variability determines inter-annual changes in stream invertebrate community assembly. *Oikos*, *127*(11), 1586–1595. https://doi.org/10.1111/oik.05329

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., 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. *Journal of Animal Ecology*, *90*(4), 886–898. https://doi.org/10.1111/1365-2656.13417

Schälchli, U. (1992). The clogging of coarse gravel river beds by fine sediment. *Hydrobiologia*, *235*, 189–197. https://doi.org/10.1007/BF00026211

Scheffer, M., Carpenter, S., Foley, J. A., Folke, C., & Walker, B. (2001). Catastrophic shifts in ecosystems. *Nature*, *413*, 591–596. https://doi.org/10.1038/35098000

Schwalm, C. R., Anderegg, W. R. L., Michalak, A. M., Fisher, J. B., Biondi, F., Koch, G., Litvak, M., Ogle, K., Shaw, J. D., Wolf, A., Huntzinger, D. N., Schaefer, K., Cook, R., Wei, Y., Fang, Y., Hayes, D., Huang, M., Jain, A., & Tian, H. (2017). Global patterns of drought recovery. *Nature*, *548*(7666), 202–205. https://doi.org/10.1038/nature23021

Sear, D. A., Armitage, P. D., & Dawson, F. H. (1999). Groundwater dominated rivers. *Hydrological Processes*, *13*(3), 255–276. https://doi.org/10.1002/(SICI)1099-1085(19990228)13:3%3C255::AID-HYP737%3E3.0.CO;2-Y

Sefton, C. E. M., Parry, S., England, J., & Angell, G. (2019). Visualising and quantifying the variability of hydrological state in intermittent rivers. *Fundamental and Applied Limnology*, *193*(1), 21–38. https://doi.org/10.1127/fal/2019/1149

Seneviratne, S. I., Nicholls, N., Easterling, D., Goodess, C. M., Kanae, S., Kossin, J., Luo, Y., Marengo, J., McInnes, K., Rahimi, M., Reichstein, M., Sorteberg, A., Vera, C., & Zhang, X. (2012). Changes in climate extremes and their impacts on the natural physical environment. In C. B. Field, V. Barros, T. F. Stocker, D. Qin, D. J. Dokken, K. L. Ebi, M. D. Mastrandrea, K. J. Mach, G.-K. Plattner, S. K. Allen, M. Tignor, & P. M. Midgley (Eds.), *Managing the risks of extreme events and disasters to advance climate change adaptation: A special report of working groups I and II of the Intergovernmental Panel on Climate Change (IPCC)* (pp. 109–230). Cambridge University Press. https://www.ipcc.ch/site/assets/uploads/2018/03/SREX-Chap3_FINAL-1.pdf

Slette, I. J., Post, A. K., Awad, M., Even, T., Punzalan, A., Williams, S., Smith, M. D., & Knapp, A. K. (2019). How ecologists define drought, and why we should do better. *Global Change Biology*, *25*(10), 3193–3200. https://doi.org/10.1111/gcb.14747

Smith, K. H., Tyre, A. J., Tang, Z., Hayes, M. J., & Akyuz, F. A. (2020). Calibrating human attention as indicator monitoring #drought in the Twittersphere. *Bulletin of the American Meteorological Society*, *101*(10), E1801–E1819. https://doi.org/10.1175/BAMS-D-19-0342.1

Smith, M. D. (2011). An ecological perspective on extreme climatic events: A synthetic definition and framework to guide future research. *Journal of Ecology*, *99*(3), 656–663. https://doi.org/10.1111/j.1365-2745.2011.01798.x

Spinoni, J., Naumann, G., Vogt, J., & Barbosa, P. (2015). European drought climatologies and trends based on a multi-indicator approach. *Global and Planetary Change*, *127*, 50–57. https://doi.org/10.1016/j.gloplacha.2015.01.012

Spinoni, J., Vogt, J. V., Naumann, G., Barbosa, P., & Dosio, A. (2018). Will drought events become more frequent and severe in Europe? *International Journal of Climatology*, *38*(4), 1718–1736. https://doi.org/10.1002/joc.5291

Stoelzle, M., Stahl, K., Morhard, A., & Weiler, M. (2014). Streamflow sensitivity to drought scenarios in catchments with different geology. *Geophysical Research Letters*, *41*(17), 6174–6183. https://doi.org/10.1002/2014GL061344

Strachan, S. R., Chester, E. T., & Robson, B. J. (2015). Freshwater invertebrate life history strategies for surviving desiccation. *Springer Science Reviews*, *3*, 57–75. https://doi.org/10.1007/s40362-015-0031-9

Stubbington, R. (2012). The hyporheic zone as an invertebrate refuge: A review of variability in space, time, taxa and behaviour. *Marine and Freshwater Research*, *63*(4), 293–311. https://doi.org/10.1071/MF11196

Stubbington, R., England, J., Wood, P. J., & Sefton, C. E. (2017). Temporary streams in temperate zones: Recognizing, monitoring and restoring transitional aquatic-terrestrial ecosystems. *WIREs Water*, *4*(4), e1223. https://doi.org/10.1002/wat2.1223

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

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

Stubbington, R., & Wood, P. J. (2013). Benthic and interstitial habitats of a lentic spring as invertebrate refuges during supra-seasonal drought. *Fundamental and Applied Limnology*, *182*(1), 61–73. https://doi.org/10.1127/1863-9135/2013/0409

Stubbington, R., Wood, P. J., & Boulton, A. J. (2009). Low flow controls on benthic and hyporheic macroinvertebrate assemblages during supra-seasonal drought. *Hydrological Processes*, *23*(15), 2252–2263. https://doi.org/10.1002/hyp.7290

Stubbington, R., Dimon, J., England, J., & Watts, G. (2022). *Chalk streams of the future: The effects of climate change on biodiversity in England's iconic river ecosystems* (p. 18). Nottingham Trent University. https://doi.org/10.6084/m9.figshare.21663269

Sutanto, S. J., Vitolo, C., Di Napoli, C., D'Andrea, M., & Van Lanen, H. A. (2020). Heatwaves, droughts, and fires: Exploring compound and cascading dry hazards at the pan-European scale. *Environment International*, *134*, 105276. https://doi.org/10.1016/j.envint.2019.105276

Szejner, P., Belmecheri, S., Ehleringer, J. R., & Monson, R. K. (2020). Recent increases in drought frequency cause observed multi-year drought legacies in the tree rings of semi-arid forests. *Oecologia*, *192*, 241–259. https://doi.org/10.1007/s00442-019-04550-6

Tachet, H., Richoux, P., Bournaud, M., & Usseglio-Polatera, P. (2010). *Invertébrés d'Eau Douce: Systématique, Biologie, Écologie*. CNRS Éditions.

Tanguy, M., Chevuturi, A., Marchant, B. P., Mackay, J. D., Parry, S., & Hannaford, J. (2023). How will climate change affect the spatial coherence of streamflow and groundwater droughts in Great Britain? *Environmental Research Letters*, *18*(6), 064048. https://doi.org/10.1088/1748-9326/acd655

Tassone, S. J., Besterman, A. F., Buelo, C. D., Ha, D. T., Walter, J. A., & Pace, M. L. (2023). Increasing heatwave frequency in streams and rivers of the United States. *Limnology and Oceanography Letters*, *8*(2), 295–304. https://doi.org/10.1002/lol2.10284

Thoms, M. C. (2006). Variability in riverine ecosystems. *River Research and Applications*, *22*(2), 115–121. https://doi.org/10.1002/rra.900

Tornwall, B. M., Swan, C. M., & Brown, B. L. (2017). Manipulation of local environment produces different diversity outcomes depending on location within a river network. *Oecologia*, *184*, 663–674. https://doi.org/10.1007/s00442-017-3891-7

Tramblay, Y., Rutkowska, A., Sauquet, E., Sefton, C., Laaha, G., Osuch, M., Albuquerque, T., Alves, M. H., Banasik, K., Beaufort, A., Brocca, L., Camici, S., Csabai, Z., Dakhlaoui, H., DeGirolamo, A. M., Dörflinger, G., Gallart, F., Gauster, T., Hanich, L., … Datry, T. (2021). Trends in flow intermittence for European rivers. *Hydrological Sciences Journal*, *66*(1), 37–49. https://doi.org/10.1080/02626667.2020.1849708

Trenberth, K. E., Dai, A., Van Der Schrier, G., Jones, P. D., Barichivich, J., Briffa, K. R., & Sheffield, J. (2014). Global warming and changes in drought. *Nature Climate Change*, *4*(1), 17–22. https://doi.org/10.1038/nclimate2067

Turner, S., Barker, L. J., Hannaford, J., Muchan, K., Parry, S., & Sefton, C. (2021). The 2018/2019 drought in the UK: A hydrological appraisal. *Weather*, *76*(8), 248–253. https://doi.org/10.1002/wea.4003

UK CEH (UK Centre for Ecology & Hydrology). (2023). *Drought inventory* [Online]. UK CEH. https://www.ceh.ac.uk/our-science/projects/drought-inventory

Vadher, A. N., Millett, J., Stubbington, R., & Wood, P. J. (2018). 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*, 121–132. https://doi.org/10.1007/s10750-018-3544-9

Van der Bolt, B., van Nes, E. H., & Scheffer, M. (2021). No warning for slow transitions. *Journal of the Royal Society Interface*, *18*, 20200935. https://doi.org/10.1098/rsif.2020.0935

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

Van Loon, A. F., Gleeson, T., Clark, J., Van Dijk, A. I. J. M., Stahl, K., Hannaford, J., Di Baldassarre, G., Teuling, A. J., Tallaksen, L. M., Uijlenhoet, R., Hannah, D. M., Sheffield, J., Svoboda, M., Verbeiren, B., Wagener, T., Rangecroft, S., Wanders, N., & Van Lanen, H. A. J. (2016). Drought in the Anthropocene. *Nature Geoscience*, *9*, 89–91. https://doi.org/10.1038/ngeo2646

Van Nes, E. H., Arani, B. M., Staal, A., van der Bolt, B., Flores, B. M., Bathiany, S., & Scheffer, M. (2016). What do you mean, 'tipping point'? *Trends in Ecology & Evolution*, *31*(12), 902–904. https://doi.org/10.1016/j.tree.2016.09.011

Van Vliet, M. T. H., Ludwig, F., Zwolsman, J. J. G., Weedon, G. P., & Kabat, P. (2011). Global river temperatures and sensitivity to atmospheric warming and changes in river flow. *Water Resources Research*, *47*(2), W02544. https://doi.org/10.1029/2010WR009198

Van Vliet, M. T. H., & Zwolsman, J. J. G. (2008). Impact of summer droughts on the water quality of the Meuse river. *Journal of Hydrology*, *353*(1–2), 1–17. https://doi.org/10.1016/j.jhydrol.2008.01.001

Vehanen, T., Huusko, A., Mäki-Petäys, A., Louhi, P., Mykrä, H., & Muotka, T. (2010). Effects of habitat rehabilitation on brown trout (*Salmo trutta*) in boreal forest streams. *Freshwater Biology*, *55*(10), 2200–2214. https://doi.org/10.1111/j.1365-2427.2010.02467.x

Vicente-Serrano, S. M., Quiring, S. M., Pena-Gallardo, M., Yuan, S., & Dominguez-Castro, F. (2020). A review of environmental droughts: Increased risk under global warming? *Earth-Science Reviews*, *201*, 102953. https://doi.org/10.1016/j.earscirev.2019.102953

Wada, Y., van Beek, L. P., Wanders, N., & Bierkens, M. F. (2013). Human water consumption intensifies hydrological drought worldwide. *Environmental Research Letters*, *8*(3), 034036. https://doi.org/10.1088/1748-9326/8/3/034036

Wade, A. J., Whitehead, P. G., Hornberger, G. M., & Snook, D. L. (2002). On modelling the flow controls on macrophyte and epiphyte dynamics in a lowland permeable catchment: The river Kennet, southern England. *Science of the Total Environment*, *282*, 375–393. https://doi.org/10.1016/S0048-9697(01)00925-1

Walker, D. W., & Van Loon, A. F. (2023). Droughts are coming on faster. *Science*, *380*(6641), 130–132. https://doi.org/10.1126/science.adh3097

Watts, G., Battarbee, R. W., Bloomfield, J. P., Crossman, J., Daccache, A., Durance, I., Elliott, J. A., Garner, G., Hannaford, J., Hannah, D. M., Hess, T., Jackson, C. R., Kay, A. L., Kernan, M., Knox, J., Mackay, J., Monteith, D. T., Ormerod, S. J., Rance, J., … Wilby, R. L. (2015). Climate change and water in the UK—past changes and future prospects. *Progress in Physical Geography*, *39*(1), 6–28. https://doi.org/10.1177/0309133314542957

Westwood, C. G., Teeuw, R. M., Wade, P. M., Holmes, N. T. H., & Guyard, P. (2006). Influences of environmental conditions on macrophyte communities in drought-affected headwater streams. *River Research and Applications*, *6*(22), 703–726. https://doi.org/10.1002/rra.934

Whelan, M. J., Linstead, C., Worrall, F., Ormerod, S. J., Durance, I., Johnson, A. C., Johnson, D., Owen, M., Wiik, E., Howden, N. J. K., Burt, T. P., Boxall, A., Brown, C. D., Oliver, D. M., & Tickner, D. (2022). Is water quality in British rivers "better than at any time since the end of the industrial revolution"? *Science of the Total Environment*, *843*, 157014. https://doi.org/10.1016/j.scitotenv.2022.157014

White, J. C., Khamis, K., Dugdale, S., Jackson, F. L., Malcolm, I. A., Krause, S., & Hannah, D. M. (2023). Drought impacts on river water temperature: A process-based understanding from temperate climates. *Hydrological Processes*, *37*, e14958. https://doi.org/10.1002/hyp.14958

Whitehead, P. G., Wilby, R. L., Battarbee, R. W., Kernan, M., & Wade, A. J. (2009). A review of the potential impacts of climate change on surface water quality. *Hydrological Sciences Journal*, *54*(1), 101–123. https://doi.org/10.1623/hysj.54.1.101

Wigley, T. M. L., & Atkinson, T. C. (1977). Dry years in south-east England since 1698. *Nature*, *265*(5593), 431–434. https://doi.org/10.1038/265431a0

Wilby, R. L., Cranston, L. E., & Darby, E. J. (1998). Factors governing macrophyte status in Hampshire chalk streams: Implications for catchment management. *Water and Environment Journal*, *12*(3), 179–187. https://doi.org/10.1111/j.1747-6593.1998.tb00170.x

Williams, A. P., Cook, E. R., Smerdon, J. E., Cook, B. I., Abatzoglou, J. T., Bolles, K., Baek, S. H., Badger, A. M., & Livneh, B. (2020). Large contribution from anthropogenic warming to an emerging North American megadrought. *Science*, *368*(6488), 314–318. https://doi.org/10.1126/science.aaz9600

WMO (World Meteorological Organization). (1992). *International meteorological vocabulary* (WMO-No. 182, 2nd ed., p. 784). WMO. https://library.wmo.int/?lvl=notice_display&id=220#.ZFehSnbMJPY

Wohl, E., Lininger, K. B., & Scott, D. N. (2018). River beads as a conceptual framework for building carbon storage and resilience to extreme climate events into river management. *Biogeochemistry*, *141*, 365–383. https://doi.org/10.1007/s10533-017-0397-7

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), 1–20. https://doi.org/10.1127/0003-9136/2004/0161-0001

Wood, P. J., & Petts, G. E. (1994). Low flows and recovery of macroinvertebrates in a small regulated chalk stream. *Regulated Rivers: Research & Management*, *9*(4), 303–316. https://doi.org/10.1002/rrr.3450090410

Wood, P. J., & Petts, G. E. (1999). The influence of drought on chalk stream macroinvertebrates. *Hydrological Processes*, *13*(3), 387–399. https://doi.org/10.1002/(SICI)1099-1085(19990228)13:3%3C387::AID-HYP745%3E3.0.CO;2-R

Woodhouse, C. A., & Overpeck, J. T. (1998). 2000 years of drought variability in the central United States. *Bulletin of the American Meteorological Society*, *79*(12), 2693–2714. https://doi.org/10.1175/1520-0477(1998)079%3C2693:YODVIT%3E2.0.CO;2

Woodward, G., Papantoniou, G., Edwards, F., & Lauridsen, R. B. (2008). Trophic trickles and cascades in a complex food web: Impacts of a keystone predator on stream community structure and ecosystem processes. *Oikos*, *117*(5), 683–692. https://doi.org/10.1111/j.0030-1299.2008.16500.x

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

Wright, J. F., Clarke, R. T., Gunn, R. J., Winder, J. M., Kneebone, N. T., & Davy-Bowker, J. (2003). Response of the flora and macroinvertebrate fauna of a chalk stream site to changes in management. *Freshwater Biology*, *48*(5), 894–911. https://doi.org/10.1046/j.1365-2427.2003.01058.x

Wright, J. F., Clarke, R. T., Gunn, R. J. M., Kneebone, N. T., & Davy-Bowker, J. (2004). Impact of major changes in flow regime on the macroinvertebrate assemblages of four chalk stream sites, 1997–2001. *River Research and Applications*, *20*(7), 775–794. https://doi.org/10.1002/rra.790

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

Wright, J. F., & Symes, K. L. (1999). A nine-year study of the macroinvertebrate fauna of a chalk stream. *Hydrological Processes*, *13*(3), 371–385. https://doi.org/10.1002/(SICI)1099-1085(19990228)13:3%3C371::AID-HYP744%3E3.0.CO;2-C

Yang, Q., Ferreira, V., Wu, Q., Heděnec, P., Yuan, J., Yuan, C., Peng, Y., Wu, F., & Yue, K. (2023). Global negative effects of drought on instream invertebrate communities. *Journal of Freshwater Ecology*, *38*(1), 2203728. https://doi.org/10.1080/02705060.2023.2203728

Yuan, X., Wang, Y., Ji, P., Wu, P., Sheffield, J., & Otkin, J. A. (2023). A global transition to flash droughts under climate change. *Science*, *380*(6641), 187–191. https://doi.org/10.1126/science.abn6301

Zipper, S., Popescu, I., Compare, K., Zhang, C., & Seybold, E. C. (2022). Alternative stable states and hydrological regime shifts in a large intermittent river. *Environmental Research Letters*, *17*(7), 074005. https://doi.org/10.1088/1748-9326/ac7539

Zipper, S. C., Hammond, J. C., Shanafield, M., Zimmer, M., Datry, T., Jones, C. N., Kaiser, K. E., Godsey, S. E., Burrows, R. M., Blaszczak, J. R., Busch, M. H., Price, A. N., Boersma, K. S., Ward, A. S., Costigan, K., Allen, G. H., Krabbenhoft, C. A., Dodds, W. K., Mims, M. C., … Allen, D. C. (2021). Pervasive changes in stream intermittency across the United States. *Environmental Research Letters*, *16*(8), 084033. https://doi.org/10.1088/1748-9326/ac14ec

## SUPPORTING INFORMATION

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

**How to cite this article:** Stubbington, R., England, J., Sarremejane, R., Watts, G., & Wood, P. J. (2024). The effects of drought on biodiversity in UK river ecosystems: Drying rivers in a wet country. *WIREs Water*, e1745. https://doi.org/10.1002/wat2.1745