nature reviews biodiversity

https://doi.org/10.1038/s44358-026-00131-7

Review article

Extreme events and river biodiversity under climate change

Jonathan D. Tonkin[1,2], Tadeu Siqueira[1,3,4], Julian Merder[1], Thibault Datry[5], N. LeRoy Poff[6,7], Julia Talbot-Jones[2,8] & Julian D. Olden[9]

Abstract

Extreme climatic events (ECEs) including floods, droughts and heatwaves are increasing in severity and frequency, fundamentally reshaping riverine ecosystems. In this Review, we synthesize global evidence of the impacts of ECEs on riverine biodiversity, revealing widespread and often compounding threats. ECEs affect biodiversity in diverse ways across scales; they can erode genetic diversity, alter community composition, reduce ecosystem function and disrupt population and community synchrony across the wider river meta-network. ECEs can also amplify the impact of, and be amplified by, other global stressors, and ECEs that occur in tandem or sequentially (compound events) have potentially strong but poorly understood biodiversity impacts. Several promising statistical and mechanistic modelling frameworks now enable prediction of the impacts of ECEs under non-stationary conditions. To adequately prepare for increasing and compounding ECEs, management strategies must shift from local, reactive interventions to catchment-scale, resilience-focused approaches. Top future research priorities include high-frequency and coordinated long-term monitoring, understanding legacies and biophysical feedbacks from extremes and deconstructing the impacts of compounding events. Our synthesis provides a roadmap for advancing science and practice to confront the ecological challenges posed by an increasingly extreme future.

Sections

---

[1]School of Biological Sciences, University of Canterbury, Christchurch, New Zealand. [2]Te Pūnaha Matatini Centre of Research Excellence, University of Canterbury, Christchurch, New Zealand. [3]Department of Biodiversity, Institute of Biosciences, São Paulo State University (UNESP), Rio Claro, Brazil. [4]Centre for Research on Biodiversity Dynamics and Climate Change, Institute of Biosciences, São Paulo State University (UNESP), Rio Claro, Brazil. [5]INRAE, UR RiverLy, Centre Lyon-Grenoble Auvergne-Rhône-Alpes, Villeurbanne, France. [6]Department of Biology and Graduate Degree Program in Ecology, Colorado State University, Fort Collins, CO, USA. [7]Centre for Applied Water Science, University of Canberra, Canberra, Australian Capital Territory, Australia. [8]School of Government, Te Herenga Waka — Victoria University of Wellington, Wellington, New Zealand. [9]School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA, USA. e-mail: jonathan.tonkin@canterbury.ac.nz

Key points

- Extreme climatic events (ECEs) erode river biodiversity across organizational levels — from genes to ecosystems — through selective mortality, with evolutionary and ecological consequences that permeate across river networks. Network connectivity shapes river resilience: the hierarchical and connected structure of river networks allows the impact of ECEs to propagate across systems, while also providing pathways that support biodiversity recovery following disturbance.

- The impacts of ECEs in rivers are often exacerbated by underlying or interacting stressors, such as land-use change or pollution, and can intensify, or be intensified by, biological invasions. Recovery from ECEs can vary widely from weeks to multiple years, if ever, depending on the specifics of the event and the biodiversity metric of interest.

- Compound events can impose disproportionately large ecological impacts, but limited research to date highlights this as an emerging frontier of research.

- Predictive tools are improving, with distributional regression approaches and mechanistic or hybrid models enabling forecasting of changing extremes and their ecological consequences at scale. To adequately prepare for increasing and compounding ECEs, management strategies must shift from local, reactive interventions to catchment-scale, resilience-focused approaches that are anticipatory.

- Promising future avenues for research and application include advancing the implementation of high-resolution, high-frequency monitoring programmes; continued and coordinated long-term research programmes; broadening the collective understanding of compounding impacts; building knowledge of legacy effects; and studying the biophysical feedbacks between ECEs, river flow regimes, geomorphological dynamics and biodiversity resilience.

Introduction

Rivers are among the most diverse ecosystems on Earth – offering innumerable benefits to billions of people, including fisheries that sustain lives and livelihoods, clean drinking water, material goods and numerous cultural benefits[1]. However, freshwater biodiversity is under threat. Declines in freshwater populations continue at a greater rate than those in marine or terrestrial environments[2]. Still, more challenges will arise in the future as freshwater species face among the highest risks to climate-related extinctions[3]. Despite this deepening crisis, an ‘invisible tragedy’ remains where river ecosystems and the species within them continue to receive scant attention in comparison to the world’s lands and oceans, challenging the ability to mitigate freshwater biodiversity loss[4].

Riverine biodiversity is under pressure from widespread persistent and emerging threats, including land-use change, pollution, invasive species, infectious diseases, harmful algal blooms, flow modification, over-exploitation, salinization, pesticides, microplastics and pharmaceuticals[5]. Rivers have been dammed, diverted and channelized worldwide, modifying the natural cycles that species have evolved with, resulting in widespread impacts to biodiversity[6]. Watercourses that were once perennial now cease to flow for long periods, and others are subject to extreme flooding and excessive temperatures as a result of human activities[7]. Climate change further interacts with, and exacerbates, these threats. Climate change is altering the timing[8] and magnitude[9] of river flows and promoting widespread drying[10,11] and flooding of rivers globally[12] (Box 1).

Rivers are experiencing both gradual shifts in response to mean climate conditions and abrupt changes expressed as extreme climatic events (ECEs). ECEs such as droughts, floods, severe storms, heatwaves, coldwaves, and ice breakup and jam events are changing in multiple dimensions[12–14] (Box 1 and Fig. 1). Although ECEs are becoming more probable (Fig. 1), they are notoriously challenging to study[15,16] and thus their impacts on riverine biodiversity are only now beginning to be well documented. Emerging research has begun to elucidate the breadth of potential consequences of ECEs for riverine biodiversity, ranging from individual-level and population-level impacts through to the disruption of ecosystem functions[17–20]. Furthermore, because many rivers are already subject to considerable pressures[5], ECEs are expected to amplify the challenges facing biodiversity conservation. There is a pressing need to synthesize the current state of knowledge of the effects of ECEs on riverine biodiversity and to identify gaps and research opportunities that could help to inform conservation action in the future.

In this Review, we discuss the implications of ECEs for riverine biodiversity, using the term biodiversity in its broadest sense – encompassing levels from genetic to functional diversity. Drawing from examples from around the world, we highlight the independent effects of ECEs and explore how they have interacted with other anthropogenic stressors and how they combine to create compounding extremes that affect biodiversity. We conclude by suggesting what research is needed to proactively and accurately forecast potential biodiversity impacts of ECEs in different landscape settings, and by identifying the existing barriers constraining the application of this knowledge to management practices that seek to promote future ecosystem resilience in a world that is not stationary[21,22].

Defining extreme events in river networks

Extreme events can be defined in many ways. First, many define extreme events in rivers as statistically rare or unusual events that translate into extreme environmental change[15,23]. These impacts might or might not have equally extreme consequences for species or the ecosystems they inhabit. Second, hydrologists often invoke probability-based criteria to classify extreme floods, such as high flow events with a 100-year return interval or a 1% exceedance probability (flood magnitudes with 1-in-100 chance of being equalled or exceeded in any given year) over a defined time period[24]. Third, extreme events can be defined according to a specified biological threshold, such as when water temperatures exceed specific physiological limits (for example, critical thermal maxima) for biota[25].

This definitional inconsistency hampers progress towards understanding the ecological implications of ECEs and how to manage them[15]. In response, this Review combines criteria according to probabilities and biological responses to define an extreme event as “an episode or occurrence in which a statistically rare or unusual climatic period alters ecosystem structure and/or function well outside the bounds of what is considered typical or normal variability”[26]. We use the terms ‘ecosystem structure’ and ‘function’ in their broadest sense, including the composition of communities or abundances of populations through to functions such as nutrient processing, decomposition and production. This definition enables us to incorporate a wide

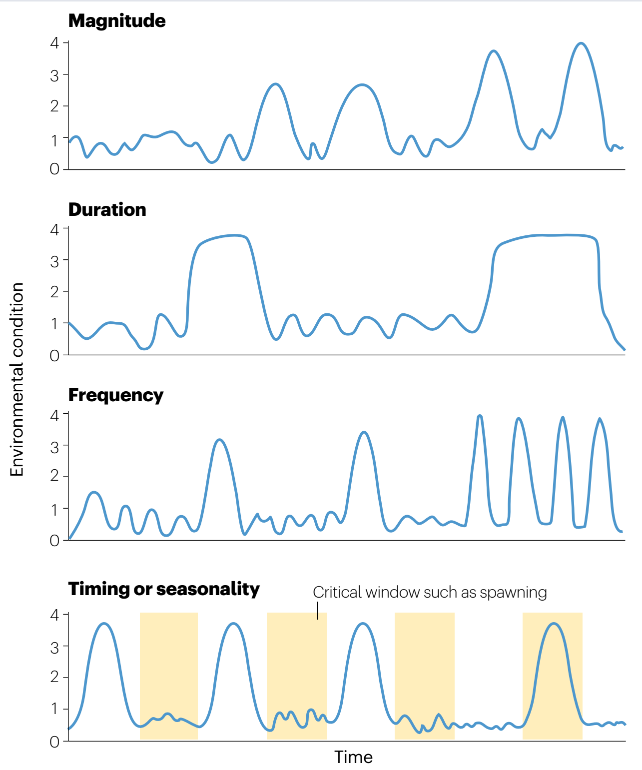
Box 1 | The changing nature of river extremes

River flow and temperature regimes are multifaceted, comprising five main components: magnitude, frequency, duration, timing and rate of change[201,202]. Our Review focuses specifically on magnitude, duration, frequency and timing (see the figure).

The frequency of flood events has increased during the twentieth century[12,24]. Floods events have also changed in timing; for instance, earlier snowmelt from global warming has ushered in earlier floods to western North America[203] and in northeastern Europe, but delayed winter storms are bringing later floods in regions of the Mediterranean coast and North Sea[8]. Flood magnitudes are growing in northwestern Europe from increasing autumn and winter rainfall, but decreased precipitation and greater evaporation in southern Europe are bringing smaller floods[9]. Changes to timing and magnitude are not necessarily concurrent, with river flow seasonality reportedly changing independently from changes in the mean discharge[204]. Importantly, an unusually timed event, or an unusually rapid onset of an event, can have detrimental impacts similar to those caused by extreme magnitudes alone.

Extreme drought events are also on the rise, mainly via increased magnitudes, longer durations and increased frequencies. Changes to the onset of the rainy season, and consequently the duration of the dry season, have led to longer dry seasons and diminished discharge in the Amazon Basin since the mid-1970s[205]. In the Colorado River Basin, warming is drying out soil, creating a water deficit that intercepts snowmelt, thereby reducing stream and river surface flows[206]. Such prolonged extreme drying can result in irreversible changes to catchment hydrology: seven years after the Millenium Drought in southeastern Australia, catchment hydrology in 37% of watersheds had not recovered indicating a threshold in what certain systems can sustain in terms of extreme drought[207].

Changing river temperature regimes are also observed globally[208,209], with extreme warm events (heatwaves) found to influence flow regimes more than moderate events[210]. Heatwaves are increasing in frequency, duration and magnitude in ocean, coastal and lake ecosystems. For example, the annual mean total number of heatwave days more than doubled, from 11 to 25, across the USA between 1996 and 2021 (ref. 13). More extreme temperature events have also been documented at high elevations in spring and summer in European mountain streams[135].



Climate change will also alter other river-ice processes such as ice formations, duration, thickness and ice jams. There is now broad agreement in the scientific literature that the duration of the ice-cover season is decreasing as a result of climate change, such as observational records from rivers in the Northern Hemisphere that consistently show later freeze-up dates and earlier ice breakup[14]. Extreme climatic events might affect the frequency and severity of extreme ice-jamming events, and milder winter temperatures can cause atypical midwinter ice breakups, such as those that have been reported in Canadian rivers[211].

range of studies in our discussion and to recognize that there are both statistical and ecological dimensions to extreme events. Notably, multiple dimensions of ECEs shape ecological responses (Fig. 2). However, the frequency and magnitude of extremes can change over time owing to trends in the distribution of climate variables (mean, variance, skewness and kurtosis) and shifts in their spatiotemporal autocorrelation structure, meaning that the threshold for what constitutes a rare or unusual event is always defined relative to the historical range of variation.

We focus specifically on ECEs in rivers, considering three broad categories of ECEs: hydrological (floods, droughts, ice breakup and jams), thermal (heatwaves and coldwaves) and meteorological (cyclones and hurricanes). Our primary focus is on floods, droughts and heatwaves owing to insufficient data availability for the other ECEs. These riverine extremes are often associated with extreme events on land, including precipitation and temperature extremes, and climate-driven storm events[27]. They can also interact with terrestrial ECEs such as forest fires, which cause landscape-scale changes in erosion, nutrient inputs and hydrologic amplification of river systems[28].

Rivers are organized into connected hierarchical dendritic networks. They receive and transmit organisms and matter, which means the impacts of ECEs will rarely be local, and instead will propagate through entire river networks, laterally onto the floodplain and vertically to the underlying groundwaters[29]. Patterns of ECE propagation are highly context-dependent, given this dendritic organization. Depending on catchment geology, river networks can, for instance, comprise patchy drying patterns or synchronized large-scale drying[7]. Similarly, a high rainfall event anywhere in a catchment is typically propagated downstream throughout the network (for example, decreases in dissolved oxygen propagate downstream following rainfall events post-wildfire[30]), but channels with strong hyporheic (shallow subsurface zone where groundwater and surface water mix)

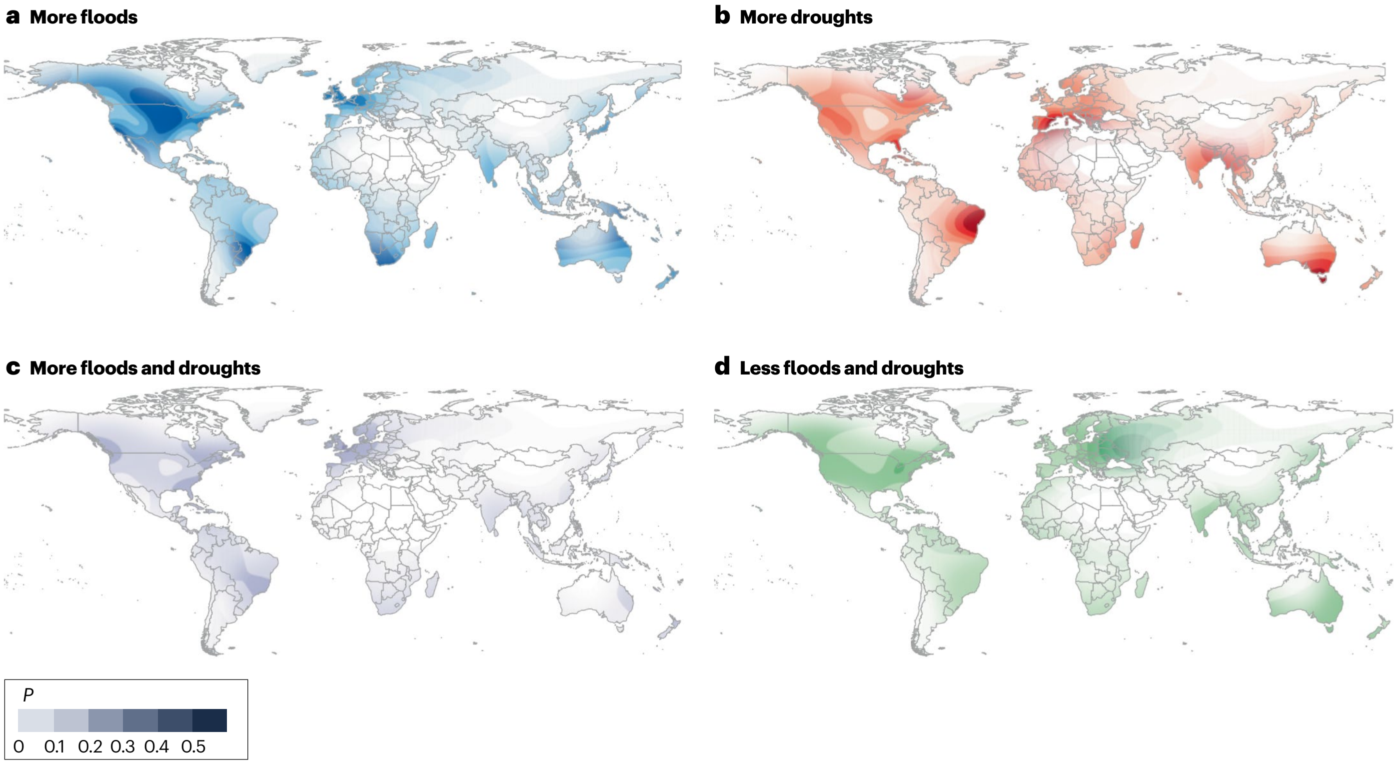


Fig. 1 | Future probability of extreme events. a, Probability (*P*) of increasing floods. **b**, Probability of increasing droughts. **c**, Probability of increasing floods and droughts. **d**, Probability of decreasing floods and droughts. Probabilities (*P*) of increasing extreme conditions were estimated using Sen's slope trends in the yearly maximum 7-day arithmetic mean (MAX7) and yearly minimum 7-day arithmetic mean (MIN7) streamflow[12]. Maps show results of a multinomial regression conducted over space, based on published data from ref. 12. **a**, Probability of increasing floods reflects positive trend in MAX7. **b**, Probability of increasing droughts reflects a negative trend in MIN7. **c**, Probability of increasing floods and droughts reflects positive MAX7 and negative MIN7 trends, respectively. **d**, Probability of decreasing floods and droughts reflects negative MAX7 and positive MIN7 trends, respectively. White areas indicate regions with no data.

exchange or losing channels that emerge over an alluvial fan (fan-shaped sediment deposit zone at the base of valleys) can exhibit limited downstream propagation. For example, although wildfires directly affected ~6% of the total river network length in the western USA from 1984 to 2014, ~11% of river network was affected owing to longitudinal propagation of impacts[29].

The effects of ECEs can amplify when multiple extremes, such as heatwaves, floods or droughts, occur together or in quick succession (also known as compound events[31,32]). For example, a heatwave followed by a prolonged drought could have a compound impact on ecosystems, in which the intense heat increases evaporation and exacerbates water shortages, further stressing already dry conditions[32]. Finally, conservation concerns arise when extremes combine to create compound biophysical effects[31,32], which can manifest in nonlinear ways[33]. As the mean of a climate variable (for example, temperature) increases, so often does the variance, which contributes to an increasing likelihood of more frequent ECEs occurring in quick succession. However, so too can the frequency of different but related event types, such as drought. For instance, in the Gila River catchment (USA), a period of drought spanning multiple seasons coincided with extreme flooding and widespread wildfires, all connected to changing climate[34,35]. In addition, repeat events can occur while a system is still actively undergoing recovery, causing catastrophic ecological impacts, such as extreme floods following a prolonged drought[32].

Effects of extremes on riverine biodiversity

Given the unpredictable nature of extreme events, empirical evidence showing their effects on freshwater biodiversity remains sparse and geographically biased[18,36]. Existing evidence comes primarily from three sources: (1) long-term data that fortuitously captured an extreme event, offering before–after control-impact evidence[17,37–39]; (2) data gathered after an extreme event[29] and (3) indirect evidence derived from studies of biodiversity responses to climatic factors associated with extreme events, such as rainfall and temperature[40,41]. These sources of evidence, combined with theory about the assembly and dynamics of freshwater communities, lend support to the notion that the effects of ECEs on biodiversity depend on the type, magnitude, frequency, duration, timing and legacy of the event and on the biodiversity responses under investigation[17,18]. Whether different facets of biodiversity will persist under novel, non-stationary conditions is an unresolved question, as this will depend on how the populations of the constituent species respond across time and space to shifting biotic and abiotic conditions.

In this section, we collate evidence (or evidence gaps) for the effect of hydrological, thermal and meteorological ECEs on riverine biodiversity across scales, from population genetic diversity to meta-system dynamics (Figs. 2 and 3).

Genetic-level and population-level responses

ECEs can induce mortality and thus exert selective pressure on populations for adaptation. Events that exceed or approach the limits of organisms' acclimatory capacities are likely to strongly influence evolution[42]. Mortality from extremes can act as a one-off selecting sweep, resulting in population bottlenecks that can reduce a population's recovery potential[43]. Such events can also reduce the resilience of populations to future extremes by eroding genetic variation. The difficulty of studying extreme event impacts limits understanding of how mass mortality following extremes diminishes genetic diversity, particularly across multiple species exposed to an ECE[44]. For example, population genomic changes (including both erosion and gain of genomic diversity) varied among stream benthic insect species in response to a 1-in-500-year rainfall event in Colorado (USA), highlighting the difficulty in generalizing evolutionary responses to ECEs[17]. Importantly, aquatic insect species with low mobility and lacking a terrestrial adult stage were locally extirpated after the high-magnitude ECE and did not return within 2 years[17], suggesting that ECEs can have long-lasting impacts on the resistance and resilience of populations to future events. However, the impacts – particularly on the resistance and resilience of populations – can be context-dependent. In response to two extreme flood events, guppy populations showed little change in genetic diversity and population structure (resistance), whereas variation in body size and male coloration were heavily affected but recovered relatively quickly (resilience)[43].

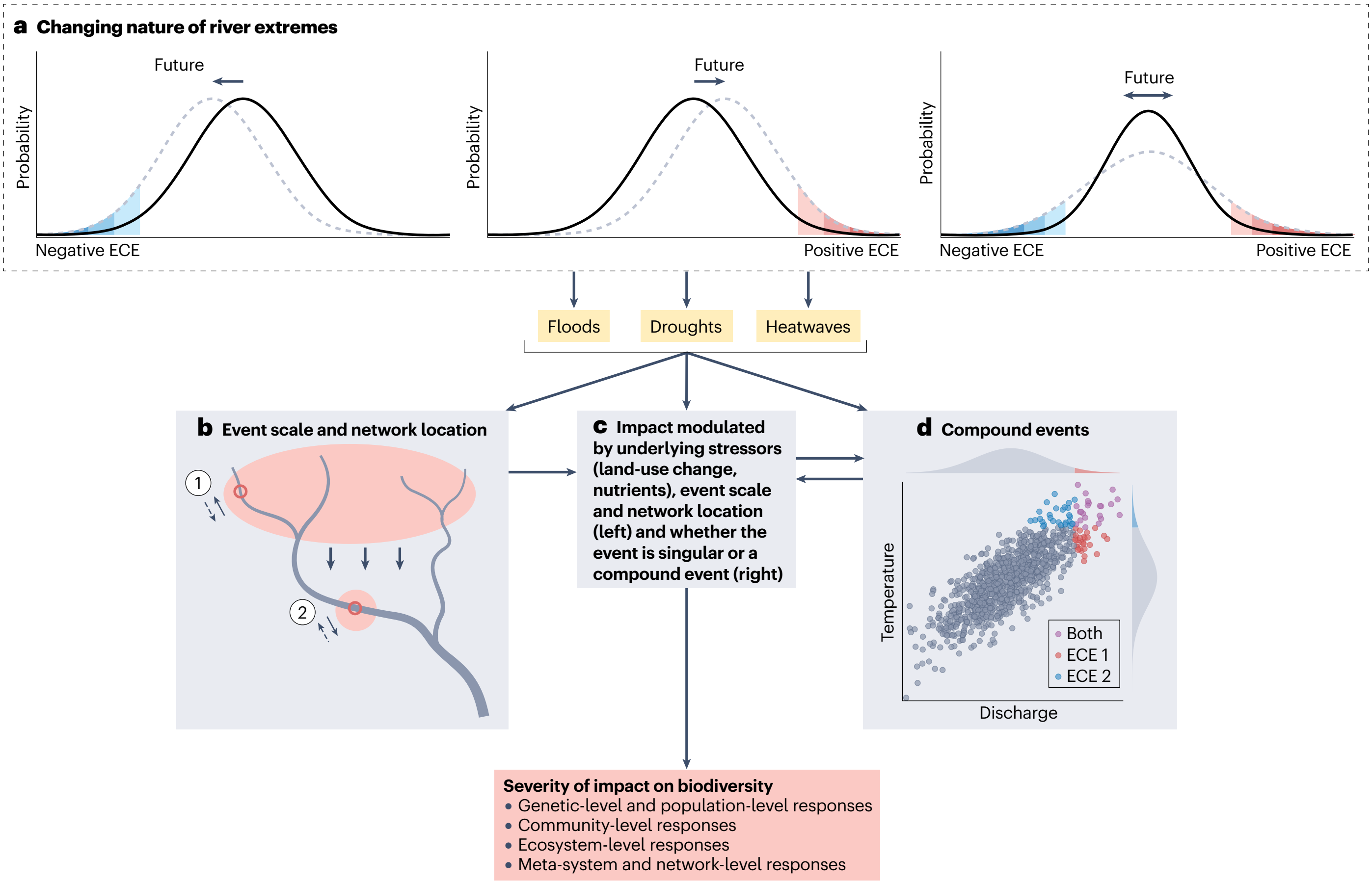
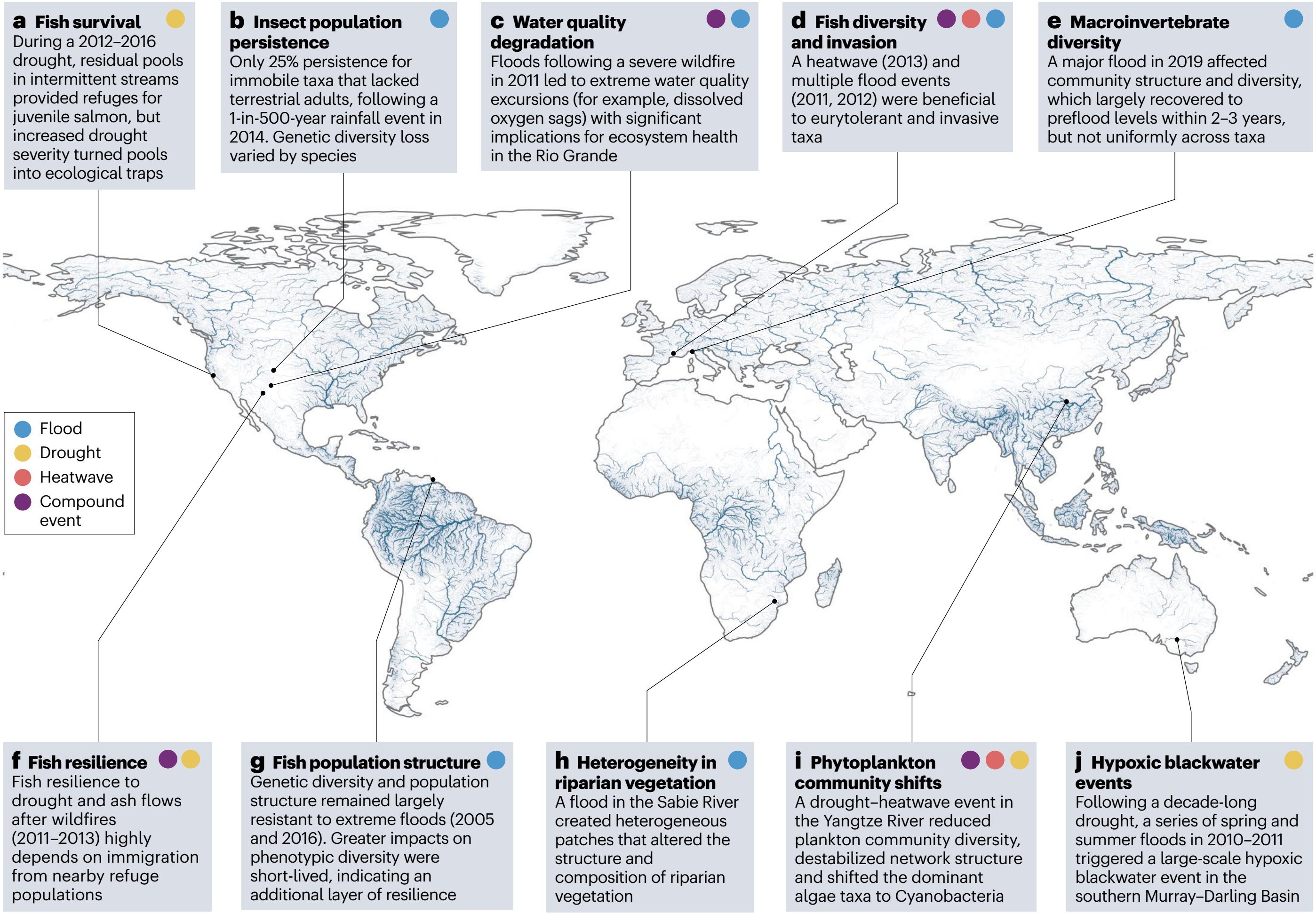


Fig. 2 | Extreme events and the ways they affect river biodiversity. a, Future changes in frequency and magnitude of extremes will be affected not only by trends in the climate variables' mean but also by changes in the scale (spread) and shape (tail heaviness and skewness) of their distributions. Changes in the scale and shape of their distributions (shifting positive, negative or increasing spread, depicted by the future dashed lines relative to historical solid lines), in particular, can result in an increasing chance of experiencing both positive (red) and negative (blue) extreme events (potential impact depicted by colour weight). Extreme climatic events (ECEs) such as floods, droughts and heatwaves (yellow boxes) affect several aspects of riverine biodiversity (red box), but the impacts depend on: the scale and location of the ECE within the connected river network (part **b**); modulation by underlying or interacting stressors (such as land-use change, nutrient enrichment) (part **c**) and whether the ECE occurs alone or as a compound event with another ECE (note that non-extreme events can also combine to form compound extremes) (part **c**). **b**, River network demonstrating the potential propagation of extreme impacts differing between upstream (1) and downstream (2) locations, and small and large spatial scale events (shaded ovals). Propagation of impacts is downstream-biased (solid arrows) and the strength of propagation depends on the scale of the event, with larger spatial scale events affecting the downstream network more severely, and events lower in the network affecting less of the catchment. **d**, When climate variables are correlated, compound extremes can occur (purple points), in which one extreme (red and blue shaded regions) is accompanied by another extreme at the same time (or shortly thereafter, in close spatial proximity or if one extreme makes the system more vulnerable for another[32]).



a Fish survival
During a 2012–2016 drought, residual pools in intermittent streams provided refuges for juvenile salmon, but increased drought severity turned pools into ecological traps

b Insect population persistence
Only 25% persistence for immobile taxa that lacked terrestrial adults, following a 1-in-500-year rainfall event in 2014. Genetic diversity loss varied by species

c Water quality degradation
Floods following a severe wildfire in 2011 led to extreme water quality excursions (for example, dissolved oxygen sags) with significant implications for ecosystem health in the Rio Grande

d Fish diversity and invasion
A heatwave (2013) and multiple flood events (2011, 2012) were beneficial to eurytolerant and invasive taxa

e Macroinvertebrate diversity
A major flood in 2019 affected community structure and diversity, which largely recovered to preflood levels within 2–3 years, but not uniformly across taxa

f Fish resilience
Fish resilience to drought and ash flows after wildfires (2011–2013) highly depends on immigration from nearby refuge populations

g Fish population structure
Genetic diversity and population structure remained largely resistant to extreme floods (2005 and 2016). Greater impacts on phenotypic diversity were short-lived, indicating an additional layer of resilience

h Heterogeneity in riparian vegetation
A flood in the Sabie River created heterogeneous patches that altered the structure and composition of riparian vegetation

i Phytoplankton community shifts
A drought–heatwave event in the Yangtze River reduced plankton community diversity, destabilized network structure and shifted the dominant algae taxa to Cyanobacteria

j Hypoxic blackwater events
Following a decade-long drought, a series of spring and summer floods in 2010–2011 triggered a large-scale hypoxic blackwater event in the southern Murray–Darling Basin

Fig. 3 | Global extreme climatic event impacts on riverine biodiversity. Selected examples of extreme floods (blue), droughts (yellow), heatwaves (red) and compound events (purple), as discussed in more detail in the main text. River network data on the background map were sourced from the HydroRIVERS dataset[192]. Reference information: **a**, ref. 107; **b**, ref. 17; **c**, ref. 30; **d**, ref. 75; **e**, ref. 50; **f**, ref. 71; **g**, ref. 43; **h**, ref. 120; **i**, ref. 122; **j**, ref. 57.

ECEs that selectively remove individuals from a population can have evolutionary consequences for species' life histories, as selective sweeps can operate on particular species traits. Life-history traits (such as the timing of reproduction relative to flood timing) can evolve to match the patterns of environmental characteristics in predictable systems[45,46]. However, because extreme flows are rare and unpredictable, they are unlikely to exert selective pressure on such synchronized life histories[47]. Instead, any evolutionary response to ECEs probably occurs via a selective sweep against specialized species and in favour of flexible species, with the strength of selection depending on the event's timing, frequency and predictability. In unpredictable systems, bet hedging strategies can emerge, the form of which depends on organisms' lifespans[46].

The evolutionary impact of ECEs in river systems is further shaped by their timing relative to life-history stages of vulnerable species[17] and their spatial scale in relation to the level of mortality they cause[47]. High-mortality events with broad spatial impact are likely to exert stronger evolutionary pressure on the life-history strategies of riverine organisms than more localized disturbances[47], but these scale-dependent pressures can depend on the predictability of cues. For example, behavioural experiments on the giant waterbug, *Abedus herbertii*, found that populations from predictable streams – where localized rainfall signalled flash floods – responded to rainfall cues rapidly by crawling away from the water to escape flash floods[48]. By contrast, populations from less predictable streams – where proximate rainfall cues did not signal flash floods – responded more slowly.

ECE impacts are most readily observed at the population level. When an ECE is physically disruptive (extreme floods) or physiologically disruptive (cessation of water flow), the immediate consequence is a reduction in the population size of vulnerable species, which, if large enough, might result in local extinctions. A species' vulnerability to certain types of ECEs depends, in part, on its biological and ecological traits. For example, when a devastating flood in Ireland caused a tenfold decline in overall community abundance, the small, abundant and aerially dispersing chironomid species were largely unaffected, whereas the larger (mayflies, stoneflies and caddisflies) and less mobile (molluscs and crustaceans) species experienced population declines that did not recover for up to ten years[49]. Similar results have been found in Italian streams for chironomids and baetid mayflies, which have been attributed to a combination of dispersal ability through drift propensity, behavioural adaptations and refuge use during floods[50]. Additionally, during the 'Millennium Drought' (1997-2009) in Australia's Murray-Darling Basin, the most affected fish species included small-bodied invertivores with low fecundity, preference for spawning in cool temperatures and relatively low upper lethal temperature limit[51].

The mechanisms enabling the stability of populations during and following ECEs vary widely. For example, tolerance to high temperature, low oxygen or desiccation can promote resistance to droughts, whereas enhanced dispersal abilities, high fecundity and rapid physiological developments can promote recovery by enabling rapid recolonization of disturbed sites. Invertebrate species inhabiting non-perennial streams typically have desiccation-resistant stages, such as eggs, cysts or dormant adult forms that can remain in dry sediments for months and be reactivated upon flow resumption[52,53]. Similarly, only fish species with high thermal tolerances persisted during the long-duration megadrought experienced in the Amazon Basin in 2023 (ref. 19).

In contrast to abrupt events such as extreme floods that remove or kill organisms, gradual stressors such as droughts and heatwaves usually affect organism physiology[36]. Slow drying lowers water depth, raises temperature and reduces oxygen, pushing organisms beyond their thermal or hydrological limits. For example, during a 2003 heatwave in France, the Saône River reached temperatures above the thermal tolerance of molluscs, increasing their metabolism until energy reserves were exhausted[54]. From 1999 to 2004, densities decreased from 520 to a mere 98 individuals per square metre at one location, with the number of species also reducing from 10 to 6 at another location[54]. Larger species such as bivalves died in large numbers because they could not meet their energy demands, whereas smaller gastropod populations survived slightly longer before collapsing[54]. Similarly, drought reduces habitat and causes hypoxia and heat stress, forcing fish to expend energy just to survive[55]. Over time, these stressors limit growth and reproduction, especially in large or immobile species.

Community-level responses

Among the immediate community-level responses to ECEs are a direct change in taxonomic diversity owing to decreases in population sizes and subsequent species loss. A 2023 meta-analysis found that reductions in water flow were the main cause of declines, with communities losing about 1.5 standard deviations of richness following flow reduction (95% CI 0.6–2.4)[18] (Fig. 4). Community biomass also declined in response to ECEs, with warming and reduced flow driving biomass losses of roughly one standard deviation ($\tau = -1.04$, 95% CI −1.89 to −0.19), but results were highly context-dependent among studies and groups[18] (Fig. 4). Moreover, a reduction in community biomass does not imply uniform impacts across all species; some might experience severe effects, such as local extinction owing to widespread mortality

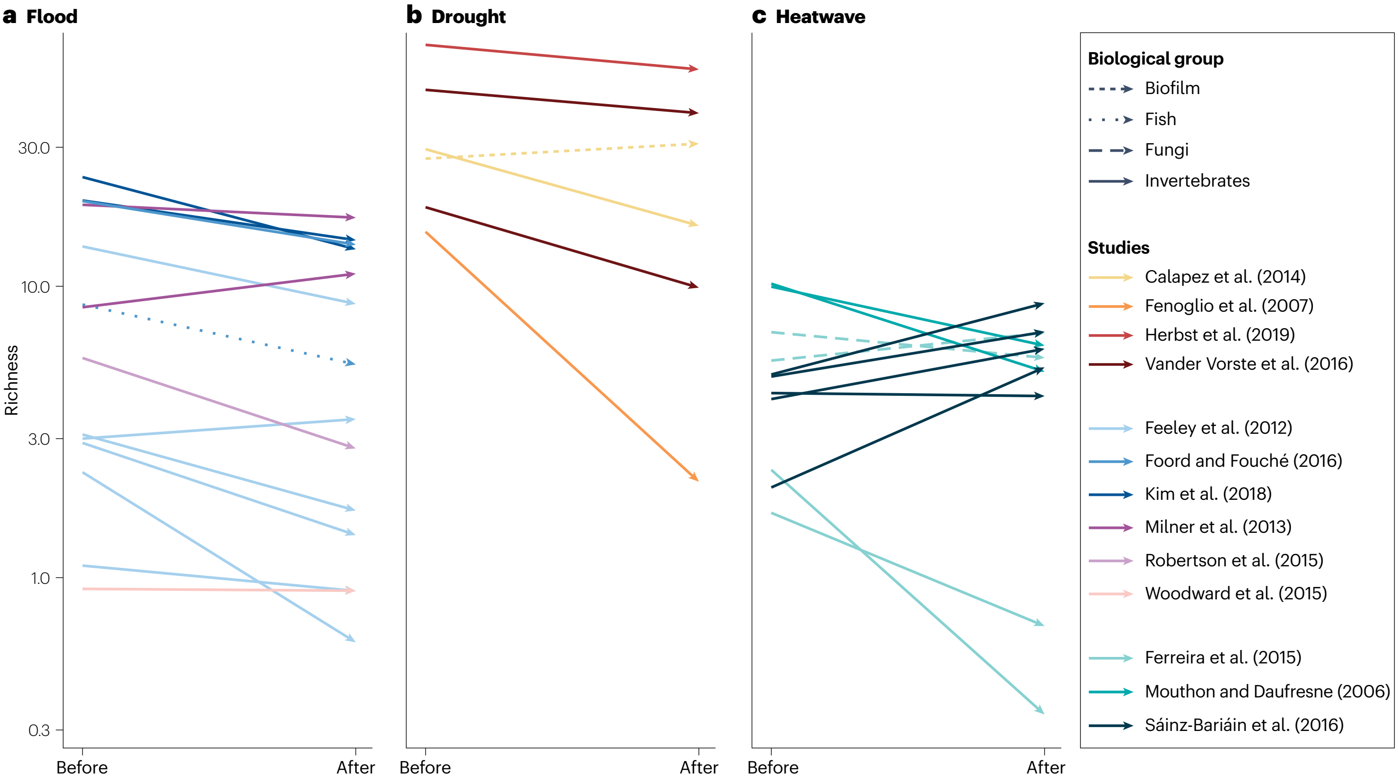


Fig. 4 | Context-dependent effects of extreme changes in water flow and temperature on species richness. Results of 13 studies in which species richness was assessed before and after an extreme event (data from the meta-analysis by ref. 18). Results are grouped by category: flood (part **a**), drought (part **b**) and heatwave (part **c**). Different biological groups are illustrated by different line types, but most studies were on invertebrates (solid lines). Flood data are from Woodward et al.[49], Robertson et al.[129], Milner et al.[185], Feeley et al.[193], Foord & Fouché[194] and Kim et al.[195]; drought data are from Vander Vorste et al.[113], Herbst et al.[196], Calapez et al.[197] and Fenoglio et al.[198]; heatwave data are from Mouthon & Daufresne[54], Ferreira et al.[199] and Sáinz-Bariáin et al.[200]. Generally, richness of species is lower following each of these three types of extreme events, but responses are context-dependent.

or displacement[56,57], whereas others might be less affected[58] depending on their species-specific traits. For instance, small changes in drought magnitude can result in substantial changes in invertebrate communities, particularly in the composition of certain traits[40]. The loss of surface water seems to be a key driver of threshold responses of stream invertebrates, especially for larger species and those with lower thermal tolerances[40]. Indeed, recovery can take considerable time, and new community trajectories can occur. For example, several years after an extreme flood event in Italian streams, new macroinvertebrate species continued to replace those lost during the event[50].

Different properties of riverine communities can recover from ECEs at different, often rapid, rates[59–61]. Specifically, properties such as population growth rates and interactions among species are unlikely to fully recover, whereas properties such as total biomass and abundance can bounce back within weeks[18,36]. These recoveries typically occur when the community includes short-lived, highly mobile species that can recolonize soon after conditions are appropriate[36] or species with resistance and resilience traits that reduce disturbance mortality[17]. For instance, following an extreme rainfall event in montane Colorado (USA) that produced flood disturbances ranging from 1-in-50 to 1-in-500 year probabilities, the average persistence across 14 streams was 84% for taxa with mobile larvae and terrestrial adult stages, compared with just 25% for those lacking terrestrial adults[17]. Similarly, a severe drought (1953–1954) that decimated the fish and invertebrate populations in Smiths Branch (USA) was quickly followed by repopulation the following year by adult invertebrates that returned from other streams and by fish that recolonized from downstream[62]. Relatively rapid (within a year) recovery of invertebrates has also been reported in Welsh streams[63], Scottish streams[64] and New Zealand streams[65].

One clear pathway by which ECEs affect communities is by facilitating the introduction, establishment and spread of invasive species through river networks. Extreme flooding events, in particular, can facilitate the movement of invasive species propagules over long distances or across physical barriers. For example, flooding events in the Mississippi River Basin were linked to the first-known introduction of black carp (*Mylopharyngodon piceus*) when floodwaters allowed fish to escape from inundated aquaculture ponds into the river[66] and to the rapid downstream dispersal of zebra mussel (*Dreissena polymorpha*) larvae[67]. Non-native fishes have also been found to circumvent dam barriers by being transported downstream over reservoir spillways during extreme high flows[68].

ECEs can decrease the capacity of resident species to use resources (nutrients, prey and space) or can increase the availability of resources for invasive species both during and after the stressor ceases[69], both of which potentially create a favourable 'window' for invasive species. The duration of the invasion window is a function of the resilience of the native community as well as the magnitude, duration, frequency and timing of the ECE. Invasive species tend to have broader environmental tolerances than co-occurring native species, as well as traits that favour rapid resource acquisition, growth and colonization of disturbed areas[70]. For example, native fish species were found to have greater sensitivity to interannual variation in climate conditions compared with non-natives in the Gila River (USA)[71]. Similarly, anomalous drought reduced native fish population abundances but had no significant effect on non-native fishes in the Salt River (USA)[72]. In riparian ecosystems across western North America, drought has contributed to the increasing prevalence of the invasive tamarisk (*Tamarix ramosissima*), in which declining water tables and increased salt in surface soils promote this species over more drought-vulnerable and salt-vulnerable native species[73]. These impacts can be self-reinforcing owing to the ability of invasive species to alter local abiotic conditions[74]. Similarly, invasive crayfish are more tolerant to desiccation than native crayfish, leading to greater numbers of invasive species surviving during drought-induced stream drying. In France's Rhône River, increases in abundance of invasive and broadly tolerant macroinvertebrates were temporally correlated with the 2003 European heatwave, as well as with severe flood events that might have contributed to increased resources[75].

ECEs can also amplify the already large negative ecological impacts of invasive species in riverine ecosystems[76]. For example, reductions in flow during extreme droughts concentrate organisms in small and often isolated habitats, increasing the frequency and magnitude of negative species interactions with both native and non-native species[77]. Drought-induced habitat loss in stream ecosystems can confine native fishes to remnant pools and intensify rates of predation by invasive fishes[78], and increase exposure of fish to non-native diseases[55]. Non-native species can also influence the response of native species to extreme flows. For example, although introduced trout are more sensitive to extreme flood events than high country river-resident galaxiids in New Zealand, their presence can impair the recovery of galaxiids by reducing their growth rates through competition for resources or behavioural changes[79].

Although ECEs often facilitate or amplify invasive species impacts, they can in some instances release native species from the pressures invasive species exert. For example, although stream warming can promote fast-growing non-native species by increasing growth rates in temperate rivers[76], in arid and semi-arid ecosystems, increased temperatures might exacerbate drought, potentially favouring drought-tolerant natives[71]. The introduced brown trout (*Salmo trutta*) in New Zealand is more susceptible than native river-resident galaxiid fishes to stresses associated with low flows, thus helping to prevent trout from eliminating galaxiid fishes in small streams[80,81]. Extreme droughts in Australia reduced many streams to small, isolated pools with depleted oxygen levels and high water temperatures where invasive common carp (*Cyprinus carpio*) were unable to survive these conditions despite native species persisting[82]. Of course, the impacts of non-natives can depend on whether the ECE is a drought or flood. In tropical streams, native fishes were reported to better cope with longer maximum durations of low flows than expected when non-native fishes were absent, but in mixed fish assemblages, longer maximum durations of low flows heightened the negative effects of non-native fishes[83]. Interestingly, extended maximum durations of high flows might have acted as a control of non-native species and dampened their negative effect on native species[83].

In summary, research to-date has shown that ECEs can affect invasion processes, but that this relationship is complex and often context-dependent. Long-standing legacies of ECEs include the integration of non-native species into contemporary communities that alters the nature and strength of ecological interactions with native species.

Ecosystem-level responses

ECEs can trigger abrupt, transient shifts in stream food web energy pathways. The resulting shifts in energy allocation can cascade through food webs, releasing smaller, faster-growing species from top-down control and reshaping community composition long after the ECE[36]. Following an extreme flood event, consumer–resource relationships in stream invertebrates shifted to more reliance on allochthonous (organic materials that enter a river from external sources, such as leaves falling into a stream) detritus inputs that entered the channel during the extreme runoff[84]. By contrast, primary consumers (mainly shrimp) shifted their food source following a hurricane (meteorological extreme) that increased stream canopy openness[39]. Before the hurricane, allochthonous carbon generally contributed more than half of the primary consumers' diet, whereas just 2 months after the hurricane, biofilm-derived (autochthonous: inputs produced within the river, such as algae or diatoms growing on river substrate) carbon became the most important source of food. Consumers eventually returned to a terrestrial resource base as the forest canopy recovered from hurricane damage 18 months later[39].

Despite the prevalence of these higher-level food-web processes, empirical evidence quantifying the effects of ECEs on biogeochemical processes is rare[18]. Nonetheless, several ecosystem processes have been investigated in terms of response to ECEs. One of the most studied processes is leaf litter decomposition, which connects terrestrial and aquatic ecosystems through material fluxes mediated by physical forces and dispersal[85]. This process, largely driven by fungi, bacteria and shredder invertebrates, with contributions from physical abrasion and photodegradation[86], responds differently to various ECEs. First, severe flooding often flushes downstream or laterally[87,88], not altering decomposition rates but potentially stimulating physical abrasion during transport or modifying nutrient stoichiometry of relocated litter[89]. Less extreme flooding, by contrast, can reduce decomposition by negatively affecting shredder communities[90,91]. Changes in flood magnitude and frequency can also affect nutrient processing and retention, as high flows often minimize in-stream nutrient cycling by allowing transport to override retention[92].

River drying can also slow or even halt the decomposition of leaf litter, with effects that vary across the stage of drying[93]. Initially, flow cessation can increase biotic interactions among microbial and shredding communities, ultimately slowing litter decomposition[94], whereas the complete disappearance of surface water halts all biotic components of decomposition[85,93] leading to accumulation of leaf litter in dry streambeds[95]. These negative effects of drying can persist for several months upon rewetting[96–98].

Abrupt or prolonged flow reductions have been reported to modify other ecosystem processes. For example, primary productivity was found to be significantly reduced by flow reductions in a meta-analysis[18]. Such reductions will presumably lead to increased consumer dependence on detrital sources relative to before drying. In boreal headwater streams, drought led to increased water residence time, which decreased aerobic metabolism and increased concentrations of reduced solutes in both stream and subsurface water, causing water quality degradation[99]. Increased drying can also increase contact between water and sediment, promoting nutrient retention and shifting energy sources towards in-stream production, particularly during hydrologically disconnected periods[92]. During extreme reductions in flow, isolated pools can develop hypoxic, acidic conditions, potentially increasing denitrification and raising ammonium concentrations through multiple biogeochemical pathways[92]. In hydrologically disconnected river networks, this process can increase spatial heterogeneity in nutrient concentrations and can lead to extreme levels of primary production for extended periods[100].

Finally, heatwaves can substantially alter decomposition of leaf litter in streams. In general, high temperatures can increase decomposition rates, particularly in winter[101]. Nevertheless, severe temperature increases (more than 40 °C) can indirectly reduce the decomposition of litter through lethal effects on detritivore species[102]. Severe or extreme heatwaves were shown to cause increased heterotrophy (reliance on organic carbon rather than in-stream photosynthesis) in a study of 48 streams across the USA[20]. Gross primary productivity declined up to 82%, whereas ecosystem respiration increased up to 47%. This thermally induced increase in heterotrophy suggests that, during severe heatwaves, rivers' contribution to atmospheric CO_2 levels will probably increase. More research is needed to identify temperature thresholds (and their frequency and timing) that impair river ecosystem processes in streams and rivers[103].

Meta-system and network-level responses

The hierarchical, longitudinally connected nature of river networks provides both threats (for example, propagation of impacts through the network via flow; Fig. 2) and opportunities (for example, fragmented drying) for resilience to ECEs. This connectivity means that the effects of ECEs can spread well beyond the localities where they occur. For example, a severe drought can directly affect communities in specific locations while also disrupting hydrological connectivity across the river network, leading to negative consequences even in localities not affected or long after the ECE has ceased. Droughts can also affect stream metabolism beyond dried channels, as accumulated organic material is subsequently flushed downstream[104]. Similarly, the effect of droughts on aquatic communities can be detected months after the end of the event[105,106].

Loss of connectivity (fragmentation) can also threaten population persistence (Box 2), particularly for migratory species with vulnerable life-history stages that rear in headwater streams. The impact of the loss of connectivity among stream pools on migratory fish can be mediated by the duration of time a pool is disconnected from the wider river network. During California's record-breaking 2012–2016 drought, when the duration of pool disconnection increased from 0 to 78 days, survival of endangered juvenile Coho salmon declined from 0.59 (95% CI 0.39–0.70) to 0.11 (95% CI 0.04–0.24)[107]. However, survival of juvenile salmon varied among pools within the stream network, and this variability increased during drought years. The mean coefficient of variation in cumulative survival rose from 41% in non-drought years to 103% during drought years, indicating that certain pools acted as critical drought refuges that were important for population persistence in the face of accelerated mortality in other pools[107].

The dendritic and heterogeneous nature of river networks provides a level of spatial insurance for biodiversity in response to ECEs[108,109] (Box 2). In particular, refuges are critical for the resistance and resilience of biodiversity to ECEs in river networks[77,110]. The ability of native fish communities in the Gila River, USA, to recover from severely reduced population sizes following a combination of drought and wildfires, depended on immigration from nearby refuges[71]. The capacity to recolonize from refuges, such as perennial reaches, can promote a rapid recovery of communities after extreme drying events[111,112]. For example, the hyporheic zone of gravel-bed rivers can be the major source of recolonization after drying events for invertebrates[113,114] or fish[115]. During flood events, such refuges might be off-channel habitats in the floodplain. However, the impacts of extreme floods can also affect communities in off-channel floodplain environments, as demonstrated by substantial changes to macrophyte communities in floodplain lakes and backwaters in the Parana River, Brazil, following a rare flood event[116].

Although the interconnected nature of riverine networks might facilitate the spatial propagation of ECE effects, it can also make

Box 2 | Temporal and spatial stability in river networks

The capacity of ecosystems to maintain consistent properties over time (temporal stability) emerges from complex interactions among intrinsic population and community dynamics, environmental heterogeneity and spatial connectivity[212]. At local scales, diverse communities stabilize aggregate ecological properties through portfolio effects[213] (statistical averaging among species with independent fluctuations), and compensatory dynamics (negative covariance in population abundances) further reduces variability[214,215].

Temporal stability increases with spatial scale in river networks. Local populations might fluctuate strongly, but catchment-level dynamics are stabilized when these fluctuations are asynchronous[118]. For example, non-native fish increased population variability, destabilizing native communities at stream reaches, but spatial asynchrony diluted these effects at the basin scale[216]. In the context of ECEs, asynchronous dynamics in less-disturbed habitats is expected to maintain basin-scale stability via buffering processes offered by spatial scaling.

Spatial synchrony, defined as correlated fluctuations across locations, drives regional stability[217,218]. For example, mobile predators can enhance spatial asynchrony by switching prey resources across habitats[117], and natural flow intermittence can maintain it through environmental heterogeneity[219]. ECEs such as basin-wide droughts can override these stabilizing mechanisms by synchronizing population fluctuations via uniform stressors (the Moran effect), thereby reducing regional stability. For example, heatwaves have been found to destabilize stream algal communities by spatially homogenizing them in the absence of top predators that controlled herbivores[119].

The spatial insurance hypothesis[220] provides a biodiversity-focused framework that integrates these temporal stability and spatial synchrony concepts. In river networks, spatial insurance manifests through three key mechanisms that will be subject to change from ECEs. First, dispersal-mediated recolonization describes how mobile species or life stages (such as aquatic insects with aerial adults or migratory fish) disperse from undisturbed refuges to previously disturbed habitats. For example, perennial reaches can buffer the impacts of drought by acting as sources of recolonists in drying streams[111,112]. Second, trait-mediated compensation explains how species with contrasting traits (for example, desiccation-resistant but immobile versus desiccation-prone but mobile taxa) respond asynchronously to ECEs. Hyporheic zones shelter invertebrates during drying[113], whereas mobile fish exploit transient habitats, maintaining aggregate ecosystem functions[221]. Third, heterogeneity-enhanced asynchrony in which habitat diversity (pools and riffles) and spatial heterogeneity reduce synchrony might influence how river biodiversity responds to ECEs. For instance, fish populations in headwaters exhibited a more rapid decline in synchrony over distance compared with those in the mainstem[222], potentially because headwater populations have limited dispersal opportunity and experience more heterogeneous environments.

Theoretically, ECEs can erode temporal stability in river networks through different pathways:

- Floods. Extreme floods homogenize habitat conditions across river reaches, increasing the synchrony of local dynamics. This homogenization reduces the habitat heterogeneity required to buffer environmental fluctuations, as demonstrated by the persistent community shifts 12 years post-flood in an Alaskan river[121].
- Droughts. By fragmenting river systems, droughts impede the movement of mobile predators, such as fish, between interconnected reaches[223]. If widespread, prolonged drying can also erode spatial heterogeneity in both abiotic and biotic conditions, thus increasing spatial synchrony[107].
- Heatwaves. Elevated temperatures associated with heatwaves can exceed the physiological tolerances of many aquatic organisms, leading to mass mortality events and shifts in distributions. The resulting decline in local diversity and altered trophic dynamics may increase the synchrony of community responses, thereby substantially eroding temporal stability across river networks[224].

These impacts often interact. For example, habitat homogenization from droughts can compound physiological stress during heatwaves, accelerating biodiversity loss. Although predictions highlight risks, empirical evidence remains sparse, particularly regarding cross-scale feedbacks and recovery thresholds.

networks more temporally stable in the face of ECEs (Box 2). If local areas within a riverscape are sufficiently heterogeneous to exhibit asynchronous hydrologic and associated ecological dynamics, the system might offer buffering against the impacts of localized ECEs, assuming that hydrologic connectivity exists between local sites. For instance, in Bristol Bay (USA), salmon returns were considerably less variable over five decades as a result of the maintenance of hundreds of discrete populations than if they were a single homogeneous population[108]. Additionally, top mobile predators can increase asynchrony in local food webs by switching between more and less preferable food resources across the riverscape[117,118]. For example, heatwaves destabilized stream algal communities by spatially homogenizing them in the absence of top predators[119]; predators were thought to enhance spatial variability in algal communities (thereby increasing temporal stability) through their influence on macroinvertebrate herbivores. Finally, ECEs themselves might promote spatial heterogeneity in certain contexts, such as in the structure of floodplain vegetation following an extreme flood[120]. Nevertheless, under ECEs, freshwater ecosystems are expected to become more synchronized at local scales, resulting in reduced capacity of networks to buffer against abrupt changes (Box 2). As a result, the temporal stability exhibited at larger geographical scales might erode, making riverine networks even more susceptible to further disturbance events over time.

Evidence remains limited regarding whether ECEs alter the emergence and maintenance of temporal stability in riverine systems. Multiple mechanisms (including compositional shifts, extinction and colonization rates; referred to as stability components) could influence temporal stability following ECEs, but they have rarely been tested. Two extreme flood events occurring 8 years apart (2005 and 2014) in an Alaskan river disrupted the processes that typically drive stability following disturbance – manifesting as a decoupling of different stability components (increased ‘dimensionality’ of stability), which typically exhibit correlated responses[121]. Major shifts in community composition persisted 12 years after the initial extreme flood, suggesting a decoupling of species–environment deterministic relationships or the presence of a strong legacy effect. Explanations for these patterns include the limited dispersal capacity of certain displaced taxa and potential colonizers, as well as an increased sensitivity to subsequent stochastic environmental variations[121].

Interactive and combined effects

The impacts of ECEs are exacerbated when ecosystems face compound events (Fig. 2). Compound events can be categorized as: preconditioned, when a pre-existing condition amplifies impacts (for example, heavy rainfall on saturated soils or snow); multivariate, when multiple hazards occur together (for example, drought and heatwave); temporally compounding, when hazards occur in sequence (for example, sequences of heatwaves or floods following drought); or spatially compounding, when hazards occur simultaneously across regions (for example, widespread floods)[32]. The impacts of these events are often multiplicative, in which the combined effects of multiple stressors are greater than the sum of their individual effects. Compound events can overwhelm species' physiological and ecological coping mechanisms or cause periods of chronic stress in which, in the case of temporally compounding events, the gap between ECEs provides insufficient recovery time. Importantly, although individual events might not be extreme in isolation, their impacts are made extreme in combination. For instance, coinciding droughts and heatwaves (multivariate compound event) can have severe effects on biodiversity. A multivariate drought–heatwave compound event in the Yangtze River not only reduced alpha diversity in phytoplankton and microbial communities and shifted dominance towards cyanobacteria (known to produce harmful algal blooms) but also drove an 11-fold increase in algal gene quantity, a 31 ± 22% rise in particulate organic carbon content and an 18 ± 8% increase in the proportion of labile particulate organic carbon across the basin[122]. The greatest changes in community composition of invertebrates in an Irish river were found to be when a low flow and high flow event followed each other in sequence (temporally compounding), relative to one-off events[49]. In New Mexico (USA), rainfall events following a catastrophic forest fire caused large-scale flash flood impacts on ecosystem health that propagated 50 km downstream[30]. Runoff from burn areas resulted in considerable fluctuations in turbidity, dissolved oxygen, pH and conductivity, with dissolved oxygen dropping to levels that can be lethal for fish and invertebrates. In the Murray–Darling Basin (Australia) in 2010–2011, a series of flood events following prolonged drought caused organic matter pulses that depleted dissolved oxygen, leading to hypoxic blackwater events affecting more than 2,000 km of river network[57]. Understanding how compound events reshape species interactions, community structure and ecosystem resilience remains an urgent frontier, crucial to predicting biodiversity responses under climate change.

Compound events can be exacerbated in river networks that are highly modified through water management and withdrawals[56,57]. For instance, in 2018–2019 in the Lower Darling River (Australia), three major fish-kill events resulted from extreme drought conditions followed by sudden cool weather events that de-stratified managed weir pools, exposing unusually large fish biomasses to anoxic conditions[123]. A similar fish-kill event occurred in the Oder River (Germany) in 2022 when drought conditions, high temperatures, nutrient enrichment and salinity from various sources including municipal and industrial sewage discharge resulted in a harmful algal bloom[124]. These studies highlight that flow management actions can exacerbate the impacts of ECEs on riverine biodiversity. ECEs also have the potential to intensify the ecological impacts caused by dam operations such as hydropeaking, which have already led to the near extirpation of entire insect orders in sections of the Colorado River (USA)[125,126].

The impacts of ECEs on riverine biodiversity can also be modulated by underlying stressors to the system (Fig. 2). For instance, the abundance of impervious surfaces in urban environments leads to erratic flow regimes that can amplify the effects of extreme rainfall events. Alternatively, human-induced stressors, such as land-use change, fragmentation, water extraction and water quality, can modify how ecosystems respond to and recover from extreme droughts[127]. For example, fragmentation of river networks can limit the options for recolonization of fishes following extreme drought events[71,128]. Sensitivities of macroinvertebrate communities to extreme flow events in the Rhône River (Germany) increased through time under observed warming trends over 20 years[75]. Contrasting responses to extreme floods have been observed in Alaskan streams that were deglaciated 38–180 years ago, where differences in channel morphology and vegetation influenced how meiofauna, macroinvertebrates and fish responded to flood events[129]. Compared with older streams, younger (more recently deglaciated) streams were sparsely vegetated and more prone to erosion, leading to greater incision and loss of refuge habitats, resulting in greater declines in macroinvertebrate abundance and richness[129]. However, variation in rainfall magnitude among catchments makes it difficult to separate these effects from differences in flood magnitude[129].

Finally, an emerging area of interest is understanding the synergistic effects of ECEs such as heatwaves in combination with emerging contaminants such as micropollutants, but the results to-date have been highly varied[130]. During extreme flood events, toxic chemicals can be redistributed by the turnover of substrate, amplifying the effects of pre-existing stressors[59]. These changes further emphasize the interconnectedness of ECEs, climate change and existing stressors on ecosystems.

Anticipating biological responses to extremes

Predicting the impacts of ECEs on biodiversity is a challenging but critical task. Ecological models span a gradient from entirely correlative to highly parameterized mechanistic models. Traditional ecohydrological models, typically based on empirical correlations within historical ranges of variability and assumptions of hydroclimatic stationarity, might be limited when anticipating the impacts of ECEs, for several reasons. First, extremes are rare events located in the tails of statistical distributions (Fig. 2a), thereby challenging conventional methods that focus on central tendencies, and providing questionable insight into, and opportunities to learn from, the dynamics of extreme values. Second, the effects of extremes can propagate across levels of ecological organization and among components of a species' life history[46]. For instance, an extreme flood that occurs within the pre-spawning stage of a riverine fish can affect egg development and recruitment success, with lagged effects on population size — the indicator of interest — across several years. Third, anomalous events are treated as statistical anomalies that are scrubbed from the data before analyses. In the light of these and other challenges, we discuss promising avenues for modelling frameworks that can be used to predict the impacts of ECEs ranging from near-term forecasts to longer-term scenario projections. Given persistent uncertainties in both climate projections and biological responses — and the need to effectively communicate associated risks, thresholds and uncertainties to decision makers — accurately quantifying and tracking these uncertainties is paramount[131,132].

Statistical approaches

Estimating the probability or magnitude of ECEs at a given location or time is a crucial step for assessing risk and impacts on biodiversity. To address the challenges of modelling ECEs, researchers typically subset datasets by focusing on specific thresholds or quantiles or aggregating to a lower resolution (for example, yearly maxima from daily flow data) before applying classical regression techniques[23,133]. However, subsetting reduces sample size, increases uncertainty, can violate standard distributional assumptions, and filtering by extremes leads to a higher proportion of outliers. Robust methods including Theil–Sen regression are commonly used to mitigate outliers[12,134,135], whereas generalized extreme value distributions have been used to readjust for the asymmetric conditional distribution of the remaining tail of the data[23,136]. This loss of data, however, diminishes statistical power and predictive precision, particularly problematic for machine-learning and artificial intelligence approaches that require large training datasets. Quantile regression directly estimates chosen quantiles (such as the 0.99 quantile) from the full dataset without imposing a specific distributional form[137,138]. Because each quantile is fitted independently, however, these techniques can suffer from different quantile fits crossing, and rapidly deteriorating precision in the extreme tails[139]. Another approach to model extremes in many health and environmental applications has been to define a critical threshold and use logistic regression or machine learning to model the probability of exceedance. Although straightforward, this binary classification creates severe class imbalance when the threshold is in the tail, inflating uncertainty and underestimating the probability of rare events[140].

Truly understanding the changing nature and impacts of ECEs requires unified approaches that simultaneously capture shifts in the entire distribution of hydroclimatic and biodiversity variables, including both location and shape, while retaining full data and statistical power. Such approaches can, for example, differentiate whether ECEs are becoming more common because the entire distribution of the hydroclimatic variable is drifting upward or because its variance, skewness or tail heaviness is changing, making ECEs more likely even if the mean of the hydroclimatic variable remains constant. Distributional regression frameworks, such as Generalized Additive Models for Location, Scale and Shape (GAMLSS)[141], are well suited to interrogating extreme events as they leverage the full data to model how covariates affect all parameters of the response distribution, including location (mean and median), scale (variance), skewness and tail heaviness from which quantiles, exceedance probabilities or ECE frequency and magnitude can be inferred all at once[142]. When ECEs are used as covariates – such as minimum monthly streamflow, which can have nonlinear effects on ecological responses – GAMLSS can capture these patterns using smoothing splines, integrate machine-learning techniques, such as random forests and neural networks, and account for temporal structure through simple autocorrelation terms[141]. This flexibility makes GAMLSS well suited to predict not only ECEs but also their effects on ecological responses. GAMLSS supports a wide range of distributions[143], including zero-adjusted (for example, daily river flow with days of no flow), discrete (for example, number of species) or bounded distributions (for example, beta diversity indices). When models are adequately validated, distributional regression provides a powerful and flexible framework for predicting the full conditional distribution of ECEs and ecological responses and, in turn, the effects and risk of ECEs on river ecosystems.

Combining GAMLSS with models that integrate real-time, web-accessible hydrologic and ecological time-series data offers a powerful way forward in future near-term ecological risk assessment. Such near-term iterative forecast models enable adaptive refinement as new data are collected, iteratively improving models sequentially and fully tracking uncertainties through model stages[144,145]. These near-term forecasts leverage the autoregressive nature of time-series data to predict ecological dynamics from hourly to decadal scales. They are particularly well suited for integration with adaptive management cycles in managed systems, in which interventions are planned and implemented as a function of model forecasts and iterated appropriately[144] (for example, triggering actions such as dam reoperation to maintain connectivity during droughts; Fig. 5). Finally, to move beyond correlation and towards understanding underlying drivers, these models can be further extended with causal inference frameworks that disentangle direct and indirect effects, which are being increasingly used in ecology[61,146–148], enabling targeted, mechanism-based management interventions under uncertainty.

Mechanistic and hybrid approaches

Mechanistic models seek to explicitly link critical biological processes with climate dynamics, enabling predictions outside the historical range of variation. This direct causal mapping of multiscale ecological processes across a wide range of environmental dynamics makes mechanistic models ideal for studying feedback mechanisms and tipping points, including evaluating future risks from ECEs ahead of time. By modelling the component parts of a system, mechanistic models particularly excel at exploring emergent phenomena in response to changing conditions. For example, multispecies, stage-structured demographic models[149] projected riparian plant interaction networks across a full suite of future flow regime scenarios in a dryland river in the southwest USA[150]. Similarly, multispecies demographic models revealed a shift from a native dominant to a non-native dominant fish assemblage, aligning with increased drought frequency over a 50-year time period (1964–2017) in the Verde River, USA[151]. The vulnerability of commercially important Coho salmon to projected future summer extreme low flows was similarly predicted using a stage-based life-cycle model in which recruitment depended on river discharge during critical freshwater stages[152]. By incorporating key processes or demographic information, such as stage-specific vital rates (growth, survival and fecundity), and expressing them quantitatively in terms of environmental variation (individual high or low flow events and sequences), mechanistic models help to reveal how complex ecological communities might reorganize under novel flow regimes.

Mechanistic models can incorporate a wide range of mechanisms, including (1) physiology; (2) demography, life history and phenology; (3) dispersal, colonization and range dynamics; (4) species interactions; (5) responses to environmental variation; and (6) evolutionary potential and population differentiation[153] (Fig. 5). Although parameterization of mechanistic models presents substantial challenges, some unique to the extreme event being modelled, tailoring models towards particular mechanisms allows for a better understanding of the impacts of rare or unusual ECEs. For instance, modelling physiological responses to heatwaves might require parameters such as critical thermal maximum (CT_{max}) values from laboratory experiments; modelling the recovery of species or communities might require species-level dispersal kernels or trait-based approaches; and modelling population demographic responses might require information on stage-based survivorship and fecundity[153]. Acquiring data to inform such models can be challenging, but is critical to enable mechanistic predictions into non-analogue futures[22,153]. Additionally, fully mechanistic models

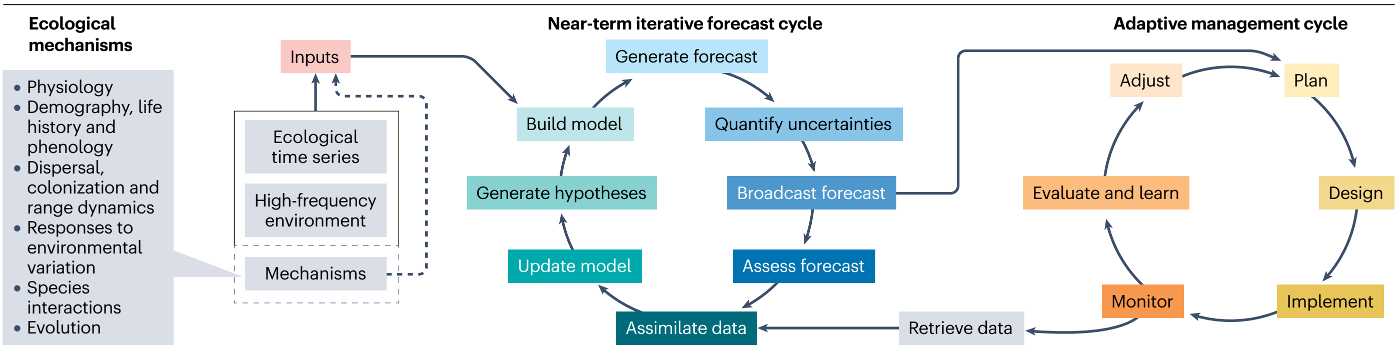


Fig. 5 | Relationship between ecological mechanisms, iterative forecast cycles and adaptive management. Ecological time-series data and high-frequency environmental data are inputs for near-term forecasts (middle) that predict future ecological conditions (from hours to years, depending on the model) in an iterative cycle. Quantifying uncertainty helps to target new data collection continuously, including adaptive monitoring. This iterative cycle couples well with adaptive management cycles (right), in which decisions are informed by model forecasts. Decisions are made adaptively in an iterative cycle. Incorporating ecological mechanisms (left) in predictive models can lengthen the forecast horizon (the period over which predictions remain reliable) and support scenario projections that explore the longer-term consequences of alternative interventions. The high-frequency nature of near-term iterative forecasts is well positioned to update models based on extreme events as they arise.

typically require simplification of ecological complexity, such as focusing on single mechanisms or grouping species by functional traits, to remain computationally tractable, potentially limiting their realism in highly diverse river ecosystems.

One solution to the persistent parameterization challenge lies in hybrid statistical–mechanistic models that fit parameters within mechanistic frameworks directly from available data[154–157]. These emerging approaches leverage the strengths of both statistical and mechanistic modelling, capitalizing on existing datasets while maintaining causal relationships. For instance, hybrid models might combine time-series data on population abundances with stage-structured population models to project trajectories under novel conditions (integrated population modelling)[158], or infer parameters from observational datasets via inverse modelling[159]. By combining the mechanistic depth with the flexibility and robustness of advanced statistical methods, these approaches hold promise to improve the forecasting of biodiversity responses to ECEs. Despite their potential, however, such models require further development to optimize computational efficiency, manage parameter uncertainty and ensure generalizability across diverse ecological systems. Future advances in these areas will be crucial for improving the prediction and management of ECEs in the context of climate change and increasing anthropogenic pressures.

River management in a time of extremes

Managing rivers for biodiversity in the face of increasing ECEs is an unprecedented challenge for water managers, particularly in terms of scale. Management approaches have traditionally been local (site-based) initiatives that have been reactive in nature. For example, environmental flows management is a direct response to disruption caused by water infrastructure operations such as dams[160]. Increasingly, ECEs will require water managers to introduce proactive measures at the network or catchment scale to allow for movement and redistribution of individuals and species through the river network (meta-system) during and after an ECE[161]. In this context, managing for biodiversity in the light of ECEs can be better framed as managing for resilience.

At the catchment scale, several key features relating to geomorphic integrity (the natural structure of river channels and floodplains) can help to build biodiversity resilience under a changing climate[162–164]. First, natural spatial and temporal variability in riverine environments, such as those associated with discharge, temperature and sediment flux, can be used to define the habitat conditions that shape species distributions[165]. In the past, places where anthropogenic forces caused the dampening or amplification of variability have been the focus of restoration efforts for biodiversity[166]. To manage for extremes, river restoration should be process-based[167] and explicitly focus on restoring both connectivity and spatiotemporal variability[168,169]. Second, ensuring heterogeneity in geomorphic habitats can create refuges (cool groundwater upwelling, stable physical habitats, deepwater pools and perennial habitats) that increase resistance to large flood events or drought events[164,170]. Third, ensuring connectivity of heterogeneous habitats through a river system's dendritic network of channels can facilitate meta-system processes (including dispersal and gene exchange) that help to maintain catchment-wide diversity. A heterogeneous catchment with naturally variable processes and connectivity will increase the likelihood of refuges and recolonization that are considered crucial to sustaining biodiversity in river ecosystems[110]. At the scale of the river network, refuges and connectivity are both important: if species can move through the network, they can use these refuges to persist during ECEs and recolonize afterwards. Importantly, permanent fragmentation (by dams, weirs and other barriers) and temporary fragmentation (by drying events) can jeopardize these dynamics[171].

A challenge for developing proactive management strategies is identifying how the capacity for a catchment to support biodiversity varies in response to the combination of catchment size (from small streams to large rivers) and human modification of catchment integrity (such as fragmentation by dams or intensity of land-use change). As catchment scale increases, management for biodiversity shifts from a focus on alpha diversity to beta and gamma diversity. However, the likelihood of potential intervention success is reduced as the cumulative impacts of human modifications increase[172].

Addressing this management challenge requires defining a typology of rivers and river catchment properties that differ in their potential to provide resilience to ECEs (Table 1). This typology provides a framework for evaluation of potentially effective management strategies at different spatial extents. Likewise, adopting a vulnerability (or risk) analysis approach to managing biodiversity in riverine landscapes could help to navigate the challenge of managing under increasing ECEs. This approach involves at least three components. First, metrics for catchment resilience can be used to identify the sensitivity of biodiversity responses to ECEs in terms of catchment size and human impacts[162] (Table 1). Targets for biodiversity management could include sustaining keystone species critical to ecosystem function or keystone communities that are enabled via dispersal through connected river networks[173]. Second, the exposure of a catchment type to ECEs needs to be characterized. Methods to robustly project ECEs are limited, but near-term forecasting could be used to anticipate near-future ECEs. The overlay of catchment sensitivity and biodiversity exposure to ECEs would provide critical information about where to target proactive management actions that could increase catchment resilience (including removal of waterway barriers, improvement of land cover and so on)[174]. Third, decision support tools can be used to better anticipate which management interventions will deliver the greatest net gain and how to triage competing demands given resource constraints. The RAD framework (resist–accept–direct) that is currently used by science-based land management agencies offers an example of a decision support tool that could help decision-making for ECEs[175]. The RAD framework enables managers to assess the vulnerability of ecosystems to transformation at landscape scales and the feasibility of management interventions to sustain ecosystem function. Opportunities exist to extend the RAD framework to also account for social and economic adaptation — as well as ecological resilience — in the face of ECEs[176].

Water management plans and policies that consider trade-offs among multiple ecological, social and economic goals must also be embedded within the decision process[177]. One area at the nexus of such decision-making is in managing rivers in response to increasing extreme flood risks. Although hard engineering infrastructure might be required to protect infrastructure and livelihoods from increasing ECEs, nature-based solutions such as giving rivers room to move can offer a mutually beneficial solution for both humans and ecosystem health[164]. Coordinating efforts at multiple spatial and temporal scales is also possible by using eco-engineering decision scaling tools (EEDS[178]) to evaluate how different management options for water infrastructure can achieve stakeholder-defined biodiversity objectives under non-stationarity. This bottom-up decision tool could be combined with iterative near-term climate forecasting to guide and update management decisions in an adaptive management cycle (Fig. 5).

Summary and future directions

Climate change is exerting widespread impacts on riverine biodiversity[179]. ECEs in particular are reshaping river ecosystems in complex ways, interacting with other stressors to amplify risks to biodiversity across multiple levels from genes to ecosystems and across spatial scales. River ecosystems, with their connected hierarchical structures, are particularly vulnerable to these changes, including repeat events that have compounding impacts. Much of historical river ecology and management is founded on the assumption of stationarity: that the conditions we have observed in the past will continue into the future in a kind of dynamic equilibrium. Mounting evidence is challenging this assumption, however, with models indicating that these events will accelerate as climate disruption continues. Ultimately,

Table 1 | A typology of river settings that differ in the potential to provide catchment resilience to extreme climatic events

River setting	Context	Native biodiversity potential	Feature	Management action (RAD)	Outcome
Free-flowing stream or river	Connected to larger free-flowing river	High	Well-connected catchment with presumably high resilience (variability and heterogeneity)	Resist changes in land cover management at the catchment scale to maintain natural flow (discharge), sediment, temperature processes and connectivity	Maintains catchment resilience and high beta and gamma diversity
Tributary to stream or river impounded downstream	Tributaries to a river that itself is impounded by a nearby downstream dam	Medium	Limited connectivity in catchment interrupted by a downstream dam. Might not help migratory species that cannot pass dam and impounded river	Resist degradation of free-flowing tributaries in catchment, assist in re-establishing connectivity above impounded river. High priority catchments might hold unique biodiversity	Maintains high beta and gamma diversity and supports system resilience through variability, heterogeneity and connectivity
Tributary to stream or river impounded upstream	Tributaries that flow into regulated river (that is, one impounded by a nearby upstream dam)	Medium	Set of potentially unconnected tributaries, but habitat potentially accessible to downstream migratory species. Natural flow regime entering modified mainstem	Protect undammed tributaries to dammed river (that is, those flowing into regulated river)	Helps to support beta diversity of system, and protects native species and resilience through supporting colonists
Isolated stream or river	Regulated river (that is, one downstream of dam that modifies flow, sediment, temperature and connectivity)	Medium-low	Single, linear habitat that is disconnected from catchment-scale meta-processes	Direct management of environmental flow and/or thermal (for example, cold water) releases from reservoir for key species	Provides improved flow and temperature regimes that support alpha diversity in regulated river
Isolated stream or river hydrologically disconnected from other streams	Affected river (that is, one that flows through a highly urbanized catchment)	Low	Disconnected from meta-processes and thus low resilience	Accept that system cannot be managed towards a more resilient state to support biodiversity	May offer limited opportunities to support biodiversity

RAD, resist–accept–direct.

Glossary

Compound event	An extreme climate event in which multiple climate drivers or hazards occur simultaneously or sequentially, interacting to produce impacts that are greater than would be expected from each event acting alone.
Conditional distribution	A conditional distribution characterizes the probability distribution of a response variable given fixed values of one or more covariates (explanatory variables).
Dendritic	A hierarchical, tree-like branching network formed by repeated bifurcation, characteristic of river systems.
Distribution	A probability distribution specifies the probabilities of all possible values of a random variable and reflects key features such as central tendency, variability, skewness and tail shape.
Distributional regression	Methods that model the conditional distribution of an outcome, allowing parameters such as mean, variance, skewness and tail heaviness to depend on explanatory variables, rather than just the mean.
Generalized Additive Models for Location, Scale and Shape (GAMLSS)	A widely used framework for distributional regression that can incorporate nonlinear relationships through smoothing splines and other machine-learning architectures, enabling the prediction of central tendency, quantiles and exceedance probabilities of thresholds, which are essential for assessing variability, extreme event risk and magnitude.
Generalized extreme value distribution	A family of continuous distributions encompassing the Gumbel, Fréchet and Weibull type distributions, often used to approximate the tails of other distributions, or when modelling the maxima or minima sampled within specific spatiotemporal intervals.
Hybrid statistical–mechanistic model	A model that combines elements of both statistical and mechanistic models, including those that estimate parameters within mechanistic frameworks directly from observed data.
Hydrological connectivity	Water-mediated transfer of matter, energy or organisms between components of a hydrological system, linking habitats and influencing nutrient fluxes, sediment transport, ecological interactions and pollutant spread.
Mechanistic models	Parametric models grounded in hypothesized, anticipated or known functional relationships among underlying biological, chemical or physical processes. Also known as process-oriented or process-based models.
Meta-system	Sets of spatially structured ecological units — including metapopulations, metacommunities and meta-ecosystems — that interact through the movement of organisms, energy or materials across space.
Near-term iterative forecast	A near-horizon to medium-horizon prediction framework in which forecasts are repeatedly updated as new observations become available, making it particularly useful for dynamic systems in which conditions change rapidly.
Perennial	A perennial stream maintains continuous flow throughout the year under normal climatic conditions and is not subject to seasonal drying.
Quantile regression	A framework that models conditional quantiles of a response variable given explanatory variables, rather than focusing solely on the conditional mean.
RAD framework	A decision-making framework that helps resource managers to develop strategies for responding to socio-ecological changes, including those caused by climate change, by resisting, accepting or directing.
Refuge	An area where organisms find protection from adverse conditions, such as predation or extreme environmental factors, allowing them to persist when surrounding habitats are inhospitable.
Resilience	The ability of a system to absorb shocks and recover to a similar form and function.
Stationary	Stationarity signifies that the statistical properties of a time series, such as mean, variance and covariance, remain constant over time; an assumption increasingly challenged in hydrodynamic systems under climate change (in other words, non-stationarity).
Tail heaviness	How quickly probabilities decline in the tails of a distribution, with heavy-tailed distributions (for example, Cauchy) being more likely to produce extreme values than light-tailed ones (for example, normal).
Tails	The tails of a statistical distribution are the regions at both extremes, corresponding to the smallest and largest values.

safeguarding river biodiversity in an era of extremes will depend on shifting from reactive to proactive and anticipatory, catchment-scale management that acknowledges both the uncertainty and inevitability of future change. In addition to the ideas discussed in the prior sections, we outline promising future avenues for research and application subsequently. By addressing these priorities, researchers and practitioners can convert fragmented evidence into predictive frameworks, helping society to protect riverine biodiversity against increasingly frequent ECEs. Closing geographic research gaps is also critical, as most documented examples of ECE impacts originate from well-studied, high-income countries in the Global North.

High-resolution, high-frequency monitoring programmes are urgently needed to provide the data necessary to better understand and predict the impacts of ECEs on biodiversity. Monitoring programmes must move beyond static, infrequent sampling and instead adopt high-resolution, real-time data collection that integrates both biotic and abiotic indicators[180]. Incorporating technologies such as remote sensing, environmental DNA and automated sensor networks can enhance spatial and temporal coverage, allowing researchers to monitor riverine ecosystems at the spatial and temporal scales needed to detect ECEs[181,182] and measure shifts in species distribution and community structure[183]. Integrative and more representative gauge networks are needed to measure river discharge globally[184]. Additionally, coupling these data with predictive ecological models will improve the capacity to forecast biodiversity responses and inform adaptive river management strategies in the face of accelerating climate change (see the ‘Anticipating biological responses to extremes’ section).

Additional to the above priority is the need for continued funding of long-term research and monitoring programmes. A critical challenge in understanding how ECEs affect riverine biodiversity lies in the scarcity of empirical evidence, which is often based on opportunistic observations from long-term datasets. For instance, a 30-year time series enabled understanding the impacts of a major flood event on salmon, macroinvertebrate and meiofauna communities that caused clear geomorphic change to the stream channel[185]. Researchers and funding agencies must prioritize long-term ecological research and multiscale monitoring networks. Pairing these efforts with experiments, such as mesocosms that mimic dendritic networks, will allow researchers to isolate mechanisms such as drought-induced fragmentation or flood homogenization. Global initiatives using standardized protocols for rapid sampling (for example, CELLDEX[186]) can potentially reduce the burden on individual researchers to spatially replicate by sharing effort among researcher networks.

A major research frontier is to separate the inherent natural variability of river systems from the persistent imprints that ECEs leave on ecological structure and function – including physical (such as habitat simplification), demographic (such as altered age structure), structural (such as species composition) and biogeochemical (such as nutrient depletion). Resolving this distinction is fundamental for determining whether such legacy effects represent transient recovery phases or permanent changes in stability thresholds. Overcoming this challenge requires approaches that integrate multiple lines of evidence. First, studies using palaeoecological archives, such as sediment cores that track invertebrate remains or isotopic analysis of fish otoliths, can rebuild historical baselines of stability and identify tipping points. For example, isotopic signatures in otoliths provide a means to reconstruct individual exposure to past hydrological conditions, which can be linked to population fluctuations and recovery. Second, mechanistic models that explicitly incorporate stochastic variability can help to identify when observed changes exceed the bounds of expected fluctuations. Models could also account for processes such as delayed predator recovery, which can amplify disturbance impacts and push systems towards threshold breaches. Third, experimental platforms such as Drought-Net[187], expanded to riverine systems, could impose disturbances such as controlled drying gradients to test resilience limits, helping to understand the mechanisms underpinning ECE impacts on riverine biodiversity.

Unlike legacies, which leave persistent imprints, feedbacks operate contemporaneously, shaping how rivers respond to and propagate ECEs. An urgent frontier for future research is to understand the biophysical feedback loops among the intensification of ECEs, river flow regimes, geomorphological dynamics and biodiversity resilience[162,188,189]. The link between physical and biological processes in river-floodplain systems is bidirectional, including positive feedback mechanisms in which riparian vegetation can strongly influence river geomorphology and vice versa. Altered flow regimes destabilize this relationship, amplifying the role of vegetation, particularly invasive species[74], in shaping river geomorphology, and weakening the influence of hydrology[164]. ECEs have the potential to substantially and irreversibly disrupt this relationship, resulting in reduced habitat complexity critical for buffering future disturbances, diminishing the resilience of river ecosystems to subsequent extremes. Given the potential role of river channels to store carbon[190], and the negative impacts of ECEs on river geomorphology, increasing ECEs could also indirectly promote further ECEs[191]. Understanding how the degradation of riverine biophysical processes exacerbates climate extremes, and vice versa, requires an integrated approach that couples hydrology, geomorphology, ecology and atmospheric science. New research should prioritize experimental river restoration designed to test flow–geomorphology–biodiversity interactions and predictive modelling frameworks that account for these dynamic, bidirectional feedbacks. Only by embracing these complex interconnections can researchers fully grasp how rivers shape – and are shaped by – an increasingly extreme climate.

References

1. Lynch, A. J. et al. People need freshwater biodiversity. *WIREs Water* **10**, e1633 (2023).
2. WWF. *Living Planet Report 2024 — A System in Peril* (WWF, 2024).
3. Urban, M. C. Climate change extinctions. *Science* **386**, 1123–1128 (2024).
4. Tickner, D. et al. Bending the curve of global freshwater biodiversity loss: an emergency recovery plan. *BioScience* **70**, 330–342 (2020).
5. Reid, A. J. et al. Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biol. Rev.* **94**, 849–873 (2018).
6. He, F. et al. Hydropower impacts on riverine biodiversity. *Nat. Rev. Earth Environ.* **5**, 755–772 (2024).
7. Datry, T. et al. Non-perennial segments in river networks. *Nat. Rev. Earth Environ.* **4**, 815–830 (2023).
8. Blöschl et al. Changing climate shifts timing of European floods. *Science* **357**, 588–590 (2017).
9. Blöschl et al. Changing climate both increases and decreases European river floods. *Nature* **573**, 108–111 (2019).
10. Tramblay, Y. et al. Trends in flow intermittence for European rivers. *Hydrol. Sci. J.* **66**, 37–49 (2020).
11. Zipper, S. C. et al. Pervasive changes in stream intermittency across the United States. *Environ. Res. Lett.* **16**, 084033 (2021).
12. Gudmundsson, L. et al. Globally observed trends in mean and extreme river flow attributed to climate change. *Science* **371**, 1159–1162 (2021).
13. Tassone, S. J. et al. Increasing heatwave frequency in streams and rivers of the United States. *Limnol. Oceanogr. Lett.* **8**, 295–304 (2022).
14. Burrell, B. C., Beltaos, S. & Turcotte, B. Effects of climate change on river-ice processes and ice jams. *Int. J. River Basin Manag.* **21**, 421–441 (2022).
15. McPhillips, L. E. et al. Defining extreme events: a cross-disciplinary review. *Earth's Future* **6**, 441–455 (2018).
16. Mahecha, M. D. et al. Biodiversity and climate extremes: known interactions and research gaps. *Earth's Future* **12**, e2023EF003963 (2024).
17. Poff, N. L. et al. Extreme streams: species persistence and genomic change in montane insect populations across a flooding gradient. *Ecol. Lett.* **21**, 525–535 (2018).
18. Sabater, S. et al. Extreme weather events threaten biodiversity and functions of river ecosystems: evidence from a meta-analysis. *Biol. Rev.* **98**, 450–461 (2022).
19. Braz-Mota, S. & Luis Val, A. Fish mortality in the Amazonian drought of 2023: the role of experimental biology in our response to climate change. *J. Exp. Biol.* **227**, jeb247255 (2024).
20. Tassone, S. J., Kelly, M. C., Beidler, O. N., Pace, M. L. & Marcarelli, A. M. Impacts of riverine heatwaves on rates of ecosystem metabolism in the United States. *Limnol. Oceanogr. Lett.* **10**, 464–472 (2025).
21. Milly, P. C. D. et al. Stationarity is dead: whither water management? *Science* **319**, 573–574 (2008).
22. Tonkin, J. D. et al. Prepare river ecosystems for an uncertain future. *Nature* **570**, 301–303 (2019).
23. Katz, R. W., Parlange, M. B. & Naveau, P. Statistics of extremes in hydrology. *Adv. Water Resour.* **25**, 1287–1304 (2002).
24. Milly, P. C. D., Wetherald, R. T., Dunne, K. A. & Delworth, T. L. Increasing risk of great floods in a changing climate. *Nature* **415**, 514–517 (2002).
25. Ledger, M. E. & Milner, A. M. Extreme events in running waters. *Freshw. Biol.* **60**, 2455–2460 (2015).
26. Smith, M. D. et al. An ecological perspective on extreme climatic events: a synthetic definition and framework to guide future research. *J. Ecol.* **99**, 656–663 (2011).
27. Easterling, D. R. et al. Climate extremes: observations, modeling, and impacts. *Science* **289**, 2068–2074 (2000).
28. Paul, M. J. et al. Wildfire induces changes in receiving waters: a review with considerations for water quality management. *Water Resour. Res.* **58**, 1–28 (2022).
29. Ball, G., Regier, P., González-Pinzón, R., Reale, J. & Van Horn, D. Wildfires increasingly impact western US fluvial networks. *Nat. Commun.* **12**, 2484 (2021).
30. Dahm, C. N., Candelaria-Ley, R. I., Reale, C. S., Reale, J. K. & Van Horn, D. J. Extreme water quality degradation following a catastrophic forest fire. *Freshw. Biol.* **60**, 2584–2599 (2015).
31. Zscheischler, J. et al. Future climate risk from compound events. *Nat. Clim. Change* **8**, 469–477 (2018).
32. Zscheischler, J. et al. A typology of compound weather and climate events. *Nat. Rev. Earth Environ.* **1**, 333–347 (2020).

33. Bastos, A. et al. A joint framework for studying compound ecoclimatic events. *Nat. Rev. Earth Environ.* **4**, 333–350 (2023).
34. Dennison, P. E., Brewer, S. C., Arnold, J. D. & Moritz, M. A. Large wildfire trends in the western United States, 1984–2011. *Geophys. Res. Lett.* **41**, 2928–2933 (2014).
35. Gergel, D. R., Nijssen, B., Abatzoglou, J. T., Lettenmaier, D. P. & Stumbaugh, M. R. Effects of climate change on snowpack and fire potential in the western USA. *Clim. Change* **141**, 287–299 (2017).
36. Woodward, G. et al. The effects of climatic fluctuations and extreme events on running water ecosystems. *Philos. Trans. R. Soc. B Biol. Sci.* **371**, 20150274 (2016).
37. Giller, P. S., Sangpradub, N. & Twomey, H. Catastrophic flooding and macroinvertebrate community structure. *SIL. Proc.* 1922–2010 **24**, 1724–1729 (1991).
38. Bogan, M. T. & Lytle, D. A. Severe drought drives novel community trajectories in desert stream pools: drought causes community regime shifts. *Freshw. Biol.* **56**, 2070–2081 (2011).
39. Gutiérrez-Fonseca, P. E., Pringle, C. M., Ramírez, A., Gómez, J. E. & García, P. Hurricane disturbance drives trophic changes in neotropical mountain stream food webs. *Ecology* **105**, e4202 (2023).
40. Aspin, T. W. H. et al. Extreme drought pushes stream invertebrate communities over functional thresholds. *Glob. Change Biol.* **25**, 230–244 (2018).
41. Colls, M., Timoner, X., Font, C., Sabater, S. & Acuña, V. Effects of duration, frequency, and severity of the non-flow period on stream biofilm metabolism. *Ecosystems* **22**, 1393–1405 (2019).
42. Gutschick, V. P. & BassiriRad, H. Extreme events as shaping physiology, ecology, and evolution of plants: toward a unified definition and evaluation of their consequences. *N. Phytol.* **160**, 21–42 (2003).
43. Blondel, L., Paterson, I. G., Bentzen, P. & Hendry, A. P. Resistance and resilience of genetic and phenotypic diversity to 'black swan' flood events: a retrospective analysis with historical samples of guppies. *Mol. Ecol.* **30**, 1017–1028 (2021).
44. Grant, P. R. et al. Evolution caused by extreme events. *Philos. Trans. R. Soc. B Biol. Sci.* **372**, 20160146 (2017).
45. Lytle, D. A. & Poff, N. L. Adaptation to natural flow regimes. *Trends Ecol. Evol.* **19**, 94–100 (2004).
46. Hernández-Carrasco, D., Tylianakis, J. M., Lytle, D. A. & Tonkin, J. D. Ecological and evolutionary consequences of changing seasonality. *Science* **388**, eads4880 (2025).
47. Lytle, D. A. Disturbance regimes and life-history evolution. *Am. Nat.* **157**, 525–536 (2001).
48. Lytle, D. A., Bogan, M. T. & Finn, D. S. Evolution of aquatic insect behaviours across a gradient of disturbance predictability. *Proc. R. Soc. B Biol. Sci.* **275**, 453–462 (2007).
49. Woodward, G., Bonada, N., Feeley, H. B. & Giller, P. S. Resilience of a stream community to extreme climatic events and long-term recovery from a catastrophic flood. *Freshw. Biol.* **60**, 2497–2510 (2015).
50. Marino, A., Fenoglio, S. & Bo, T. The impact of catastrophic floods on macroinvertebrate communities in low-order streams: a study from the Apennines (Northwest Italy). *Water* **16**, 2646 (2024).
51. Chessman, B. C. Identifying species at risk from climate change: traits predict the drought vulnerability of freshwater fishes. *Biol. Conserv.* **160**, 40–49 (2013).
52. Stubbington, R. & Datry, T. The macroinvertebrate seedbank promotes community persistence in temporary rivers across climate zones. *Freshw. Biol.* **58**, 1202–1220 (2013).
53. Hay, S. E., Jenkins, K. M. & Kingsford, R. T. Diverse invertebrate fauna using dry sediment as a refuge in semi-arid and temperate Australian rivers. *Hydrobiologia* **806**, 95–109 (2017).
54. Mouthon, J. & Daufresne, M. Effects of the 2003 heatwave and climatic warming on mollusc communities of the Saône: a large lowland river and of its two main tributaries (France). *Glob. Change Biol.* **12**, 441–449 (2006).
55. Whitney, J. E. et al. Physiological basis of climate change impacts on North American inland fishes. *Fisheries* **41**, 332–345 (2016).
56. Hladyz, S., Watkins, S. C., Whitworth, K. L. & Baldwin, D. S. Flows and hypoxic blackwater events in managed ephemeral river channels. *J. Hydrol.* **401**, 117–125 (2011).
57. Whitworth, K. L., Baldwin, D. S. & Kerr, J. L. Drought, floods and water quality: drivers of a severe hypoxic blackwater event in a major river system (the southern Murray–Darling Basin, Australia). *J. Hydrol.* **450–451**, 190–198 (2012).
58. Piniewski, M. et al. Hydrological modelling of the Vistula and Odra river basins using SWAT. *Hydrol. Sci. J.* **62**, 1266–1289 (2017).
59. Death, R. G., Fuller, I. C. & Macklin, M. G. Resetting the river template: the potential for climate-related extreme floods to transform river geomorphology and ecology. *Freshw. Biol.* **60**, 2477–2496 (2015).
60. Reich, P. & Lake, P. S. Extreme hydrological events and the ecological restoration of flowing waters. *Freshw. Biol.* **60**, 2639–2652 (2014).
61. Tabi, A., Siqueira, T. & Tonkin, J. D. Species interactions drive continuous assembly of freshwater communities in stochastic environments. *Sci. Rep.* **12**, 21747 (2023).
62. Larimore, R. W., Childers, W. F. & Heckrotte, C. Destruction and re-establishment of stream fish and invertebrates affected by drought. *Trans. Am. Fish. Soc.* **88**, 261–285 (1959).
63. Cowx, I. G., Young, W. O. & Hellawell, J. M. The influence of drought on the fish and invertebrate populations of an upland stream in Wales. *Freshw. Biol.* **14**, 165–177 (1984).
64. Morrison, B. R. S. Recolonisation of four small streams in central Scotland following drought conditions in 1984. *Hydrobiologia* **208**, 261–267 (1990).
65. Caruso, B. S. Temporal and spatial patterns of extreme low flows and effects on stream ecosystems in Otago, New Zealand. *J. Hydrol.* **257**, 115–133 (2002).
66. Nico, L. G., Williams, D. & Jelks, H. L. *Black Carp: Biological Synopsis and Risk Assessment of an Introduced Fish* (American Fisheries Society, 2005).
67. Tucker, J. K., Cronin, F. A., Soergel, D. W. & Theiling, C. H. Predation on zebra mussels (*Dreissena polymorpha*) by common carp (*Cyprinus carpio*). *J. Freshw. Ecol.* **11**, 363–372 (1996).
68. Schultz, A. A., Maughan, O. E., Bonar, S. A. & Matter, W. J. Effects of flooding on abundance of native and nonnative fishes downstream from a small impoundment. *North Am. J. Fish. Manag.* **23**, 503–511 (2003).
69. Diez, J. M. et al. Will extreme climatic events facilitate biological invasions? *Front. Ecol. Environ.* **10**, 249–257 (2012).
70. Sorte, C. J. B. et al. Poised to prosper? A cross-system comparison of climate change effects on native and non-native species performance. *Ecol. Lett.* **16**, 261–270 (2012).
71. Gido, K. B. et al. Pockets of resistance: response of arid-land fish communities to climate, hydrology, and wildfire. *Freshw. Biol.* **64**, 761–777 (2019).
72. Ruhí, A., Holmes, E. E., Rinne, J. N. & Sabo, J. L. Anomalous droughts, not invasion, decrease persistence of native fishes in a desert river. *Glob. Change Biol.* **21**, 1482–1496 (2014).
73. Stromberg, J. Dynamics of Fremont cottonwood (*Populus fremontii*) and saltcedar (*Tamarix chinensis*) populations along the San Pedro River, Arizona. *J. Arid. Environ.* **40**, 133–155 (1998).
74. Carneiro, L. et al. Typology of the ecological impacts of biological invasions. *Trends Ecol. Evol.* **40**, 563–574 (2025).
75. Daufresne, M., Bady, P. & Fruget, J.-F. Impacts of global changes and extreme hydroclimatic events on macroinvertebrate community structures in the French Rhône River. *Oecologia* **151**, 544–559 (2007).
76. Rahel, F. J. & Olden, J. D. Assessing the effects of climate change on aquatic invasive species. *Conserv. Biol.* **22**, 521–533 (2008).
77. Magoulick, D. D. & Kobza, R. M. The role of refugia for fishes during drought: a review and synthesis. *Freshw. Biol.* **48**, 1186–1198 (2003).
78. Labbe, T. R. & Fausch, K. D. Dynamics of intermittent stream habitat regulate persistence of a threatened fish at multiple scales. *Ecol. Appl.* **10**, 1774 (2000).
79. Lennox, R. S. et al. Introduced trout hinder the recovery of native fish following an extreme flood disturbance. Preprint at *BioRxiv* https://doi.org/10.1101/2024.09.05.611377 (2024).
80. Leprieur, F. et al. Hydrological disturbance benefits a native fish at the expense of an exotic fish. *J. Appl. Ecol.* **43**, 930–939 (2006).
81. Hore, O. R., Tonkin, J., Boddy, N. C. & McIntosh, A. Flow matters: unravelling the interactive influences of flow alterations and non-native trout on vulnerable galaxiids. *River Res. Appl.* **41**, 1131–1142 (2025).
82. Lake, P. S. Ecological effects of perturbation by drought in flowing waters. *Freshw. Biol.* **48**, 1161–1172 (2003).
83. Myers, B. J. E. et al. The effects of flow extremes on native and non-native stream fishes in Puerto Rico. *Freshw. Biol.* **69**, 1292–1306 (2024).
84. Larson, E. I., Poff, N. L., Atkinson, C. L. & Flecker, A. S. Extreme flooding decreases stream consumer autochthony by increasing detrital resource availability. *Freshw. Biol.* **63**, 1483–1497 (2018).
85. Sarremejane, R. et al. Drying and fragmentation drive the dynamics of resources, consumers and ecosystem functions across aquatic-terrestrial habitats in a river network. *Oikos* **2024**, e10135 (2024).
86. Gessner, M. O., Chauvet, E. & Dobson, M. A perspective on leaf litter breakdown in streams. *Oikos* **85**, 377 (1999).
87. Corti, R. & Datry, T. Invertebrates and sestonic matter in an advancing wetted front travelling down a dry river bed (Albarine, France). *Freshw. Sci.* **31**, 1187–1201 (2012).
88. Jacobson, P. J. & Jacobson, K. M. Hydrologic controls of physical and ecological processes in Namib Desert ephemeral rivers: implications for conservation and management. *J. Arid Environ.* **93**, 80–93 (2013).
89. Glazebrook, H. S. & Robertson, A. I. The effect of flooding and flood timing on leaf litter breakdown rates and nutrient dynamics in a river red gum (*Eucalyptus camaldulensis*) forest. *Aust. J. Ecol.* **24**, 625–635 (1999).
90. Chauvet, E. Leaf litter decomposition in large rivers: the case of the River Garonne. *Limnetica* **13**, 65–70 (1997).
91. Langhans, S. D. & Tockner, K. The role of timing, duration, and frequency of inundation in controlling leaf litter decomposition in a river-floodplain ecosystem (Tagliamento, northeastern Italy). *Oecologia* **147**, 501–509 (2005).
92. Bernal, S., von, Schiller, D., Sabater, F. & Martí, E. Hydrological extremes modulate nutrient dynamics in Mediterranean climate streams across different spatial scales. *Hydrobiologia* **719**, 31–42 (2012).
93. del Campo, R., Foulquier, A., Singer, G. & Datry, T. in *The Ecology of Plant Litter Decomposition in Stream Ecosystems* (eds Swan, C. M. et al.) 73–100 (Springer International, 2021).
94. Corti, R., Datry, T., Drummond, L. & Larned, S. T. Natural variation in immersion and emersion affects breakdown and invertebrate colonization of leaf litter in a temporary river. *Aquat. Sci.* **73**, 537–550 (2011).
95. Datry, T. et al. A global analysis of terrestrial plant litter dynamics in non-perennial waterways. *Nat. Geosci.* **11**, 497–503 (2018).
96. Datry, T., Corti, R., Claret, C. & Philippe, M. Flow intermittence controls leaf litter breakdown in a French temporary alluvial river: the 'drying memory'. *Aquat. Sci.* **73**, 471–483 (2011).

97. Pinna, M. et al. Influence of aperiodic summer droughts on leaf litter breakdown and macroinvertebrate assemblages: testing the drying memory in a Central Apennines River (Aterno River, Italy). *Hydrobiologia* **782**, 111–126 (2016).
98. Di Sabatino, A., Coscieme, L. & Cristiano, G. Effects of antecedent drying events on structure, composition and functional traits of invertebrate assemblages and leaf-litter breakdown in a former perennial river of Central Apennines (Aterno River, Abruzzo, Central Italy). *Ecohydrology* **15**, e2358 (2021).
99. Gómez-Gener, L., Lupon, A., Laudon, H. & Sponseller, R. A. Drought alters the biogeochemistry of boreal stream networks. *Nat. Commun.* **11**, 1795 (2020).
100. Acuña, V., Giorgi, A., Muñoz, I., Uehlinger, U. & Sabater, S. Flow extremes and benthic organic matter shape the metabolism of a headwater Mediterranean stream. *Freshw. Biol.* **49**, 960–971 (2004).
101. Ferreira, V. & Canhoto, C. Future increase in temperature may stimulate litter decomposition in temperate mountain streams: evidence from a stream manipulation experiment. *Freshw. Biol.* **60**, 881–892 (2015).
102. Pérez, J., Correa-Araneda, F., López-Rojo, N., Basaguren, A. & Boyero, L. Extreme temperature events alter stream ecosystem functioning. *Ecol. Indic.* **121**, 106984 (2021).
103. Battin, T. J. et al. River ecosystem metabolism and carbon biogeochemistry in a changing world. *Nature* **613**, 449–459 (2023).
104. López-Rojo, N. et al. Alternating drying and flowing phases control stream metabolism through short- and long-term effects: insights from a river network. *J. Geophys. Res. Biogeosci.* **130**, e2024JG008369 (2025).
105. Piano, E. et al. If Alpine streams run dry: the drought memory of benthic communities. *Aquat. Sci.* **81**, 32 (2019).
106. Crabot, J., Heino, J., Launay, B. & Datry, T. Drying determines the temporal dynamics of stream invertebrate structural and functional beta diversity. *Ecography* **43**, 620–635 (2019).
107. Vander Vorste, R., Obedzinski, M., Nossaman Pierce, S., Carlson, S. M. & Grantham, T. E. Refuges and ecological traps: extreme drought threatens persistence of an endangered fish in intermittent streams. *Glob. Change Biol.* **26**, 3834–3845 (2020).
108. Schindler, D. E. et al. Population diversity and the portfolio effect in an exploited species. *Nature* **465**, 609–612 (2010).
109. Loreau, M. et al. Biodiversity as insurance: from concept to measurement and application. *Biol. Rev.* **96**, 2333–2354 (2021).
110. Van Looy, K. et al. The three Rs of river ecosystem resilience: resources, recruitment, and refugia. *River Res. Appl.* **35**, 107–120 (2019).
111. Bogan, M. T., Boersma, K. S. & Lytle, D. A. Flow intermittency alters longitudinal patterns of invertebrate diversity and assemblage composition in an arid-land stream network. *Freshw. Biol.* **58**, 1016–1028 (2013).
112. Chester, E. T. & Robson, B. J. Anthropogenic refuges for freshwater biodiversity: their ecological characteristics and management. *Biol. Conserv.* **166**, 64–75 (2013).
113. Vander Vorste, R., Malard, F. & Datry, T. Is drift the primary process promoting the resilience of river invertebrate communities? A manipulative field experiment in an intermittent alluvial river. *Freshw. Biol.* **61**, 1276–1292 (2015).
114. Priest, H. J. & Finn, D. S. Bucketloads of aquatic invertebrates in a dry intermittent stream. *Ecology* **104**, e3936 (2023).
115. Kawanishi, R., Inoue, M., Dohi, R., Fujii, A. & Miyake, Y. The role of the hyporheic zone for a benthic fish in an intermittent river: a refuge, not a graveyard. *Aquat. Sci.* **75**, 425–431 (2013).
116. Padial, A. A. et al. The role of an extreme flood disturbance on macrophyte assemblages in a Neotropical floodplain. *Aquat. Sci.* **71**, 389–398 (2009).
117. McCann, K. S., Rasmussen, J. B. & Umbanhowar, J. The dynamics of spatially coupled food webs. *Ecol. Lett.* **8**, 513–523 (2005).
118. Siqueira, T. et al. Understanding temporal variability across trophic levels and spatial scales in freshwater ecosystems. *Ecology* **105**, e4219 (2023).
119. Ross, S. R. P.-J. et al. Predators mitigate the destabilising effects of heatwaves on multitrophic stream communities. *Glob. Change Biol.* **28**, 403–416 (2021).
120. Parsons, M., McLoughlin, C. A., Kotschy, K. A., Rogers, K. H. & Rountree, M. W. The effects of extreme floods on the biophysical heterogeneity of river landscapes. *Front. Ecol. Environ.* **3**, 487 (2005).
121. Eagle, L. J. B. et al. Extreme flood disturbance effects on multiple dimensions of river invertebrate community stability. *J. Anim. Ecol.* **90**, 2135–2146 (2021).
122. Lyu, J. et al. Extreme drought–heatwave events threaten the biodiversity and stability of aquatic plankton communities in the Yangtze River ecosystems. *Commun. Earth Environ.* **6**, 171 (2025).
123. Sheldon, F. et al. Assessment of the causes and solutions to the significant 2018–19 fish deaths in the Lower Darling River, New South Wales, Australia. *Mar. Freshw. Res.* **73**, 147–158 (2021).
124. Absalon, D., Matysik, M., Woźnica, A. & Janczewska, N. Detection of changes in the hydrobiological parameters of the Oder River during the ecological disaster in July 2022 based on multi-parameter probe tests and remote sensing methods. *Ecol. Indic.* **148**, 110103 (2023).
125. Kennedy, T. A. et al. Flow management for hydropower extirpates aquatic insects, undermining river food webs. *BioScience* **66**, 561–575 (2016).
126. Abernethy, E. F. et al. Hydropeaking intensity and dam proximity limit aquatic invertebrate diversity in the Colorado River Basin. *Ecosphere* **12**, e03559 (2021).
127. Datry, T. et al. Causes, responses, and implications of anthropogenic versus natural flow intermittence in river networks. *BioScience* **73**, 9–22 (2022).
128. Gido, K. B., Osborne, M. J., Propst, D. L., Turner, T. F. & Olden, J. D. Megadroughts pose mega-risk to native fishes of the American southwest. *Fisheries* **48**, 204–214 (2023).
129. Robertson, A. L., Brown, L. E., Klaar, M. J. & Milner, A. M. Stream ecosystem responses to an extreme rainfall event across multiple catchments in southeast Alaska. *Freshw. Biol.* **60**, 2523–2534 (2015).
130. Polazzo, F. et al. Combined effects of heatwaves and micropollutants on freshwater ecosystems: towards an integrated assessment of extreme events in multiple stressors research. *Glob. Change Biol.* **28**, 1248–1267 (2021).
131. Dietze, M. C. Prediction in ecology: a first-principles framework. *Ecol. Appl.* **27**, 2048–2060 (2017).
132. Johnson, T. F. et al. Revealing uncertainty in the status of biodiversity change. *Nature* **628**, 788–794 (2024).
133. Perkins, S. E. & Alexander, L. V. On the measurement of heat waves. *J. Clim.* **26**, 4500–4517 (2013).
134. Sen, P. K. Estimates of the regression coefficient based on Kendall's tau. *J. Am. Stat. Assoc.* **63**, 1379–1389 (1968).
135. van Hamel, A. & Brunner, M. I. Trends and drivers of water temperature extremes in mountain rivers. *Water Resour. Res.* **60**, e2024WR037518 (2024).
136. Bardsley, E. & Vetrova, V. The bounded inverse Weibull distribution: an extreme value alternative for application to environmental maxima? *Watershed Ecol. Environ.* **3**, 57–63 (2021).
137. Fasiolo, M., Wood, S. N., Zaffran, M., Nedellec, R. & Goude, Y. Fast calibrated additive quantile regression. *J. Am. Stat. Assoc.* **116**, 1402–1412 (2020).
138. Olivetti, L., Messori, G. & Jin, S. A quantile generalized additive approach for compound climate extremes: pan-Atlantic extremes as a case study. *J. Adv. Model. Earth Syst.* **16**, e2023MS003753 (2024).
139. Rigby, R., Stasinopoulos, D. & Voudouris, V. Discussion: a comparison of GAMLSS with quantile regression. *Stat. Model.* **13**, 335–348 (2013).
140. King, G. & Zeng, L. Logistic regression in rare events data. *Polit. Anal.* **9**, 137–163 (2001).
141. Rigby, R. A. & Stasinopoulos, D. M. Generalized additive models for location, scale and shape. *J. R. Stat. Soc. Ser. C Appl. Stat.* **54**, 507–554 (2005).
142. Merder, J. et al. Geographic redistribution of microcystin hotspots in response to climate warming. *Nat. Water* **1**, 844–854 (2023).
143. Rigby, R. A., Stasinopoulos, M. D., Heller, G. Z. & De Bastiani, F. *Distributions for Modeling Location, Scale, and Shape: Using GAMLSS in R* (Chapman and Hall/CRC, 2019).
144. Dietze, M. C. et al. Iterative near-term ecological forecasting: needs, opportunities, and challenges. *Proc. Natl Acad. Sci. USA* **115**, 1424–1432 (2018).
145. Lewis, A. S. L. et al. The power of forecasts to advance ecological theory. *Methods Ecol. Evol.* **14**, 746–756 (2022).
146. Pearl, J., Glymour, M. & Jewel, N. *Causal Inference in Statistics: A Primer* (John Wiley & Sons, 2016).
147. Kimmel, K., Dee, L. E., Avolio, M. L. & Ferraro, P. J. Causal assumptions and causal inference in ecological experiments. *Trends Ecol. Evol.* **36**, 1141–1152 (2021).
148. Siegel, K. & Dee, L. Foundations and future directions for causal inference in ecological research. *Ecol. Lett.* **28**, e70053 (2025).
149. Lytle, D. A. & Tonkin, J. D. Matrix community models for ecology and evolution. *npj Biodivers.* **2**, 26 (2023).
150. Tonkin, J. D., Merritt, D. M., Olden, J. D., Reynolds, L. V. & Lytle, D. A. Flow regime alteration degrades ecological networks in riparian ecosystems. *Nat. Ecol. Evol.* **2**, 86–93 (2017).
151. Rogosch, J. S. et al. Increasing drought favors nonnative fishes in a dryland river: evidence from a multispecies demographic model. *Ecosphere* **10**, e02681 (2019).
152. Ohlberger, J. et al. Effects of past and projected river discharge variability on freshwater production in an anadromous fish. *Freshw. Biol.* **63**, 331–340 (2018).
153. Urban, M. C. et al. Improving the forecast for biodiversity under climate change. *Science* **353**, aad8466 (2016).
154. Ibáñez, I. et al. Integrated assessment of biological invasions. *Ecol. Appl.* **24**, 25–37 (2014).
155. Evans, M. E. K., Merow, C., Record, S., McMahon, S. M. & Enquist, B. J. Towards process-based range modeling of many species. *Trends Ecol. Evol.* **31**, 860–871 (2016).
156. Briscoe, N. J. et al. Forecasting species range dynamics with process-explicit models: matching methods to applications. *Ecol. Lett.* **22**, 1940–1956 (2019).
157. Koerich, G., Fraser, C. I., Lee, C. K., Morgan, F. J. & Tonkin, J. D. Forecasting the future of life in Antarctica. *Trends Ecol. Evol.* **38**, 24–34 (2023).
158. Schaub, M. & Abadi, F. Integrated population models: a novel analysis framework for deeper insights into population dynamics. *J. Ornithol.* **152**, 227–237 (2010).
159. González, E. J., Martorell, C. & Bolker, B. M. Inverse estimation of integral projection model parameters using time series of population-level data. *Methods Ecol. Evol.* **7**, 147–156 (2016).
160. Arthington, A. H. et al. Accelerating environmental flow implementation to bend the curve of global freshwater biodiversity loss. *Environ. Rev.* **32**, 387–413 (2024).
161. Messager, M. L. et al. A metasystem approach to designing environmental flows. *BioScience* **73**, 643–662 (2023).
162. Grantham, T. E., Matthews, J. H. & Bledsoe, B. P. Shifting currents: managing freshwater systems for ecological resilience in a changing climate. *Water Secur.* **8**, 100049 (2019).
163. Ciotti, D. C., Mckee, J., Pope, K. L., Kondolf, G. M. & Pollock, M. M. Design criteria for process-based restoration of fluvial systems. *BioScience* **71**, 831–845 (2021).
164. McCabe, C. L., Matthaei, C. D. & Tonkin, J. D. The ecological benefits of more room for rivers. *Nat. Water* **3**, 260–270 (2025).
165. Naiman, R. J., Latterell, J. J., Pettit, N. E. & Olden, J. D. Flow variability and the biophysical vitality of river systems. *Comptes Rendus Géosci.* **340**, 629–643 (2008).

166. Palmer, M. A., Hondula, K. L. & Koch, B. J. Ecological restoration of streams and rivers: shifting strategies and shifting goals. *Annu. Rev. Ecol. Evol. Syst.* **45**, 247–269 (2014).
167. Beechie, T. J. et al. Process-based principles for restoring river ecosystems. *BioScience* **60**, 209–222 (2010).
168. Backus, G. A., Clements, C. F. & Baskett, M. L. Restoring spatiotemporal variability to enhance the capacity for dispersal-limited species to track climate change. *Ecology* **105**, e4257 (2024).
169. da Silva, J. P. et al. The role of connectivity in conservation planning for species with obligatory interactions: prospects for future climate scenarios. *Glob. Change Biol.* **30**, e17169 (2024).
170. Mason, R. J. et al. Rebalancing river lateral connectivity: an interdisciplinary focus for research and management. *WIREs Water* **12**, e1766 (2024).
171. Cid, N. et al. From meta-system theory to the sustainable management of rivers in the Anthropocene. *Front. Ecol. Environ.* **20**, 49–57 (2021).
172. Craig, L. S. et al. Meeting the challenge of interacting threats in freshwater ecosystems: a call to scientists and managers. *Elem. Sci. Anthr.* **5**, 72 (2017).
173. Mouquet, N., Gravel, D., Massol, F. & Calcagno, V. Extending the concept of keystone species to communities and ecosystems. *Ecol. Lett.* **16**, 1–8 (2012).
174. Patrick, C. J. et al. The application of metacommunity theory to the management of riverine ecosystems. *WIREs Water* **8**, 1–21 (2021).
175. Lynch, A. J. et al. Managing for RADical ecosystem change: applying the Resist–Accept–Direct (RAD) framework. *Front. Ecol. Environ.* **19**, 461–469 (2021).
176. Olsson, R. C., Wyborn, C. A. & van Kerkhoff, L. E. How the Resist–Accept–Direct framework is being used by communities for socio-economic climate adaptation: a case study in Australia's Murray–Darling Basin. *Reg. Environ. Change* **24**, 136 (2024).
177. Grupper, M. A., Horne, A. C., Webb, J. A. & Olden, J. Identifying and approaching barriers to environmental flow implementation using social–ecological systems thinking. *WIREs Water* **12**, e1764 (2025).
178. Poff, N. L. et al. Sustainable water management under future uncertainty with eco-engineering decision scaling. *Nat. Clim. Change* **6**, 25–34 (2015).
179. Tonkin, J. D. in *Encyclopedia of Inland Waters* (eds Mehner, T. & Tockner, K.) 653–664 (Elsevier, 2022).
180. Kuehne, L. M. et al. The future of global river health monitoring. *PLoS Water* **2**, e0000101 (2023).
181. Pekel, J.-F., Cottam, A., Gorelick, N. & Belward, A. S. High-resolution mapping of global surface water and its long-term changes. *Nature* **540**, 418–422 (2016).
182. Tomsett, C. & Leyland, J. Remote sensing of river corridors: a review of current trends and future directions. *River Res. Appl.* **35**, 779–803 (2019).
183. Pawlowski, J. et al. The future of biotic indices in the ecogenomic era: integrating (e) DNA metabarcoding in biological assessment of aquatic ecosystems. *Sci. Total Environ.* **637–638**, 1295–1310 (2018).
184. Krabbenhoft, C. A. et al. Assessing placement bias of the global river gauge network. *Nat. Sustain.* **5**, 586–592 (2022).
185. Milner, A. M., Robertson, A. L., McDermott, M. J., Klaar, M. J. & Brown, L. E. Major flood disturbance alters river ecosystem evolution. *Nat. Clim. Change* **3**, 137–141 (2012).
186. Tiegs, S. D. et al. Human activities shape global patterns of decomposition rates in rivers. *Science* **384**, 1191–1195 (2024).
187. Smith, M. D. et al. Extreme drought impacts have been underestimated in grasslands and shrublands globally. *Proc. Natl Acad. Sci. USA* **121**, e2309881120 (2024).
188. Stecca, G., Hicks, D. M., Measures, R. & Henderson, R. Numerical modeling prediction of vegetation trajectories under different flow regimes in New Zealand braided rivers. *J. Geophys. Res. Earth Surf.* **128**, e2023JF007397 (2023).
189. Harris, H. A. L., Tonkin, J. D. & McIntosh, A. R. in *Resilience and Riverine Landscapes* (eds Thoms, M. & Fuller, I.) 157–175 (Elsevier, 2024).
190. Wohl, E., Dwire, K., Sutfin, N., Polvi, L. & Bazan, R. Mechanisms of carbon storage in mountainous headwater rivers. *Nat. Commun.* **3**, 1263 (2012).
191. Mahecha, M. D. et al. Biodiversity loss and climate extremes — study the feedbacks. *Nature* **612**, 30–32 (2022).
192. Lehner, B. & Grill, G. Global river hydrography and network routing: baseline data and new approaches to study the world's large river systems. *Hydrol. Process.* **27**, 2171–2186 (2013).
193. Feeley, H. B., Davis, S., Bruen, M., Blacklocke, S. & Kelly-Quinn, M. The impact of a catastrophic storm event on benthic macroinvertebrate communities in upland headwater streams and potential implications for ecological diversity and assessment of ecological status. *J. Limnol.* **71**, 109–318 (2012).
194. Foord, S. & Fouché, P. Response of instream animal communities to a short-term extreme event and to longer-term cumulative impacts in a strategic water resource area, South Africa. *Afr. J. Aquat. Sci.* **41**, 29–40 (2016).
195. Kim, D. G., Yoon, T. J., Baek, M. J. & Bae, Y. J. Impact of rainfall intensity on benthic macroinvertebrate communities in a mountain stream under the East Asian monsoon climate. *J. Freshw. Ecol.* **33**, 489–501 (2018).
196. Herbst, D. B., Cooper, S. D., Medhurst, R. B., Wiseman, S. W. & Hunsaker, C. T. Drought ecohydrology alters the structure and function of benthic invertebrate communities in mountain streams. *Freshw. Biol.* **64**, 886–902 (2019).
197. Calapez, A. R., Elias, C. L., Almeida, S. F. P. & Feio, M. J. Extreme drought effects and recovery patterns in the benthic communities of temperate streams. *Limnetica* **33**, 281–296 (2014).
198. Fenoglio, S., Bo, T., Cucco, M. & Malacarne, G. Response of benthic invertebrate assemblages to varying drought conditions in the Po river (NW Italy). *Ital. J. Zool.* **74**, 191–201 (2007).
199. Ferreira, V., Chauvet, E. & Canhoto, C. Effects of experimental warming, litter species, and presence of macroinvertebrates on litter decomposition and associated decomposers in a temperate mountain stream. *Can. J. Fish. Aquat. Sci.* **72**, 206–216 (2015).
200. Sáinz-Bariáin, M. et al. Changes in Mediterranean high mountain Trichoptera communities after a 20-year period. *Aquat. Sci.* **78**, 669–682 (2015).
201. Poff, N. L. et al. The natural flow regime. *BioScience* **47**, 769–784 (1997).
202. Olden, J. D. & Naiman, R. J. Incorporating thermal regimes into environmental flows assessments: modifying dam operations to restore freshwater ecosystem integrity. *Freshw. Biol.* **55**, 86–107 (2009).
203. Stewart, I. T., Cayan, D. R. & Dettinger, M. D. Changes toward earlier streamflow timing across western North America. *J. Clim.* **18**, 1136–1155 (2005).
204. Wang, H. et al. Anthropogenic climate change has influenced global river flow seasonality. *Science* **383**, 1009–1014 (2024).
205. Marengo, J. A. & Espinoza, J. C. Extreme seasonal droughts and floods in Amazonia: causes, trends and impacts. *Int. J. Climatol.* **36**, 1033–1050 (2015).
206. Udall, B. & Overpeck, J. The twenty-first century Colorado River hot drought and implications for the future. *Water Resour. Res.* **53**, 2404–2418 (2017).
207. Peterson, T. J., Saft, M., Peel, M. C. & John, A. Watersheds may not recover from drought. *Science* **372**, 745–749 (2021).
208. Isaak, D. J., Wollrab, S., Horan, D. & Chandler, G. Climate change effects on stream and river temperatures across the northwest U.S. from 1980–2009 and implications for salmonid fishes. *Clim. Change* **113**, 499–524 (2011).
209. van Vliet, M. T. H. et al. Global river discharge and water temperature under climate change. *Glob. Environ. Change* **23**, 450–464 (2013).
210. Anderson, S. & Chartrand, S. The streamflow response to multi-day warm anomaly events: sensitivity to future warming and spatiotemporal variability by event magnitude. *Earth's Future* **12**, e2024EF004962 (2024).
211. Beltaos, S. & Prowse, T. D. Climate impacts on extreme ice-jam events in Canadian rivers. *Hydrol. Sci. J.* **46**, 157–181 (2001).
212. Kéfi, S. et al. Advancing our understanding of ecological stability. *Ecol. Lett.* **22**, 1349–1356 (2019).
213. Thibaut, L. M. & Connolly, S. R. Understanding diversity–stability relationships: towards a unified model of portfolio effects. *Ecol. Lett.* **16**, 140–150 (2012).
214. Gonzalez, A. & Loreau, M. The causes and consequences of compensatory dynamics in ecological communities. *Annu. Rev. Ecol. Evol. Syst.* **40**, 393–414 (2009).
215. Schindler, D. E., Armstrong, J. B. & Reed, T. E. The portfolio concept in ecology and evolution. *Front. Ecol. Environ.* **13**, 257–263 (2015).
216. Erős, T. et al. Effects of nonnative species on the stability of riverine fish communities. *Ecography* **43**, 1156–1166 (2020).
217. Wang, S., Lamy, T., Hallett, L. M. & Loreau, M. Stability and synchrony across ecological hierarchies in heterogeneous metacommunities: linking theory to data. *Ecography* **42**, 1200–1211 (2019).
218. Lamy, T. et al. The dual nature of metacommunity variability. *Oikos* **130**, 2078–2092 (2021).
219. Gianuca, A. T. et al. River flow intermittence influence biodiversity–stability relationships across spatial scales: implications for an uncertain future. *Glob. Change Biol.* **30**, e17457 (2024).
220. Loreau, M., Mouquet, N. & Gonzalez, A. Biodiversity as spatial insurance in heterogeneous landscapes. *Proc. Natl Acad. Sci. USA* **100**, 12765–12770 (2003).
221. Hershkovitz, Y. & Gasith, A. Resistance, resilience, and community dynamics in Mediterranean-climate streams. *Hydrobiologia* **719**, 59–75 (2012).
222. Larsen, S. et al. The geography of metapopulation synchrony in dendritic river networks. *Ecol. Lett.* **24**, 791–801 (2021).
223. Jaeger, K. L., Olden, J. D. & Pelland, N. A. Climate change poised to threaten hydrologic connectivity and endemic fishes in dryland streams. *Proc. Natl Acad. Sci. USA* **111**, 13894–13899 (2014).
224. Steel, E. A. et al. Thermal landscapes in a changing climate: biological implications of water temperature patterns in an extreme year. *Can. J. Fish. Aquat. Sci.* **76**, 1740–1756 (2019).

Acknowledgements

J.D.T. is supported by a Rutherford Discovery Fellowship administered by the Royal Society Te Apārangi (RDF-18-UOC-007), Te Pūnaha Matatini, a Centre of Research Excellence funded by the Tertiary Education Commission, New Zealand. J.D.T. and J.M. acknowledge funding from the Ministry of Business, Innovation and Employment (Fish Futures: preparing for novel freshwater ecosystems; CAWX2101). J.D.O. is supported by the Richard C. and Lois M. Worthington Endowed Professor in Fisheries Management from the School of Aquatic and Fishery Sciences, University of Washington. T.D. was supported through the DRYvER project, which has received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement no. 869226. T.S. is supported by a productivity grant (309496/2021-7) administered by the Brazilian National Council for Scientific and Technological Development (CNPq). T.S. acknowledges funding from the São Paulo Research Foundation (FAPESP; 2021/00619-7 and 2021/10639-5). J.T.-J. acknowledges funding from the Royal Society Te Apārangi (Fresh ideas for water economics and policy - VUW2006) and Te Pūnaha Matatini, a Centre of Research Excellence funded by the Tertiary Education Commission, New Zealand.

Author contributions

J.D.T., T.S. and J.D.O. conceptualized the main ideas. J.D.T. led the writing of the manuscript, with all authors leading sections of the first draft and contributing to revisions. J.D.T. and J.M. produced the figures.

Competing interests

The authors declare no competing interests.

Additional information

Peer review information *Nature Reviews Biodiversity* thanks Juan David González-Trujillo and the other, anonymous, reviewer(s) for their contribution to the peer review of this work.