Climate Change and Extreme Events in Shaping River Ecosystems

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Glossary

Beta diversity Differences in ecological communities among multiple locations. More specifically, variability in species composition among locations within a region.

Ecological trap A situation where rapid environmental change leaves organisms in poor-quality habitats. Whether the habitat quality or the environmental cue changes rapidly to the point that one no longer reliably indicates the other, organisms mistakenly prefer habitats where their fitness is lower than in other habitats.

Extreme event "A rare or unusual weather or climatic occurrence (e.g., extreme of precipitation, temperature or wind) and/or the resultant extreme physical phenomena in river catchments (e.g., fluvial floods, hydrologic droughts, storm surges, fire or cryosphere-related effects)"; taken from Ledger and Milner (2015). See "Extreme events defined" section for full explanation.

Flow regime The long-term sequence of high (floods) and low (droughts) flows, characterized by five key components: magnitude, frequency, duration, timing, and rate of change.

Nonstationarity Generally, where a system no longer fluctuates within a range of variability that persists through time (no longer fixed underlying probability distribution). More specifically, differences in statistical characteristics, such as mean or variance, or in statistical relationships, through time.

Press disturbance Disturbances that arise rapidly and then maintain a constant level, such as the building of a dam to alter a flow regime or river connectivity.

Pulse disturbance Short-term and sharply delineated disturbances, such as flood events.

Ramp disturbance A disturbance where the strength of disturbance steadily increases over time, such as gradual land-use change, the spread of an invasive species, or long-term drought.

Resilience The capacity of a population or community to recover following a disturbance event.

Resistance The ability of a population or community to withstand a disturbance event.

Species range shift Changes in the distribution limits of a species, generally along altitudinal or latitudinal gradients.

Introduction

In June 2021, a large low-pressure mass built up over the Tasman Sea to the west of New Zealand before proceeding to pick up moisture-rich air from the Pacific Ocean to the north and slamming into the east coast of New Zealand's South Island. This event caused widespread destruction across the Canterbury region of New Zealand, with many of the large rivers draining the eastern slopes of the Southern Alps flooding, damaging critical infrastructure and putting lives at risk. Although this was described as a

one-in-two-hundred-year event, the reality of climate change means these kinds of events will recur at much higher frequencies than in the past (IPCC, 2021). In the weeks that followed this event, we witnessed catastrophic floods unfolding elsewhere in New Zealand, as well as across Europe and China. This is a recurring trend: over recent years, we have seen increasing frequencies of various extreme climatic events, including high profile drought and wildfire events across western North America and eastern Australia, causing tens of billions of dollars of economic losses, severe losses of biodiversity, and loss of human life (WMO, 2020).

Such events serve as a reminder that the main way in which humans will feel climate change is via increasing frequencies of what we currently consider extreme events. Climate change-driven disturbances are predicted to continue to intensify by more than an order of magnitude over the next 100 years (IPCC, 2021). We continue to see records being broken in terms of heat across the globe (WMO, 2020), with July 2021 being the hottest month ever recorded on Earth (NOAA, 2021). The threats to human infrastructure are clear. More nuanced, however, are the threats to freshwater biodiversity and to the ecosystem goods and services provided by rivers.

Rivers and streams are highly dynamic environments, with natural cycles of floods and droughts (Poff et al., 1997). Organisms that inhabit these ecosystems have evolved life histories to cope with, and indeed capitalize on, these natural disturbance regimes (Lytle and Poff, 2004). However, these regimes are rapidly changing in terms of their magnitude, frequency, timing, and duration (Blöschl et al., 2017, 2019; Stewart et al., 2005).

Climate change and extreme events are dynamically entwined in river ecosystems. In addition to magnifying and increasing the frequency of extreme events, climate change has the potential to alter many other aspects of river ecosystems, such as modifying temperatures and inducing species range shifts, or interacting with various other anthropogenic stressors, including invasive species, land-use change and flow alteration (Dudgeon et al., 2006). The physical basis of climate change has never been clearer: with an increasingly high level of confidence, science indicates that climate change will continue to intensify in coming decades (IPCC, 2021). The need to understand the effects of climate change on riverine ecosystems has, therefore, never been more pressing. In this chapter, I review the broad ways in which climate change will influence river ecosystems, and the role of climate-driven extreme events in shaping river ecosystems, including their structure and function.

The physical basis of climate change and extreme events

Extreme events defined

Climate change research has often focused on shifting mean conditions, but one of the key ways in which climate change will impact freshwater ecosystems is via increasing variation around increasing means; i.e., by amplifying the magnitudes and frequencies of extreme events. There is no consistent definition for what constitutes an extreme event in running waters. This lack of coherent definition is an issue that has transcended disciplines, which may have hampered our ability to understand and manage extreme events (McPhillips et al., 2018). Extreme events in rivers are typically considered statistically rare or unusual events (often climatically-driven) that translate into extreme physical effects, such as through floods or droughts, which may or may not have extreme consequences on the ecosystem. Extreme climatic events include prolonged droughts, heatwaves, or rainfall events associated with unusually large and infrequent storms.

Many have used probability-based definitions, such as extreme floods being those with a 100-year return interval or 1% excedence probability; or threshold-based, such as temperature crossing certain thresholds (Ledger and Milner, 2015). However, what is considered an extreme event in the present day based on certain thresholds or magnitudes will likely be revised as the climate continues to warm (McPhillips et al., 2018).

For the purpose of this chapter, I will focus mostly on climate-related extreme events, which largely reflect flood and drought regimes (flow regimes). My definition of an extreme event is deliberately broad, with no particular threshold or probability. Thus, I will loosely define an extreme event following the definition used by Ledger and Milner (2015): "a rare or unusual weather or climatic occurrence (e.g., extreme of precipitation, temperature or wind) and/or the resultant extreme physical phenomena in river catchments (e.g., fluvial floods, hydrologic droughts, storm surges, fire or cryosphere-related effects)." It is important to note that this definition also considers more than just the magnitude of events. For instance, if a major event falls well outside the typical timing of such events historically, it may have just as detrimental an effect as an extreme event defined by magnitude alone.

From historical range of variability to novel future regimes

Research has now demonstrated considerable change has already occurred to flow regimes across the world in recent decades (Blöschl et al., 2017, 2019; Stewart et al., 2005). Extreme flood events have increased substantially in frequency over the 20th century (Milly et al., 2002). These changes play out differently across the globe and within regions. Existing water stressed regions (Fig. 1) are set to become more challenged by water shortages. For instance, floods are arriving earlier in northeastern Europe due to warmer temperatures driving earlier snowmelt, later around the North Sea and parts of the Mediterranean coast due to delayed winter storms, and earlier in western Europe due to earlier soil moisture maxima (Blöschl et al., 2017). Similarly, flood magnitudes are increasing in northwestern Europe due to increasing autumn and winter rainfall, and decreasing in both southern and eastern Europe due to decreasing precipitation and increasing evaporation in southern regions, and decreasing snow cover and melt in eastern regions (Blöschl et al., 2019). In western North America, the onset of spring snowmelt and associated increases in river discharge is occurring earlier across the region (Stewart et al., 2005). Similarly, increases have been found in river temperatures over a 30-year period in northwestern United States (Isaak et al., 2012), a trend that is set to continue with increased climate change, not
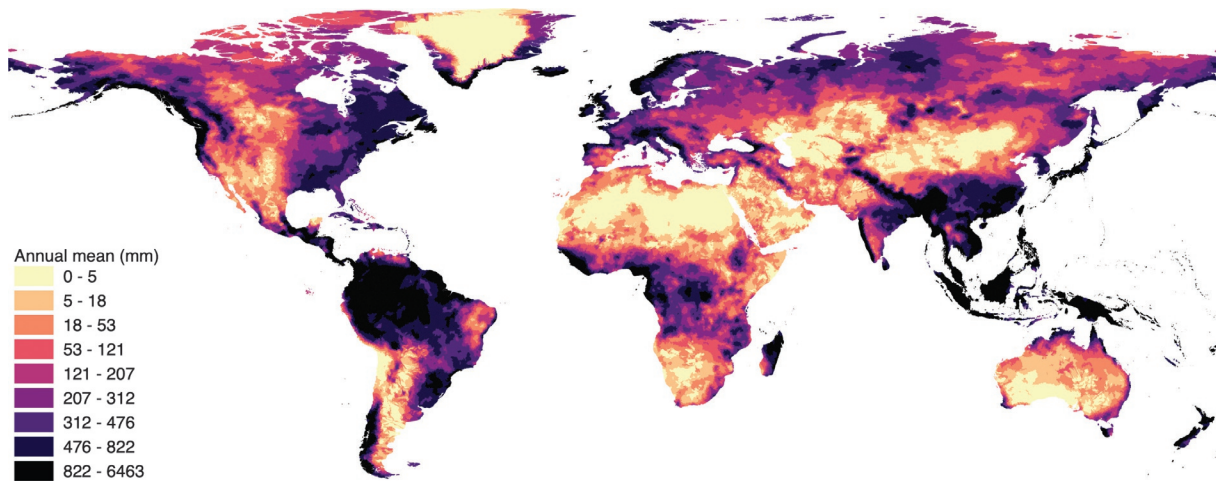
Fig. 1 Global map of land surface runoff (mm year^{-1}), based on long-term (1971–2000) averages, highlighting existing water stressed regions at risk of further climate change. Data were sourced from the HydroATLAS database (Linke et al., 2019).

just in North America, but across the globe (van Vliet et al., 2013). This shifting physical template of rivers presents critical challenges for the species that inhabit them, let alone the management of river flows for human wellbeing.

Effects on river ecosystems

The mechanisms by which extreme events influence biodiversity are varied depending on their nature, and effects can be direct or indirect. Extreme floods can significantly alter the physical template of rivers (Death et al., 2015), or cause direct mortality on individuals, but may also enable previously isolated populations to disperse and reconnect, particularly in arid landscapes where stream drying isolates permanently flowing channels (Datry et al., 2016; Tonkin et al., 2018a). By contrast, extreme droughts can fragment freshwater habitats or push temperatures and pollutant concentrations beyond tolerable limits for organisms (Palmer and Ruhi, 2019). Thus, ecological responses to extreme events, like everything in ecology, are context dependent. However, testing the effects of extreme climatic events on riverine biodiversity is challenging given the rarity of extreme events and the general associated lack of pre-event data (Poff et al., 2018). Thus, case studies on the effects of extreme events on riverine ecosystems are not common.

Nonetheless, evidence of the effects of these climate change-induced extreme events is beginning to accumulate. For instance, unprecedented droughts such as Australia's Millennium Drought or California's recent drought, can completely alter river and riparian ecosystems, shifting ecological communities over new thresholds (Aspin et al., 2019; Bogan and Lytle, 2011; Thomson et al., 2012). Further, the intensity and duration of drying can regulate rates of gross primary productivity (Colls et al., 2019) and litter decomposition (Mora-Gómez et al., 2020). At the other extreme, intensified floods can also have major impacts on the functioning of rivers (Palmer and Ruhi, 2019), including leading to population genetic changes as a result of mass mortality events (Poff et al., 2018).

Coupled geomorphological-ecological responses

Extreme floods resulting from climate change also have the potential to significantly change the geomorphological template of rivers (Death et al., 2015). Beyond the negative direct effects of large floods on organisms, such channel-altering floods, can provide significant benefits for resident biota by resetting physical conditions, opening up habitat for flood-adapted species, and removing nuisance accumulations of primary producers and exotic weeds. However, channel-altering floods can also multiply the effects of other stressors on aquatic life such as by redistributing toxic chemicals, in addition to their direct effects on human infrastructure (Death et al., 2015).

The geomorphological and ecological context can also influence the ecological response of stream ecosystems to extreme events. Robertson et al. (2015) examined the response of meiofauna, macroinvertebrates and fish to an extreme flooding event in southeast Alaska across four recently deglaciated catchments. The ecological responses to this event differed across the four catchments, which reflected both the local intensity of rainfall and factors related to the age of each stream (38–180 years), including channel morphology, and catchment vegetation type and cover. However, many questions remain unanswered regarding the effects of extreme floods on river geomorphology and ecology (Death et al., 2015).

Resistance vs. resilience

Given the inherent dynamism of rivers, riverine species are often relatively resistant and/or resilient to extreme flood events (Blondel et al., 2021; Lytle and Poff, 2004), as a result of the evolution of behavioral, morphological or life-history adaptations (Lytle and Poff, 2004). However, there is often a tradeoff between resistance and resilience to flood disturbances (McMullen et al., 2017). For instance, Poff et al. (2018) examined population genomic responses of aquatic insects to a one-in-500-year rainfall event in

Colorado streams. Local species responses depended on traits related to resistance and resilience, but persistence was lowest at locations with highest disturbance. Persistence was lowest for immobile taxa, with a greater chance of persistence for species with mobile larvae or terrestrial adult stages present during the flood event. Despite a clear role of resistance and resilience traits in determining species persistence, genomic changes were much less predictable for the six species examined. Resistance and resilience to extreme floods can also differ within populations depending on what aspects of the population are considered. For example, Blondel et al. (2021) found genetic diversity and population structure of native riverine guppies to be resistant, and phenotypic diversity, represented by body size and male coloration, to be resilient to extreme flood events. More specifically, minimal changes were observed in genetic diversity and population structure compared to preflood patterns whereas phenotypic diversity was more heavily impacted by the flood events, but these larger impacts were short-lived.

Altered flow regimes

Of the many changes that will occur to flow regimes as a result of ongoing climate change, one of the more concerning for native riverine organisms is changes to the timing of flow events. Flow timing is a critical component of the natural flow regime (Poff et al., 1997), and one for which species have evolved various strategies to capitalize on (Lytle and Poff, 2004). The predictability of flow regimes is a critical structuring agent of riverine biodiversity, with more predictably seasonal flow regimes able to harbor greater biodiversity (Tonkin et al., 2017). Riverine species have adapted to capitalize on these seasonal rhythms. This is not surprising given the predictability of flow regimes in many parts of the world (Fig. 2). For instance, in western North America, cottonwood (*Populus* spp.) release their seeds after the annual peak river flows that come with spring snowmelt, which facilitates dispersal and establishment into the floodplain (Mahoney and Rood, 1998). Shifting the timing of these peak flows may help non-native *Tamarix* to outcompete cottonwoods through time (Lytle et al., 2017), as has been seen below dams that have altered timing and magnitudes of peak flows (Merritt and Poff, 2010).

Fish are also fundamentally attuned to the natural timing of flow events in rivers. For instance, the timing of winter events is often critical for the reproductive strategies of coldwater fish species (Shuter et al., 2012). Given the existing evidence that the timing of flood events has already changed (Blöschl et al., 2017), it is not surprising that phenologies of riverine fish have already shifted (Shuter et al., 2012). Mismatched phenologies are a critical threat to freshwater fish as river flows continue to change, ranging from
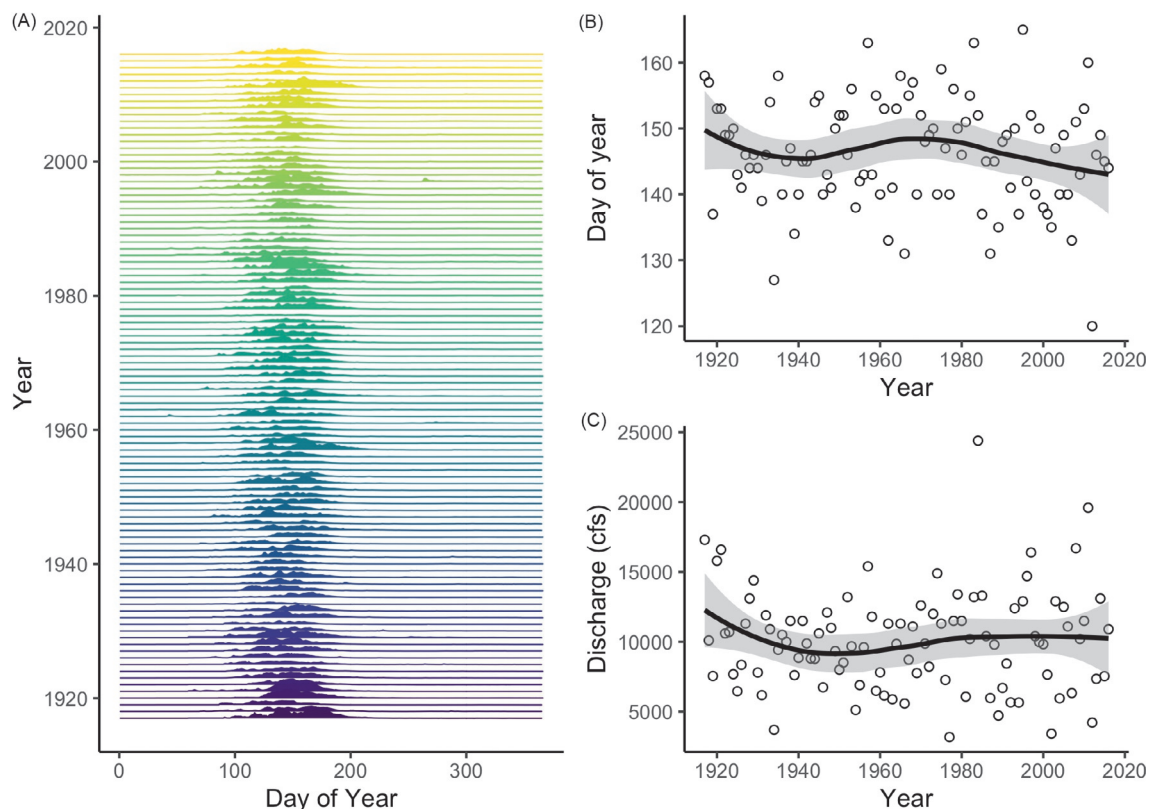

Fig. 2 (A) Ridgeline plot of flows in the unregulated Yampa River, a tributary of the Colorado River at Maybell, Colorado over a 100-year period. Each line is an annual hydrograph demonstrating the consistency of the spring snowmelt flood pulse from 1916 to 2016. Species such as riparian cottonwoods have evolved intricate relationships with these predictable pulses. Although difficult to discern here, climate change is already altering the natural phenology of river flows globally, and bringing spring snowmelt earlier across most of western North America (Stewart et al., 2005). (B) The day at which 50% of annual flow has passed the gage. (C) Annual peak in daily discharge over the 100 years. Trendlines in both B and C represent locally weighted smoothing (loess) curves.

increased larval mortality due to premature hatching to mismatched feeding phenologies between different stage classes shifting interactions between predation and competition (Shuter et al., 2012).

Human-altered flow regimes can be extreme in and of themselves. For instance, hydropeaking, where dams release different volumes of water throughout the day in response to energy demand imparts a novel pattern of flow variability into a river (Ruhi et al., 2018). These flows have been shown to reduce functional diversity of invertebrate communities downstream of a large dam on the Chattahoochee River in Georgia, United States (Ruhi et al., 2018), and lead to the near complete extirpation of mayflies, stoneflies and caddisflies in sections of the Colorado River subject to high levels of hydropeaking (Abernethy et al., 2021). Such alterations are analogous to the effects of urbanization, which can severely alter flow regimes and lead to exacerbation of flow extremes and their effects on riverine biodiversity (Palmer and Ruhi, 2019). Streams draining urban catchments are subject to regular, intense flow events due to their increased impervious surface and more concentrated runoff. In certain cases, this can lead to a cycling between flow extremes and extreme anoxia events (Blaszczak et al., 2019).

Complex and nonlinear responses to change

Biodiversity change in response to changing river conditions is complex and varied. For instance, Larsen et al. (2018) found no change in metrics typically used to detect biodiversity change but uncovered more nuanced underlying changes. Using a 30-year time-series dataset of benthic macroinvertebrates from southern Wales, they found no change in taxonomic or functional alpha diversity or spatial beta diversity. However, underlying this apparent stasis in widely-used metrics of biodiversity change was a temporal change in mean species composition. These changes reflected a systematic decline in mean community specialization, which was associated with a lower rate of recolonization of specialists as opposed to an increased local extinction rate.

Other studies have found clear evidence of change at multiple levels over recent decades attributable to climate change, but trends are often nonlinear. Using a comprehensive 42-year long dataset (1969–2010) of weekly species-level insect abundances from the Breitenbach Stream in central Germany, Baranov et al. (2020) uncovered major shifts in insect community structure, including an 82% decline in overall abundance and a 9% increase in richness. These changes occurred in the absence of any other ongoing stressors beyond a climate change-induced 1.9 °C water temperature increase and an altered flow regime, characterized by the change in four annual discharge patterns: dry years, wet years, aseasonal spate years and extreme spring spate years. Their research, again, uncovered often-missed mechanisms of change: peak insect emergence arrived 13 days earlier over the study period and the duration of emergence increased by 15 days. Understanding these mechanistic changes can enable a more comprehensive picture of how species may or may not adapt to ongoing warming. Although evidence suggests the responses of biodiversity to extreme climatic events is highly idiosyncratic and unpredictable (van de Pol et al., 2017), taking a more mechanistic approach to understand responses will likely uncover generalities that can transcend species, ecosystems and locations.

Understanding ecological responses to environmental regimes is often carried out by focusing on mean environmental conditions as the key drivers of ecological dynamics. However, in reality, one-off or extreme events may play an equal or larger role in shaping biodiversity in running waters than long-term trends through a legacy effect. Jourdan et al. (2018) compared the role of long-term climatic change and antecedent climatic conditions in predicting European stream invertebrate communities across a set of long-term ecological research network (LTER) sites sampled for between 10 and 24 years. They found that antecedent climatic conditions, measured as the mean temperature and daily precipitation, and the number of extreme hot, cold and high precipitation days over the preceding 12 months, were better predictors of community metrics than background long-term change. This highlights the need to both understand the mechanistic responses to individual flow events, including both ecosystem states and rates (Tonkin et al., 2019), and continue investment into long-term monitoring programs to help detect longer-term trends.

Species range shifts, community reorganization and invasion

One of the most apparent responses of biodiversity to ongoing climate change is caused by species moving their range to track shifting isotherms. In Europe, climate change projections have indicated a decline in climatically suitable habitat for more than 50% of invertebrate species and losses could be as great as 40% by late this century (Domisch et al., 2013). These models have indicated that species facing the largest decline in climatically suitable areas were cold-adapted species, whereas warm-adapted species were expected to gain suitable habitat (Domisch et al., 2013). Haase et al. (2019) analyzed changes in stream invertebrate community composition over 25 years across central Europe and found clear evidence of community reorganization, and in particular, evidence of a decline in cold-adapted species, with warm-adapted species appearing to replace them. The biggest distribution shifts were apparent with elevation rather than latitude, and these changes were apparent despite the temperature only having changed by 0.5 °C over this period. Systematic shifts have been found for riverine fish upstream and in elevation across France at rates faster than many terrestrial organisms but not rapid enough to track changing climate (Comte and Grenouillet, 2013).

Flow alteration and temperature change combine to threaten riverine species. Across western United States, projected climate-induced flow alteration has been shown to be equally as important as warming in its risk for stream invertebrate communities (Pyne and Poff, 2017). However, the vulnerability to projected gradients of temperature and hydrologic change varies widely across the ecoregions of the western United States—from the wet forests of the northwest to the desert of Arizona: communities in some ecoregions are more sensitive to warming and others to reduced flow (Pyne and Poff, 2017). Similarly, both increased water temperature and discharge reduction have played a key role in the disappearance of invertebrate species from the Middle Loire River in France over a 30-year period (Floury et al., 2013). During this period, species that specialize in slow flowing or standing waters, including invasive species, increased in number. Similar patterns have been uncovered for riverine fish with species

that prefer warm- and slow-water habitats increasing in dominance across the globe (Comte et al., 2021), changes that are exaggerated in human-modified regions (Comte et al., 2021).

Climate change-induced reorganization is already widespread across the globe. For example, stream invertebrate communities appear to be homogenizing through time in New Zealand (Mouton et al., 2020). Homogenization often accompanies invasion by non-native species, and many have found climate change to help facilitate the invasion of non-native fish species (Radinger and García-Berthou, 2020; Rogosch et al., 2019; Ruhí et al., 2016). Using a community-wide modeling approach, Rogosch et al. (2019) revealed non-native fish species in the southwest United States replaced native species as river flow regimes became increasingly affected by drought. These replacements reflected differences in mortality to the major flow events, including spring and summer floods, and droughts. Ruhí et al. (2016), using time-series techniques on multi-decadal ecohydrological data, uncovered high quasi-extinction risks of native species, and asserted that continuing current stream flow trends would further increase these risks for native species but decrease the risks to non-native species.

Dispersal becomes a critical tool in a species' toolbox for its response to ongoing change. Poor dispersers will be less capable of tracking shifting climatic conditions, and species that are restricted to dispersing along the river network will be more vulnerable to extinction than those that can also disperse overland (Tonkin et al., 2018a). Furthermore, species moving upwards in elevation along the river network are threatened by the "summit trap" effect, whereby further dispersal up hillsides is capped at mountain peaks (Sauer et al., 2011). Thus, the extent to which communities will reorganize will depend on a host of factors, including river network structure, dispersal ability and mode, and barriers to invasion.

Interactions with other stressors

There are very few rivers left in the world that have not been impacted by human activities. Understanding the true effects of climate change on riverine ecosystems requires a much broader understanding of species vulnerabilities beyond thermal tolerances to incorporate flow regimes and various other anthropogenic stressors including land use change (Comte et al., 2021). Human-altered systems are potentially more at risk both ecologically and economically from increased extreme events, such as dam failures that may occur with extreme future floods (Palmer et al., 2008). Dams, by altering the natural temperature regime of downstream flows, can also alter the natural responses of biodiversity to shifting climatic conditions. For example, Bruno et al. (2019) found contrasting changes between cold- and warm-adapted species from the 1970s to the 2010s between free-flowing and dam-altered rivers in alpine catchments of south-eastern France. Cold-adapted taxa decreased in both river types, but there tended to be a replacement of cold-adapted taxa by warm-adapted taxa in the free-flowing catchment over time. Such replacement was less pronounced in the regulated catchment, which led to a decline in taxonomic diversity, potentially due to the direct effect of flow regulation on habitat suitability and heterogeneity (Bruno et al., 2019). Dams or other instream barriers can also fragment rivers, which can exacerbate the effects of climate change on fishes (Marshall et al., 2021; Radinger and García-Berthou, 2020). For instance, instream barriers can limit the potential recovery of stream fishes following prolonged drought due to blocking colonists (Marshall et al., 2021). However, there is also a tradeoff associated with increasing connectivity, whereby the spread of non-native species may be worsened under climate change (Radinger and García-Berthou, 2020).

The relative vulnerability of human-altered ecosystems to species loss or diminished ecosystem function when faced with further environmental change or extremes is well illustrated when various stressors combine, leading to catastrophic ecological effects. Between December 2018 and January 2019, millions of fish died across three separate events near the town of Menindee in the Darling River, Australia. Ultimately, these events occurred as a result of human alteration of the river's water through a series of weirs, including substantial harvesting of water upstream, combined with an extremely hot and dry climate during 2018 (Vertessy et al., 2019). Specifically, the fish die-offs resulted from a series of events, including large fish biomass accrual, algal bloom development and thermal stratification of weir pools leading to hypoxic bottom-water conditions. These events culminated in rapid oxygen deprivation resulting from weir pool destratification following sudden cool weather changes (Vertessy et al., 2019). The result of this is likely to be ongoing impacts on fish populations both locally and potentially in the wider Darling catchment for some time to come. The key take home here is that ongoing (or press) disturbances related to climate change are likely to make a system more vulnerable to combined anthropogenic stressors such as the over-allocation of water that can further increase water temperatures and lead to a cascading series of events similar to those at Menindee.

The effects of large transient (or pulse) disturbances (e.g., extreme floods) on top of existing ramp or press disturbances (ongoing climate change shifting mean conditions over decadal scales) is an area in need of further attention. For instance, heat waves can result in fire regimes that can increase flood intensity due to combustion of forest vegetation. When extreme events of different forms combine, the results can be particularly detrimental. Dahm et al. (2015) found flash floods that followed a catastrophic forest fire led to major reductions in water quality that persisted for 50 km downstream. Indeed, combining events that may not be extreme in isolation can make them extreme via their combination (McPhillips et al., 2018). Vieira et al. (2004) studied the response of stream invertebrate communities to repeated flood disturbances after a wildfire in New Mexico, United States, and found that total insect density and taxonomic richness declined to near zero following the first 100-year flood after the wildfire. However, density returned to pre-fire levels rapidly due to the colonization of aquatic insects including simuliids, chironomids and baetid mayflies; taxa with resilience traits (including high dispersal ability) that are often associated with disturbance regimes (McMullen et al., 2017). By contrast, taxonomic richness and community composition were much slower to return to pre-fire levels as less resilient species slowly recolonized (Vieira et al., 2004).

The interaction between ongoing land-use alteration and climate change presents a key challenge for river ecosystem resilience as rates of change continue to intensify (Van Looy et al., 2019). For instance, catchment-scale land use can mediate the local-scale responses to extreme events (Woodward et al., 2016). Collier and Quinn (2003) found that invertebrate communities in streams draining pastoral catchments (representing an underlying press disturbance) can be more influenced by flooding than those draining forested catchments. Similarly, climate change-driven changes to water temperature and flow alteration are interacting with land-use change to reorganize riverine fish communities around the world (Comte et al., 2021).

Land use alteration and climate change, representing ongoing press or ramp disturbances, can combine to interact both synergistically (amplifying effects) and antagonistically (buffering effects) to affect river ecosystems, and the nature of these interactions is context dependent. For instance, both synergistic and antagonistic interactive effects of climate change and land use change are predicted to influence the future distributions of fish diversity in the Elbe basin in Spain, resulting in a predicted increase in average species richness of 0.7–2.9 species by 2050 across the entire river network (Radinger et al., 2016). Antagonistic effects of land use and climate change were predicted for up to 75% of the network, and synergistic and additive effects up to 20% and 16% of the network, respectively (Radinger et al., 2016). Further, improvement in water quality from historical degradation has been found to mask the long-term effects of changing climate on stream invertebrate communities (Vaughan and Ormerod, 2014), potentially via the arrival of pollution-sensitive taxa (Floury et al., 2013). Such improvements can make detecting climate change impacts challenging for freshwaters. These examples demonstrate that the multi-pronged effects of long-term environmental change must be studied together to get a clear picture of the true effects of climate change on freshwater biodiversity.

Thresholds and regime shifts

Ongoing changes in the environment, such as unprecedented drought, can potentially push communities and ecosystems into novel states. Bogan and Lytle (2011) examined aquatic insect community changes in two stream pools in French Joe Canyon, Arizona between 2003 and 2009 in response to multi-year drought. They found an abrupt shift between community states during this prolonged drought, which reflected a transition from a perennial to intermittent flow regime (Fig. 3). While richness of communities may recover following, or remain stable during, multi-year drought in streams, there is often an underlying reorganization of communities, such as a replacement of long-lived, weaker dispersers with short-lived, strong dispersers (Bogan and Lytle, 2011). Aspin et al. (2019) used experimental mesocosms to examine trait-based responses to drought intensification and found that intensifying stream drying events can push stream invertebrate communities over functional thresholds, a point whereby statistical changes in traits were more rapid than changes in drought intensity. They found that the specific traits responding depended on the intensity of drought: moderate drought levels resulted in shifts in morphological traits, whereas extreme drought, where surface water was lost, saw shifts in morphological and physiological traits including body size, respiration mode and thermal tolerance (Aspin et al., 2019). Riparian ecosystems are similarly at threat from climate-induced changes to flow regimes. Using a mechanistic modeling approach, Tonkin et al. (2018b) found that an increasingly dry future would lead to the collapse of networks of interacting riparian plant species and a loss of keystone species in the southwest of the United States. Unraveling interaction networks could have negative consequences for community stability and resistance to invasion, whereas losing keystone species could lead to the loss of important ecosystem services including habitat provision, flood mitigation and nutrient cycling.

Extreme drought associated with climate change can also lead to previously suitable habitat becoming an ecological trap for native species. Vander Vorste et al. (2020) found that endangered juvenile Coho salmon survival in intermittent Californian stream pools differed markedly depending on the duration of disconnection between upstream and downstream habitats. Approximately half of the pools studied that were previously able to sustain juvenile salmon in non-drought years appeared to transition into ecological traps—defined by survival being markedly reduced—during drought.

Geographic differences

The threats of climate change will likely play out differently around the globe. Scenario projections have predicted up to 75% of local fish biodiversity will be threatened by extinction by 2070 as a result of the combined effects of climate change and human water demand, but these differ geographically due to baseline differences in climatic conditions (Xenopoulos et al., 2005). Based on physiological estimates of thermal sensitivity, more recent research suggests that freshwater fish faunas will be most at risk of climate change in Northern Hemisphere regions, particularly at high latitudes (Comte and Olden, 2017). This disproportionate threat to high latitude biodiversity in rivers is not limited to fishes (Nilsson et al., 2015). Threats include greater temperatures, increased rainfall and altered timing of stream flow events as a result of altered snowmelt dynamics, many of which will translate into extreme forms, such as unusually large floods (Nilsson et al., 2015). Northern regions will also likely see the arrival of many new species as the climate warms. Emergent aquatic macrophytes have already expanded their distributions northwards in boreal regions over the past several decades, and models suggest this will continue over the next century due to increasing growing degree days (Alahuhta et al., 2011).

No region is spared from the ongoing effects of climate change, however. For example, increased drying associated with climate change in dryland regions will further threaten endemic fishes, particularly through hydrologic fragmentation (Jaeger et al., 2014). Reductions in network-wide hydrologic connectivity through drying is expected to be as severe as 6–9% over the space of the year and up to 12–18% during spring spawning season by the mid- to late-century in the Verde River Basin, United States (Jaeger et al., 2014). Tropical regions are particularly threatened by the considerable ongoing habitat loss and agricultural expansion that will
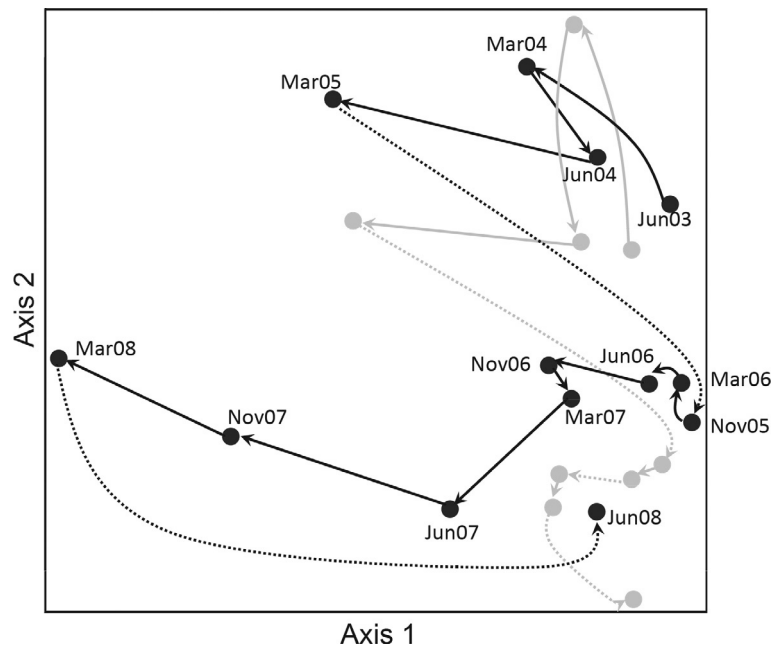
Fig. 3 Ordination plot of aquatic insect community changes in two pools (black vs. gray) in French Joe Canyon, Arizona between 2003 and 2009 in response to prolonged drought. Each point represents a community at one time-point, with those closer together reflecting more similar community composition. Trajectories of change through time are shown by the arrows (dates are labeled only on the black pool). Solid lines reflect times when continuous surface flow was available between both sampling dates. Dotted lines indicate the stream dried in between samples. March 2005 represents a transition from a perennial to intermittent flow regime. Reprinted with permission from Bogan MT and Lytle DA (2011) Severe drought drives novel community trajectories in desert stream pools: Drought causes community regime shifts. *Freshwater Biology* 56: 2070–2081. doi: 10.1111/j.1365-2427.2011.02638.x.

exacerbate the effects of climate change on river ecosystems (Sundar et al., 2020). However, considerable changes have already been observed in tropical Hong Kong stream invertebrate communities over recent decades in the absence of non-climate change drivers (Dudgeon et al., 2020).

Solutions

Many solutions are available for protecting riverine biodiversity, and indeed humans, from the growing threat of climate change and extreme events in river ecosystems. It is clear that the tools are here—the challenge is in the impetus and implementation—and I list a small selection of these tools below. First, in order to be able to better protect freshwater biodiversity from ongoing climate change, we need to go beyond observational data and correlational approaches, and understand mechanistic responses to individual events and whole regimes (Tonkin et al., 2019). This is particularly important for extreme events (van de Pol et al., 2017), and a mechanistic approach will enable a shift towards more robust forecasts and projections of future scenarios. Nevertheless, greater investment into coordinated monitoring programs is required to detect trends across broad regions.

The cost of anticipatory or proactive action will be cheaper than mitigation at a later date (Palmer et al., 2008). By focusing on employing adaptive or anticipatory management policies, much needed flexibility will be promoted to cope with the rapid rate at which systems are changing. Anticipatory or adaptive management aligns particularly well with ecological forecasting. Adaptive management and ecological forecasting can be coupled in an adaptive iterative cycle of model development, prediction and testing (Dietze et al., 2018). Moreover, frameworks such as eco-engineering decision scaling (EEDS) enable a quantitative assessment of trade-offs among potentially conflicting engineering and ecological targets across a variety of possible management regimes under uncertain hydroclimatic settings (Poff et al., 2016).

One key target to build resilience into rivers to rapidly changing futures is to embrace natural riverscape variability. This can be at both local and regional scales. For instance, giving rivers more room to move will enable a greater capacity to self-organize in response to extreme events. Even without the pending threat of climate change altering the frequency of large floods, rivers often naturally overtop their banks at regular frequencies. However, given the likelihood of large-scale river floods becoming more frequent and the fact that human infrastructure is often built on river floodplains, strategic decisions are required about where to give rivers the room they need to move and where to continue to lock in protective structures.

At more regional scales, there is a need to consider streams as metasystems from a dynamic perspective as flow regimes continue to change (Datry et al., 2016; Van Looy et al., 2019). Managing for variability and spatial connectivity across the landscape will

accommodate uncertainty and promote the resilience of river networks to change. Spatial environmental heterogeneity enables broad ecological responses (response diversity) to changing conditions, thereby imparting resilience by enhancing adaptive capacity at the landscape scale.

Designing and implementing spatial ecological networks that enable multiple species to persist, disperse and migrate, and that are robust to multiple climatic and environmental futures is possible using multi-criteria decision making (Albert et al., 2017). Without facilitating unhindered movement of organisms in this manner, managed relocation or assisted migration of species (Olden et al., 2011) or whole communities (Jourdan et al., 2019) will be required in many instances. Balancing local-scale optimal conservation goals while maintaining and promoting the variability that is inherent in natural systems remains key, but it presents major challenges for prioritization in the broader geographic context given the inherent tradeoffs and complexity in decision making required.

Often, the focus of management efforts is too local. Instead, effort should be put into strategic spatial prioritization of management actions for maximizing targets regionally while maintaining resilience at the landscape scale (Poff, 2018). Dammed river catchments may be more at risk from climate change than free flowing rivers via a reduced capacity to reorganize and absorb additional disturbances (Palmer et al., 2008). On the flip side, however, water-control infrastructure, such as dams, provides opportunities for managers to build both resilience and precision into human-altered systems (Tonkin et al., 2021). Although most research on designing environmental flows for human-altered rivers has so far focused on single dams, there is potential to apply this notion to portfolios of hydrologic infrastructure to minimize shortfall risk (in hydropower, water yields) while maximizing regional ecological outcomes. It is, nonetheless, a major societal challenge to achieve an appropriate balance between ecosystem conservation and water resource development.

Conclusions

Humans have extensively exploited river systems for their services, such as food and water supply, power, transport, and recreation, but at the cost of severe ecological degradation (Dudgeon et al., 2006). Climate change is now pushing river ecosystems into new domains of variation by altering regional precipitation and temperature regimes and extremes. The excursion of natural hydrologic variability outside the range of the historical undercuts assumptions of water resources management (Milly et al., 2008) and threatens ecosystems (Tonkin et al., 2019).

The alarming signals we are seeing from Siberian wildfires, extreme floods around the world, to deadly western United States heatwaves each represent the no-analog futures that atmospheric scientists have been predicting for some time. Only time will tell just how devastating these events will be for freshwater biodiversity. But the evidence provided in this chapter highlight that the effects will be wide ranging, from local species extirpations, range shifts, food web collapses, and homogenization. Riverine biodiversity is naturally resilient to dynamic fluctuations in the environment, but we need to be prepared to help increase this resilience through any means possible.

Acknowledgments

See Also: Structures and functions of Inland Waters - Rivers: Ecological and Evolutionary Consequences of Disturbance in Freshwater Ecosystems; Environmental Flows: Ecological Effects of Hydrologic Alterations, Assessment Methods for Rivers, Challenges and Global Uptake; High Latitude Rivers: Ecosystems Shaped by Environmental Extremes; River Resilience

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