



Future of Freshwater Ecosystems in a 1.5°C Warmer World

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Freshwater ecosystems are highly vulnerable to global warming because 1) their chief drivers, water quality and flow regimes, are highly sensitive to atmospheric warming, and 2) they are already extremely threatened by a wide range of interacting anthropogenic pressures. Even relatively modest global warming of 1.5°C poses a considerable threat to freshwater ecosystems and the many critical services these provide to people. Shifts in the composition and function of freshwater ecosystems are widely anticipated with adverse consequences for ecosystem services, including those underpinning water and food security. While the extent and severity of effects is likely to be significantly reduced if global warming is limited to 1.5°C, concerted efforts to implement widely recognised priorities for policy and management are required to mitigate unavoidable impacts and reduce the likelihood of perverse outcomes of climate mitigation and adaptation efforts in other sectors—all of which rely on fresh water supply. Freshwater ecosystems and their services, including provision of fresh water, must therefore be considered first and foremost when developing and implementing any climate action.

Keywords: aquatic biodiversity, climate change, flow regimes, rivers, lakes

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1 INTRODUCTION

It is now almost inevitable that by some time in the middle of this century (2041–2060), global temperature will exceed 1.5°C warming relative to a 1850–1900 baseline, after which it will either stabilise or, in all but the very lowest emissions scenarios, continue to rise (IPCC, 2021). Freshwater ecosystems are particularly sensitive to warming because their chief drivers, water quality and water quantity, are strongly influenced by atmospheric temperature regimes. Air temperature determines both water temperature and many chemical attributes contributing to water quality (e.g., dissolved oxygen levels), and its suitability for supporting freshwater biodiversity and maintaining critical ecological functions and services. Surface and ground water regimes, including precipitation, snow melt, run-off, soil moisture, river discharge, and aquifer recharge, are similarly sensitive to warming, with significant changes to hydrology attributed to temperature increases already apparent across the world (Cai and Cowan 2008). The vulnerability of freshwater ecosystems to warming is exacerbated by their disproportionately high levels of modification and degradation which both aggravate their sensitivity to temperature change and constrain their capacity to autonomously adapt (Capon et al., 2013; Reid et al., 2019). Indeed, rates of freshwater biodiversity loss over recent decades far outstrip those of terrestrial or marine species (Tickner et al., 2020), and even relatively modest global warming of 1.5°C poses a considerable threat to many freshwater species and ecosystems already on the brink of extinction.

Current global ambitions for climate change mitigation to limit planetary warming to 1.5°C, an objective since the 2015 COP21 Paris agreement (UNFCCC 2015), dramatically reduce the extent and magnitude of climate risks faced by freshwater ecosystems, although these remain significant. Of

further concern, however, is the additional threat to freshwater ecosystems presented by human responses to climate change (e.g., dam building for water security, meeting increased water demand for cooling), including many of the mitigation approaches being pursued to limit global temperature rise to 1.5°C (e.g., increasing hydroelectrical power generation, carbon sequestration plantations). Strong relationships exist between climate change mitigation and adaptation and the management of water resources and freshwater ecosystems (Koutroulis et al., 2018) and it is well recognised that water is the principal medium through which most people and environments are likely to experience climate change (World Meteorological Society, 2021). Consequently, it is critical that freshwater ecosystems and the many services these provide, including provision of fresh water, are considered first and foremost when developing and implementing any climate action.

Despite widespread acknowledgment of the pivotal role of freshwater ecosystems to the world's future under climate change, substantial knowledge gaps remain. Furthermore, conservation policy and management of freshwater ecosystems are often buried within a broader dialogue concerning terrestrial conservation, or else obscured by an overly narrow focus on meeting human water demands. Here, six years after the 2015 Paris agreement and with revised ambitions presented at COP26, we highlight the significant effects that even 1.5°C global warming can be expected to incur for freshwater ecosystems, and consider their implications for freshwater biodiversity and the many fundamental ecosystem services provided to people. We also emphasise widely agreed priorities for policy and management of freshwater ecosystems that will ensure the best possible futures for these critical components of our environments, economies, and cultures.

2 EFFECTS OF 1.5°C WARMING ON FRESHWATER ECOSYSTEMS

2.1 Water Quality and Quantity

Global warming of 1.5°C has many implications for freshwater ecosystems, with effects varying regionally, in relation to climate, and locally between different habitat types (Xia et al., 2015). Effects of increased temperature on water quality and hydrological regimes, themselves intricately intertwined (Whitehead et al., 2009), are likely to be the most significant aspects of abiotic change given their overriding influence on ecological patterns and processes in freshwater ecosystems.

At broad scales, water temperature is closely correlated to air temperature, with higher water temperatures generally evident in equatorial regions and lower water temperatures in mid-high latitudes, except in large river systems where there is significant lateral movement of water between regions of differing climates or where precipitation and/or snow melt contribute to aquatic thermal systems (Liu et al., 2020). Anthropogenic heat pollution also exacerbates increases in water temperature. In general, however, an upwards global trend in mean and extreme river water temperatures is apparent, with average warming of 0.163°C per decade observed globally but up to

1°C per decade (1960–2014) in some regions such as the Congo (Liu et al., 2020). Warming can be expected to continue in many river basins although seasonal cooling of river water may occur in some in response to the earlier snow melt or heavier seasonal precipitation also driven by atmospheric warming (IPCC, 2021). The distribution of lake thermal regimes will also shift over the coming century with higher latitude lakes coming to resemble those of lower latitudes. In both cases, the extent and magnitude of change will be limited under 1.5°C warming. Under low emissions scenarios (RCP 2.6), for example, around 12% of all lakes are predicted to shift into a thermal regime of a lower latitude, as opposed to 27 and 66% under the higher emissions scenarios of RCP 6.0 and 8.5, respectively (Maberly et al., 2020).

Rising water temperatures affect a wide range of biogeochemical processes underpinning water quality, most of which tend to occur at faster rates under warmer conditions (Whitehead et al., 2009). Warmer waters can also aggravate chemical pollution (Liu et al., 2020). Solubility of oxygen in water, however, declines with greater water temperature and low levels of dissolved oxygen can pose a considerable threat to aquatic biodiversity dependent on oxygen availability (e.g., fish), particularly in slow flowing and standing waters (Sheldon et al., 2021). In many places, including much of Australia and the United States, water quality will be further impacted by altered fire regimes, which can lead to elevated sediment and nutrient loads (Emmerton et al., 2020; Dupuis and Hann 2009). Flow regimes modified by climate change will additionally influence water quality by affecting patterns and processes of material transport, deposition, and transformation.

Modification of hydrological regimes by global warming can occur directly through its effects on precipitation, soil moisture, runoff, and extreme climatic events (e.g., floods, droughts and storms), as well as indirectly through broader changes to drainage networks and their catchments (e.g., land cover change). In general, the global water cycle is expected to continue to intensify with historically wet areas becoming wetter and drier regions becoming drier (Hoegh-Guldberg et al., 2019; IPCC, 2021). Higher precipitation is mostly projected in equatorial regions and higher latitudes while overall declines are expected in the subtropics, drylands and the Mediterranean. Such changes are very likely to be reflected by shifts in the overall magnitude of runoff and stream flows. In snow-driven catchments, seasonality of peak flows will also be altered where warming leads to reduced snow cover and earlier snow melt as well as higher summer temperatures and evaporation, subsequently elevating late winter and early spring flows and reducing late spring and summer flows (Donnelly et al., 2017). More frequent extreme rainfall events and associated flooding and drought, are further anticipated in most regions in response to warming, along with a higher proportion of the most intense tropical cyclones (IPCC, 2021).

Effects on hydrological regimes are largely expected to increase as warming exceeds 1.5°C, but not always and the direction of mean run-off changes projected under 1.5°C and 2°C can differ (Betts et al., 2018). In Europe, for example, intensification of droughts is limited under 1.5°C to western France, Spain and Portugal but the areas affected expand as warming increases

beyond this level (IPCC, 2021). Predicted changes to river flows, however, exhibit more variation at 1.5°C than under warmer scenarios due to anticipated seasonal variations related to altered snow patterns (Donnelly et al., 2017).

Both water regimes and water quality will additionally be affected by sea level rise, of which at least 0.28–0.55 m globally can be expected during the 21st century even under the lowest emissions scenario (SSP1-1.9; Marzeion et al., 2018). Because considerable glacier loss is already underway due to historic emissions, its contribution to sea level rise is not likely to differ significantly between 1.5°C and 2°C global warming (Marzeion et al., 2018). However, even modest sea level rise can substantially alter the character of low lying coastal freshwater ecosystems, rapidly shifting them into more brackish or saline systems unable to support their characteristic freshwater biodiversity (Grieger et al., 2020). As Siegert and Pearson (2021) note, under high emissions scenarios, we cannot rule out 2 m of sea level rise by 2100, and up to 5 m by 2150.

2.2 Freshwater Biodiversity

Freshwater biodiversity in the Anthropocene is already highly vulnerable, threatened by a wide range of interacting pressures (e.g., flow modification, land cover change, pollution, species invasions etc.) that tend to promulgate throughout catchments with the direction of flow (Capon et al., 2013). Climate change poses an umbrella pressure that directly impacts organisms as well as interacting, usually antagonistically, with other existing stressors. Rising temperatures and altered flow regimes can both be expected to drive considerable changes in freshwater biodiversity with effects encompassing biological patterns and processes across all levels of ecological organisation, from genes to landscapes. Of 31 ecological processes fundamental to the function of freshwater ecosystems, at least 23 have already been noticeably influenced by climate change with responses observed including altered species distributions, shifting phenological patterns, reductions in body size, more algal blooms, and decoupled interactions between species (Scheffers et al., 2016). Furthermore, climate change is estimated to significantly threaten around half of the world's freshwater fish species (Darwall and Freyhof, 2015).

Temperature plays a key role in determining the distribution of freshwater species and influences most critical biological processes including those associated with reproduction (e.g., spawning cues, triggers for egg hatching and seed germination etc.) and growth. Some taxa may benefit from projected changes, however. Cyanobacteria, for example, is expected to be favoured over eukaryotic algae under warmer water temperatures and higher CO₂ concentrations (Visser et al., 2016). For many other taxa, projected warming is very likely to exceed the thermal tolerances of freshwater organisms, especially as general warming will probably be accompanied by more frequent and intense heat waves (IPCC, 2021). Many freshwater species, including fish, invertebrates, amphibians, and reptiles, are ectotherms—unable to self-regulate internal temperatures and often exhibiting limited ability to avoid heat (Dupuis and Hann, 2009). Tropical ectotherms are particularly

sensitive to warming since they tend to exist closer to the limits of their thermal tolerance than temperate species (Nash et al., 2021). Temperature also tends to be the most important environmental factor determining sex in fish and warming is highly likely to promote greater proportions of males in many populations (Geffroy and Wedekind 2020).

Threats to freshwater organisms posed by rising water temperatures and associated declines in dissolved oxygen will be exacerbated by climate change impacts on flow regimes (Frakes et al., 2021). Because impacts on water quality and flow regimes will be more or less commensurate to global warming, prospects for freshwater biodiversity are considerably improved under scenarios in which temperature rise is limited to 1.5°C. Of 11,500 riverine fish species considered, for example, Barbarossa et al. (2021) estimate that approximately 4% will have more than half of their current range exposed to climatic extremes beyond those historically experienced under a warming scenario of 1.5°C, compared to 9% under 2°C and 36% with 3.2°C warming.

Further to these effects on aquatic organisms, significant changes in riparian biodiversity can be expected in response to both warming and modified flow regimes (Capon et al., 2013). Shifts in riparian vegetation composition and structure are very likely and have important implications for aquatic biodiversity through impacts on key ecological functions provided by riparian ecosystems (e.g., food subsidies and habitat provision). In many places, warming and increased CO₂ levels, as well as altered water and disturbance regimes, are resulting in woody encroachment and thickening of non-wooded wetland ecosystems (Saintilan and Rogers 2015). In coastal regions, however, saline intrusion has already resulted in widespread tree mortality in coastal swamps, generating 'ghost forests' (Grieger et al., 2020).

2.3 Ecosystem Services

Freshwater ecosystems support a diverse range of critical ecosystem services that benefit people both locally and across large spatial scales. Most services supported by freshwater ecosystems can be expected to be affected by global warming and its secondary effects on water quality, water quantity and freshwater biodiversity, with negative impacts widely anticipated (Capon and Bunn 2015). Riparian ecosystems, which support disproportionately high values and ecosystem services at catchment scales, are likely to be particularly sensitive to climate change, with further implications for the aquatic systems which they regulate and support (Capon et al., 2013). Indeed, the value of some freshwater ecosystem services, such as the provision of drought refuges, shading by riparian vegetation or provision of longitudinal corridors for wildlife movement, will likely grow as climate change progresses (Capon et al., 2013).

Changes in water quality and flow regimes have considerable implications for the supply of fresh water of suitable quality for a range of human needs including consumption and sanitation, agriculture, cooling, and industry. Many regions will experience water stress due to reductions in precipitation, runoff and rivers flows, although the extent and severity of these effects are expected to be significantly reduced if warming is limited to 1.5°C (Donnelly et al., 2017). Water security will be threatened

not only in regions experiencing drier climates, but also in those subject to increased precipitation due to accompanying shifts in the seasonality of rainfall and flows as well as declining water quality, for example because of sea level rise (Capon and Bunn 2015). Greater intensity of precipitation also alters the distribution of water resources across the landscape, reducing water storage in soils and generating higher inflows to reservoirs, thereby threatening rain-dependent agriculture, and promoting reliance on irrigation (Eekhout et al., 2018). Greater soil erosion and sediment inputs to water storages can also be expected in response to more frequent intense rainfall and runoff events, further threatening water security (Eekhout et al., 2018).

Provisioning services associated with freshwater biodiversity (fish, fibre etc.) are also directly threatened by projected effects of warming on water quality and flow regimes, especially where ecological populations are already at risk from overexploitation or other anthropogenic stressors (e.g., environmental pollution). Loss of economically significant cold-water fish species (e.g., salmonoids) is of particular concern in many regions (Maberly et al., 2020). Overall, food security is highly vulnerable to projected changes in water regimes, regardless of whether wetter or drier conditions are forecast, although the extent and magnitude of risks are expected to be considerably lower under 1.5°C than 2°C and higher global warming (Betts et al., 2018).

In addition to economic impacts and risks to human livelihoods, global warming also threatens the many social, cultural and spiritual values that people derive from freshwater ecosystems, including aesthetic appreciation of the environment (Auer 2019).

2.4 Priorities for Policy and Management

The two major drivers of change that are already impacting aquatic ecosystems, and will continue to increase in severity, each require specific management interventions. Changes to precipitation will yield dramatically altered flow regimes to which native species will not necessarily have adapted, while changes to temperature and seasonality will reduce available thermal habitat for native species and lead to asynchronous phenology for many species. Advances in freshwater ecology over recent decades provide a roadmap to mitigate these impacts, blending nature-based solutions with engineering approaches. Here, we highlight five management priorities for policy and management to best protect, restore and enhance freshwater ecosystems and their services under global warming:

- 1) Protect unmodified, unregulated freshwater systems, their riparian zones and catchments as freshwater refuges;
- 2) Actively manage flow regimes in regulated freshwater systems, prioritising key flood pulse attributes needed for biodiversity and ecosystem function;
- 3) Revegetate riparian zones and then catchments, prioritising upper reaches then moving downstream;
- 4) Design and implement flexible, adaptive management of water resources infrastructure; and
- 5) Monitor, evaluate and learn from progress made in comparable settings, sharing information openly and willingly.

2.4.1 Protect Unmodified, Unregulated Freshwater Systems, Their Riparian Zones and Catchments as Freshwater Refuges

There are very few remaining regions of the world that have wholly intact catchments and unregulated rivers. However, those that are left support a wide array of biodiversity and deliver 20% of the world's freshwater (Harrison et al., 2016). Intact catchments, and their riparian zones especially, provide a buffer against extreme temperature change and intense precipitation events. Riparian shading of narrow streams, particularly those with east-west orientation, reduces solar radiation reaching streams, moderating water temperature extremes (Rutherford et al., 2004). Equally, catchment vegetation helps retain soil moisture (Rodriguez-Iturbe and Porporato, 2004) and slows the flow of water across the landscape during extreme rain events (Istanbulluoglu and Bras, 2006). In addition to biodiversity value, protecting unmodified freshwater systems also supports ecosystem services provided by healthy functioning aquatic ecosystems. Improved planning for hydropower projects, widely viewed as a means to generating low-carbon energy and therefore part of many climate change mitigation strategies, will be particularly important for protecting the world's remaining free-flowing rivers (Thieme et al., 2021).

2.4.2 Actively Manage Flow Regimes in Regulated Freshwater Systems, Prioritising Key Flood Pulse Attributes Needed for Biodiversity and Ecosystem Function

Changes to flow regimes due to climate change are already affecting aquatic ecosystems and will exacerbate the impacts of altered flow regimes that are already evident around the world (Döll and Bunn 2014). Predictive ecological models indicate key elements of biodiversity may be lost without appropriate environmental flow mitigation (e.g., Rivaes et al., 2013). The non-stationarity of future climate change makes delivering environmental flows that recreate the natural flow regime additionally challenging (Poff, 2018); rivers with altered flow regimes will require more active management than those that flow freely (Palmer et al., 2008). While there is little chance of recreating historical natural flow regimes in already highly altered rivers (Poff, 2018), an integral part of this management must be strategically delivered environmental flows to support biodiversity and ecosystem function (Tonkin et al., 2019).

2.4.3 Revegetate Riparian Zones and Then Catchments, Prioritising Upper Reaches Then Moving Downstream

Catchment vegetation is critical to aquatic ecosystem health and ecosystem services (Allan, 2004), with headwater streams contributing disproportionately to catchment ecosystem function and maintenance of biodiversity (Alexander et al., 2007; Meyer et al., 2007). In addition to slowing the flow of water across the landscape, intact vegetation also reduces erosion and nutrient runoff, increasing "green water" in the soil which will be critical to water security under global warming (Eekhout

et al., 2018). Riparian zones themselves offer a wide range of specific ecosystem services for humans (Capon et al., 2013; Riis et al., 2020) and directly support the health of aquatic ecosystems by moderating stream temperatures and providing habitat for aquatic organisms (Sheldon et al., 2012). With changing thermal and hydrological regimes already altering the composition of aquatic biodiversity, most dramatically in modified catchments, active catchment management to moderate this process is vital (Comte et al., 2021). Minimising nutrient inputs to lakes by protecting and restoring their riparian vegetation, for example, is critical to limit the occurrence of harmful cyanobacterial blooms which are expected to be favoured over eukaryotic algae under higher water temperatures and increased CO₂ levels (Visser et al., 2016).

Recent research has shown how revegetation of riparian zones can offset the impacts of climate change and protect biodiversity by protecting cool water thermal habitat and restricting the range of invasive species, which would otherwise expand their range (Lawrence et al., 2014; Turschwell et al., 2018). Along with active revegetation approaches, passive restoration (i.e., protecting natural regrowth) can also be an effective approach to revegetating large floodplain areas, such as those in agroecological landscapes where crop production may no longer be viable under climate change (Zivec et al., 2021). Importantly in riparian habitats, revegetation needs to be coupled with adaptive management and novel approaches to water resources development (Capon and Pettit 2018).

2.4.4 Design and Implement Flexible, Adaptive Management of Water Resources Infrastructure

While conservation of biodiversity is critical for freshwater systems, we must also manage river systems for people which will inevitably require further infrastructure development (Tonkin et al., 2019). With increased variability in precipitation expected and a growing population in developing regions of the world, we need to strive for strategic deployment of traditional infrastructure in conjunction with nature-based solutions (Seddon et al., 2020). Combining existing ecosystem services provided by healthy catchments with investments in water resource infrastructure provides a cost-effective way to achieve water security in the face of climate change while minimising our impact on aquatic ecosystems (Vörösmarty et al., 2021). Deploying such water resource development and catchment management at regional-scales will require the use of decision support tools that accommodate hydrology, biophysical processes and economic constraints (e.g., Payet-Burin et al., 2019). Implementing flexible adaptive management of existing water resources infrastructure will be enhanced by participatory decision support tools that integrate real-time data describing biophysical and economic processes to manage systems under short term stresses of drought and floods that are going to increase in frequency (e.g., Phan et al., 2020). Rebuilding and retrofitting existing water resources infrastructure is also likely to be required to cope with hydrological changes (e.g., more intense rainfall and run-off events) and to reduce ecological impacts (e.g., controls to

reduce cold water pollution by dams; Olden and Naiman 2010). Across all scales, the critical input to adaptive management and decision support is high quality data.

2.4.5 Monitor, Evaluate and Learn From Progress Made in Comparable Settings, Sharing Information Openly and Willingly

After a sustained period of stability during the Holocene, it is becoming clear that the future entails the opposite and we must grapple with non-stationarity, particularly for aquatic ecosystems (Milly et al., 2008). This means that we cannot rely only on ecological relationships established in the preceding, relatively stationary decades for the conservation of aquatic biodiversity and management of aquatic ecosystem services (Poff 2018). More than ever, effective management of aquatic ecosystems and biodiversity relies on monitoring aquatic systems and integrating such monitoring with novel ecosystem models and frameworks for management (Horne et al., 2019; Tonkin et al., 2019). While we have a very good foundation for the future, derived from decades of aquatic ecological research and hydrological management, effective data collection and innovative research in the coming years will ensure we can learn from ongoing changes in aquatic ecosystems and enhance capacity to adapt to further, as yet unforeseen changes.

3 THE THREAT OF 2°C WARMING

Although the global community agreed to attempt to restrict warming to 1.5°C (UNFCCC 2015), there is already substantial evidence that this goal may not be met. Global warming of 2°C is highly likely to be exceeded in the middle of this century under all emissions scenarios except those involving steep and immediate reductions in greenhouse gas emissions (IPCC, 2021). While significant impacts to freshwater ecosystems and their services can be expected under 1.5°C warming, as described here, these are very likely to increase in severity and extent with greater levels of warming, sometimes disproportionately so. The frequency and intensity of heat waves, extreme rainfall events and agricultural and ecological droughts, will increase substantially with global warming of 2°C and higher, the latter particularly in drier regions (IPCC, 2021). Changes to hydrological regimes and water quality will also be greater with more warming. A doubling or more of flows in the Ganges River, for example, is projected in a world with 2°C warming (Betts et al., 2018). Similarly, almost a third of lakes are projected to shift into a thermal regime of a lower latitude under a 2°C scenario, more than twice as many as those likely to shift if warming is limited to 1.5°C (Maberly et al., 2020).

With the more severe thermal and hydrological changes expected under 2°C warming, considerably more freshwater species will also be exposed to extremes beyond the historical conditions in which they have evolved, including around 9% of riverine fish species, more than doubling the number of species affected at 1.5°C (Barbarossa et al., 2021). Commensurate declines

in the provision of ecosystem services, such as freshwater fisheries production and manageable supply of water for irrigation, can also be anticipated. The loss of such ecosystem services is likely to result in unprecedented risks to food security with several countries including Saudi Arabia, India and Brazil particularly exposed to these risks (Betts et al., 2018). In this comparatively bleak future, implementing the five management priorities described above may not be sufficient to mitigate these impacts and maintain freshwater systems and the ecosystem services they provide, making immediate action to reduce global carbon emissions more critical than ever before.

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DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/Supplementary Material, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct, and intellectual contribution to the work and approved it for publication.

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