Twenty-five essential research questions to inform the protection and restoration of freshwater biodiversity

Meagan Harper[†*], Fish Ecology and Conservation Physiology Laboratory, Department of Biology, Carleton University, Ottawa, Ontario, Canada. ORCID iD: 0000-0002-8462-2039

Hebah S. Mejbel[†], Department of Biology, University of Ottawa, Ottawa, Ontario, Canada. ORCID iD: 0000-0001-5737-7608

Dylan Longert[†], Department of Biology, University of Ottawa, Ottawa, Ontario, Canada

Robin Abell, Conservation International, Arlington, Virginia, USA

T. Douglas Beard, Jr, U.S. Geological Survey National Climate Adaptation Science Center, Madison, Wisconsin, USA. ORCID iD: 0000-0003-2632-2350

Joseph R. Bennett, Department of Biology and Institute of Environmental and Interdisciplinary Science, Carleton University, Ottawa, Ontario, Canada. ORCID iD: 0000-0002-3901-9513

Stephanie M. Carlson, Environmental Science, Policy, and Management, University of California, Berkeley, California, USA. ORCID iD: 0000-0003-3055-6483

William Darwall, Freshwater Biodiversity Unit, IUCN Global Species Programme, Cambridge, UK

Anthony Dell, National Great Rivers Research and Education Center, East Alton, Illinois and Washington University in St. Louis, St. Louis, Missouri, USA

Sami Domisch, Leibniz-Institute of Freshwater Ecology and Inland Fisheries (IGB), Berlin, Germany. ORCID iD: 0000-0002-8127-9335

David Dudgeon, Division of Ecology & Biodiversity, School of Biological Sciences, The University of Hong Kong, Hong Kong. ORCID iD: 0000-0003-4632-3473

Jörg Freyhof, Museum für Naturkunde, Leibniz Institute for Evolution and Biodiversity Science, Berlin, Germany. ORCID iD: 0000-0002-7042-3127

Ian Harrison, Moore Center for Science, Conservation International, Arlington, Virginia, USA. ORCID iD: 0000-0001-8686-8502

Kathy A. Hughes, WWF-UK, Living Planet Centre, Woking, England

Sonja C. Jähnig, Leibniz Institute of Freshwater Ecology and Inland Fisheries (IGB), Berlin, Germany and Humboldt-Universität zu Berlin, Geography Department, Berlin, Germany. ORCID iD: 0000-0002-6349-9561

Jonathan M. Jeschke, Leibniz Institute of Freshwater Ecology and Inland Fisheries (IGB), Berlin, Germany, the Freie Universität Berlin, Institute of Biology, Berlin, Germany and the Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), Berlin, Germany. ORCID iD: 0000-0003-3328-4217

Richard Lansdown, IUCN SSC Freshwater Plant Specialist Group, Gloucestershire UK. ORCID iD: 0000-0003-0984-4552

Mark Lintermans, Centre for Applied Water Science, Institute for Applied Ecology, University of Canberra, Australian Capital Territory, Australia

Abigail J. Lynch, U. S. Geological Survey, National Climate Adaptation Science Center, Reston, Virginia, USA. ORCID iD: 0000-0001-8449-8392

Helen M. R. Meredith, Amphibian Survival Alliance, % Synchronicity Earth, London, UK

Sanjay Molur, Zoo Outreach Organization, Tamil Nadu, India

Julian D. Olden, School of Aquatic and Fishery Sciences, University of Washington, Seattle Washington, USA. ORCID iD: 0000-0003-2143-1187

Steve J. Ormerod, Water Research Institute, School of Biosciences, Cardiff University, Cardiff, UK and Freshwater Biological Association, the Ferry Landing, Cumbria, UK

ORCID iD: 0000-0002-8174-302X

Harmony Patricio, IUCN World Commission on Protected Areas Freshwater Specialist Group

Andrea J. Reid, Centre for Indigenous Fisheries, Institute for the Oceans and Fisheries, The University of British Columbia, Vancouver, Canada. ORCID iD: 0000-0001-7251-7824

Astrid Schmidt-Kloiber, Institute of Hydrobiology and Aquatic Ecosystem Management, University of Natural Resources and Life Sciences, Vienna (BOKU), Austria. ORCID iD: 0000-0001-8839-5913

Michele Thieme, World Wildlife Fund-US, Washington, DC, USA. ORCID iD: 0000-0003-3216-9129

David Tickner, WWF-UK, Living Planet Centre, Woking, England

Eren Turak, NSW Department of Planning, Industry and the Environment, Parramatta, New South Wales, Australia. ORCID iD: 0000-0001-7383-9112

Olaf L.F. Weyl[#], South African Institute for Aquatic Biodiversity, Makhanda, South Africa.

Steven J. Cooke, Fish Ecology and Conservation Physiology Laboratory, Department of Biology and Institute of Environmental and Interdisciplinary Science, Carleton University, Ottawa, Ontario, Canada. ORCID iD: 0000-0002-5407-0659

*Correspondence: meaganharper@cmail.carleton.ca

†Authors contributed equally

[#]Deceased

Abstract

1. Freshwater biodiversity is declining at an unprecedented rate. Freshwater conservationists and environmental managers have enough evidence to demonstrate that action must not be delayed but have insufficient evidence to identify those actions that will be most effective in reversing the current trend.
2. Here, the focus is on identifying essential research topics that, if addressed, will contribute directly to restoring freshwater biodiversity through supporting "bending the curve" actions (i.e., those actions leading to the *recovery* of freshwater biodiversity, not simply deceleration of the current downward trend).
3. The global freshwater research and management community was asked to identify unanswered research questions that could address knowledge gaps and barriers associated with "bending the curve" actions. The resulting list was refined into six themes and 25 questions.
4. Although context-dependent and potentially limited in global reach, six overarching themes were identified: (1) learning from successes and failures, (2) improving current practices, (3) balancing resource needs, (4) rethinking built environments, (5) reforming policy and investments, and (6) enabling transformative change.
5. Bold, efficient, science-based actions are necessary to reverse biodiversity loss. We believe that conservation actions will be most effective when supported by sound evidence, and that research and action must complement one another. These questions are intended to guide global freshwater researchers and conservation practitioners, identify key projects, and signal research needs to funders and governments. Our questions can

act as springboards for multidisciplinary and multisectoral collaborations that will improve the management and restoration of freshwater biodiversity.

Key Words: "bending the curve", freshwater conservation, horizon scanning, priority setting, research questions

1. Introduction

Freshwater biodiversity faces unprecedented threats from human activities (Dudgeon et al., 2006; Reid et al., 2019). Many of these threats have been increasing in severity in recent decades (e.g., invasive species, fragmentation of rivers by dams, habitat loss) but there are also emerging threats (e.g., novel pollutants and pathogens, climate change), as well as interactions and cumulative effects (Birk et al., 2020), that further threaten freshwater biodiversity (Reid et al., 2019). Given how catchments function, everything that occurs in upland areas has the potential to impact freshwater ecosystems downstream. Even activities that happen well beyond the floodplain and riparian areas can have dramatic effects on freshwater biodiversity (Hynes, 1975; Weijters et al., 2009). Recent estimates have shown that, on average, the abundance of monitored freshwater vertebrate populations in the Freshwater Living Planet Index has declined by an average of 84% over the past five decades (WWF, 2020), double the rate of decline seen in marine and terrestrial realms. This has led to the recognition of the current global freshwater biodiversity emergency (Tickner et al., 2020). Additionally, roughly 30% of International Union for Conservation of Nature (IUCN) assessed freshwater species are threatened (i.e., Critically Endangered, Endangered or Vulnerable to global extinction; IUCN 2012) in the Americas, over 20% are threatened in Africa, and in Europe and Central Asia 37% of freshwater fish, 45% of freshwater snails, and 23% of amphibians are threatened (Watson et al., 2018). To facilitate management interventions that can effectively curtail or even reverse the decline in freshwater biota (i.e., "bending the curve" of biodiversity loss to enable the recovery of freshwater biodiversity), research and conservation practices must continue to be coordinated to address key knowledge gaps that currently impede progress (Mace et al., 2018; van Rees et al., 2020; Tickner et al., 2020).

Often, current research remains focused on improving understanding of natural history and the current status of freshwater biodiversity, and identifying the effects of various anthropogenic threats. This research is critical, but it is also essential to ensure there is dedicated research on actions that will directly alter and reverse the current downward trajectory of biodiversity loss. We define "bending the curve" actions in freshwater biodiversity conservation as those that will lead to the *recovery* of freshwater biodiversity (sensu Tickner et al., 2020) as opposed to the deceleration or stabilization of the current downward trend. "Bending the curve" actions aim to guide restoration and conservation, engage with the public and decision-makers, and target investments in tools, research and policy. Those actions that will reverse the impacts of direct threats (e.g., point source pollution) to, and indirect drivers (e.g., climate change) of, freshwater biodiversity loss are also included here. Research on the status of, and identification of new threats to, freshwater life is an essential part of conservation but knowledge gaps in these areas are already well-recognized (e.g., Reid et al., 2019). Instead, inspired by recent calls to motivate change (i.e., van Rees et al., 2020; Tickner et al., 2020) we focus on identifying essential research areas in the natural and social sciences that will support freshwater biodiversity recovery efforts.

In contrast to marine science (see Parsons et al., 2014), which is better represented in conservation science in general (Boon & Baxter, 2016), there have been few research agendas in freshwater science focused directly on biodiversity. Current freshwater biodiversity research agendas include one focused on migratory fishes (Lennox et al., 2019), a broader European agenda focused on overall biodiversity loss with freshwater content (European Commission, 2011), a preliminary unpublished freshwater research agenda (BioFresh, 2011), and various national agendas (e.g., Jähnig et al., 2019). None of these explicitly focus on research that will help in "bending the curve". Despite the recent development of frameworks detailing the major causes of freshwater biodiversity loss (e.g., Strayer & Dudgeon, 2010; Garcia-Moreno et al., 2014; Flitcroft et al., 2019) and efforts to support post-2020 policy agendas (van Rees et al., 2020), the issue of targeting research to facilitate freshwater biodiversity recovery remains challenging.

To address this challenge, a broad sample of the global freshwater research and management community was solicited to identify unanswered research questions in freshwater biodiversity conservation. Through this outreach, six overarching themes were identified that encompass important areas for future research. Within these themes, both foundational and cross-cutting issues and specific strategies and challenges inherent to freshwater biodiversity conservation are presented together to ensure that future research efforts are built on robust foundations and provide useable outcomes. Broad questions within these themes were identified, as were examples of possible research questions (ranging from narrow to broad) that would aid the freshwater community in effectively reversing freshwater biodiversity loss. These themes and questions are intended to serve as a guide for freshwater scientists, conservation practitioners, research funders, and policymakers by pointing to possible future projects and identifying pressing research topics and priorities related to "bending the curve" of freshwater biodiversity loss. We acknowledge that there are other broader conservation science questions that extend across realms (e.g., marine, terrestrial, freshwater) especially related to social science (see

Bennett et al., 2017b), as well as critical social justice issues pertaining to freshwater health (e.g., Mascarenhas, 2007). The questions presented here are those specifically related to freshwater biodiversity conservation.

2. Question Derivation and Theme Identification

The best practices identified in Sutherland et al. (2011) were adopted to guide this exercise. Original questions were solicited through an online questionnaire (i.e., surveyplanet.com) and requests for participation were distributed by the authors through targeted emails, list-serves and social media between September 23 and November 1, 2019. The call for questions was shared as broadly as possible by the authors and their network contacts with no limits on outreach (i.e., snowball approach or chain-referral sampling). It was therefore not possible to quantify the full extent of the call for question's reach, which is typical of the Sutherland et al. (2011) approach for these exercises. It is not known how many individuals or nations received a request to participate (or were aware of the survey) and chose not to respond. Those who did respond were asked to provide questions that would help address the knowledge gaps and barriers associated with "bending the curve" of freshwater biodiversity loss, as well as to provide information on their sector, role and geographic location. To obtain as many questions as possible and to allow participants to contribute fully, there were no limits to the number of times an individual could participate.

The call for questions achieved global reach with participants active in 45 countries (Table 1; Figure S2); however, it is important to note that 27 of these 45 countries (60%) had a single respondent. The top three participating countries were Canada (n=25 participants), the United States (n=23), and Australia (n=18). Participants represented all sectors: *Industry* (n=2;

1.2%), *Government* (n=30; 18.5%), *Not-for-profit* (n=48; 29.6%) and *Academic* (n=61; 37.7%), and an additional 21 participants (13%) who self-identified as *Other* (Figure 1a). Several participants (n=11) selected more than one sector. The most common primary role was *Researcher* (n=74; 43.3%), followed by *Practitioner* (n=35; 20.5%), *Decision maker* (n=20; 11.7%), *Other* (n=25; 14.6%) and *Student/post-doc* (n=17; 9.9%); the only unrepresented primary role was *Funder* (Figure 1b). As with sector, participants often selected more than one primary role; a total of 21 participants selected two or more.

(insert Figure 1a and b, and Table 1)

An initial list of 424 questions, submitted by 144 participants, was screened by the review team (MH, HSM, DL, and SJC). Questions that were deemed less applicable to the aim of bending the curve were removed. Questions removed included those that were: 1) highly region specific, 2) extremely taxonomic specific (e.g., regarding life history of a single species), 3) focused on threat identification (e.g., the impact of X on Y) and 4) those based on natural history (e.g., where does X species spawn?). Questions aimed at guiding restoration and conservation, educating the public and decision-makers, and targeting investments in tools, research and policy to lead to the *recovery* of freshwater biodiversity were retained (see Supporting Information for more detailed methodology and expanded results, and Table S2 for the complete list of submitted questions). After the initial screening by the review team, a short list of questions was evaluated by all authors to: 1) group or split specific questions, 2) suggest re-wording for clarity and 3) assess the likelihood of a question leading to research that would advance “bending the curve” actions. Additionally, all authors had the opportunity to advocate for questions that had been initially removed or to suggest their own. The final list of questions was selected through an iterative process and edited by all authors, including the review team, and were then condensed to six major themes (Figure 2) using the methods described in Sutherland et al. (2011).

(insert Figure 2)

Six major themes are presented, each including several broad "essential questions" (25 questions in total) which represent knowledge gaps and areas of concern identified by the respondents to our call for questions and by our author team. While Tickner et al. (2020) present six curve-bending actions for freshwater biodiversity (representing one framework for thematizing questions), the essential questions (and research needs) presented here transcend and cut across those actions. They are, therefore, grouped into slightly different themes (Table S3). The 25 essential questions are presented in no particular order, as priorities are inevitably context-dependent and will vary by geographic region and the socio-economic and political realities on the ground. These questions could be arranged under a variety of overlapping and cross-boundary themes, while themes and questions can interact in the development of specific hypotheses. This selection was further expanded with a limited subset of 75 possible research questions (Table 2) ranging from narrowly focused to broadly applicable. These additional example questions reflect some of the diversity of interests and the stage of development of freshwater biodiversity research globally. Such lists could be virtually endless, so these 75 further examples are just that – examples of specific questions which, if answered, could help further "bend the curve" of freshwater biodiversity loss.

(Insert Table 2)

3. Six Themes and Twenty-Five Questions

Theme 1: Learning from Successes and Failures

This theme considers what can be learned from previous successes and failures in biodiversity conservation and how that knowledge can be applied to current and future initiatives. Understanding what strategies and tactics are most effective and efficient in terms of producing lasting conservation impact, at scale, in the face of complex and increasingly dynamic socio-economic, political, cultural and governance challenges are essential components of learning from successes and failures. Questions included in this theme assess the characteristics of protected areas for freshwater organisms, consider the spatial scale of conservation initiatives, the effectiveness of flagship and umbrella species in freshwater biodiversity restoration, and the benefits of effective monitoring. The identification of successful conservation initiatives, when scaled up (see Bennett et al., 2016), can lead to improvements in freshwater biodiversity.

(1) *Opportunities for Learning: Where and why have past conservation efforts been successful or failed, and how can we learn from these outcomes?*

In disciplines such as business, it is common practice to engage in extensive, formal reflective processes to learn from success and failure (e.g., Lant & Montgomery, 1987). Only recently has this idea been fully embraced by the conservation science community (see Knight, 2006), but often successes are celebrated and failures forgotten. Also troubling is the fact that many current efforts in freshwater biodiversity conservation appear to be ineffective in the face of an increasing number of persistent, emerging, and synergistic or additive stressors (Craig et al., 2017). Efforts to understand the enabling factors for success can be illuminating and further research on factors that extend beyond the ecological realm (including economic, institutional, social, and cultural factors) can contribute to determining the ultimate success of conservation initiatives. Learning from success and failure, with a focus on identifying enabling factors, provides opportunities to support evidence-based conservation for long-term freshwater conservation outcomes.

(2) *Optimizing Scale: At what spatial and temporal scales are management interventions best applied to benefit freshwater biodiversity?*

To improve management of freshwater biodiversity, the spatial and temporal scales of conservation initiatives must be considered. The scales at which conservation efforts are implemented is a primary factor in how freshwater biodiversity is enhanced and which species and populations benefit (e.g., Lintermans, 2013). Delivering freshwater conservation at effective scales often involves trade-offs of terrestrial or aquatic resource exploitation with downstream consequences. It is necessary to assess the effectiveness and interactions of strategies at different scales to mitigate, restore, or avoid adverse impacts (Feld et al., 2018). A key determinant of success in conserving freshwater biodiversity is the development of integrative assessments of appropriate catchment scales required for effective results, recognizing that conservation efforts must adapt through time. For example, increasing habitat connectivity at different scales can promote species diversity (Shao et al., 2019) and enhance population resilience to climate change (Jaeger, Olden & Pelland, 2014), if done responsibly to avoid unintended consequences (e.g., species invasions).

(3) *Protected Areas: What are the characteristics of current protected areas and networks, as well as lands and waters stewarded and managed by Indigenous people, that lead to improved status of freshwater biodiversity and how can these be employed in future conservation efforts?*

The use of protected areas in freshwater ecosystems, relative to marine or terrestrial ecosystems (Hermoso et al., 2016), often lags (Loury et al., 2018). Resource use in IUCNrecognised protected areas varies widely and ecosystem protection is inconsistent as a consequence. The responses of freshwater organisms to protected areas remains variable, but there is a growing body of evidence that suggests that protected areas can be a useful tool for freshwater biodiversity conservation provided their design and management is robust [see Acreman et al., (2019) for a systematic review specifically related to freshwater protected area impacts]. Indigenous lands may function similarly, although less is known about aquatic systems on these lands (but see Schuster et al., 2019 for a terrestrial example). Although catchment scale protected areas are highly desirable (Saunders, Meeuwig & Vincent, 2002), protected areas are often more limited in size. Research related to understanding how to enable broader implementation and management of protected areas for both groundwater and surface water, and the optimal configurations and management approaches when full catchment scale protection is not possible, is necessary (for a fuller discussion on systematic conservation planning, see Question 15). This will require considering alternatives to traditional top-down approaches to protected area implementation; for an example, consider the community-level fish sanctuaries employed in Thailand which have benefited both fish biodiversity and community members who depend on these fisheries (Koning et al., 2020).

(4) *Flagship/umbrella Species: How can flagship or umbrella species be effectively used to both increase restoration and protection of freshwater biodiversity and increase public involvement in freshwater biodiversity restoration initiatives?*

The concepts of flagship and umbrella species have been applied successfully in terrestrial systems (e.g., giant pandas serving as both; Li & Pimm, 2016) and could be similarly successful in freshwater environments (e.g., freshwater turtles; Kalinkat et al., 2017). Flagship species act as ambassadors for conservation, are used to raise conservation funding, and to attract public attention. Umbrella species are expected to benefit a wide range of co-occurring species. Questions remain regarding which species to select and whether they should be endemic or threatened, megafauna, or from often overlooked groups [e.g., benthic invertebrates (Ormerod et al., 2010) or macrophytes], or if they truly function as intended. Similarly, whether more general systematic techniques for choosing flagship species (e.g., Veríssimo et al., 2014; McGowan et al., 2020) are applicable to aquatic ecosystems is uncertain. Working across disciplines with marketing and communications professionals to select species that resonate with the public and that meet ecological goals, may increase the success of these initiatives (Kalinkat et al., 2017).

(5) *Monitoring: How can we improve monitoring metrics and resources to guide restoration, conservation, and sustainable management of freshwater biodiversity?*

Some freshwater ecosystems are subject to comprehensive and long-term monitoring, yet it often remains unclear how those data feed into decision-making (Dixon & Chiswell, 1996). In other instances, monitoring is haphazard or nonexistent and it is likely that some freshwater species will be imperiled, or even extinct, before their existence is known (Burkhead 2012). Major investments in different interventions (such as restoration) often occur with little to no monitoring of effectiveness (Cooke et al., 2018). Well designed and executed monitoring plans should feed directly into current and future management planning cycles. Many of the metrics currently used in conservation (e.g., habitat quality, species richness, species abundance) are inadequate to quantify biodiversity losses in freshwater habitats (Turak et al., 2017) and research is needed to improve monitoring metrics. Additionally, community science (a.k.a., "citizen science") can make a huge contribution to biodiversity monitoring (Chandler et al., 2017), but more work is needed to determine how this capacity can be enhanced for freshwater biodiversity and how different forms of knowledge (e.g., conventional science or traditional knowledge) can be blended in ways that are more comprehensive and strategically focused in relation to the aims and objectives of conservation and restoration efforts.

Theme 2: Improving Current Practices

Questions in this theme identify gaps in current knowledge of measures to protect and restore freshwater biodiversity and ecosystems successfully. This includes identification of high priority biodiversity conservation areas, improvement of current pollution control and remediation measures, identification of methods which proactively manage the effects of global change (e.g., species invasions) and the discovery of solutions which mitigate the effects of synergistic threats. The identification and utilization of these measures can enhance future action to "bend the curve" of freshwater biodiversity loss.

(6) *Key Biodiversity Areas: What are the Key Biodiversity Areas that need to be prioritized for conservation of freshwater biodiversity?*

Key Biodiversity Areas are sites that contribute significantly to the global persistence of biodiversity (IUCN, 2016). While recent research has contributed to the identification of Key Biodiversity Areas in the freshwater realm (e.g., Carrizo et al., 2017), more work is necessary to identify what attributes of these areas ensure the conservation of freshwater biodiversity. For example, catchments are recognized as useful planning and management units, but efforts to manage at catchment scales have often failed to prevent biodiversity loss (Hermoso et al., 2016). Additionally, determining which locations and species should be given conservation priority remains challenging (Whitehead et al., 2014), but should not be a barrier to conservation. Improving identification and protection of these areas is essential for biodiversity conservation.

(7) *Pollution: What approaches to pollution reduction and remediation efforts will most benefit freshwater biodiversity?*

Point source and non-point source pollution continues to threaten freshwater ecosystem functions and biodiversity (Reid et al., 2019) necessitating better management and mitigation techniques for both ground and surface waters. Stopping pollution at the source with better licensing and harm-reduction policies is essential, but finding strategies for water resource management practitioners to meet their obligations and objectives once a pollutant is present is equally important. Reduction and remediation measures have been effectively applied to some freshwater systems (Søndergaard et al., 2007), but finding measures that will ensure long-term success continues to be a challenge for some pollutants, especially from non-point sources. With the identification of new pollutants (e.g., microplastics, pharmaceuticals), further research into improving existing pollution reduction and remediation techniques is necessary. Additionally, researching and adopting new measures (such as the use of nature-based solutions; Liquete et al., 2016) that are developed specifically for freshwater ecosystems, could benefit freshwater biodiversity.

(8) *Tool Development: What research innovations are needed to help restore freshwater biodiversity?*

Understanding of freshwater ecosystem integrity and function has dramatically increased over the past few decades. However, many threats to freshwater biodiversity are increasing in severity and frequency, while new threats continue to emerge (Reid et al., 2019). Leveraging new research techniques such as big data analytics, knowledge synthesis, community science, or novel field techniques could advance conservation efforts (Cheruvelil & Soranno, 2018). Further developing techniques that allow for decreased field work intensity (i.e., remote offload; Lennox et al., 2017) and approaches that do not require lethal sampling (e.g., environmental DNA, camera traps, remote sensing) is essential. Improving existing methods through facilitating longer-term field research (e.g., Mirtl et al., 2018), study reproducibility (Fidler et al., 2017), or co-developing decision-support tools with conservation managers (Kuehne, Strecker, & Olden, 2020) and community scientists could lead to the development of more effective conservation tools and initiatives. To be clear, this is not research for the acquisition of knowledge *per se*, but rather exploiting innovations in research to meaningfully advance freshwater conservation.

(9) *Climate Change: How do we proactively incorporate climate change adaptation into freshwater biodiversity conservation?*

The effects of climate change continue to severely impact freshwater ecosystems despite considerable research into the topic (e.g., the Fish Climate Change Database https://ficli.shinyapps.io/database/; Krabbenhoft et al., 2020). It is essential that measures that enhance the resilience of freshwater systems to the effects of climate change are employed (e.g., Huang et al., 2019). Understanding of how to proactively mitigate and manage the impacts of climate change requires improvements to overall understanding of the effectiveness of conservation strategies to support freshwater ecosystem function. For instance, some researchers advocate strategies that consider species vulnerability, exposure, and adaptive capacity (e.g., Dawson et al., 2011) to improve effective protections for freshwater habitats and species. Novel approaches could harness synergistic interactions where biodiversity gain arises from mitigation (e.g., carbon sequestration, reduced emissions), adaptation (e.g., restored riparian forest) and nature-based solutions (e.g., flood-risk management), but more evidence on their effectiveness is needed (Thomas, Griffiths & Ormerod, 2016).

(10) *Invasive Species: What are the best ways to manage freshwater invasive species and diseases to ensure proactive and meaningful improvements to freshwater biodiversity?*

The introduction and proliferation of invasive species and diseases in freshwater ecosystems can cause serious economic and conservation losses (e.g., Johnson & Paull, 2011; Pyšek et al., 2020). Unfortunately, these impacts are expected to become more extensive through new pathways (e.g., easy access to invasive species through e-commerce; Peres et al., 2018) and a changing climate (Rahel & Olden, 2008). Although increasingly studied, knowledge of effective prevention and management options is often limited by insufficient information (e.g., Rytwinski et al., 2018). Strategies for better managing intentional introductions (e.g., fisheries enhancements for economic opportunities or vegetation control) that result in negative impacts (e.g., Ellender et al., 2014) are needed to meet conservation goals. Although improving current control and prevention methods will be challenging, better understanding and communication of the impacts and management of invasive species will facilitate meaningful advances.

(11) *Riparian Zones: What are the optimal riparian management actions that contribute to the protection of freshwater biodiversity?*

Riparian areas, including floodplains, have long been regarded as important for freshwater ecosystems and a variety of management actions are used by practitioners to protect riparian areas and adjacent freshwaters (Naiman, Decamps & McClain, 2010). Many questions remain regarding the importance of maintaining longitudinal riparian zone continuity and lateral connectivity to floodplains, and the role of groundwater-riparian zone interactions on freshwater biodiversity. Riparian buffers and setbacks are common tools that have been shown to reduce flooding, limit erosion, and protect aquatic and terrestrial habitats. Benefits could also arise for pollution reduction, thermal damping, enhanced energetic subsidies and habitat provision (Feld et al., 2018). Current guidelines on setback requirements and design criteria in some regions need further development and evaluation (Olugunorisa, 2009; Haley et al., 2016). While setback widths are often defined by the size of the drainage area (National Research Council, 2000) and fixed-width buffers are standard practice (Richardson, Naiman & Bisson, 2012), more research is needed to determine the influence of landscape types on setback effectiveness. Defining best management practices and providing recommendations for riparian area and floodplain management could help protect freshwater biodiversity and freshwater ecosystem functioning.

(12) *Synergistic Threats: How can we develop conservation and restoration measures that most effectively and efficiently address synergistic threats to freshwater biodiversity?*

Multiple threats can lead to combined effects being greater (synergism), less than (antagonism) or equal to the sum of (additive) their individual effects or can manifest in the opposite direction to independent effects (reversals) leading to unanticipated ecological responses (e.g., warming can reverse the trend of increasing phytoplankton biomass observed under cold acidification conditions; Christensen et al., 2006). A recent synthesis indicated that the net effects of paired alterations to freshwater ecosystems were more frequently antagonistic (41%) than synergistic (28%), additive (16%), or reversed (15%) (Jackson et al., 2016). Moreover, conservation projects targeting single threats often fail to address synergistic and additive effects (Craig et al., 2017). Given multiple and sometimes synergistic stressors, it is necessary to target limited resources so that the most significant stressors or threats are addressed and the most restorative blend of actions is identified.

<u>Theme 3: Balancing Resource Needs</u>

There is a constant tension between human development and freshwater biodiversity conservation, especially in ecosystems where the high economic benefits gained by some groups through ecosystem resource exploitation is juxtaposed with the ecosystem management necessary to maintain biodiversity. Conventional approaches to economic development often focus on a narrow set of priorities at the cost of wider biodiversity (Flitcroft et al., 2019). This theme is focused on generating solutions that lead to positive outcomes for freshwater biodiversity and for humans. Questions related to this theme include balancing resource extraction, sustainable food production and energy generation with the needs of freshwater biodiversity. Raising the priority of freshwater biodiversity and considering trade-offs in resource use and development will help in "bending the curve" and supporting wider sustainability in development outcomes.

(13) *Sustainable Food: What are the joint priorities for sustainable food production and freshwater biodiversity conservation?*

Demands from aquatic and terrestrial food production put pressure on freshwater ecosystems (e.g., through land-use conversion, overexploitation, nutrient enrichment, pollution, water abstraction; Cottrell et al., 2018). Although efforts have been made to integrate terrestrial biodiversity into sustainable food systems (e.g., FOLU, 2019), less work has focused specifically on freshwater biodiversity. Freshwater conservation initiatives require integration with agriculture, aquaculture and inland fishery practices to minimize the negative impacts of these pressures while providing food sustainability (Phang et al., 2019). Protecting freshwater biodiversity through the development and uptake of new methods in the food sector, such as alternative water sources (Intriago et al., 2018) or production intensification (Tanentzap et al., 2015), is challenging and sometimes controversial (e.g., balanced harvest; Zhou et al., 2019).

These methods will be heavily influenced by geographic region and socio-economic context, so must be tailored to specific situations. Questions remain regarding implementation of new techniques and harmonization of conservation and food-sustainability goals.

(14) *Dams and associated infrastructure: How can the need for dams and associated infrastructure be balanced with connectivity, health, and flow requirements of freshwater ecosystems and biodiversity?*

Dams and associated infrastructure enable water storage, flood control and energy production, but are increasingly recognized as threats to freshwater ecosystems and biodiversity. Even small barriers and small hydropower plants have negative impacts on aquatic ecosystems (Couto & Olden, 2018; Lange et al., 2018; Belletti et al., 2020). There are growing calls to transform the use of dams to balance their benefits and costs and to address associated impacts and externalities more effectively during all phases of planning and design (Moran et al., 2018). Expanding energy portfolios to further develop alternative energy sources beyond hydropower will also lead to improved freshwater biodiversity outcomes. While there are some recent examples (e.g., Opperman et al., 2019; Hurford et al., 2020), there is a need for further research on how to assess trade-offs across social, environmental and economic variables [e.g., fisheries, agriculture and hydropower; Pittock, Dumaresque and Orr (2017)]. Additional research on the improvement of regulatory enforcement and site selection is necessary. Ensuring connectivity, improving operational flow regimes and incorporating freshwater biodiversity into policies affecting dam design and operation remains challenging but necessary (Poff & Olden, 2017).

(15) *Conflicting Needs: How can we better balance conflicting interests between human demand for natural resources and freshwater biodiversity?*

Conflicts between natural resource demands (e.g., ground and surface water abstraction for agriculture, industry, sanitation and domestic consumption, forestry, extraction of aggregates) and freshwater biodiversity will continue as human population grows and per capita consumption increases (Motesharrei et al., 2016). Efficient consumption of resources that explicitly considers the protection of freshwater biodiversity and ecological limits is essential. Systematic approaches for freshwater conservation planning (Linke, Turak & Nel, 2011) and frameworks to improve decision-making in resource use (e.g., Huysman et al., 2015) could help balance these goals. However, shifts in economic practices (Martin, Maris & Simberloff, 2016), improved legislation and policy (Bringezu et al., 2016), and development of new technologies (Czech, 2008) will likely be necessary to avoid many of the trade-offs to conservation gains. Promoting research of multidisciplinary solutions and applying limits in areas of current demand are important efforts to reduce risks to freshwater biodiversity.

Theme 4: Rethinking Built Environments

This theme is representative of the increasing need to consider new avenues for freshwater biodiversity conservation such as in urban and suburban areas previously considered to be biodiversity poor. Questions relating to this concept aim at improving recognition of opportunities and facilitating development of programmes, policies and infrastructure that actively seek to incorporate freshwater biodiversity conservation to help expand understanding of valuable freshwater spaces. Considering indirect effects from infrastructure development (e.g., river aggregate extraction; Koehnken et al., 2020) and working to rethink and explicitly design infrastructure for freshwater conservation will facilitate “bending the curve” of freshwater biodiversity loss.

(16) *Urbanization: What policies, programmes and activities can we implement to turn the risks associated with urbanization into benefits/opportunities for freshwater biodiversity enhancement?*

Frameworks for including biodiversity in urban development can mitigate the effects of urban growth and intensification (e.g., Biodiversity Sensitive Urban Design; Garrard et al., 2018), but freshwater biodiversity has rarely been considered. Focusing on evaluating the persistence of freshwater species and ecosystems in development initiatives and capitalizing on opportunities realized during the development process can lead to improved outcomes (e.g., wetlands used for stormwater management in China's Sponge Cities; Chan et al., 2018). Influencing the distribution of people in cities to maximize species diversity is one possible strategy (Geschke et al., 2018). However, identifying ways to enable co-existence of humans and freshwater biodiversity through urban planning (Nel et al., 2009) and stormwater management (Hassall & Anderson, 2015) may be even more effective. These opportunities require rethinking targets and indicators (e.g., freshwater reptiles; Turak et al., 2020) in efforts to protect and improve urban biodiversity.

(17) *Infrastructure: How can freshwater biodiversity conservation be better integrated into infrastructure planning, implementation and operation?*

Infrastructure development, including transportation, navigation, power, water supply, irrigation, stormwater management and sanitation, has generally proceeded without consideration for freshwater biodiversity. These activities can alter hydrology and ecosystems, negatively affecting freshwater biodiversity. Massive investments in water-associated infrastructure often fail to include sufficient expenditures to protect aquatic ecosystems (Bunn, 2016), but calls for considering ecosystems as infrastructure are increasing (da Silva & Wheeler, 2017). Determining how to alter or replace current infrastructure and how infrastructure and biodiversity planning can be harmonized will lead to better cost-sharing approaches (Sleight & Neeson, 2018). Also needed is a greater understanding of how urban planning, building standards, construction supply chains, recycling and reuse of construction materials, and aggregate extraction practices can take better account of ecosystem impacts to maintain the health of many freshwater ecosystems. Additionally, improving engineering strategies and planning for multi-use infrastructure enables the integration of resource use and freshwater biodiversity needs (e.g., planning irrigation with both agriculture and fisheries in mind; Lynch et al., 2019).

(18) *Novel/designed Ecosystems: What is the role of novel and designed ecosystems in conservation and how can these systems be managed to benefit freshwater biodiversity?*

Novel ecosystems are self-assembling, self-sustaining and inadvertently arise through human activity (e.g., new wetlands following peat harvesting; Collier, 2014), while designed ecosystems, such as retention ponds or large reservoirs, result from deliberate planning for human benefit and often require intensive intervention to maintain (Higgs, 2017). The contribution of novel and designed ecosystems to biodiversity conservation is unclear. Some argue that they allow for flexible management of systems unlikely to return to historical conditions (e.g., 'designer' flows; Acreman et al., 2014); others argue that adopting these ecosystems may lead to de-prioritizing restoration activities (see Miller & Bestelmeyer, 2016). It remains to be seen whether these ecosystems can provide suitable habitats for native species (but see Ebner, Lintermans & Dunford, 2011). Increased research will lead to new conservation opportunities (Heger et al., 2019).

Theme 5: Reforming Policy and Investments

This theme highlights the growing need to implement and enforce strong policies that benefit freshwater biodiversity while recognizing the need for increased financial investments in freshwater conservation and restoration efforts. Policy and investment are necessarily both regionally and socio-economically dependent and must be addressed at the level of implementation in a targeted manner. Questions related to this theme aim at understanding what government structures and strategies are needed to implement change, as well as determining mechanisms to scale up public and private sector financial investments and improve investments for implementation of specific conservation efforts. Effective policy and the identification of investment models for scaling up conservation financing can promote incentives that will ultimately lead to the protection of freshwater biodiversity.

(19) *Policy and Legislation: What public policy measures can most effectively promote conservation and restoration of freshwater biodiversity?*

Effective policy and legislation with a focus on freshwater ecosystems are necessary for future conservation efforts (Harrison et al., 2018; van Rees et al., 2020). However, conservation policy and legislation are often designed primarily for terrestrial or oceanic environments and do not fully account for the needs of freshwater ecosystems (Castello & Macedo, 2016). For example, freshwater biodiversity was not specifically mentioned in the United Nations' Sustainable Development Goal (SDG) 14: "Life Under Water" (United Nations, 2018), although many SDGs implicitly require conservation of freshwater (Lynch et al., 2017) and recent efforts reveal how freshwater fish and fisheries, for example, are integral to achieving the SDGs (Lynch et al., 2020). Understanding how to better account for environmental costs and consider trade-offs that favour solutions that benefit biodiversity, people and the economy would provide major improvements in freshwater biodiversity policy. There is also a need to explore policy options related to incentivising conservation actions that protect freshwater biodiversity and embracing nature-based solutions.

(20) *Financial Investment: How can we scale up and optimize financial investments from government, private sector and other sources such that there is a step change in funding for global freshwater conservation and restoration efforts?*

While funding for conservation and restoration programs has increased, there is a growing concern that consistent funding may not be available to support the long-term effectiveness of conservation efforts (Huwyler et al., 2014). Conservation financing has typically been provided on a small-scale and investment opportunities remain underdeveloped. Generating economic and management benefits from conservation funding programs and describing how they might create returns similar to traditional business models could provide a way forward (Huwyler et al., 2014). Highlighting improvements in efficiency, cost-reductions and supply chain stability can support a solid business case for investment in conservation efforts by major corporations and insurance companies, among others (Clark, Reed & Sunderland, 2018). By identifying methods and incentives for scaling up financial investments and capitalizing on opportunities that reduce business risk, conservation financing could create significant contributions towards sustainable development and protection of freshwater biodiversity for the future.

(21) *Environmental Flows: What are the social and natural science investments needed to develop and implement environmental flows that benefit freshwater biodiversity?*

Knowledge of environmental flow requirements has improved, but implementation requires the continued collaboration of a variety of stakeholders, especially considering the diversity and interdependencies of human/flow relationships (Anderson et al., 2019).

Collaboration could be enhanced by investments in social initiatives to improve support and grow understanding, and investments in the natural sciences to improve knowledge of effective environmental flow regimes. Continued research on incorporating environmental flows into policy and governance (Arthington et al., 2018) and creating mechanisms for their practical implementation is necessary. Setting reliable environmental flows, incorporating them into water management (i.e., at what scale; Opperman, Kendy & Barrios, 2019) and adapting flow-management strategies in the face of changing hydro-ecological conditions (Capon et al., 2018) will enable further improvements in environmental flows to support freshwater biodiversity needs.

(22) Ex situ *Conservation: What type of investments in* ex situ *conservation (e.g., captive breeding, reintroduction, managed relocation) are most effective for imperiled freshwater biodiversity?*

Despite attempts to conserve freshwater taxa *in situ*, increasing rates of habitat loss and climate change highlight the need for investments in alternative conservation tools (Olden et al., 2011; Brütting, Hensen & Wesche, 2013). *Ex situ* conservation is the process of conserving biological diversity at the gene, population and species level, outside the environment where it evolved. This technique can raise awareness of the plight of the species, but is expensive and requires extensive investments in time, tools and research. This is especially true given the number of imperiled freshwater organisms which need species-specific *ex situ* conservation strategies and the scale at which such efforts would be needed (Snyder et al., 1996; Fischer & Lindenmayer, 2000). Identifying the most appropriate and cost-effective *ex situ* methods for different freshwater species, especially those with complex life cycles and unique ecosystem and habitat requirements (for example, the development of an extensive captive breeding and reintroduction program for Kihansi spray toads after the loss of their unique spray wetland; Lee et al., 2006) could lead to investments in *ex situ* conservation that create positive results for freshwater biodiversity restoration and improved technical guidelines for global cooperation.

Theme 6: Enabling Transformative Change

This theme features research gaps that need to be addressed to enable transformative changes in individual human behaviour, societal actions and practice. Underpinning such efforts is the need to enhance knowledge exchange and raise awareness of the current state of freshwater biodiversity through better communication among researchers, between researchers and decision makers, and between researchers and the general public. Questions relating to this theme include identifying methods to develop and enhance management frameworks for restoring biodiversity, sharing science and communicating findings, and increasing public engagement to lead to changes in individual behaviour to help "bend the curve" of freshwater biodiversity loss. Promoting better research practices could lead to improved conservation initiatives and, by translating these findings into more accessible forms, will increase public support and political will for restoring freshwater biodiversity.

(23) *Management Frameworks: How do we develop management frameworks and evidence-bases that gain greater traction with stakeholders and managers?*

Conceptual management frameworks are tools by which complex systems, interactions and research gaps can be explained. While more recent frameworks (MA, 2005; IPBES, 2019) and a growing evidence-base (Schreckenberg, Mace & Poudyal, 2018) have highlighted the strong linkages among freshwater biodiversity, human well-being, ecosystem services, and government systems, active engagement by stakeholders and policy makers remains low. There remains a lack of empirical and targeted guidance for processes that consider complex dynamic interactions between these linkages. Related to this, guidance must necessarily be focused on a variety of different scales (geographically, socio-economically and in terms of governance) to reflect the context in which management decisions and conservation efforts are made. Frameworks for the management of freshwater biodiversity that not only foster evidence-based action, but also embed authentic participation by stakeholders and partners, are needed to realistically design and plan for conservation intervention (Langhans et al., 2019).

(24) *Science Communication: What steps should be taken to better communicate and share evidence and knowledge about the science of freshwater biodiversity among stakeholders?*

One of the key requirements for improving conservation of freshwater biodiversity is the establishment of stronger partnerships across sectors (Dudley et al., 2016). Building partnerships that create meaningful freshwater biodiversity outcomes requires effective communication between researchers, conservationists, practitioners, policymakers and the public. Utilizing methods such as collaborative alliance models (Gray & Wood, 1991) or co-design would allow for the integration of researchers and stakeholders in the planning and conduct of research on complex problems. This would improve the interpretation of results and the communication and use of findings. This can further be achieved by effectively translating scientific findings into material that is comprehensive, usable and accessible to other stakeholders. Communication among disparate knowledge-users requires enhancement and long-term maintenance of data-publishing and sharing platforms (Schmidt-Kloiber et al., 2019), improvement of evidence syntheses (Cooke et al., 2017) and the general implementation and acceptance of open-access publishing (Tennant et al., 2016) to ensure the availability of high-quality evidence.

(25) *Changing Mindsets: How can we increase the level of public engagement to change mindsets and build social license and political will to "bend the curve" of freshwater biodiversity loss?*

Awareness of the current state of freshwater biodiversity among the general public remains low (Darwall et al., 2018). Engaging the public, and local political representatives, through community science, environmental education (Sousa et al., 2016) or unique collaborations (e.g., with public aquariums; Murchie, Knapp & McIntyre, 2018) could result in improved understanding and willingness to support freshwater biodiversity initiatives. Changing attitudes and perspectives is difficult, especially if biodiversity initiatives are perceived as detrimental to human livelihoods (e.g., turtle bycatch reduction strategies; Nguyen et al., 2013), but is not impossible (Larocque et al., 2020). Designing methods to motivate involvement (e.g., community science activities) in environmental initiatives and to foster greater understanding and support for freshwater conservation will be challenging, and will likely require long-term efforts and collaboration across the natural and social sciences. Increased public engagement and incorporation of diverse worldviews into these messages can raise the profile of freshwater biodiversity leading to necessary actions directed toward improved conservation.

4. Discussion

In many areas of freshwater biodiversity conservation there is extensive evidence to demonstrate that actions to "bend the curve" must not be delayed. Conservation actions will be most effective when supported by sound evidence. If addressed comprehensively, the research questions presented here will fill critical knowledge gaps to better inform conservation activities and improve the effectiveness of current and future initiatives.

Themes and Questions

The six themes presented here are broadly applicable to many freshwater biodiversity conservation initiatives. Although specific questions submitted by participants tended to have a narrower focus (see Table 2), they were collectively generalized into broader groups that cut across boundaries. The themes included: 1. *Learning from Successes and Failures*; 2. *Improving Current Practices*; 3. *Balancing Resource Needs*; 4. *Rethinking Built Environments*; 5. *Reforming Policy and Investment*; and 6. *Enabling Transformative Change.* One concept that connects all six themes is the need for interdisciplinary research, communication and collaboration with those beyond the freshwater conservation community. Examples of successful research efforts that have led to positive change for freshwater biodiversity highlight the effectiveness of these efforts (Boon & Baxter, 2020). There are many social science questions that can be asked for each of the research questions posed here (e.g., understanding barriers to change; Bennett et al., 2017a) and furthering research at the intersection of the natural and social sciences will only improve conservation outcomes, especially when paired with active and adaptive management as new knowledge becomes available.

The broad questions developed during this process tended to include concepts of proactive and meaningful development of policies, tools and metrics that would enhance and prioritize the effective management of freshwater biodiversity conservation initiatives at a variety of spatial and temporal scales. Additionally, they include a focus on scaling up investment and integrating various levels of research, public engagement and policy to balance priorities and provide optimal benefits for freshwater biodiversity and human needs. The 25 essential questions in this list provide starting points for identifying future research and a loose framework within which to prioritize more specific initiatives. The many cross-cutting and foundational issues contained in these questions (e.g., spatial scale, human behaviour) highlight how interconnected solutions and policies will be necessary in the future. The answers to these questions are not solely sufficient to “bend the curve” of freshwater biodiversity loss (Tickner et al., 2020) and these questions should by no means constrain research in other areas. We therefore call on the freshwater conservation community to continue to add new questions to this list, and to promote and implement recommended actions resulting from current or future research.

By our definition, “bending the curve” questions are those whose answers will lead to actions for the *recovery* of freshwater biodiversity. Many of the submitted questions included calls to improve understanding of understudied regions and habitats (e.g., tropical ecosystems and non-perennial streams and wetlands), underrepresented taxa (including macrophytes, algae, invertebrates and microbes), and emerging threats (e.g., invasive pathogens). These would, therefore, not directly produce the knowledge needed for changing the current trajectory of freshwater biodiversity loss. Additionally, many of the original questions submitted were very specific to location or taxa. We recognize the importance of these types of questions to inform local-scale conservation and encourage the community to continue their efforts in these areas. Questions relating to these understudied topics are included in the complete list of submitted questions (see Supporting Information).

Limitations

The call for questions attempted to reach the broadest possible audience, but there are limitations in the methodology. Despite being largely untargeted and freely available to anyone who wished to participate, the questionnaire was distributed only in English. Distribution through the professional and social networks of the authors likely limited its reach and accessibility to English-speaking nations and individuals. Most responses were received from Canada, the United States, Australia, and other high-income nations (Table 1, Figure S2). As a result, the list of research questions may better reflect the interests of nations with well-developed conservation programmes, freshwater sciences and western science perspectives. Many nations were represented by a single participant resulting in a list of questions that may not have been adequately representative of broad geographic and socio-economic concerns. The lack of more comprehensive representation likely influenced both the questions submitted and the resulting final list. Despite recruiting a diverse team of coauthors with regional, taxonomic, and disciplinary expertise, the full diversity of research needs in freshwater biodiversity conservation may not have been captured. To help mitigate this, any missing topics considered essential by the authors could be brought forward for consideration at other phases of question thematization and refinement. The relative importance of questions in this list will necessarily vary by geography, socio-economic and political conditions, knowledge systems, and cultural norms. Our list is not intended to provide a specific road map, but rather to provide a list of potential areas to consider when establishing research agendas. We believe that providing this list is important for continuing conversations surrounding future "bending the curve" actions.

Although attempts were made to reach out beyond research institutions, more responses were received from researchers (43%) compared with practitioners (20.5%) and decision makers (12%). Students/post-docs and other roles make up the remaining 24.5% (Figure 1b). No responses were received from funders (Figure 1b). Since practitioners and decision makers are less well represented in the responses, it is possible that questions seeking directly applicable solutions may not have been submitted. However, practitioners and decision makers represent the on-the-ground experts in many regions and additional effort is needed to collate their experiences and knowledge to share with the broader community. Because practitioners may tend to maintain the status quo when engaging in conservation actions (Pullin & Knight, 2003;

Nguyen, Young & Cooke, 2017), concerted efforts to disrupt these norms and ensure that work is founded on best available evidence will improve conservation outcomes (Sutherland et al., 2004; Cooke et al., 2017). Several new journals (e.g., Ecological Solutions and Evidence, Conservation Science & Practice) have been developed to provide mechanisms for practitioners to share their knowledge and findings at the interface between practical experience, management, and theory, allowing for increased representation in research and decision-making. We encourage the community to utilize these and other avenues for increased knowledge sharing.

Thinking Globally

The implementation and enforcement of strong policies that benefit freshwater biodiversity are necessary both regionally and globally, and must be addressed in a targeted and equitable manner. Understanding the key role of freshwater biodiversity in contributing to ecosystems services is often overlooked at the international policy level. For instance, the Convention of Biological Diversities (CBD) 2020 Aichi Biodiversity Targets had no direct linkages to "bending the curve" for freshwater biodiversity (Tickner et al., 2020). The post-2020 framework for biodiversity, currently under negotiation at CBD, should ensure that there is an explicit goal focused on protection of freshwater biodiversity. Direct engagement on the discussion of the United Nations plan to protect 30% of the Earth's surface by 2030 (Dinerstein et al., 2019) at upcoming CBD plenaries focused on protecting freshwater systems will be important to ensure that freshwater is not ignored in selection of criteria for siting protected areas (or development of targets to measure progress toward agreed goals).

Further, to ensure that freshwater biodiversity research needs are identified, engagement of experts focused on aspects of freshwater biodiversity in ongoing initiatives (such as the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) proposed assessments on the nexus between food, water, energy and health, and transformative change) will be important to highlight the importance of freshwater biodiversity (www.ipbes.net). Engagement with the climate community, through the Intergovernmental Panel on Climate Change (IPCC), can help to ensure that science assessments focused on reducing carbon emissions will not unduly impact freshwater biodiversity as a trade-off for increased energy development.

Conclusion

Our aspiration is that the essential questions presented here will serve as a springboard for multidisciplinary and multisectoral collaborations that succeed in tackling the challenges of the freshwater biodiversity crisis. Bold, efficient, science-based actions are necessary to halt and reverse biodiversity loss (Mace et al., 2018), especially for freshwater biodiversity (Tickner et al., 2020). Addressing many of the research questions listed here will require the allocation of significant resources, but not all questions need to be addressed in all regions. Regional priorities need to be developed and funding strategies identified, which will require coordinated efforts from key non-governmental organizations, governments, and communities (including rights- and stakeholders). The extensive focus on social sciences and policy in these questions showcases the need for collaboration and multi- and trans-disciplinary efforts that bridge the gap between research, public participation and policy. Targeted, multi-disciplinary research funding will enhance urgent efforts to protect the world's freshwater biodiversity by making conservation and restoration efforts more effective and applicable at scale. Additionally, global syntheses emerging from distributed empirical research will also be needed to enable evidence-based decision making. Conservation actions will be most effective when supported by sound evidence, but we are also emphatic that action should not be delayed in the face of uncertainty (O'Riordan

& Cameron, 1994; Rytwinski et al2021). The themes and questions presented here help to highlight current research needs in freshwater biodiversity conservation. Addressing these questions comprehensively is achievable and necessary.

Conflict of interest

The authors declare no conflicts of interest.

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Table 1. Participants by geographic region.

Region	No. Participants
North America	48
Central and South America	4
Asia-Pacific	35
Europe	49
Africa	16

Table 2. Example research questions for each of the 25 essential questions. Note: the inclusion of a specific example research question does not imply it has any particular importance or priority over others. The examples are just that, and were selected to emphasize the diversity of ways in which the essential question can be addressed, from very localized, perhaps taxon-specific research, to broader, multi-regional or even global research that spans taxa and systems.

Theme	Essential Question	Example Research Questions
1. Learning from Successes and Failures	1. Where and why have past conservation efforts been successful or failed, and how can we learn from these outcomes?	1. What lessons stand to be gained from successful efforts for expanding the application of freshwater conservation policies? 2. How can conservation success stories be translated into increased resilience and resistance to perturbation for freshwater species' populations? 3. What are the different contributing factors and elements of success for different types of freshwater ecosystems?
	2. At what spatial scale and temporal scales are management interventions best applied to benefit freshwater biodiversity?	1. How can we develop a better understanding of the interconnectedness of terrestrial and aquatic ecosystems for improved freshwater restoration? 2. How can catchment approaches be delivered on a sufficiently broad scale to reverse freshwater biodiversity decline? 3. To what extent can local-scale management interventions (e.g., property scale) reduce threats to freshwater biodiversity and what are the cost/benefit implications of making changes at different scales?
	3. What are the characteristics of current protected areas and networks, as well as lands and waters stewarded and managed by Indigenous people, that lead to improved status of freshwater biodiversity and how can these be employed in future conservation efforts?	1. What spatial gaps in protected areas need to be addressed to ensure successful management strategies? 2. How and where should freshwater protected areas be established? 3. How can protected-area networks incorporate connectivity between terrestrial, freshwater, and marine systems to successfully protect freshwater ecosystems?
	4. How can flagship or umbrella species be effectively used to both increase restoration and protection of freshwater biodiversity and increase public involvement in freshwater biodiversity restoration initiatives?	1. Which threatened taxa are umbrella species candidates for freshwater conservation? 2. How can the often-overlooked components of freshwater biodiversity (plants, invertebrates, amphibians etc.) be prioritized for flagship and/or umbrella species? 3. What is the umbrella potential of freshwater mega-fauna?
	5. How can we improve monitoring metrics and resources to guide restoration, conservation, and sustainable management of freshwater biodiversity?	1. Is freshwater biodiversity conservation improved by concentrating efforts in a single location or spreading efforts over multiple locations? 2. How can we improve freshwater biodiversity monitoring in historically under-represented regions and habitat types? 3. What are the key elements in a successful global freshwater biodiversity monitoring program and how can they be implemented in the most cost-effective manner?
1. Improving Current Practices	6. What are the Key Biodiversity Areas that need to be prioritized for conservation of freshwater biodiversity?	1. How can we prioritize key sites that, if restored, would provide the greatest improvements to the condition of freshwater ecosystems and freshwater biodiversity? 2. How should we select areas from which future human activities should be barred through strict conservation initiatives? 3. How can the protection of freshwater Key Biodiversity Areas be improved, both through legal, and physical means (i.e., barriers)?
	7. What approaches to pollution reduction and remediation efforts will most benefit freshwater biodiversity?	1. How can we effectively communicate, to industrial and commercial entities, the dangers of dumping waste (physical and chemical) into freshwater systems and provide cost-effective solutions to the creation and safe disposal of waste? 2. To what extent are nature-based solutions applicable to point and non-point source pollution control in freshwater ecosystems? 3. How can the effects of newly emerging contaminants such as pharmaceuticals, microplastics etc. in freshwater systems be detected and mitigated more effectively?
	8. What research innovations are needed to help restore freshwater biodiversity?	1. How can established management tools, such as repatriation of local biota, field assessments, and stocking in freshwater biodiversity conservation, be improved? 2. What novel techniques (e.g., drones, eDNA, community science) could be applied to develop knowledge for improved freshwater biodiversity monitoring, conservation, and restoration activities?

		3. How can resilience assessments inform decision-making for freshwater biodiversity conservation?
	9. How do we incorporate climate change adaptation into freshwater biodiversity conservation?	1. Are current, conventional measures and metrics adequate to evaluate climate change effects (e.g., securing fish passage, water quality) and, if not, how can we improve them? 2. How can restoration projects incorporate resilience to a variety of climate impacts? 3. How should the climate change impacts on water resources best be mitigated to maintain optimal ecosystem function and services?
	10. What are the best ways to manage freshwater invasive species and diseases to ensure proactive and meaningful improvements to freshwater biodiversity?	1. What are emerging pathways of new species introductions and how can they be managed to prevent harmful invasions from occurring in the future? 2. How can we improve measures to control or slow the spread of invasive species, including using techniques such as integrated risk assessments, biotechnology, and community science? 3. How can proactive invasive species risk management, rather than reactive management (i.e., eradication), be integrated with current practices?
	11. What are the optimal riparian management actions that contribute to the protection of freshwater biodiversity?	1. How do riparian zone setbacks modulate impacts of land-use change? 2. How can lateral continuity be better maintained in riparian zones? 3. What evidence will convince developers and planning authorities that human activities in riparian zones have dramatic effects on freshwater biodiversity and should be avoided?
	12. How can we develop conservation and restoration measures that most effectively and efficiently address synergistic threats to freshwater biodiversity?	1. How can field-based experiments be improved in terms of scale and scope to identify management strategies that effectively decrease the negative effects of synergistic and additive stressors? 2. What management approaches used for individual threats could be utilized for effective management of multiple threats? 3. What measures could be applied to mitigate the confounding effects of climate change and warming-induced weather events (e.g., wildfires, hurricanes) on freshwater biodiversity?
3. Balancing Resource Needs	13. What are the joint priorities for sustainable food production and freshwater biodiversity conservation?	1. How can we move away from traditional/industrialized in-land fisheries management towards sustainable harvesting and improved conservation practices? 2. How can land-based agricultural practices (e.g.., ranching or irrigation) be reformed to integrate freshwater biodiversity? 3. What steps can aquaculture take to ensure freshwater biodiversity is protected from escapees, disease, and genetic alterations?
	14. How can the need for dams and associated infrastructure balanced with connectivity, health, and flow requirements of freshwater ecosystems and biodiversity?	1. How can we enhance and operate existing dams to reduce impact on freshwater species, and achieve energy production and conservation objectives? 2. How can site selection for new large and small hydropower projects be improved to reduce impacts on freshwater biodiversity? 3. What are the alternatives to traditional hydropower (i.e., dams) and how can these non-traditional options be adopted?
	15. How can we better balance conflicting interests between human demand for natural resources and freshwater biodiversity?	1. How can we regulate human activities and resource use to better accommodate the needs of natural systems? 2. How can water abstraction (i.e., groundwater or surface water extraction) be mitigated to reduce the impacts on freshwater ecosystems and habitats? 3. What types of innovative technological efficiencies can decrease the impacts of, and demand for, resource extraction (e.g.., sand alternatives) and benefit freshwater biodiversity?
4. Rethinking Built Environments	16. What policies, programmes, and activities can we implement to turn the risks associated with urbanization into benefits/opportunities for freshwater biodiversity enhancement?	1. Which urban restoration and rehabilitation actions provide the most effective results for enhancing freshwater biodiversity? 2. How can the distribution of people in cities be optimized to avoid destruction or degradation of wetlands and floodplains? 3. When should rivers and wetlands be completely protected from urban development and when should preference be given to effective co-existence?
	17. How can freshwater biodiversity conservation be better integrated into economic infrastructure planning, implementation, and operation?	1. How can water allocation systems be redesigned to ensure sufficient water for freshwater ecosystems? 2. How can wastewater infrastructure be adapted to contribute to freshwater habitat development? 3. What changes to transportation infrastructure could decrease fragmentation and reinstate movement of freshwater species through enhanced freshwater connectivity?

	18. What is the role of novel and designed ecosystems in conservation, and how can these systems be managed to benefit freshwater biodiversity?	1. How do we recognize ecosystems that cannot be returned to pre-disturbance conditions and how do we intervene to restore new biodiversity value, despite the changes experienced? 2. How can ecosystems, such as retention ponds and similar human-made features, be designed to provide sanctuaries for threatened species? 3. What management approaches are most applicable in novel and designed ecosystems to support native freshwater biodiversity?
5. Reforming Policy and Investment	19. What public policy measures can most effectively promote conservation and restoration of freshwater biodiversity?	1. How can we aid decision-makers in improving their understanding of the state of freshwater biodiversity to gain additional political support in complementary legislation? 2. What policy strategies can be used to improve long-term funding stability for freshwater conservation management projects? 3. How can government strategies be improved to integrate freshwater biodiversity into policy to avoid contradictory regulatory objectives?
	20. How can we scale up and optimize financial investments from government, private sector, and other sources such that there is a step change in funding for global freshwater conservation and restoration efforts?	1. Would quantification and communication of the economic consequences of freshwater biodiversity loss be an effective method to convince stakeholders to increase investment? 2. How can data portals and knowledge platforms be used to help decrease conservation costs and to optimize the reallocation of funds? 3. What valuation methods should we use to embed freshwater biodiversity in freshwater ecosystem services, to make protection and restoration more adoptable?
	21. What are the social and natural science investments needed to develop and implement environmental flows that benefit freshwater biodiversity?	1. What methods can we use to better link the components of artificially altered hydrology to biodiversity in perennial and non-perennial streams? 2. How can we mainstream and implement the principles of environmental flows within national legislation? 3. What scale of environmental flow implementation leads to improved freshwater biodiversity outcomes?
	22. What type of investments in *ex situ* conservation (e.g., captive breeding, reintroduction, managed relocation) are most effective for imperiled freshwater biodiversity?	1. At what thresholds or trends of population abundance or decline does it make sense to invest in ex situ initiatives for different taxa? 2. Under what conditions do the benefits outweigh the risks/costs for ex situ conservation of threatened freshwater species? 3. What policies could be implemented to avoid genetic homogenization in ex situ conservation initiatives?
6. Enabling transformative change	23. How do we develop management frameworks and evidence-bases that gain greater traction with stakeholders and managers?	1. How can disparate evidence-bases (e.g., academic, corporate, Indigenous) be integrated to support improved conservation outcomes? 2. How can prioritization frameworks be adapted to improve inclusion of stakeholders in conservation and restoration? 3. Can specific freshwater biodiversity frameworks be developed to improve conservation outcomes and returns at national and international levels?
	24. What steps should be taken to better communicate and share evidence and knowledge about the science of freshwater biodiversity among stakeholders?	1. How can we do a better job of translating scientific findings into actions for on-the-ground practitioners? 2. How do we improve communication and exchange of scientific findings with underrepresented regions, especially where language or restricted dissemination of research creates barriers? 3. How can Findable Accessible Interoperable Reusable (FAIR) data principles be best implemented into freshwater biodiversity science for the longevity of research findings (e.g., systematic publishing processes for data)?
	25. How can we increase the level of public engagement to change mindsets and build social license and political will to “bend the curve” of freshwater biodiversity loss?	1. What innovative new techniques can be developed for more effectively engaging the general public and fostering greater understanding of (and caring for) our freshwater biodiversity and ecosystems? 2. What is needed to shift mindsets and inspire the next generation to be excellent ambassadors and custodians of freshwater biodiversity? 3. How can we broaden the current models and orthodoxies at the science-policy interface to integrate worldviews from Indigenous and multicultural understandings?

Figure Legends

Figure 1. a) Frequency (%) of participants from different sectors involved in freshwater biodiversity research and protection including industry, government, not-for-profit organizations, and other sectors. b) Frequency (%) of participants with different primary roles including students/post-docs, decision makers, practitioners, researchers and other primary roles. No funders participated in our call for questions.

Figure 2. Six major themes for "bending the curve" of freshwater biodiversity loss. *Learning from Successes and Failures* and *Improving Current Practices* focus on improving conservation and protection of freshwater biodiversity; *Balancing Resource Needs*, and *Rethinking Built Environments* consider balancing human and freshwater biodiversity needs; *Reforming Policy and Investment* and *Enabling Transformative Change* emphasize the need to improve funding, knowledge exchange and public engagement in freshwater biodiversity research and conservation.

Fig. 1

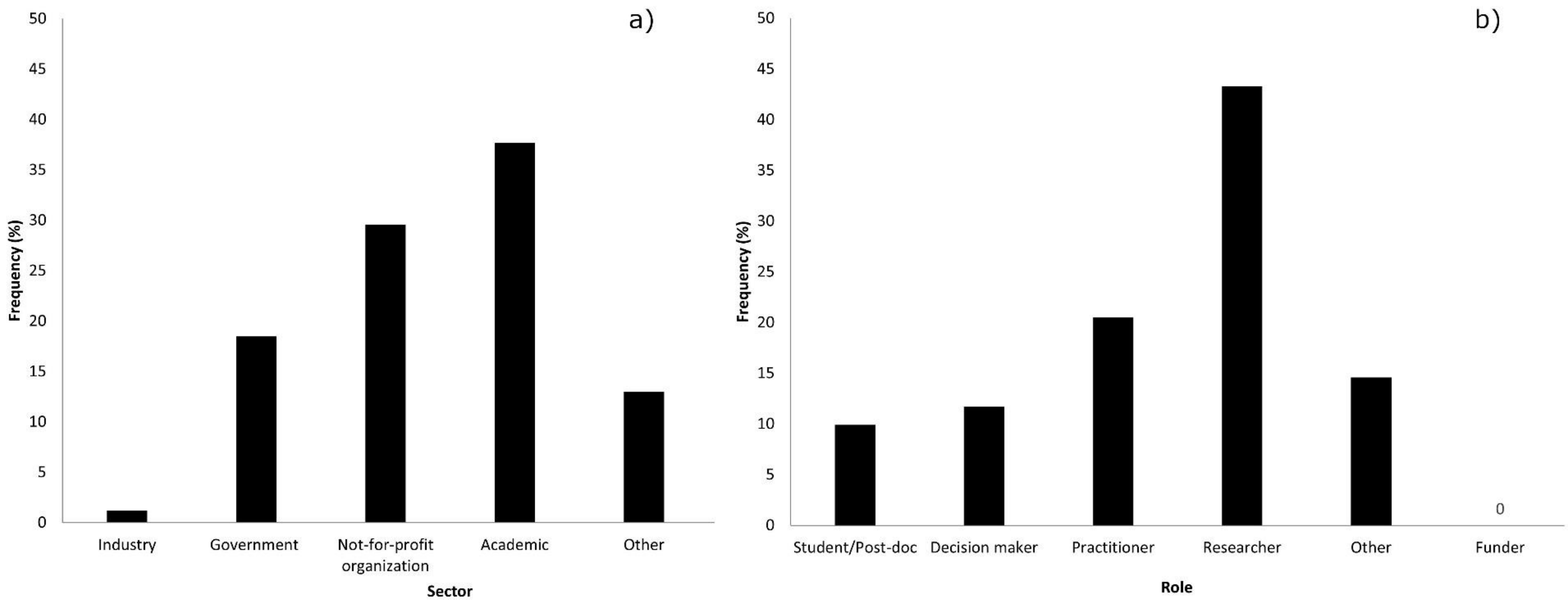
a)
Frequency (%)
50
45
40
35
30
25
20
15
10
5
0
Industry
Government
Not-for-profit organization
Academic
Other
Sector
b)
Frequency (%)
50
45
40
35
30
25
20
15
10
5
0
0
Student/Post-doc
Decision maker
Practitioner
Researcher
Other
Funder
Role

Fig. 2


1
Learning from Successes and Failures
2
Improving Current Practices
3
Balancing Resource Needs
4
Rethinking Built Environments
5
Reforming Policy and Investment
6
Enabling Transformative Change
6
Themes
25
Umbrella Questions
75
Example Research Questions

Supporting Information

Microsoft Word Document (.docx), 441 KB

Expanded methods and results. Includes information on methodology and results of outreach.

Figure S1. Authors represent nine countries (brown) globally.

Figure S2. Participant countries. The gradient in colour indicates the number of participants per country, with Canada, the United States and Australia having the most participants. Kiribati is indicated by *.

Table S1. Questions and information requested of participants on the online. Questions could be answered by selecting categories or by including free form narratives.

Table S2. Full question list from 144 participants. A total of 424 individual questions were submitted (submissions from participants were split where necessary if more than one question was included). Questions indicated with (*) were edited for clarity. Questions indicated with (†) were not applicable to "bending the curve" (i.e., threats, current status, overly specific, lists etc.) and were excluded from further consideration.

Table S3. Alignment of "bending the curve" research questions and the Emergency Recovery Plan priority actions (Tickner et al., 2020). For each theme and priority action, questions that would meeting the requirements of "bending the curve" and grow knowledge of priority actions are listed (e.g., 'Question 21: Environmental Flows' is in the theme Reforming Policy and Investments and aligns with the priority action 'accelerate implementation of environmental flows').