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

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1 **Abstract**

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

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

25 **Key Words:** “bending the curve”, freshwater conservation, horizon scanning, priority setting,
26 research questions

27 **1. Introduction**

28 Freshwater biodiversity faces unprecedented threats from human activities (Dudgeon et
29 al., 2006; Reid et al., 2019). Many of these threats have been increasing in severity in recent
30 decades (e.g., invasive species, fragmentation of rivers by dams, habitat loss) but there are also
31 emerging threats (e.g., novel pollutants and pathogens, climate change), as well as interactions
32 and cumulative effects (Birk et al., 2020), that further threaten freshwater biodiversity (Reid et
33 al., 2019). Given how catchments function, everything that occurs in upland areas has the
34 potential to impact freshwater ecosystems downstream. Even activities that happen well beyond
35 the floodplain and riparian areas can have dramatic effects on freshwater biodiversity (Hynes,
36 1975; Weijters et al., 2009). Recent estimates have shown that, on average, the abundance of
37 monitored freshwater vertebrate populations in the Freshwater Living Planet Index has declined
38 by an average of 84% over the past five decades (WWF, 2020), double the rate of decline seen in
39 marine and terrestrial realms. This has led to the recognition of the current global freshwater
40 biodiversity emergency (Tickner et al., 2020). Additionally, roughly 30% of International Union
41 for Conservation of Nature (IUCN) assessed freshwater species are threatened (i.e., Critically
42 Endangered, Endangered or Vulnerable to global extinction; IUCN 2012) in the Americas, over
43 20% are threatened in Africa, and in Europe and Central Asia 37% of freshwater fish, 45% of
44 freshwater snails, and 23% of amphibians are threatened (Watson et al., 2018). To facilitate
45 management interventions that can effectively curtail or even reverse the decline in freshwater

46 biota (i.e., “bending the curve” of biodiversity loss to enable the recovery of freshwater
47 biodiversity), research and conservation practices must continue to be coordinated to address key
48 knowledge gaps that currently impede progress (Mace et al., 2018; van Rees et al., 2020; Tickner
49 et al., 2020).

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

66 In contrast to marine science (see Parsons et al., 2014), which is better represented in
67 conservation science in general (Boon & Baxter, 2016), there have been few research agendas in
68 freshwater science focused directly on biodiversity. Current freshwater biodiversity research

69 agendas include one focused on migratory fishes (Lennox et al., 2019), a broader European
70 agenda focused on overall biodiversity loss with freshwater content (European Commission,
71 2011), a preliminary unpublished freshwater research agenda (BioFresh, 2011), and various
72 national agendas (e.g., Jähnig et al., 2019). None of these explicitly focus on research that will
73 help in “bending the curve”. Despite the recent development of frameworks detailing the major
74 causes of freshwater biodiversity loss (e.g., Strayer & Dudgeon, 2010; Garcia-Moreno et al.,
75 2014; Flitcroft et al., 2019) and efforts to support post-2020 policy agendas (van Rees et al.,
76 2020), the issue of targeting research to facilitate freshwater biodiversity recovery remains
77 challenging.

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

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

95 **2. Question Derivation and Theme Identification**

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

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

114 1.2%), *Government* (n=30; 18.5%), *Not-for-profit* (n=48; 29.6%) and *Academic* (n=61; 37.7%),
115 and an additional 21 participants (13%) who self-identified as *Other* (Figure 1a). Several
116 participants (n=11) selected more than one sector. The most common primary role was
117 *Researcher* (n=74; 43.3%), followed by *Practitioner* (n=35; 20.5%), *Decision maker* (n=20;
118 11.7%), *Other* (n=25; 14.6%) and *Student/post-doc* (n=17; 9.9%); the only unrepresented
119 primary role was *Funder* (Figure 1b). As with sector, participants often selected more than one
120 primary role; a total of 21 participants selected two or more.
121 (insert Figure 1a and b, and Table 1)

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

136 iterative process and edited by all authors, including the review team, and were then condensed
137 to six major themes (Figure 2) using the methods described in Sutherland et al. (2011).

138 *(insert Figure 2)*

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

155 *(Insert Table 2)*

156 **3. Six Themes and Twenty-Five Questions**

157 Theme 1: Learning from Successes and Failures

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

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

170 In disciplines such as business, it is common practice to engage in extensive, formal reflective
171 processes to learn from success and failure (e.g., Lant & Montgomery, 1987). Only recently has
172 this idea been fully embraced by the conservation science community (see Knight, 2006), but
173 often successes are celebrated and failures forgotten. Also troubling is the fact that many current
174 efforts in freshwater biodiversity conservation appear to be ineffective in the face of an
175 increasing number of persistent, emerging, and synergistic or additive stressors (Craig et al.,
176 2017). Efforts to understand the enabling factors for success can be illuminating and further
177 research on factors that extend beyond the ecological realm (including economic, institutional,
178 social, and cultural factors) can contribute to determining the ultimate success of conservation
179 initiatives. Learning from success and failure, with a focus on identifying enabling factors,

180 provides opportunities to support evidence-based conservation for long-term freshwater
181 conservation outcomes.

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

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

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

201 The use of protected areas in freshwater ecosystems, relative to marine or terrestrial
202 ecosystems (Hermoso et al., 2016), often lags (Loury et al., 2018). Resource use in IUCN-

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

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

222 The concepts of flagship and umbrella species have been applied successfully in
223 terrestrial systems (e.g., giant pandas serving as both; Li & Pimm, 2016) and could be similarly
224 successful in freshwater environments (e.g., freshwater turtles; Kalinkat et al., 2017). Flagship
225 species act as ambassadors for conservation, are used to raise conservation funding, and to attract

226 public attention. Umbrella species are expected to benefit a wide range of co-occurring species.
227 Questions remain regarding which species to select and whether they should be endemic or
228 threatened, megafauna, or from often overlooked groups [e.g., benthic invertebrates (Ormerod et
229 al., 2010) or macrophytes], or if they truly function as intended. Similarly, whether more general
230 systematic techniques for choosing flagship species (e.g., Veríssimo et al., 2014; McGowan et
231 al., 2020) are applicable to aquatic ecosystems is uncertain. Working across disciplines with
232 marketing and communications professionals to select species that resonate with the public and
233 that meet ecological goals, may increase the success of these initiatives (Kalinkat et al., 2017).

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

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

249 be blended in ways that are more comprehensive and strategically focused in relation to the aims
250 and objectives of conservation and restoration efforts.

251

252 Theme 2: Improving Current Practices

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

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

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

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

273 Point source and non-point source pollution continues to threaten freshwater ecosystem
274 functions and biodiversity (Reid et al., 2019) necessitating better management and mitigation
275 techniques for both ground and surface waters. Stopping pollution at the source with better
276 licensing and harm-reduction policies is essential, but finding strategies for water resource
277 management practitioners to meet their obligations and objectives once a pollutant is present is
278 equally important. Reduction and remediation measures have been effectively applied to some
279 freshwater systems (Søndergaard et al., 2007), but finding measures that will ensure long-term
280 success continues to be a challenge for some pollutants, especially from non-point sources. With
281 the identification of new pollutants (e.g., microplastics, pharmaceuticals), further research into
282 improving existing pollution reduction and remediation techniques is necessary. Additionally,
283 researching and adopting new measures (such as the use of nature-based solutions; Liqueste et al.,
284 2016) that are developed specifically for freshwater ecosystems, could benefit freshwater
285 biodiversity.

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

288 Understanding of freshwater ecosystem integrity and function has dramatically increased
289 over the past few decades. However, many threats to freshwater biodiversity are increasing in
290 severity and frequency, while new threats continue to emerge (Reid et al., 2019). Leveraging
291 new research techniques such as big data analytics, knowledge synthesis, community science, or
292 novel field techniques could advance conservation efforts (Cheruvilil & Soranno, 2018). Further
293 developing techniques that allow for decreased field work intensity (i.e., remote offload; Lennox

294 et al., 2017) and approaches that do not require lethal sampling (e.g., environmental DNA,
295 camera traps, remote sensing) is essential. Improving existing methods through facilitating
296 longer-term field research (e.g., Mirtl et al., 2018), study reproducibility (Fidler et al., 2017), or
297 co-developing decision-support tools with conservation managers (Kuehne, Strecker, & Olden,
298 2020) and community scientists could lead to the development of more effective conservation
299 tools and initiatives. To be clear, this is not research for the acquisition of knowledge *per se*, but
300 rather exploiting innovations in research to meaningfully advance freshwater conservation.

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

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

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

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

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

331 Riparian areas, including floodplains, have long been regarded as important for
332 freshwater ecosystems and a variety of management actions are used by practitioners to protect
333 riparian areas and adjacent freshwaters (Naiman, Decamps & McClain, 2010). Many questions
334 remain regarding the importance of maintaining longitudinal riparian zone continuity and lateral
335 connectivity to floodplains, and the role of groundwater-riparian zone interactions on freshwater
336 biodiversity. Riparian buffers and setbacks are common tools that have been shown to reduce
337 flooding, limit erosion, and protect aquatic and terrestrial habitats. Benefits could also arise for
338 pollution reduction, thermal damping, enhanced energetic subsidies and habitat provision (Feld

339 et al., 2018). Current guidelines on setback requirements and design criteria in some regions
340 need further development and evaluation (Olugunorisa, 2009; Haley et al., 2016). While setback
341 widths are often defined by the size of the drainage area (National Research Council, 2000) and
342 fixed-width buffers are standard practice (Richardson, Naiman & Bisson, 2012), more research is
343 needed to determine the influence of landscape types on setback effectiveness. Defining best
344 management practices and providing recommendations for riparian area and floodplain
345 management could help protect freshwater biodiversity and freshwater ecosystem functioning.

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

348 Multiple threats can lead to combined effects being greater (synergism), less than
349 (antagonism) or equal to the sum of (additive) their individual effects or can manifest in the
350 opposite direction to independent effects (reversals) leading to unanticipated ecological
351 responses (e.g., warming can reverse the trend of increasing phytoplankton biomass observed
352 under cold acidification conditions; Christensen et al., 2006). A recent synthesis indicated that
353 the net effects of paired alterations to freshwater ecosystems were more frequently antagonistic
354 (41%) than synergistic (28%), additive (16%), or reversed (15%) (Jackson et al., 2016).
355 Moreover, conservation projects targeting single threats often fail to address synergistic and
356 additive effects (Craig et al., 2017). Given multiple and sometimes synergistic stressors, it is
357 necessary to target limited resources so that the most significant stressors or threats are addressed
358 and the most restorative blend of actions is identified.

359

360 Theme 3: Balancing Resource Needs

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

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

374 Demands from aquatic and terrestrial food production put pressure on freshwater
375 ecosystems (e.g., through land-use conversion, overexploitation, nutrient enrichment, pollution,
376 water abstraction; Cottrell et al., 2018). Although efforts have been made to integrate terrestrial
377 biodiversity into sustainable food systems (e.g., FOLU, 2019), less work has focused specifically
378 on freshwater biodiversity. Freshwater conservation initiatives require integration with
379 agriculture, aquaculture and inland fishery practices to minimize the negative impacts of these
380 pressures while providing food sustainability (Phang et al., 2019). Protecting freshwater
381 biodiversity through the development and uptake of new methods in the food sector, such as
382 alternative water sources (Intriago et al., 2018) or production intensification (Tanentzap et al.,
383 2015), is challenging and sometimes controversial (e.g., balanced harvest; Zhou et al., 2019).

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

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

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

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

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

418 Theme 4: Rethinking Built Environments

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

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

431 Frameworks for including biodiversity in urban development can mitigate the effects of
432 urban growth and intensification (e.g., Biodiversity Sensitive Urban Design; Garrard et al.,
433 2018), but freshwater biodiversity has rarely been considered. Focusing on evaluating the
434 persistence of freshwater species and ecosystems in development initiatives and capitalizing on
435 opportunities realized during the development process can lead to improved outcomes (e.g.,
436 wetlands used for stormwater management in China's Sponge Cities; Chan et al., 2018).
437 Influencing the distribution of people in cities to maximize species diversity is one possible
438 strategy (Geschke et al., 2018). However, identifying ways to enable co-existence of humans and
439 freshwater biodiversity through urban planning (Nel et al., 2009) and stormwater management
440 (Hassall & Anderson, 2015) may be even more effective. These opportunities require rethinking
441 targets and indicators (e.g., freshwater reptiles; Turak et al., 2020) in efforts to protect and
442 improve urban biodiversity.

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

445 Infrastructure development, including transportation, navigation, power, water supply,
446 irrigation, stormwater management and sanitation, has generally proceeded without
447 consideration for freshwater biodiversity. These activities can alter hydrology and ecosystems,
448 negatively affecting freshwater biodiversity. Massive investments in water-associated
449 infrastructure often fail to include sufficient expenditures to protect aquatic ecosystems (Bunn,
450 2016), but calls for considering ecosystems as infrastructure are increasing (da Silva & Wheeler,

451 2017). Determining how to alter or replace current infrastructure and how infrastructure and
452 biodiversity planning can be harmonized will lead to better cost-sharing approaches (Sleight &
453 Neeson, 2018). Also needed is a greater understanding of how urban planning, building
454 standards, construction supply chains, recycling and reuse of construction materials, and
455 aggregate extraction practices can take better account of ecosystem impacts to maintain the
456 health of many freshwater ecosystems. Additionally, improving engineering strategies and
457 planning for multi-use infrastructure enables the integration of resource use and freshwater
458 biodiversity needs (e.g., planning irrigation with both agriculture and fisheries in mind; Lynch et
459 al., 2019).

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

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

473 Theme 5: Reforming Policy and Investments

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

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

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

497 related to incentivising conservation actions that protect freshwater biodiversity and embracing
498 nature-based solutions.

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

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

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

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

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

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

532 Despite attempts to conserve freshwater taxa *in situ*, increasing rates of habitat loss and
533 climate change highlight the need for investments in alternative conservation tools (Olden et al.,
534 2011; Brütting, Hensen & Wesche, 2013). *Ex situ* conservation is the process of conserving
535 biological diversity at the gene, population and species level, outside the environment where it
536 evolved. This technique can raise awareness of the plight of the species, but is expensive and
537 requires extensive investments in time, tools and research. This is especially true given the
538 number of imperiled freshwater organisms which need species-specific *ex situ* conservation
539 strategies and the scale at which such efforts would be needed (Snyder et al., 1996; Fischer &
540 Lindenmayer, 2000). Identifying the most appropriate and cost-effective *ex situ* methods for
541 different freshwater species, especially those with complex life cycles and unique ecosystem and
542 habitat requirements (for example, the development of an extensive captive breeding and

543 reintroduction program for Kihansi spray toads after the loss of their unique spray wetland; Lee
544 et al., 2006) could lead to investments in *ex situ* conservation that create positive results for
545 freshwater biodiversity restoration and improved technical guidelines for global cooperation.

546

547 Theme 6: Enabling Transformative Change

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

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

561 Conceptual management frameworks are tools by which complex systems, interactions
562 and research gaps can be explained. While more recent frameworks (MA, 2005; IPBES, 2019)
563 and a growing evidence-base (Schreckenberg, Mace & Poudyal, 2018) have highlighted the
564 strong linkages among freshwater biodiversity, human well-being, ecosystem services, and
565 government systems, active engagement by stakeholders and policy makers remains low. There

566 remains a lack of empirical and targeted guidance for processes that consider complex dynamic
567 interactions between these linkages. Related to this, guidance must necessarily be focused on a
568 variety of different scales (geographically, socio-economically and in terms of governance) to
569 reflect the context in which management decisions and conservation efforts are made.
570 Frameworks for the management of freshwater biodiversity that not only foster evidence-based
571 action, but also embed authentic participation by stakeholders and partners, are needed to
572 realistically design and plan for conservation intervention (Langhans et al., 2019).

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

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

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

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

605 **4. Discussion**

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

611 *Themes and Questions*

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

626 The broad questions developed during this process tended to include concepts of
627 proactive and meaningful development of policies, tools and metrics that would enhance and
628 prioritize the effective management of freshwater biodiversity conservation initiatives at a
629 variety of spatial and temporal scales. Additionally, they include a focus on scaling up
630 investment and integrating various levels of research, public engagement and policy to balance
631 priorities and provide optimal benefits for freshwater biodiversity and human needs. The 25
632 essential questions in this list provide starting points for identifying future research and a loose
633 framework within which to prioritize more specific initiatives. The many cross-cutting and
634 foundational issues contained in these questions (e.g., spatial scale, human behaviour) highlight

635 how interconnected solutions and policies will be necessary in the future. The answers to these
636 questions are not solely sufficient to “bend the curve” of freshwater biodiversity loss (Tickner et
637 al., 2020) and these questions should by no means constrain research in other areas. We therefore
638 call on the freshwater conservation community to continue to add new questions to this list, and
639 to promote and implement recommended actions resulting from current or future research.

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

651 *Limitations*

652 The call for questions attempted to reach the broadest possible audience, but there are
653 limitations in the methodology. Despite being largely untargeted and freely available to anyone
654 who wished to participate, the questionnaire was distributed only in English. Distribution
655 through the professional and social networks of the authors likely limited its reach and
656 accessibility to English-speaking nations and individuals. Most responses were received from
657 Canada, the United States, Australia, and other high-income nations (Table 1, Figure S2). As a

658 result, the list of research questions may better reflect the interests of nations with well-
659 developed conservation programmes, freshwater sciences and western science perspectives.
660 Many nations were represented by a single participant resulting in a list of questions that may not
661 have been adequately representative of broad geographic and socio-economic concerns. The lack
662 of more comprehensive representation likely influenced both the questions submitted and the
663 resulting final list. Despite recruiting a diverse team of coauthors with regional, taxonomic, and
664 disciplinary expertise, the full diversity of research needs in freshwater biodiversity conservation
665 may not have been captured. To help mitigate this, any missing topics considered essential by the
666 authors could be brought forward for consideration at other phases of question thematization and
667 refinement. The relative importance of questions in this list will necessarily vary by geography,
668 socio-economic and political conditions, knowledge systems, and cultural norms. Our list is not
669 intended to provide a specific road map, but rather to provide a list of potential areas to consider
670 when establishing research agendas. We believe that providing this list is important for
671 continuing conversations surrounding future “bending the curve” actions.

672 Although attempts were made to reach out beyond research institutions, more responses
673 were received from researchers (43%) compared with practitioners (20.5%) and decision makers
674 (12%). Students/post-docs and other roles make up the remaining 24.5% (Figure 1b). No
675 responses were received from funders (Figure 1b). Since practitioners and decision makers are
676 less well represented in the responses, it is possible that questions seeking directly applicable
677 solutions may not have been submitted. However, practitioners and decision makers represent
678 the on-the-ground experts in many regions and additional effort is needed to collate their
679 experiences and knowledge to share with the broader community. Because practitioners may
680 tend to maintain the status quo when engaging in conservation actions (Pullin & Knight, 2003;

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

688 *Thinking Globally*

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

701 Further, to ensure that freshwater biodiversity research needs are identified, engagement
702 of experts focused on aspects of freshwater biodiversity in ongoing initiatives (such as the
703 Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES)

704 proposed assessments on the nexus between food, water, energy and health, and transformative
705 change) will be important to highlight the importance of freshwater biodiversity
706 (www.ipbes.net). Engagement with the climate community, through the Intergovernmental
707 Panel on Climate Change (IPCC), can help to ensure that science assessments focused on
708 reducing carbon emissions will not unduly impact freshwater biodiversity as a trade-off for
709 increased energy development.

710 *Conclusion*

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

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

730

731 **Conflict of interest**

732 The authors declare no conflicts of interest.

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748

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1237 Table 1. Participants by geographic region.

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

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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?	<ol style="list-style-type: none"> 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?	<ol style="list-style-type: none"> 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?	<ol style="list-style-type: none"> 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?	<ol style="list-style-type: none"> 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?	<ol style="list-style-type: none"> 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?	<ol style="list-style-type: none"> 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?	<ol style="list-style-type: none"> 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?	<ol style="list-style-type: none"> 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?	<ol style="list-style-type: none"> 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?	<ol style="list-style-type: none"> 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?	<ol style="list-style-type: none"> 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?	<ol style="list-style-type: none"> 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?	<ol style="list-style-type: none"> 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?	<ol style="list-style-type: none"> 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?	<ol style="list-style-type: none"> 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?	<ol style="list-style-type: none"> 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?	<ol style="list-style-type: none"> 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?	<ol style="list-style-type: none"> 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?	<ol style="list-style-type: none"> 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?	<ol style="list-style-type: none"> 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?	<ol style="list-style-type: none"> 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 <i>ex situ</i> conservation (e.g., captive breeding, reintroduction, managed relocation) are most effective for imperiled freshwater biodiversity?	<ol style="list-style-type: none"> 1. At what thresholds or trends of population abundance or decline does it make sense to invest in <i>ex situ</i> initiatives for different taxa? 2. Under what conditions do the benefits outweigh the risks/costs for <i>ex situ</i> conservation of threatened freshwater species? 3. What policies could be implemented to avoid genetic homogenization in <i>ex situ</i> conservation initiatives?
6. Enabling transformative change	23. How do we develop management frameworks and evidence-bases that gain greater traction with stakeholders and managers?	<ol style="list-style-type: none"> 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?	<ol style="list-style-type: none"> 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?	<ol style="list-style-type: none"> 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

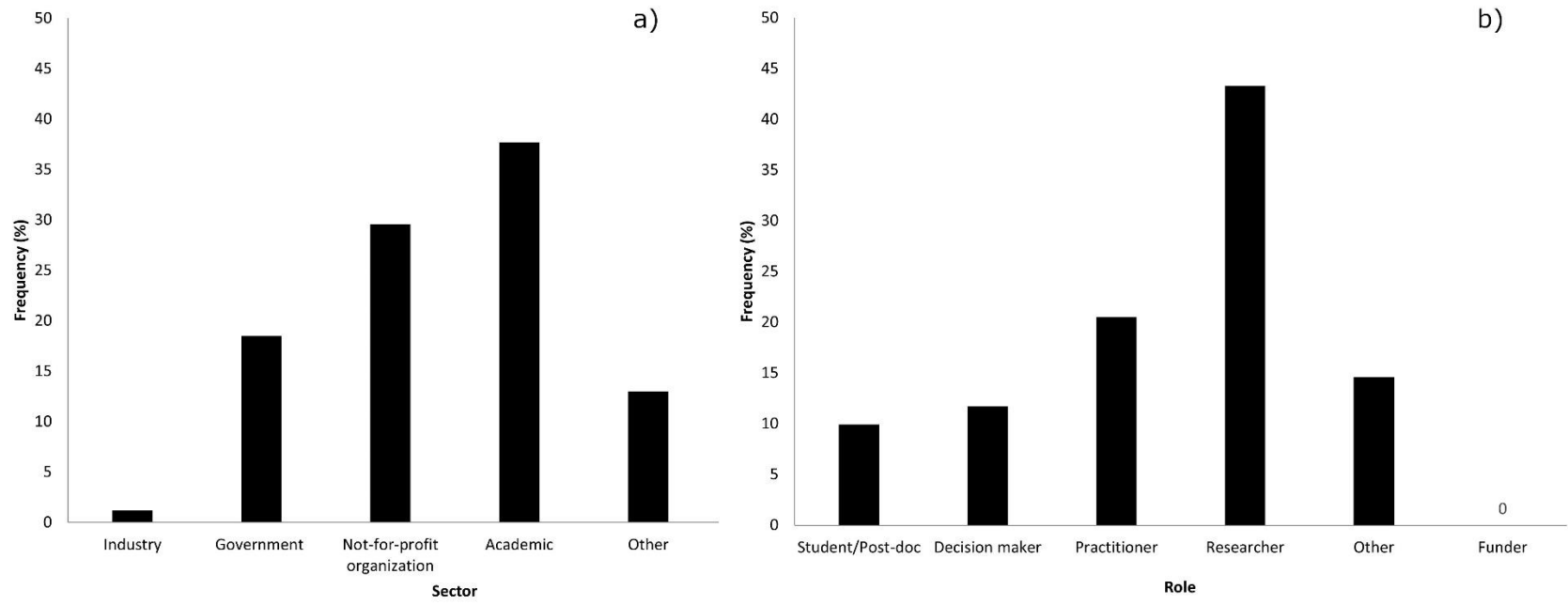


Fig. 2



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’).