Global Swimways for the conservation of migratory freshwater fishes

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Anthropogenic activities have severely degraded the ecological integrity of global freshwater systems. Migratory freshwater fishes are especially threatened by the cumulative effects of multiple stressors and fragmentation, particularly those that impede access to critical habitats. To stimulate the conservation and protection of these species, we propose a "Global Swimways" program to identify rivers that support the migration routes of biologically and/or socioeconomically important freshwater fishes. We test the utility of the International Union for Conservation of Nature Red List data to support the identification of Global Swimways and present case study regions containing rivers with either high species richness (west-central Africa and Southeast Asia), high numbers of threatened species (Eastern Europe and Central Asia), or multiple endemic species (the Rift Valley lakes in East Africa). We hope the Global Swimways program will provide metrics that can be used to identify rivers requiring increased protection or restoration, track trends, and stimulate the greater inclusion of migratory freshwater fishes in global policy mechanisms.

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Of the 18,201 freshwater fish species described to date (as of July 2021) (van der Laan 2021), the majority undertake some form of between-habitat movement as part of their life history (Brink *et al.* 2018). Of these species, more than 1000 are considered truly migratory and as such their survival is dependent on completing these migrations (Brink *et al.* 2018).

In a nutshell:

- Humans have severely degraded the world's rivers, with migratory freshwater fishes particularly affected by reduced access to critical habitats
- We propose development of a "Global Swimways" program to catalog rivers that support the entire migration routes of biologically and/or socioeconomically important freshwater fishes
- Analysis of data from the International Union for Conservation of Nature Red List demonstrates that biological metrics such as species richness and the number of threatened or endemic species can be used to identify Global Swimways
- We outline the future directions for improving identification and implementation of Global Swimways to fully capture the benefits migratory freshwater fishes provide to people

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Migratory fishes can play critical roles in ecosystem functioning, for instance as vectors transporting nutrients from the ocean into freshwater and terrestrial realms (Holmlund and Hammer 1999) and vice versa. Migratory fishes also deliver key ecosystem services, including the provision of dietary protein (Dugan *et al.* 2010) and income from both commercial (Hoeinghaus *et al.* 2009) and recreational (Butler *et al.* 2009) fisheries, as well as symbolic and cultural importance to numerous communities (Close *et al.* 2002). Conservation of migratory fishes is therefore not only of ecological necessity but also of socioeconomic value.

In-stream infrastructure development has reduced the extent of remaining free-flowing rivers (Grill *et al.* 2019), with consequent fragmentation and flow alteration severely degrading the ecological integrity of many of the world's rivers (Revenga *et al.* 2000; Nilsson *et al.* 2005). Migratory fish species are particularly impacted by river infrastructure (Limburg and Waldman 2009; but see Barbarossa *et al.* 2020), as fragmentation impedes critical movements between habitats, often resulting in local extinctions (Liermann *et al.* 2012). The most complete global assessment of migratory freshwater fish populations to date revealed an average 76% reduction in abundance for 1406 populations of 247 species from 1970 to 2016 (Deinet *et al.* 2020). However, despite the myriad threats they face, migratory freshwater fishes are largely overlooked by current policy mechanisms; for example, few are listed in the Convention on Migratory Species (CMS) Appendix I (species threatened with extinction) or Appendix II (species requiring transboundary cooperative conservation efforts). Listing on the appendices encourages signatories of the CMS to cooperate on conserving those species and their habitats.

To encourage greater conservation and management of migratory freshwater fishes, we propose the development of a

"Global Swimways" program. We define Global Swimways as rivers and their associated ecosystems that support the entire migration routes of biologically and/or socioeconomically important freshwater fishes. A Global Swimways program and their subsequent mapping would provide a spatially explicit set of metrics against which the impacts of current and future river infrastructure development could be assessed to identify rivers requiring increased protection or restoration. Our main goal here is to "start the discourse" on Global Swimways and provide a basis for further discussion on the range of biological, economic, and social criteria that would drive their identification and monitoring. Using data on migratory fish species assessed under the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (www.iucnredlist.org), we highlight case study regions containing rivers that could be identified as Global Swimways, based on the biological metrics of species richness, endemism, or number of threatened species. We also call attention to data gaps, such as economic or social criteria, that currently inhibit a holistic assessment of Global Swimways and the ecosystem services conferred by migratory fishes.

Building on the Flyways concept

A Global Swimways approach builds on the Flyways concept developed for migratory birds. Initially focusing on wading birds, Flyways facilitated joint conservation efforts along identified global bird migration routes (Boere and Stroud 2006). Flyways are defined as "the entire range of a migratory bird species (or groups of related species or distinct populations of a single species) through which it moves on an annual basis from the breeding grounds to non-breeding areas, including intermediate resting and feeding places as well as the area within which the birds migrate" (Boere and Stroud 2006). Recognition of multispecies flyways in the mid-20th century acted as a stimulus for establishment of the Convention on Wetlands of International Importance in 1971, resulting in the protection of wetland sites of high importance for migratory birds (UNEP/CMS Secretariat 2012). One of the founding principles of the Flyways approach is to facilitate cooperation between signatory nations, which reduces the number of formal instruments required to enact conservation mechanisms (UNEP/CMS Secretariat 2012). We envision an analogous approach for fish migration routes promoting similar protection and cooperation efforts within and among nations. In the future, we will aim to achieve consensus on a globally accepted set of criteria to distinguish and describe the most important fish migration routes, which we term Global Swimways. Recognition of these swimways will in turn help to fill a knowledge gap for prioritizing rivers for protection and restoration, and facilitate identification of migration routes that are critical to the life histories of many fishes.

Biological criteria for Global Swimways

Fundamental to identifying Global Swimways is knowledge of migratory freshwater fish distributions and their migration pathways. Other than these spatial elements, information on species abundance, threat status, and endemism, among other factors, would also be required. Ideally, data would be globally comprehensive and capture a consistent and complete set of metrics that fully describe the biological attributes of migratory freshwater fishes. However, knowledge of freshwater fish distributions, life histories, and conservation status is often geographically biased toward temperate regions of Europe and North America (eg Deinet *et al.* 2020). Most data on population abundances are currently limited to either harvest data or counts at fish passage facilities (eg fish ladders and lifts), although environmental DNA (eDNA) holds promise for development of reliable abundance indices. The IUCN and Nature Metrics eBioAtlas (https://ebioatlas.org) is an example of a current project whose goal is to provide species presence data and (potentially) abundance indices from rivers by utilizing a global network of scientists, including citizen scientists.

While not providing data for the full suite of biological criteria, one source of data that may be useful for identifying Global Swimways is the range maps and descriptions of migratory freshwater fish species maintained in the IUCN Red List database (IUCN 2021). To explore the utility of the IUCN Red List for identifying Global Swimways data, we present four case study regions (WebPanel 1) with rivers that, based on simple biological metrics, could be considered Global Swimways. The case study regions were selected because rivers within them contain high species richness, high numbers of threatened species, or large numbers of endemic species. Our analysis includes only regions for which the majority of fish species have been comprehensively assessed and mapped and for which data are available in the IUCN Red List (WebPanel 1).

Of the assessed regions, we found that rivers with high migratory freshwater fish richness are concentrated primarily in west-central Africa and Southeast Asia (Panel 1), with the lower portions of the Niger River supporting >60 species. These findings largely align with patterns of species richness across multiple freshwater taxa, including freshwater fishes in general (Tisseuil *et al.* 2013; Collen *et al.* 2014; He *et al.* 2018). It should be noted that the IUCN Red List data currently lack information for some areas of high freshwater taxa richness (eg Amazon and East Asia; see below), which, once addressed, will likely identify other potential Global Swimways rich in migratory freshwater fish species. Potential Global Swimways based on the presence of multiple species of threatened migratory freshwater fishes are concentrated in Eastern Europe and Central Asia (Panel 2). This can partly be explained by the presence of several species of threatened sturgeon (*Acipenser* spp and *Huso huso*), with connectivity in these basins fragmented by numerous large dams (Barbarossa *et al.* 2020). Endemism in the migratory freshwater fishes included in our dataset was generally low and limited to small numbers of species in a few rivers concentrated in Africa and southern and Southeast Asia. The highest numbers of endemic species were found in the Rift Valley lakes of East Africa (Panel 3), with

Panel 1. Regions of high species richness for migratory freshwater fishes

We mapped the location of 665 migratory fish species (WebPanel 1). Within our dataset, potential Global Swimways that had multiple river segments (median segment length 2.5 km, range: 0.003–118.8 km) supporting high species richness were found in west-central Africa (Figure 1a) and Southeast Asia (Figure 1b). The west-central Africa region hosts several major rivers (including the Congo, Niger, Senegal, and Volta) that harbor substantial freshwater biodiversity, including many migratory fish species, a high proportion of which are threatened (Smith *et al.* 2009; Brooks *et al.* 2011). One major threat to these fishes is pollution from agricultural, mining, and industrial operations, and from urban areas as well, which often creates chemical barriers to fish passage. Management of water resources for irrigation and increasingly for hydropower is also impacting the free-flowing nature of these rivers, through construction of physical barriers that block migration and reduce water flows.

Several river basins in Southeast Asia could also be potentially considered Global Swimways based on the scope of the inland fisheries they support. For example, the Mekong River provides over 15% of the global inland fish catch, which supports livelihoods and provides a key source of animal protein; migratory fishes represent a key component of this resource (Dugan *et al.* 2010; FAO 2020). From the early 1990s to the late 2000s, this region experienced enormous increases in human pressure on the environment (Venter *et al.* 2016). Many of the rivers in Southeast Asia are impacted by moderate to high levels of fragmentation (Grill *et al.* 2019), conditions that will be further exacerbated by construction of additional planned dams (Zarfl *et al.* 2015). For instance, the Mekong fishery is threatened by continued hydropower dam construction throughout the basin, with barriers impacting spawning migrations of many economically important species (Dugan *et al.* 2010).

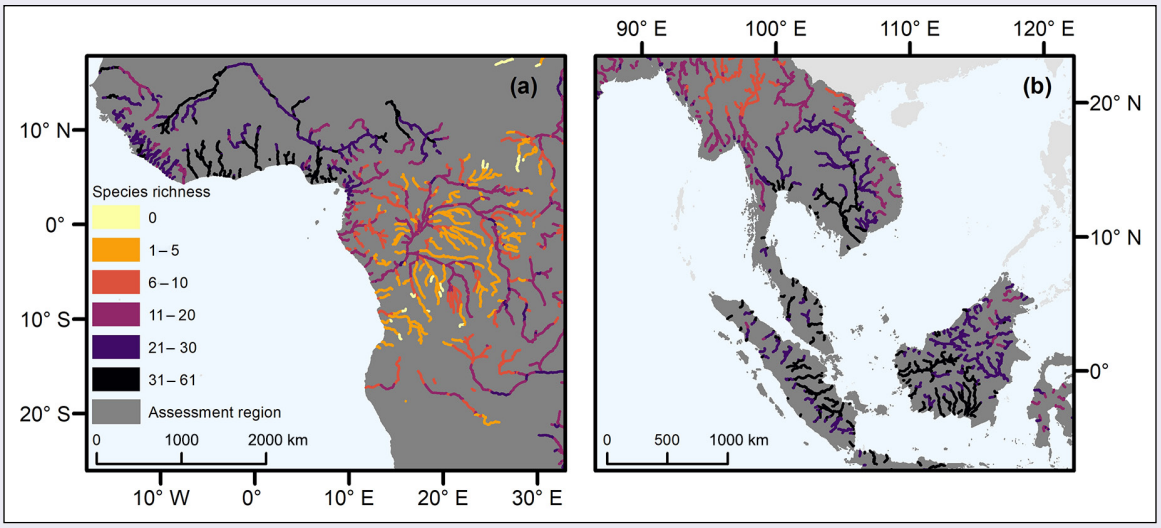

Figure 1. Species richness of migratory freshwater fishes in the rivers of (a) west-central Africa and (b) Southeast Asia.

these ancient lakes known to support high fish diversity including endemic freshwater species that migrate up the rivers feeding into the lakes (Collen *et al.* 2014; Hanly *et al.* 2017; Winemiller 2018).

These results highlight some important conclusions. First, there is variation in which regions are highlighted, suggesting that for biological criteria alone a range of metrics is needed to comprehensively identify Global Swimways (see also Collen *et al.* 2014). Second, there are multiple pressures that threaten migratory freshwater fishes, with the threat of river fragmentation apparent for several rivers (for example, Volga River, Niger River, and Chao Phraya River) (Grill *et al.* 2019). Although factors related to the socioeconomic value (eg exploitation for subsistence or economic income) of migratory species have been highlighted in most regions, metrics quantifying these values are generally lacking.

Our analysis illustrates some of the (biological) criteria that could be used to map Global Swimways. However, the ability to do so is currently limited by the spatial and species coverage available in Red List assessments (WebPanel 1), resulting in an incomplete picture of the global distribution of migratory freshwater fishes. This is particularly pertinent given that the current data gaps in Red List assessments include areas of high freshwater richness and endemism (eg the Amazon and East Asia; Tisseuil *et al.* 2013). Comprehensive coverage of all migratory fish distributions within Red List assessments is anticipated by mid-2022. In addition, there is the potential to incorporate other sources of migratory fish distribution data (eg Jézéquel *et al.* [2020] for the Amazon) to fill gaps in global datasets. However, this would require a consistent approach to ascertaining which freshwater fishes are migratory and, where possible, a common set of metrics to be recorded for each species.

For greater utility in conservation planning, the Global Swimways program would also benefit from integration of other key variables, such as community composition, functional traits, and abundance (Fleishman *et al.* 2006). Incorporating data on

Panel 2. High numbers of threatened migratory freshwater fishes in the rivers of Eastern Europe and Central Asia

Of the 665 migratory fish species included in our analysis, 109 are identified as "threatened" (critically endangered, endangered, and vulnerable) based on their IUCN Red List assessments (WebPanel 1). The rivers supporting the highest number of threatened species are those draining into the Black Sea and the Caspian Sea (Figure 2), with the Volga River in Russia alone containing ten threatened migratory species. These potential Global Swimways support populations of several threatened species of sturgeon (*Acipenser* spp and *Huso huso*), two species of shad (*Alosa* spp), two barbels (*Luciobarbus* spp), alburnus (*Alburnus sarmaticus*), European eel (*Anguilla anguilla*), and common carp (*Cyprinus carpio*). The rivers within the Ponto-Caspian region are a hotspot for Acipenseriformes (sturgeons and paddlefishes), large-bodied, long-lived species that have experienced major declines due to overexploitation, dredging, ship strikes, and habitat degradation impeding migration and reproduction (Billard and Lecointre 2000). Globally, sturgeon species have undergone precipitous declines, with populations of the 14 species of Acipenseridae for which data are available having decreased by 91% on average between 1970 and 2016 (Deinet *et al.* 2020).

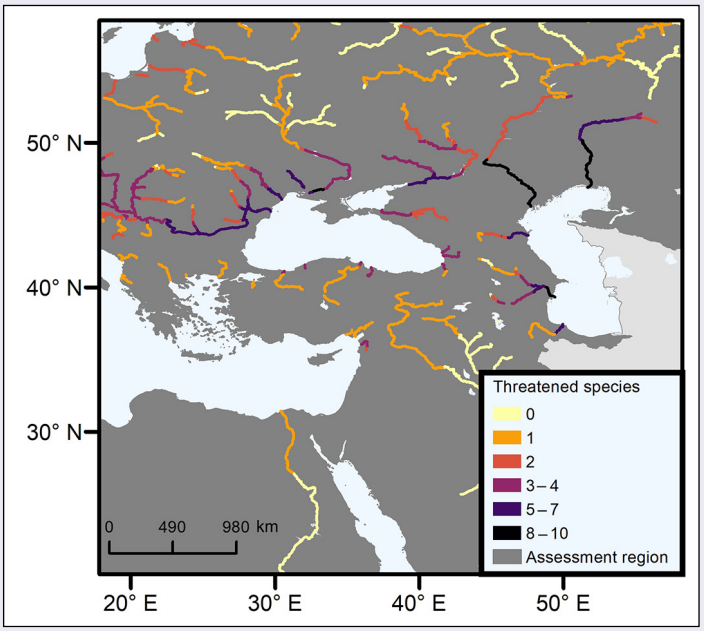

Figure 2. The number of threatened migratory freshwater fish species in the rivers of Eastern Europe and Central Asia. Only lakes (Messager *et al.* 2016) greater than 1000 km^2 in size are shown.

species abundance is of critical importance; however, as identified in the Living Planet Index, data on migratory freshwater fish abundance are largely absent, including for areas that support the greatest diversity and are subject to the most pressing threats (Deinet *et al.* 2020). Aggregate metrics may mask particular biological attributes of species inhabiting certain river systems or unique aspects of the rivers themselves. For instance, three species of amphidromous gobioid fishes in Hawaii (*Awaous guamensis*, *Lentipes concolor*, and *Sicyopterus stimpsoni*) are morphologically adapted to undertake vertical migrations to ascend waterfalls (Fitzsimons *et al.* 2007), and as such represent species displaying unique migratory behaviors despite low overall richness in these rivers. Flexibility in the further development of the program will be critical, enabling Global Swimways to be assigned based on a range of widely agreed upon biological metrics (eg high species richness; endemism; genetically distinct populations; or rare riverine habitats that support fish migrations, such as the chalk stream rivers of southern England) that fully capture the variability in freshwater fishes and their migrations.

Economic criteria for Global Swimways

Estimated to employ 60 million people in developing countries (Kelleher *et al.* 2012), inland fisheries are often small scale and subsistence-oriented, providing a source of income and protein to rural low-income communities (Lynch *et al.* 2016). However, there are also examples of larger scale commercial freshwater fisheries. For instance, commercial fisheries in the upper reaches of the Mississippi River in the US were estimated to generate revenues of US$2 million annually between 2000 and 2013, with migratory shovelnose sturgeon (*Scaphirhynchus platorynchus*) and American eel (*Anguilla rostrata*) forming major components (Klein *et al.* 2018). Recreational freshwater fisheries are generally more prevalent in the developed world, with global annual expenditures conservatively estimated at more than US$190 billion (Kelleher *et al.* 2012; Bower *et al.* 2020). In certain contexts, migratory species are likely to form large components of subsistence, commercial, and recreational catches, and although available for some species and some locations, data are often absent, aggregated to the national level, or not usable for identification at the species level. These shortcomings render attributing economic values to individual rivers challenging and represent a critical research need (eg recreational fisheries data in developing countries; Holder *et al.* 2020).

Social criteria for Global Swimways

Inland fisheries play critical roles in providing food security in many parts of the world, although their true value is often masked due to poor data availability (Youn *et al.* 2014). Incorporating data on subsistence fisheries based on migratory fish, including their nutritional value, would aid in the identification of rivers providing food security (often to vulnerable communities) and facilitate a more holistic assessment of the potential impacts of river management. The role of migratory

Panel 3. Endemism in the Rift Valley lakes of East Africa

We identified a total of 91 endemic migratory fish species globally, with endemism defined as a species whose range is confined to a single basin (median area 55,927 km^2; WebPanel 1). Endemism is generally low, and only a limited number of Global Swimways are likely to be identified based on this metric alone. However, the systems that supported the highest number of endemic species – the Rift Valley lakes of East Africa – did not rank highly based on our other metrics, and as such endemism highlights areas that may be overlooked when considering richness measures. Within the Rift Valley lakes, five potamodromous species (*Labeo victorianus*, *Gnathonemus longibarbis*, *Labeobarbus altianalis*, *Pollimyrus nigricans*, and *Hippopotamyrus grahami*) inhabit the Lake Victoria basin in the headwaters of the White Nile in Kenya and Uganda, and six species (*Engraulicypris sardella*, *Enteromius arcislongae*, *Enteromius litamba*, *Opsaridium microcephalum*, *Opsaridium microlepis*, and *Synodontis njassae*) are found in Lake Malawi/Niassa/Nyasa and the upper Shire River, Malawi, Mozambique, and Tanzania (Figure 3). For many of these species, migrations take the form of upriver movements to spawning grounds. Although these migrations are not as extensive as for other species, they represent movements between ecosystems and across national borders, presenting challenges for species management and conservation. The Rift Valley lakes sustain fisheries that provide a source of food and income for millions of people, and are known to support large numbers of endemic freshwater species (Darwall *et al.* 2011; Tisseuil *et al.* 2013). However, unsustainable exploitation and loss or degradation of riparian habitats, along with water-quality issues and flow modifications, pose serious threats to many of these species (Odada *et al.* 2003; Darwall *et al.* 2011).

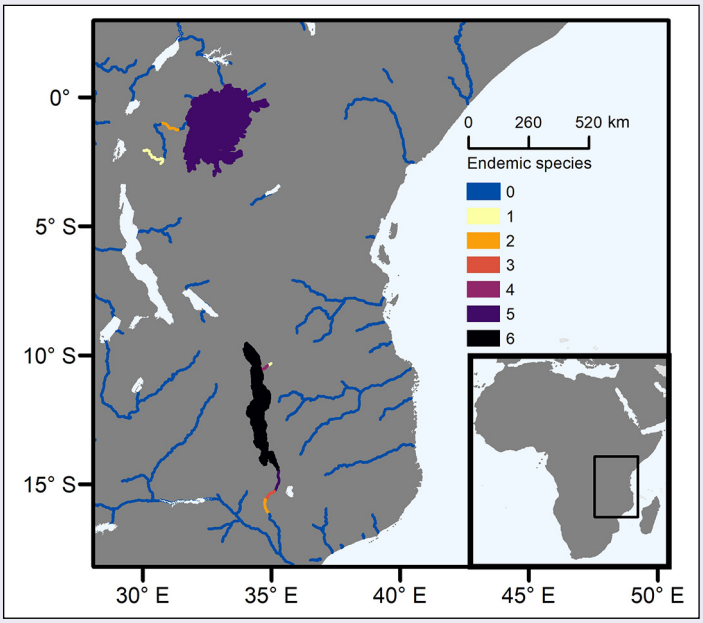

Figure 3. The number of endemic migratory freshwater fish species in the rivers and Rift Valley lakes of East Africa. Only lakes (Messager *et al.* 2016) greater than 1000 km^2 in size are shown.

fishes in supporting these values is often well understood, but data are often underreported, and acquiring globally standardized statistics is challenging and costly (Romulo *et al.* 2017). Migratory fishes also provide many less tangible social benefits, such as religious or cultural value. For example, Indigenous peoples across the North Pacific Rim have harvested various species of Pacific salmon (*Oncorhynchus* spp) for millennia, with salmon resource management incorporating cultural and spiritual beliefs (Atlas *et al.* 2021). Because quantifying these non-monetized benefits is challenging and resource-intensive (Chan *et al.* 2012), the Global Swimways program should be based on a framework whereby difficult-to-quantify metrics can be identified on a case-by-case basis, yet still be robust and quantified to enable comparisons between rivers. Moreover, the status associated with being recognized as a Global Swimway may inspire local communities to self-report or develop useful data on non-monetary values that can then be incorporated into assessments.

Future directions

Our primary objective here is to initiate discussion about the Global Swimways concept. Future research, policy, and conservation activities centered on dialogue with global and regional experts, and consultation with relevant civil society, government agencies, and conservation organizations, are needed to evaluate, improve, and standardize methods for identifying Global Swimways. Below, we outline some key opportunities for and challenges to implementation of the Global Swimways program.

Quantifying and refining migration routes

In addition to identifying Global Swimways based on species' broad distributions, mapping of the actual migration routes of fishes within basins and the relative scale of migration will be critical, as it will allow more accurate evaluation of the impact of human activities (eg dam construction, pollution, climate change). For anadromous and catadromous species, this will include the marine phase of their life history; however, at present, movements during marine phases are often even less well known than when in freshwater. As such, increased monitoring of freshwater fish movements will be required, with the potential for new techniques (eg eDNA, eBioAtlas, and more affordable global positioning system tracking tags) to provide data cost-effectively and at scale.

Global engagement to address data gaps

Some of the factors that describe a Global Swimway are less amenable to the creation of spatial metrics (eg religious or cultural values, species with unique migratory behaviors). These metrics are unlikely to be quantified, modeled, or mapped consistently at the global scale, and therefore data will not be available for all rivers. However, there is an opportunity to engage researchers, organizations, and communities with the Global Swimways program (eg Twardek *et al.* 2020) as a means of developing local-scale data for these metrics and determining candidate rivers.

Identification of a Global Swimway

As highlighted above, a holistic Global Swimways program will be underpinned by metrics of different types and across different scales. It is important that the framework be flexible enough to incorporate a range of data, requiring considerable discussion and debate on how best to compare swimways across these metrics. The framework should permit metrics to be used independently to identify Global Swimways. For instance, some of the less easily quantifiable metrics, such as spiritual values or unique biological attributes, may trigger swimway inclusion regardless of the candidate river's ranking with respect to more easily quantifiable metrics such as species richness. For metrics that can be quantified consistently and globally, the thresholds that trigger inclusion as a Global Swimway will need to be standardized and may vary depending on the scale of assessment (see below).

Developing a hierarchical approach

Once fully developed, we envisage that the Global Swimways program could be applied across a range of scales, as is the case for key biodiversity areas (KBAs). For instance, a swimway may be triggered at global, regional, or national levels, ensuring recognition of rivers important in a local context that might otherwise be overlooked using broad-scale delineations alone.

Creating a global standard

Overall, our long-term vision is that in the future Global Swimways will be identified based on an agreed global standard, similar to the system developed for KBAs (eg IUCN 2019), and as such would underpin the conservation and restoration of migratory freshwater fishes both in terms of global policy and in implementation.

Embedding Global Swimways within conservation policy

We expect that, once fully developed, Global Swimways will lead to greater inclusion of migratory freshwater fishes and the ecosystems that support them in conservation policy mechanisms. Where fish migrations are transboundary, data such as those captured within the Global Swimways program are needed to facilitate international cooperation (Lennox *et al.* 2019), for instance listing of species on the CMS appendices. The mapping of Global Swimways would also provide an impetus to grant greater protection to systems that support populations of biologically and/or socioeconomically important freshwater fishes. For example, the Río Matos Ramsar site in Bolivia (https://rsis.ramsar.org/ris/2093) supports many of the freshwater fishes inhabiting the Amazon basin, including 50 of which that are migratory. Likewise, in Europe, the EU biodiversity strategy aims to restore 25,000 km of free-flowing rivers by 2030.

Conclusions

Our goal here is to stimulate wider discussion of a Global Swimways program that would increase understanding of the status of the world's migratory fishes and the rivers that support them, and focus protection and/or restoration actions on maintaining the ecological, social, economic, and cultural benefits provided by these species and ecosystems. Rivers with the greatest existing or potential fish migrations were identified using range maps and descriptions of migratory freshwater fish species from the IUCN Red List database, in tandem with examining the number of threatened and endemic migratory species in these systems. Our analyses suggest that a suite of metrics is needed to comprehensively identify Global Swimways across broad geographic areas. We envisage a flexible further development of Global Swimways incorporating additional biological metrics, such as genetically distinct populations or rare riverine habitats. In addition, to fully describe and identify Global Swimways, the framework will need to be expanded to include data on the economic value and social benefits of migratory freshwater fishes, which will require dialogue with multiple actors at global and regional levels to provide information for regions where data are limited or unavailable. Finally, we have outlined several of the key opportunities and challenges for the Global Swimways program. We hope that this study will provide a building block upon which the conservation and research communities can collaborate to identify and prioritize Global Swimways.

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Data Availability Statement

Data are already published and publicly available, with those publications properly cited in this submission. The raw

data used to develop the case study regions are available from the International Union for Conservation of Nature (www.iucnredlist.org/resources/spatial-data-download).

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