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Spatial priorities for freshwater fish conservation in relation to protected areas

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Abstract

1. Freshwater habitats are vital for both humans and nature owing to their exceptional biodiversity and valuable ecosystem services, but they are currently facing serious threats. The designation and management of protected areas have been proposed as the most feasible way to ensure conservation objectives for the future. However, traditional approaches have not protected freshwater fauna effectively, especially freshwater fish.
2. Previous studies have identified the most irreplaceable terrestrial places to achieve conservation goals. Here, the aim was to investigate how the present network of protected areas preserves irreplaceable rivers for freshwater fish.
3. The irreplaceability of the world's river basins was calculated using International Union for the Conservation of Nature Red List distribution maps, considering the rarity, richness, and conservation status of their freshwater fish fauna. The overlap between irreplaceable basins and the present network of protected areas was also calculated.
4. The results highlight the conservation significance of tropical rivers, particularly those in the Neotropics. The subset of the basins covering 30% of the most irreplaceable land surface (in line with the United Nations 30by30 target) encompasses 99% of freshwater fish species. However, protected areas do not seem to provide sufficient protection to these basins, as 89% of their surface area lies outside protected areas. Only 7% of freshwater ecoregions meet the United Nations 30by30 target.
5. Given the context of climate change, allocating new protected areas becomes crucial in providing better survival opportunities for freshwater fish species. Despite the limitations inherent to the absence of total knowledge of freshwater fish biogeography and the irreplaceability index itself, this study identifies priority sites for their conservation that may help inform decision-making in the future to establish more effective protected areas.

KEYWORDS
freshwater biodiversity, irreplaceability, IUCN Red List, knowledge gap, spatial prioritization, threatened species

1 | INTRODUCTION

Freshwater ecosystems are exceptionally diverse, containing up to 30% of the world's vertebrate diversity in less than 1% of the Earth's surface (Darwall et al., 2018). These ecosystems also provide humans with numerous ecosystem services (Darwall et al., 2011b), ranging from water provision and security, and the regulation of nutrient flows, to recreational activities, spiritual values, and food and fibre production (Carpenter, Stanley & Vander Zanden, 2011; Green et al., 2015).

Despite their importance, freshwater ecosystems may rank among the most threatened on Earth, and they are considered endangerment hotspots (Dudgeon et al., 2006; Vörösmarty et al., 2010). The increasing concentration of people and settlements around freshwater systems and increasing human demands for water are leading to high levels of degradation and threats to freshwater biodiversity (Strayer & Dudgeon, 2010; Arthington et al., 2016), including water extraction, invasive species, construction of dams, river channelization, overfishing, pollution, and climate change (Collen et al., 2014). Therefore, 28% of all freshwater vertebrates are threatened with extinction, according to the International Union for the Conservation of Nature (IUCN) Red List (IUCN, 2022). As a result, in 2010 the Convention on Biological Diversity (CBD) adopted the Strategic Plan for Biodiversity 2010–2020 and its 20 Aichi Biodiversity Targets to address global declines in biodiversity (Butchart et al., 2010). Target #11 requested that 'by 2020, at least 17 per cent of terrestrial and inland water (…), especially areas of particular importance for biodiversity and ecosystem services, are conserved through effectively and equitably managed, ecologically representative and well-connected systems of protected areas and other effective area-based conservation measures, and integrated into the wider landscapes and seascapes' (CBD [Convention on Biological Diversity], 2011). This target was hardly met, according to the Protected Planet Report 2020. Moreover, there are several biases in the way spatial protection has been awarded to terrestrial ecosystems (Venter et al., 2018). In December 2022, the 15th Conference of Parties to the United nations (UN) Convention on Biological Diversity adopted the Kunming–Montreal Global Biodiversity Framework (GBF), targeting the effective conservation and management of at least 30% of the world's lands, inland waters, coastal areas, and oceans by 2030, with emphasis on areas of particular importance for biodiversity and ecosystem functioning and services.

Protected areas (PAs) play a crucial role in maintaining a healthy environment, both for people and nature. They are vital for conserving biodiversity and provide numerous beneficial ecosystem services. Millions of people benefit from tourism to these areas, and they offer protection from climate change and natural disasters for local communities and habitats (UNEP-WCMC and IUCN, 2016). Despite the steady increase in the number and extent of PAs over the last few decades, global protection levels barely reached CBD's 17% target in 2020, and many regions have fallen short (Abell et al., 2017; Almond, Grooten & Peterson, 2020). Trends in freshwater biodiversity reveal a consistent increase in the number of endangered freshwater species (Reid et al., 2019), and the low protection they receive in the present network of PAs largely stems from their design and management (Linke, Hermoso & Januchowski-Hartley, 2019). Rivers, which are viewed as elements of a landscape mosaic, constitute a complex and dynamic landscape in their own right (the riverscape) with their own ecological processes (Wiens, 2002). Traditional notions cannot be applied to fresh waters, which have received inadequate protection (Abell, Allan & Lehner, 2007) and have been largely neglected in global priorities for biodiversity conservation (Abell et al., 2011). Therefore, there is a need for a paradigm shift in effectively protecting fresh waters within PAs, incorporating the processes that sustain the functioning of wetlands and the ecosystem services they provide (Hermoso et al., 2016). Models such as the one proposed in Abell, Allan & Lehner (2007) not only consider freshwater ecosystems as focal areas but also establish management zones surrounding these areas, exceeding the limits of PAs and considering basins as conservation units (Hermoso et al., 2011).

Although there are some signs of progress and examples of the positive effects that PAs can have on freshwater biodiversity abundance (Hermoso et al., 2016), many species in freshwater systems are under serious threat and in decline. One in three freshwater species is threatened with extinction worldwide (Collen et al., 2014; Almond et al., 2022), with freshwater fish being particularly vulnerable, as 30% of them are classified as threatened by the IUCN Red List (IUCN, 2022). This threat to freshwater fish is largely caused by human activities such as dams and water management/use; invasive, non-native, or alien species; and pollution from agricultural and forestry effluents (Costa et al., 2021). Unfortunately, studies based on global trends of freshwater fish face difficulties associated with provisional information, data scarcity, and biases in databases (Pelayo-Villamil et al., 2015; Rodeles, Galicia & Miranda, 2016). Around 50% of the total freshwater fish species (Froese & Pauly, 2021) have been assessed by IUCN's Red List (IUCN, 2022), the reference guide over the last 50 years on species extinction risk (Rodrigues et al., 2006). Furthermore, 21% of assessed freshwater fish are considered Data Deficient, meaning there is a risk of leaving them out of the main conservation efforts (Bland et al., 2015).

Several biases are affecting freshwater fish protection in PAs: conservation priorities driven by terrestrial biodiversity patterns (Abell et al., 2011), existing PA networks biased towards remote places (Butchart et al., 2012), and a deficit in the degree to which PAs cover areas of particular importance for freshwater biodiversity (Juffe-Bignoli et al., 2016b). In addition, gaps in the species distribution data, mainly located in tropical areas (Miqueleiz et al., 2020), may influence certain indicators (Collen et al., 2008) that could potentially be used to identify where PAs should be established or the extent to which current PAs are protecting freshwater biodiversity.

Unfortunately, freshwater fish species have been largely overlooked in the designation of PAs in many regions of the world (Juffe-Bignoli et al., 2016b). To remedy this, specific indicators are needed to measure the effectiveness of PA networks in adequately protecting freshwater fish (Abraham & Kelkar, 2012; Pino-del-Carpio, Ariño & Miranda, 2014). In this sense, the concept of irreplaceability, defined as 'the extent to which spatial options for conservation targets are reduced if the site is lost' (Rodrigues et al., 2006), offers an effective approach to detect those high-value areas requiring urgent conservation measures. This presents several choices to achieve conservation targets (Knight et al., 2013). Irreplaceability has been used in previous studies (Le Saout et al., 2013; Tognelli et al., 2019), and whereas some studies have found that comprehensively assessed taxonomic groups can act as surrogates for broader vertebrate diversity (Rodrigues et al., 2014), others have confirmed that patterns in freshwater biodiversity cannot be represented by terrestrial vertebrate data (Darwall et al., 2011a). Therefore, the use of freshwater fish-based irreplaceability, and its relationship with PAs, remains unexplored. This research can provide new insights into the conservation of inland waters biodiversity.

This study applied an irreplaceability index to identify priority conservation freshwater areas according to their freshwater fish fauna. By studying the relationship between this index and PAs the aim was to address whether the present network of PAs adequately protects irreplaceable areas for fish. The results from this study will provide valuable information regarding where freshwater fish conservation efforts and resources should be focused.

2 | METHODS

Maps for world river basins at 30″ were obtained from the HydroSHEDS project web page (http://hydrosheds.org/) (Lehner, Verdin & Jarvis, 2008). This database provides a global dataset of catchment boundaries that divides the world's land surface into geographical units based on the water flow. It serves as a framework for water-related geospatial analysis and management at various scales or levels. For this analysis, level 8 was chosen as it aligns with the delineation of freshwater fish distribution polygons by the IUCN Red List. Data for all regions in the standard data type were downloaded and merged, resulting in a dataset that comprised a total of 190,675 units, hence called 'basins'. In contrast, the term 'catchment' was limited to entire river basins.

Data on freshwater Actinopterygii (ray-finned) fish species distributions and their global conservation status were obtained from the IUCN Red List (IUCN, 2022). Among the three available formats for information on the spatial distribution of freshwater fish (polygons, points, and freshwater HydroBASIN tables), the first ones were chosen to delineate the species' cartography. Distribution maps provide information about known, inferred, or projected sites of occurrence for the species; however, they are imperfect in some aspects. As in a previous study using similar data (Le Saout et al., 2013), only the fractions of each species' distribution where it was considered to be extant or probably extant, and where the species was native or reintroduced, were included. Areas of migratory passage or seasonal presence were not excluded, as they are considered important areas for fish species that undertake longitudinal and horizontal movements throughout their life cycles. For a description of the categories of origin, presence, and seasonality, see the metadata document Digital Distribution Maps on the IUCN Red List of Threatened Species (IUCN, 2017). In total, 10,970 freshwater fish species were included in the analysis.

River basin irreplaceability was defined as 'a measure of the degree of dependence of species on a given river basin' (adapted from Le Saout et al., 2013). This metric assesses the importance of each river basin in preventing global species extinction based on the distribution patterns of its freshwater fish fauna. It takes into account the proportion of each species' global distribution that overlaps with each basin, as well as its IUCN Red List conservation status, resulting in a vulnerability–rarity weighted richness. This metric identifies spatial priority areas for effective biodiversity conservation by considering species distribution patterns and conservation status. However, it does not consider other species extinction drivers, such as habitat modifications, exploitation, or biological invasions.

The irreplaceability score Ip of each basin p was calculated as the sum across species i of weights w_{ip} for each species in each site p. In this analysis, each species' distribution was intersected with the basin layer to determine species presence in a basin and the number of basins where a species is present. The rarity value for the species for each basin p and each species i, w_{ip}, was calculated as the proportion of the species distribution that falls within that basin (1/number of basins where the species is present). Next, the species rarity value was multiplied by its IUCN Red List conservation status V_i, assigning a value of 1 to species classified as Least Concern, 2 to Near Threatened, 3 to Vulnerable, 4 to Endangered, and 5 to Critically Endangered. Finally, the irreplaceability value for a basin was obtained by summing the values of all the fish species present in that basin:

$$Ip = \sum_i V_i * w_{\underline{ip}}$$

Direct distribution proportions were chosen for the study because the focus was on the basin as a single unit. Calculating the Ip value of the basin based on its area, as done a previous study (Le Saout et al., 2013), would have increased the Ip value in larger basins and weakened smaller ones. This approach ensured that all river basins where a species is present were equally considered. In addition, considering that this study did not include information about other factors (habitat quality, dams, proportion of freshwater surface in the basin, river branching), and as fish are restricted to the freshwater environment, basin size is not a reliable indicator of the amount of surface used by the species.

Data on PAs were obtained in October 2022 from the World Database on Protected Areas (www.protectedplanet.net), which provides the most comprehensive global dataset on marine and terrestrial PAs. Marine PAs were excluded from this analysis. Following Venter et al. (2018), only PAs with a national designation (IUCN codes I to VI) were considered. For PAs lacking a polygon representation and represented only as points, a circular buffer was created with the area of the buffer equal to the reported area of the PA around its central coordinates. Merging the polygon and buffer layers into a single one resulted in a total of 164,377 PAs.

Subsequently, the basins with higher Ip value covering 30% of the land surface were identified. These basins were classified as 'highly irreplaceable' by arbitrarily using the same surface goal established by the UN GBF 30by30 target. To achieve this, basins were ranked from highest to lowest irreplaceability. Basins without any fish species were excluded, and the most irreplaceable basins were selected (starting with the highest irreplaceability) until the total surface of the selected basins covered 30% of the area analysed. The extent to which this subset of highly irreplaceable basins covered freshwater fish species' range was analysed, especially observing the number of species that were not covered at all and basin-endemic species.

Furthermore, the study investigated how many of these highly irreplaceable basins remained outside the existing PA network, in order to provide some insights for future designation of PAs. The coverage of highly irreplaceable basins by PAs was calculated as the number of basins that fall (totally or partially) inside PAs. However, to reflect accurately the extent of basin protection, considering that PAs may only cover a fraction of the basin, the surface of the basins covered by PAs was also calculated by accounting for the proportion of each basin covered by PAs.

Finally, the surface occupied by PAs in each of the Freshwater Ecoregions of the World (Abell et al., 2008) was analysed. Ecoregions that fulfilled the UN GBF 30by30 target were identified, which included ecoregions with at least 30% of their surface covered by PAs. PAs present in more than one ecoregion were divided to assign their corresponding protected surface area to each ecoregion.

All calculations were performed using R software (R Development Core Team, 2021) and associated packages sf and ggplot2.

3 | RESULTS

Higher Ip values were predominantly distributed in tropical and subtropical regions of the world (Figure 1). In the Americas, the most irreplaceable basins were observed in Mexico, Panama, Colombia, and south-eastern Brazil. In Africa, irreplaceable basins were identified in the lower Congo catchment, the Gulf of Guinea, and the African Great Lakes region. Similarly, the Indian Western Ghats, Sri Lanka, Mekong catchment and Malay Peninsula, and Indonesia exhibited high irreplaceability values. A comprehensive list of basin Ip values can be found in the Supporting Information. The subset of highly irreplaceable basins, encompassing 30% of the Earth's surface inhabited by freshwater fishes, was established by those basins with an Ip value ≥0.0296 ($n = 46{,}552$). This selected subset covered almost all freshwater fish species, with only 27 (0.25%) species not covered at all and none of the remaining species being endemic to a single basin. In addition, only 186 (1.7%) freshwater fish species have less than 25% of their distribution range within the highly irreplaceable basins (Figure 2).

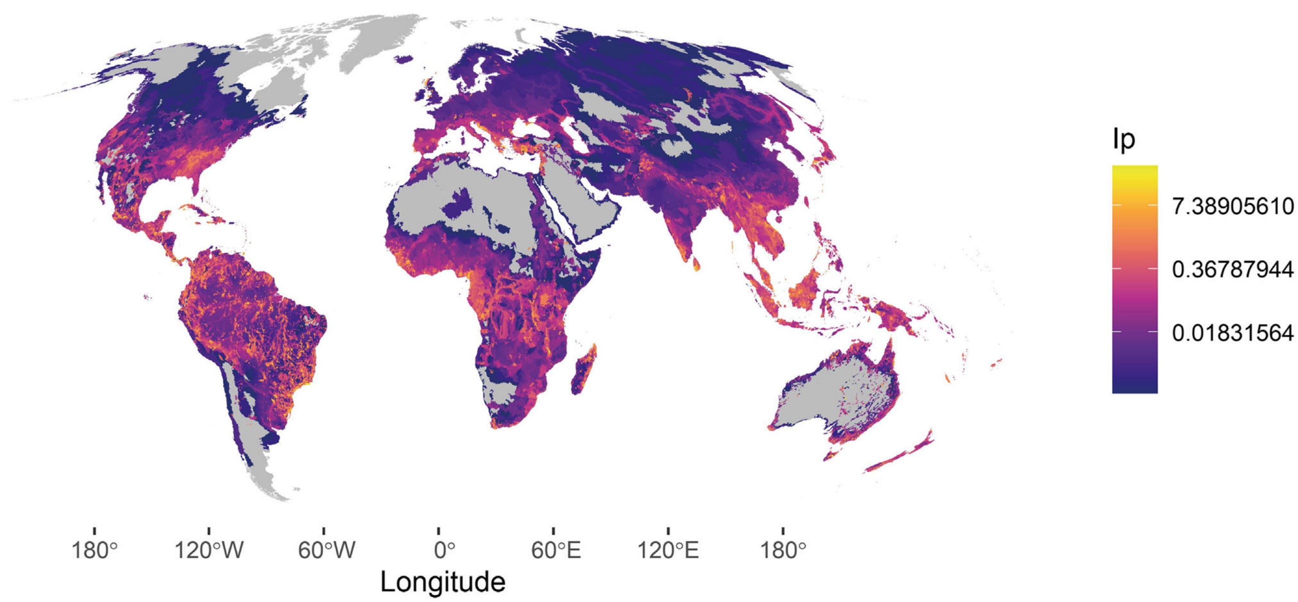

FIGURE 1 Ip index values from basins of the world. Grey land areas represent basins without spatial data on freshwater fish in the International Union for the Conservation of Nature Red List.

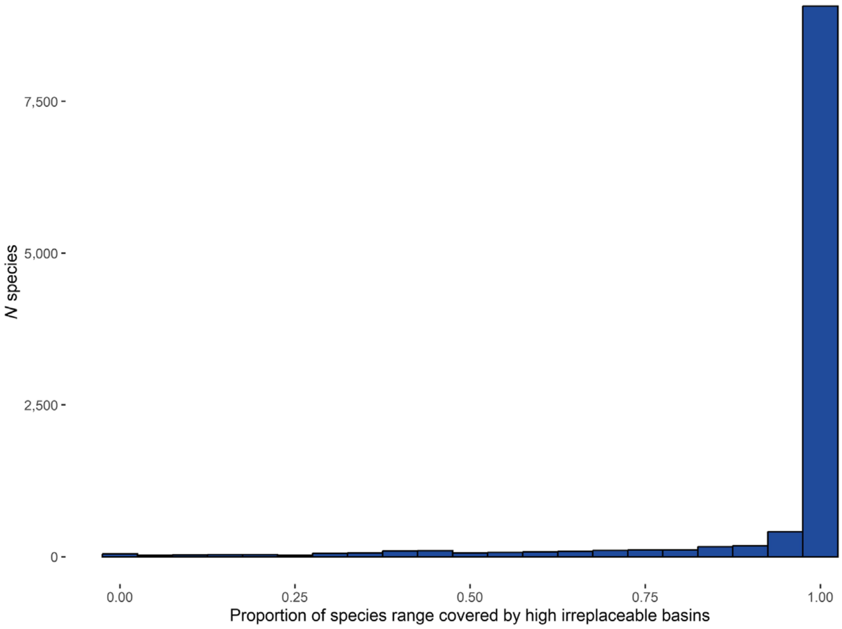

FIGURE 2 Distribution of freshwater fish species' range fraction covered by the subset of highly irreplaceable basins.

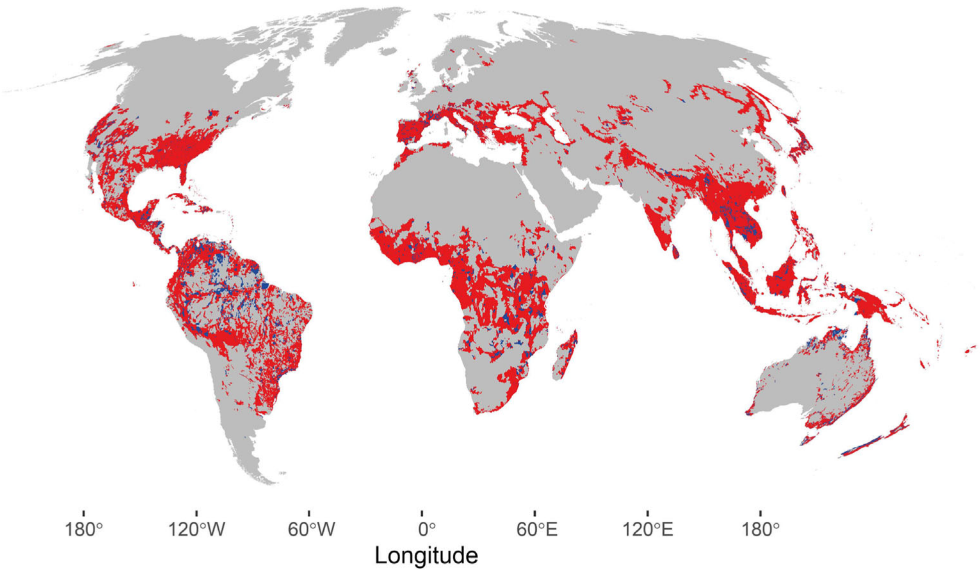

FIGURE 3 Top irreplaceable rivers covering 30% of the world surface, showing those places in (blue) and outside (red) protected areas.

3.1 | Irreplaceable rivers and PAs

Protected areas intersected (totally or partially) with 38.8% of the highly irreplaceable basins. However, the effective protection provided by PAs in these basins was significantly lower, accounting for 10.6% only of their surface (Figure 3). The coverage of PAs in all regions identified as highly irreplaceable was very low, with a few exceptions of small areas exhibiting high levels of protection (e.g. New Zealand or south-eastern Brazil). Maps depicted fragmented coverage of PAs in freshwater hotspots such as the Western Ghats, as well as regions with insufficient protection (African Great Lakes, Anatolian Peninsula, or Andean Amazon Piedmont region). Notably, the Amazonas region showed substantial PA coverage in the lower areas but lacks sufficient protection in higher altitudes.

The UN 30% protection goal is only achieved in 7% of the freshwater ecoregions (Figure 4), with some of them situated in places with low freshwater diversity, such as Greenland and central Australia.

4 | DISCUSSION

The results of the study reinforce the existence of irreplaceable basins in tropical areas as a result of their unique freshwater fish fauna. However, the protection of highly irreplaceable areas is far from being adequate, with a large proportion of the most irreplaceable rivers falling outside PAs. Although new distribution maps and species descriptions may improve these

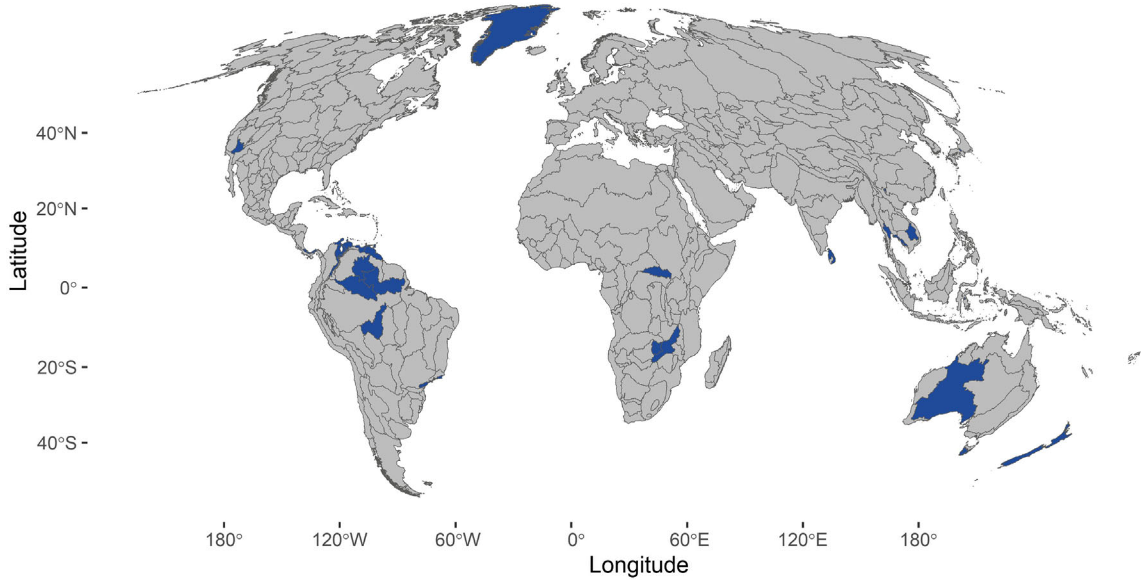

FIGURE 4 Freshwater ecoregions fulfilling 30% protected surface of the United Nations 2030 target (blue).

outcomes in the future, there is a clear need to rethink how protected and management areas are established to meet UN commitments.

The study emphasized highly irreplaceable regions that have been previously identified as freshwater biodiversity hotspots (Abell et al., 2008; Collen et al., 2014; Pelayo-Villamil et al., 2015; Jézéquel et al., 2020b), with particular importance for tropical areas of South America, Africa, and Asia, as well as areas of North America and Europe (Figure 1). Furthermore, the study highlighted precisely small irreplaceable regions where a high number of species remain confined to a few river basins, constituting a more vulnerable situation; for instance, several Mediterranean basins (Darwall et al., 2015) or Mexican endorheic systems (Contreras-MacBeath et al., 2020). Consequently, the use of high-resolution data has enabled better identification of truly irreplaceable areas that may provide opportunities for maximum biodiversity conservation (Arthington et al., 2016). Moreover, this subset of highly irreplaceable areas offers protection to 99% of freshwater fish species in a substantial fraction of their distribution range (Figure 2). The return on investment of protecting or managing this subset of the world's river basins is clear and can contribute to how the UN's 30by30 goal should be applied to meet freshwater conservation necessities.

4.1 | Role of PAs in irreplaceable river conservation

PAs offer inadequate protection to freshwater ecosystems in general, and highly irreplaceable areas in particular (Figure 3). The current target set by the UN is far from being met in most freshwater ecoregions (Figure 4). These findings highlight the need for significant efforts in this aspect, as a large proportion of the world's most irreplaceable river basins are not encompassed within PAs (89%). The patchy protection of freshwater PAs is not considered effective for conservation purposes. The effective design of freshwater PAs (Abell, Allan & Lehner, 2007) emphasizes the preservation of upstream–downstream and lateral connections that are essential for the protection of freshwater habitats (Hermoso et al., 2016). Therefore, it is essential to include these irreplaceable basins within larger management units that encompass the entire catchment area. In addition, regions where PAs currently protect few irreplaceable basins, such as the Andean Amazon Piedmont, face the threat of the dam construction boom (Closs et al., 2016; Carvajal-Quintero et al., 2017), which can disrupt water flow regimes and adversely affect river connectivity, critical factors for the survival of freshwater fish. Correspondingly, the results align with recent studies and reinforce the irreplaceable value of the upper reaches in the Amazonian catchment, whereas lower areas and the main river have lower irreplaceable values (Jézéquel et al., 2020b). Given that PAs in the Amazonian region are predominantly located in the lowlands, greater attention should be given to the irreplaceable higher reaches in the future design and establishment of PAs in the region. Furthermore, considering the potential range shifts of freshwater fish under future climate change scenarios (Frederico et al., 2021), it is likely that current PAs in this region (but also in many other regions of the world) may not provide sufficient protection. Similar challenges exist in other regions, such as African wetlands, where permissive management practices can even affect PAs (Acreman et al., 2020).

The analysis also revealed a protection bias towards areas with low freshwater diversity (Greenland or Alaska) or remote locations (such as the Amazonian lowlands or large parts of Australia). This bias has been extensively studied in scientific literature and presents a significant challenge in the rethinking of new PAs (Joppa & Pfaff, 2009). However, there are opportunities in other regions to meet both terrestrial and freshwater conservation needs. For instance, accounting for the opportunity of terrestrial PAs to incorporate freshwater ecosystems could benefit restricted-range endemic fishes in the Western Ghats (Abraham & Kelkar, 2012) and African Great Lakes (Britton et al., 2017).

Terrestrial-driven conservation patterns may unintentionally exclude irreplaceable rivers from the current PA network. This highlights the need for a more effective design and management of freshwater PAs. Prioritizations based solely on terrestrial species provide scarce freshwater benefits compared with freshwater-focused conservation measures. Integrated freshwater–terrestrial planning can improve the status of freshwater species globally without compromising terrestrial conservation aims (Leal et al., 2020). Whereas previous studies have identified the bias in PAs for terrestrial vertebrates, the implications for freshwater biodiversity have yet to be thoroughly discussed. Understanding these implications would shed light on where and how new PAs should be established in the coming decade.

Several priorities have been established to guide research in freshwater conservation for the upcoming years (Maasri et al., 2022). Regarding the role of PAs, we strongly support the ideas proposed by Acreman et al. (2020), which emphasize the importance of proper management both in PAs and the basins in which they are situated. Recognizing that complete protection of the whole planet is not feasible, we advocate a combination of spatial protection and management to achieve conservation targets, as stated by UN 2030 goals.

4.2 | Limitations and perspectives

The use of a vulnerability–rarity weighted richness index in this study has influenced the results obtained. As an example, the calculated index does not highlight Amazonian lowlands, which are known for their outstanding freshwater fish diversity (Oberdorff et al., 2019). Nevertheless, the objective of this study was to emphasize the role of PAs in freshwater fish conservation. Therefore, the protection of species-rich regions containing widely distributed species is not directly relevant to the study's objective. The calculated index strikes a balance between protecting species-rich areas and rare species, thereby highlighting several regions that can be effectively protected through the establishment of new PAs specifically focused on freshwater biodiversity. We acknowledge that the index could potentially highlight species-rich basins with widespread species. However, the richness component in these cases would be balanced by the conservation status component, acknowledging the necessity of conservation measures if such species were threatened. The value of rarity-weighted indexes has been discussed in previously in the literature (Astudillo-Scalia & de Albuquerque, 2019), and they are considered potential surrogates of biodiversity for identifying conservation priorities. Moreover, this index adequately depicts conservation priorities as the selection of the highly irreplaceable basins provides coverage for almost all freshwater fish species in a substantial fraction of their distribution range (Figure 2).

According to Collen et al. (2014), 'the extent to which existing terrestrial protected areas protect freshwater species is unknown, but they are likely to be insufficient'. Indeed, traditional PAs have offered limited protection to fresh waters owing to inadequate consideration of their unique requirements during the designing and establishment of PAs (Roux et al., 2008), often prioritizing terrestrial interests. This study demonstrates that these statements hold true for freshwater fishes. However, the effectiveness of using a single taxon (freshwater fish) to determine the value of rivers for conservation may lead to discrepancies. Previous studies have explored the use of terrestrial vertebrates as surrogates for one another (Moore et al., 2003), but they cannot serve as surrogates for freshwater fauna (Darwall et al., 2011a). On a global scale, fishes have not proved to be reliable surrogates of other vertebrates (Tisseuil et al., 2013), although there are some examples of effective surrogacy when examined at the catchment level (Lessmann et al., 2016). Given that fish are restricted to the water bodies (unlike other freshwater vertebrates), and they are better assessed than other potential surrogates (i.e. freshwater macroinvertebrates), we believe they can be used to identify priorities for spatial protection in fresh waters. Nevertheless, when conducting conservation planning at finer spatial resolutions, it is crucial to study the diversity patterns at a more detailed scale to develop optimal solutions.

The results obtained in this study were strongly conditioned by the knowledge gap existing in many areas of the world (Miqueleiz et al., 2020). Tropical areas of south-eastern Asia and South and Central America were found to have lower levels of inventory completeness (Pelayo-Villamil et al., 2015; Tognelli et al., 2016). In the Neotropical region, for instance, current rates of species discovery and publication suggest that there are likely to be more than 8,000 Neotropical freshwater fishes (Reis, 2013). Despite continuing efforts by the IUCN Red List to assess species' conservation status, the risk of undiscovered species becoming extinct without noticing remains high (Costello, May & Stork, 2013; Bland et al., 2015). Field surveys and monitoring programmes are essential to fill knowledge gaps in the distribution of fishes and biodiversity in general. Although recent efforts have been made to increase knowledge of Neotropical biodiversity (Tognelli et al., 2016; Jézéquel et al., 2020a), this tropical biodiversity gap may be influencing indicators established by the CBD (Collen et al., 2008), and urgent work is needed to sample and study Neotropical inland waters. Priority regions have been identified to help assess or reassess a significant proportion of freshwater fishes (Hermoso et al., 2017), and approaches such as the sampled Red List Index are being used for fishes and other freshwater groups (Böhm et al., 2020; Miranda et al., 2022). However, the final goal should be to achieve a comprehensive conservation assessment of freshwater species. We expect that this study, along with these efforts and others done by the IUCN Red List, will strengthen resources and actions dedicated to species description, development of distribution maps, and the protection of freshwater ecosystems.

To make informed decisions, it is crucial to assess the effectiveness of protected areas for sustaining species and to identify priority sites for their conservation (Tognelli et al., 2019), particularly for freshwater fishes in the Andean Amazon Piedmont. The study highlights the irreplaceable value of this extensive region and its key role for Neotropical freshwater fish protection. This region, and others detected by the analysis, align with previous studies and programmes,such as the Key Biodiversity Areas (KBAs) led by the IUCN. However, KBAs predominantly focus on terrestrial ecosystems, whereas freshwater ones only account for 25% of them. Some regional efforts have been made to incorporate more freshwater-focused KBAs (Carrizo et al., 2017). This study presents an opportunity to establish additional areas, as KBAs do not include fish species in many of the areas detected as highly irreplaceable and outside PAs in this study (Western Ghats, Andean Region, or southern China). Understanding the environmental drivers and evolutionary processes that shape freshwater fish diversity is feasible (Tedesco et al., 2017), but increased funding (both financial and human resources) is necessary to achieve a global assessment of freshwater fish (Juffe-Bignoli et al., 2016a).

PAs have traditionally been established in low-cost lands, a trend that has intensified over time (Venter et al., 2018). This presents a challenge when trying to establish protection in regions such as the African Great Lakes, where conservation interests go together with the social value of those areas for fishing (Gherardi et al., 2011). The introduction of Nile perch (*Lates niloticus*) in Lake Victoria in 1954 has led to the decline of native haplochromine cichlids, which were the primary source of livelihood for local fishermen (Hecky et al., 2010) and replaced traditional fishing practices with an industrial process in the hands of a small minority of fishermen (Kasulo, 2000). Effective freshwater protection in this area could benefit both native fishes with control of *L. niloticus* populations and local fishermen if they regain control over the fisheries. In regions such as the Andean Piedmont, where several dams are projected or already under construction (Carvajal-Quintero et al., 2017), connectivity analyses provide a valuable tool for informing where dam construction should be avoided to preserve freshwater biodiversity (Anderson et al., 2018).

The impacts of climate change are expected to have a significant effect on freshwater fish species (Comte & Olden, 2017), leading to climatically driven shifts in their geographical range (Pecl et al., 2017; Barbarossa et al., 2021). The present reserve network may be less effective in the face of climate change, as PAs are fixed on the land, raising concerns about their ability to adapt and maintain their conservation efficiency (Hannah, 2008). Freshwater systems are under extreme threat; the latest Living Planet Index (LPI) showed an 83% decline in population abundance of freshwater vertebrates since 1970 (Almond et al., 2022), with an alarming 89% in Central and South America. Although there may be some criticism regarding the methodology used by the LPI, the overall declining trend in freshwater vertebrate populations is undeniable (Buschke et al., 2021). Conservation actions to address these losses often prioritize areas of highest loss or threat, endemism, and so on. Enhancing the capacity of freshwater PAs to adequately cover the needs of freshwater biodiversity requires actions that also make them flexible enough to avoid unrealistic PAs (Linke, Hermoso & Januchowski-Hartley, 2019). We believe that this study serves as a foundation for future projects that estimate the cost-opportunity of freshwater PAs, an approach that has already been undertaken for terrestrial vertebrates (Venter et al., 2014). It is evident that sustainable solutions that benefit both freshwater ecosystems and humans are possible through thoughtful PAs designing and planning (Leal et al., 2020). The UN 30by30 goal represents an unprecedented opportunity to prioritize and implement protection and management efforts in regions and basins where freshwater ecosystems can be effectively safeguarded.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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