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The Spatial Discrepancy Between Colombian Freshwater Fish Suitable Habitats and Existing Protected Areas

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ABSTRACT

Aim: The increasing anthropogenic pressures on freshwater biodiversity raise the important question: how well is it represented within protected areas? We address this question using the freshwater fish fauna of a neotropical biodiversity hotspot to estimate (i) how the fish fauna is covered by the existing protected areas and (ii) to which degree alternative protected area configurations may have the potential to increase the number of fish species under protection.

Location: Colombia and neighbouring countries.

Methods: We first compiled 238,278 geographic occurrences for 1313 freshwater fish species and cleaned the species data by harmonising the nomenclature and revising the geo-referenced coordinates. Using the GMTED-digital elevation model, we delineated a stream network and extracted the corresponding 38,150 sub-catchments that served as spatial units for the analysis. We then employed ensemble species distribution modelling to project potentially suitably habitats of single fish species across the study area. Finally, we used spatial prioritisation analyses, specifically integer linear programming to account for 30% of each fish suitable habitat within newly-delineated priority areas, that is, hypothetical protected areas.

Results: We found that the newly-delineated priority areas overlap only by 25.2% with the existing protected areas. Strikingly, the required amount of area for protection is similar to that of the existing protected areas, reflecting, however, a major spatial mismatch between the two. Moreover, we found that endemic and threatened species, especially in the Magdalena-Cauca and Pacific-Choco basins, contributed towards the newly-delineated priority areas that would be integral for an efficient freshwater fish protection in this region.

Main Conclusions: Our results highlight the high discrepancy between freshwater biodiversity conservation and protected areas in Colombia and guide the integration of those areas with high ecological value yet reduced anthropogenic impact.

1 | Introduction

Freshwater biodiversity is declining globally, and freshwater populations decline faster than the terrestrial or marine counterparts (Loh et al. 2005; Strayer and Dudgeon 2010). Multiple anthropogenic factors impact freshwater ecosystems; for instance habitat change and destruction, damming, land use changes, pollution, climate change, invasive species and fish harvest (Dudgeon et al. 2006; Tickner et al. 2020). Halting the negative trend and bending the curve remain key priorities in nature conservation (Albert et al. 2021; Haase et al. 2023; Harper et al. 2021).

Protected areas are a cornerstone in safeguarding biodiversity (Margules and Pressey 2000) despite their controversy: the establishment of protected areas does not mean that the key threats affecting biodiversity are effectively ameliorated (Hilborn 2016). For example, if a non-passable hydropower dam is the core cause leading to extinction of a migratory species, establishing protected areas will not suffice the species and populations to recover if the dam remains in place. Moreover, existing protected areas were predominantly designated without consideration of freshwater biodiversity issues and have instead focused on the protection of terrestrial or marine biodiversity (Suski and Cooke 2007; Watson et al. 2014). Additionally, many protected areas were established in remote, inaccessible areas rather than in biodiversity hotspots to avoid the common opposition of people to lose access rights (Relano and Pauly 2023), or have seen ample managerial exceptions in terms of keeping access to humans (e.g., fishing with specific gears or fishing in specific times of the year), such that they may become what is known as "paper parks" (Di Minin and Toivonen 2015), especially if rule enforcement is absent (Edgar et al. 2014). At the same time, the spatial extent of protected areas has been steadily growing over past decades and they are advocated to be expanded in the future (Convention on Biological Diversity (CBD) 2020; Deinet et al. 2020; Dinerstein et al. 2017). This raises the question, to which degree do protected areas cover freshwater biodiversity, and where could new priority areas for conserving freshwater biodiversity be established?

South America and especially Colombia represents a freshwater biodiversity hotspot with an exceptionally rich freshwater fish fauna, including many endemics (Reis et al. 2016). Around 26% (or 1616) of the 6200 neotropical freshwater fish species have been taxonomically described to occur in Colombia, from which 374 species are endemic to Colombia (Albert et al. 2020; DoNascimiento et al. 2021). Colombia's diverse freshwater fish biodiversity stems from its unique biogeographic location and history (Albert et al. 2020; Jézéquel et al. 2020a). The bulk of the Colombian endemic freshwater fish species occur in the Andean mountains (Tognelli et al. 2019). Colombia's freshwater fish diversity may be viewed as a surrogate for its freshwater biodiversity (Collen et al. 2014), which is likewise subject to threats given the overexploitation by commercial or ornamental fishing, land use changes through deforestation, pollution by agriculture, legal and illegal mining or urban centres, damming and river channelling as well as the introduction of invasive species (Bezerra et al. 2019; Palacios-Torres et al. 2020; Reis et al. 2016). Future climate change is likely to add pressure on freshwater ecosystems in Colombia (Tognelli et al. 2019). There is only limited knowledge on the spatial distribution patterns and conservation status of freshwater fish biodiversity on the national scale in Colombia (Barletta et al. 2010; Lasso et al. 2016; Portocarrero-Aya and Cowx 2016; Urbano-Bonilla et al. 2018). This lack of knowledge, consequently, impedes the evaluation of existing protected areas (i.e., what biodiversity do they cover) and the spatial allocation of new areas (i.e., where to best protect biodiversity) (Miqueleiz et al. 2020). Especially Tognelli et al. (2019) and Miqueleiz et al. (2020) highlight this critical gap regarding insufficient knowledge on freshwater species distribution and endemism patterns which cascade into critical conservation gaps in this region.

Colombia's biodiversity conservation strategy heavily depends on protected areas (Negret et al. 2020). The national system of protected areas (SINAP) in Colombia and other regional and local level, being either private or public, as well as including all types of conservation status and other effective area-based conservation, cover together an area of around 316.000 km^2 or 27.6% of Colombia's territory (Protected Planet 2024; UNEP-WCMC and IUCN 2024). Its main goal is to fulfil global conservation targets by efficiently managing terrestrial and marine ecosystems. Only in recent years Colombia started to establish protected areas addressing freshwater ecosystems specifically, by selecting protected areas that cover entire catchment areas, for instance with the Ramsar site at the Rio Bita (Suárez et al. 2021). It remains, however, unclear to what extent freshwater biodiversity is included on the national scale in the protected area network of Colombia (Aldana-Domínguez et al. 2017)? To which degree are freshwater ecosystems represented in Colombian protected areas given that they are either being lumped within terrestrial protected areas, or included indirectly where, for example, rivers serve as borders to non-protected areas (Miqueleiz et al. 2020; Quenta-Herrera et al. 2022)? Historically, protected areas in Colombia have been set up predominantly in remote, species-rich areas with minor human impacts, mainly in the Amazon or Orinoco region (Forero-Medina and Joppa 2010). While Tognelli et al. (2019) showed a poor overlap between endemic fish species and protected areas in the Andean mountain range, Nogales et al. (2023) report a good representation of freshwater biodiversity within protected areas for a single sub-catchment in the Amazon basin. Given the lack of a solid baseline and the regional to national scale, informed decision making still remains a challenge. In addition, global assessments have highlighted the inadequate representation of freshwater biodiversity across different ecosystem types and gaps in connectivity between protected areas (Gavioli et al. 2023; Grantham et al. 2017; Miqueleiz et al. 2023; Tao et al. 2023).

Spatial prioritisation can be used to address this challenge, being an essential part within the broader concept of systematic conservation planning (SCP; Margules and Pressey (2000)). It aims to find the optimal solution of a spatial area network in the most cost-effective manner to achieve the long-term persistence of a habitat or species (Margules and Pressey 2000). Through a complementary approach, it identifies the set of areas to achieve predefined conservation targets, the so-called priority areas, and selects planning units, such as sub-catchments, which, given their biodiversity features, may contribute towards fulfilling this predefined conservation target (Hermoso et al. 2011). These biodiversity features, such as species occurrences, are ideally available range-wide for the entire study area (Dolezsai et al. 2015). In the real world, however, our understanding about species distribution patterns is often incomplete for many regions, a challenge also coined as the "Wallacean shortfall" (Bini et al. 2006). This challenge applies also to the Colombian ichthyofauna with unknown spatial ranges for many fish species (Bogotá-Gregory et al. 2020; Portocarrero-Aya and Cowx 2016; Urbano-Bonilla et al. 2018).

To bridge this gap, species distribution models (SDMs) provide a possible solution. They relate the species' observed geographic occurrence in space and time by correlating environmental factors at those locations to then project the potential suitable habitats in geographic space across the study area (Elith and Franklin 2013). The use of correlative SDMs has increased in recent years with advances in computational capabilities and availability of spatially explicit environmental and species occurrence data (Araújo et al. 2019). Within the freshwater realm, advances have been made to integrate the longitudinal connectivity of species into the modelling process (Radinger and Wolter 2014). Regarding conservation planning, SDMs provide the required range-wide information on species habitat suitability throughout the study area (Bini et al. 2006; Domisch et al. 2019).

Our objectives were to (i) map the spatial distribution of the freshwater fish fauna across Colombia, (ii) delineate priority areas that would cover at least 30% of each species' potentially suitable habitat — following the "30 × 30" conservation target (CBD, COP 15) — and (iii) compare the spatial representativeness of these newly-delineated priority areas against the existing protected areas of Colombia. We expected that (i) the species distribution models are able to replicate the well-known freshwater fish richness patterns following the major river systems of the Amazon and Orinoco rivers, (ii) the existing protected areas of Colombia show a low overlap with newly-delineated priority areas and that (iii) endemism and threat status of species stand out regarding their contribution towards delineating such areas. To test these hypotheses, we modelled the suitable habitats of 1313 species, including 237 endemics, and used the suitable habitats as biodiversity features for the spatial prioritisation. We highlight apparent gaps in the spatial representativeness between the newly-delineated priority areas and the existing protected areas in protecting the freshwater fish fauna, and discuss the implications of these newly-delineated priority areas in the larger context regarding freshwater biodiversity conservation in Colombia.

2 | Methods

2.1 | General Workflow

The general workflow consisted of four steps: we first (i) delineated a river network and the corresponding sub-catchments, compiled the fish occurrence records and aggregated these to the sub-catchments. We then (ii) employed ensemble species distribution models to estimate the range-wide habitat suitability probabilities for each species. This was followed by (iii) calculating newly-delineated priority areas which would fulfil a given conservation target (with and without the existing protected areas) and finally (iv) the comparison of the newly-delineated priority areas with the existing protected area network of Colombia to estimate the protection gap of the Colombian freshwater fish fauna.

2.2 | Study Area

Colombia is situated in the northwest periphery of South America between the Pacific Ocean to the west and the Caribbean Sea in the north, and intersects the Neotropics' most productive freshwater systems with the Amazon and Orinoco basins (Figure 1). The climate is heavily influenced by the large elevation gradients (0–5775 m) and varies from the tropical humid lowlands to the Andean mountains, which stretch across three mountain ranges through the country in a north–south direction (Murcia et al. 2013). These topological characteristics, in combination with a humid tropical climate, create a mosaic of different freshwater habitats (Anderson and Maldonado-Ocampo 2011).

We apply two spatial extents: (i) the larger modelling domain (Figure 1, blue outer boundary) and (ii) the spatial prioritisation domain (Figure 1, red boundary), referred to as the study area. The study area comprises Colombia and includes partly its neighbouring countries Brazil, Ecuador, Peru and Venezuela (Figure 1, red boundary). Though we focus on the Colombian fish fauna, the modelling domain exceeds the borders of Colombia to account for wider environmental gradients during the subsequent species distribution modelling (Thuiller et al. 2004), and to address the longitudinal connectivity of rivers across national borders. The area is characterised by the three large drainage basins, the Amazon, Orinoco and Magdalena-Cauca basins and two drainage basins composed of several coastal ones with similar biogeographic characteristics and proximity: the Pacific-Choco, bordering the Pacific Ocean and the Caribbean river basins in the North, flowing into the Atlantic Ocean (Figure 1, Reis et al. 2016). Note that only the Magdalena-Cauca basin is completely within the study area.

2.3 | Stream Network Delineation

We first delineated a stream network using the 1 km^2 Global Multi-Resolution Terrain Elevation Data (GMTED) digital elevation model (Danielson and Gesch 2011), obtained from http://www.earthenv.org/topography, (Amatulli et al. 2018). We then 'burned in' the waterways of South America derived from OpenStreetMap (OpenStreetMap Contributors 2022). We resampled the layer to 1 km resolution using GDAL (Rouault et al. 2024) to ensure the proper stream routing especially at the river estuaries and applied the *r.watershed* function within the GRASS-GIS software (Neteler, Bowman et al. 2012). We used a stream-initialisation threshold of 90 upstream cells, which corresponds to a minimum headwater catchment of 90 km^2. We then applied the *r.stream.basin* function to extract the sub-catchments across the network which served as the spatial units for our analyses. In total we extracted 38,150 sub-catchments with an average size of 153 km^2 which are used as planning units within the study.

2.4 | Fish Occurrence Data

We collated a total of 238,278 unique geographic occurrences of 1313 Colombian freshwater fish species from 5 sources: the Global Biodiversity Information Facility (GBIF) (2024),

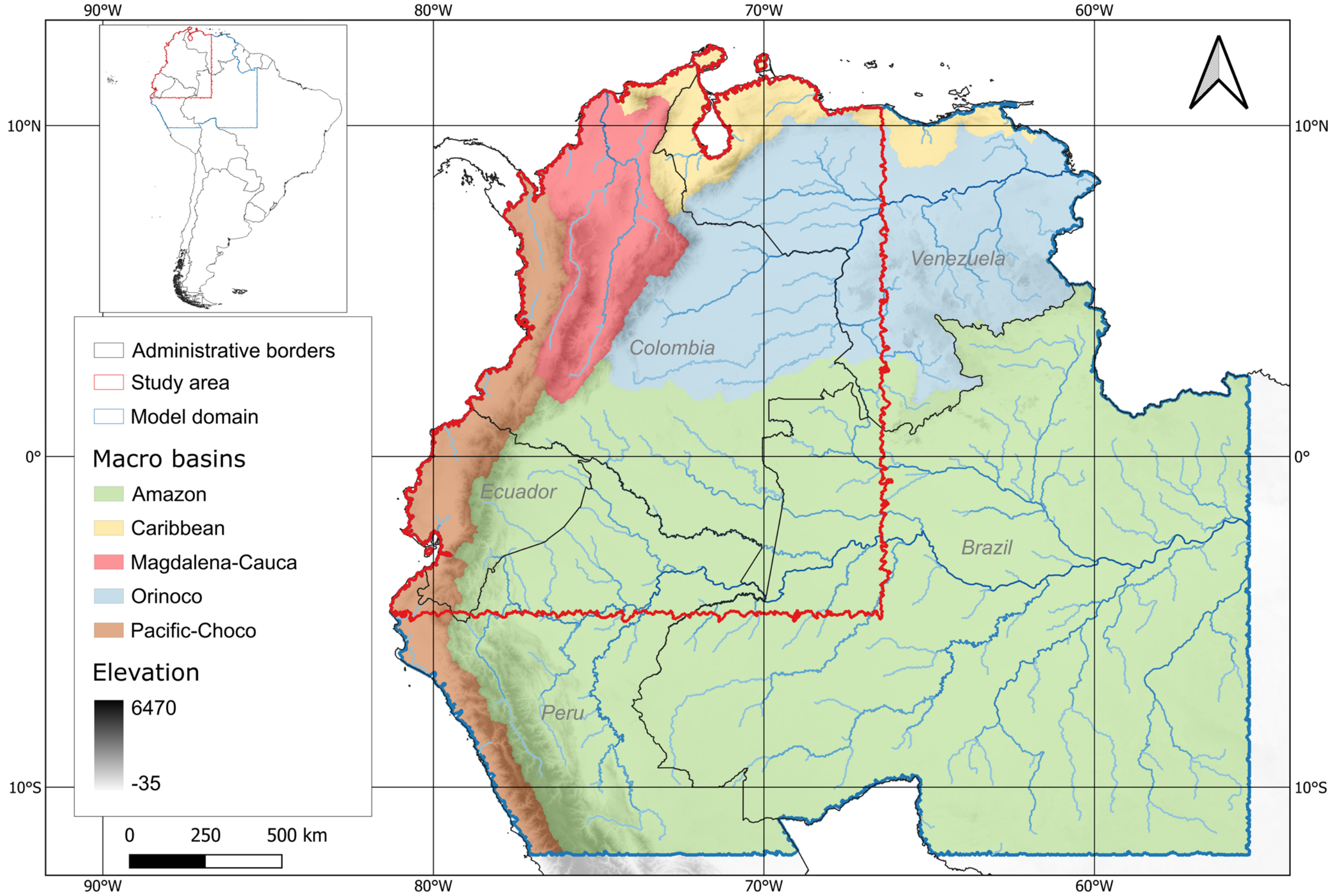

FIGURE 1 | The outer blue line shows the extent of the modelling domain of the SDMs; the red line shows the extent of the study area and spatial prioritisation; black lines in the model domain show administrative borders; the grey colour gradient represents elevation gradient (in meter); underlying colours represent the drainage basins (own illustration based on *r.stream.basins* (GRASS Development Team 2022)) and conceptually on Reis et al. (2016).

FishNet2 (2024), Species link network (Thiers et al. 2022), Integrated Digitized Biocollections (iDigBio) (2024) and Colombian taxonomist expert data derived from Prada-Pedreros et al. (2018). We first checked and corrected spelling errors in species taxonomic names against the FishBase dataset (Boettiger et al. 2012) using the *validate()* function from the 'rfishbase' R package (Boettiger et al. 2012). We then compared those species with the Colombian freshwater checklist (DoNascimiento et al. 2021) to use occurrence points of Colombian freshwater fish for all subsequent analyses. The data comprises 55 families of fish, 237 endemic species to Colombia and 69 species currently considered threatened by the International Union for Conservation of Nature (IUCN 2021). Among those threatened fish species, one is considered critically endangered, 11 endangered, 35 vulnerable and 22 near threatened (see also Table S1 for the entire species list). A total of 29 fish species are both endemic to Colombia and within one of the four above-mentioned IUCN threat categories.

We aggregated all occurrence records to the sub-catchments while removing duplicate records. Six species were omitted from the species distribution modelling since they contained occurrence points only within a single sub-catchment. We included these species however in the spatial prioritisation by assigning the sub-catchments where the species were observed as suitable habitats.

2.5 | Addressing the Longitudinal Connectivity

We addressed the longitudinal connectivity between sub-catchments by (i) preparing a species-specific network-distance layer for the species distribution modelling and (ii) creating a distance matrix across all sub-catchments for the spatial prioritisation.

For the SDMs, we calculated the network distance from each sub-catchment (corresponding to a stream segment) that contains a point record to all other connected stream segments. We first reclassified the raster cells of those segments with a point record to 1, all other stream raster cells to 0, and all remaining terrestrial and marine raster cells to NoData (NA); these represent areas fish cannot travel through. We then used the function *gridDistance()* from the 'raster' R package (Hijmans 2018) to calculate the distance from those grid cells with a 1 to all grid cells with a 0. We inverted and scaled the distances to 0–1 to obtain a layer which can be multiplied with the model predictions to (i) proportionally downweigh those predictions that are either far away, or to (ii) remove those predicted values in disconnected

TABLE 1 | The list of 13 environmental predictors used in the species distribution models: the predictor category, the predictor name, the spatial resolution, the download URL and the reference.

Predictor category	Predictor name	Spatial resolution in km	Time span	Download URL	References
Climate	Annual mean temperature Diurnal mean temperature Seasonality mean temperature	1	1980–2010	https://chelsa-climate.org/	Karger et al. (2021)
Land cover	Barren vegetation Cultivated vegetation Flooded vegetation	1	1992–2006	https://www.earthenv.org/landcover	Tuanmu and Jetz (2014)
Topography	Elevation range Elevation drop Gradient	1	2000–2010	https://www.earthenv.org/topography	Amatulli et al. (2018)
Stream-topology	Flow accumulation Stream length Sinusoid	1	2000–2010		GRASS Development Team (2022)
Hydrology	Logarithmic flow	1	1960–2015		Barbarossa et al. (2018)

drainage basins where the target species has not been observed. The habitat suitability of planning units with occurrence data remains unaltered.

For the spatial prioritisation, the stream connection between all sub-catchments is integrated into the selection process (Hermoso et al. 2011). In this way, each sub-catchment 'knows' with which sub-catchment it is connected to (Domisch et al. 2019). The connection is calculated from the final downstream sub-catchment back upstream. This step is then repeated for the next higher upstream sub-catchments and so on, until there are no higher-located upstream sub-catchments anymore. Due to computational constraints, we set a cap of 200 km river network distance between sub-catchments ID. This function is now available as *get_all_upstream_distances()* in the 'hydrographr' R package (Schürz et al. 2023). Although dams and barriers play a critical role in shaping fish distributions, we did not include this aspect in our study due to the lack of standardised and range-wide data on dams along with the corresponding fish passability information.

2.6 | Environmental Predictors

We selected topographical, climatic, land cover and hydrological environmental predictors, all available at a native 1 km^2 resolution. We obtained climate data from the CHELSA-Bioclim v. 2.1 dataset (Karger et al. 2017). It consists of high-resolution, worldwide, temperature and precipitation data for the years 1981–2010. We downloaded topographical and land cover data from the EarthEnv project (Amatulli et al. 2018; Tuanmu and Jetz 2014). We created all stream-topological predictors using the GRASS GIS function *r.stream.order* (GRASS Development Team 2022). Finally, we retrieved the mean discharge of the years 1960–2015 from the FLO1K dataset (Barbarossa et al. 2018), from which we computed the logarithmic flow. From a larger pool of predictors, we selected a subset for the modelling by excluding highly correlated predictors using the Pearson correlation coefficient $r \geq |0.7|$ as a threshold (Brunner et al. 2024) and choosing a suit of predictors frequently used in previous studies to predict the spatial distribution of freshwater fishes (Barbarossa et al. 2021; Buisson et al. 2008; Hermoso et al. 2015; Kuemmerlen et al. 2014). We then aggregated all data to the sub-catchments using the *r.univar* function in GRASS GIS, prior scaling and centring them using the *scale()* function in R. In total we used 13 environmental predictors in the SDMs (Table 1).

2.7 | Species Distribution Modelling

We used the 'biomod2' R package (Thuiller et al. 2009) and a weighted ensemble technique with four algorithms: Generalised Linear Model (GLM), Random Forest, Maximum Entropy (MaxEnt) and Classification Tree Analysis (CTA). Given the lack of absence data, we drew 10,000 random background points for each of the 10 model runs. For each run, all data is split randomly between a 70%/30% fraction regarding model training and testing, respectively (Araújo and New 2007). Model performance was estimated using the True Skill Statistic (TSS) criterion (Thuiller et al. 2016). We followed Araújo et al. (2011) and retained only those models with a TSS score > 0.4 and weighted each remaining single model proportionally given its TSS score in the final ensemble. In total, 1307 species × 4 algorithms × 10 repetitions corresponded to 52,280 individual model predictions.

The outcome of the SDM is the likelihood (ranging from 0 to 1) of habitat suitability per sub-catchment for each species across the study area. For each species, we set all probabilities below the TSS cut-off value to zero and all above the cut-off retained their original probabilities, creating a so-called semi-binary map of species suitable habitats (see also Domisch et al. (2019)). This approach has the advantage of reducing low probabilities which could sum up for many species. We multiplied the probabilities per sub-catchment by the scaled distances to account for stream connectivity following where a fish can swim. Collapsing the probabilities to a semi binary map, in combination with the distance scaling limits the number of sub-catchments that are unsuitable and inaccessible for a given species in the spatial prioritisation, thus reducing the uncertainties.

2.8 | Spatial Prioritisation

For the spatial prioritisation we employed integer linear programming using the Gurobi Optimizer software within the 'prioritzr' R package (Gurobi Optimization 2024; Hanson et al. 2024). The spatial prioritisation solves an objective function that fulfils the conservation target while minimising the selection of large, anthropogenic-influenced areas, which in turn improves the effectiveness of conservation efforts of the priority network (Linke et al. 2019).

Specifically, we created an objective function for solving a minimization problem (Hanson et al. 2024). It comprises for each planning unit (i.e., sub-catchment) the (i) individual species habitat suitability predictions as the biodiversity features and (ii) cost information in the form of the human footprint index (HFI), which can be considered as a surrogate for habitat intactness (Venter et al. 2016), as well as the (iii) sub-catchment area in km^2. For these cost information, we assumed that (i) a higher HFI in a given sub-catchment would imply a higher cost to restore this sub-catchment to its natural state, and that larger sub-catchments — if deemed for protection — would be more expensive to manage than smaller ones. We scaled and centred both cost values per sub-catchment.

We set the Gurobi solver (Gurobi Optimisation 2024) to minimise the objective function using the *add_min_set_objective()* function in prioritizr (Hanson et al. 2024). We added a connectivity constraint to emphasise the longitudinal connectedness of the resulting priority areas, where the *add_boundary_penalty()* function penalises scattered and hydrologically non-connected priority areas by increasing its costs. Moreover, smaller planning units (sub-catchments) were favoured over larger ones, assuming that larger units would increase the management and protection costs in the final prioritisation scheme (done via the *add_linear_penalties()* function). We set both penalties after iteratively testing varying settings, following a subsequent visual inspection of the outcome. The benefit of these penalties is the balance between clumped and scattered priority areas, as well as the size of the planning units in the subsequent solutions. We selected a range of fish conservation targets for each species at 20%, 30%, 40% and 50% using *add_relative_targets()* function. This means that for each target a new run is carried out keeping all parameters other than the relative target equal. Each target amounts to the proportion of suitable habitat that needs to be covered in the priority areas for each species (e.g., 30% of a species suitable habitat). The targets are chosen to encompass different conservation goals. The 30% target resembles the conservation goal set by the Convention on Biological Diversity (CBD, COP 15) in Montreal 2022 to increase protection coverage of land and ocean until 2030 (Convention on Biological Diversity (CBD) 2020), while the 50% target reflects the call advocated by different civil society actors and scientists to conserve half of the area of each existing habitat type on earth (Dinerstein et al. 2017). Note that the term "protection" is used loosely, that is, a protected area may not be a strictly protected area but instead could be managed and still allow for exploitation, provided that the use of resources is considered sustainable through properly enforced harvest regulations. We allowed a gap to optimality of 10%, which constitutes a compromise between computational time and solution accuracy. Note that with our objective function and the amount of species data, planning units and connectivity constraints, finding the optimal solution within a reasonable time and computational resources would have been challenging (Beyer et al. 2016).

In summary, the spatial prioritisation thus seeks to delineate newly-delineated priority areas that (i) address a given fish conservation target, (ii) have the lowest total HFI value by avoiding large, anthropogenic-influenced areas, (iii) favour small sized sub-catchments and (iv) contiguous, that is, longitudinally connected areas to cover a defined conservation target of suitable habitat of freshwater fish in Colombia.

The outcome of the spatial prioritisation is the information if a given planning unit is included to satisfy the objective function. At this stage, we did not lock in any protected areas to allow for the most flexibility in delineating priority areas (Domisch et al. 2019), and we refer to this as the "free-choice" scenario.

We also ran the spatial area prioritisation by locking in the existing protected areas of Colombia, obtained from the World Database of Protected Areas (Protected Planet 2024). It includes all protected areas of the region following the IUCN and CBD criteria (UNEP-WCMC 2019). We then estimated the amount of additional planning units that would be required to reach the conservation targets. Since protected areas and sub-catchments do not perfectly align spatially with each other, we defined locked-in planning units as those sub-catchments that cover at least 50% of the existing protected area using the *add_locked_in_constraints()* function (i.e., these are the "must-have" sub-catchments). The "locked-in" runs use the identical settings and conservation targets as for the "free-choice" spatial prioritisation. We then compared the spatial extent and distribution between the free-choice and locked-in scenarios with the existing protected areas. The newly-delineated hypothetical priority areas are then used for comparison with the existing protected areas in the study area. Moreover, we assessed the coverage of the newly-delineated priority areas within the major drainage basins, as well as the Strahler stream order (Strahler 1957) of the sub-catchments within the newly-delineated priority areas. We show the results for the 30% target and refer to the Appendixs S1 and S2 for the results of the other targets.

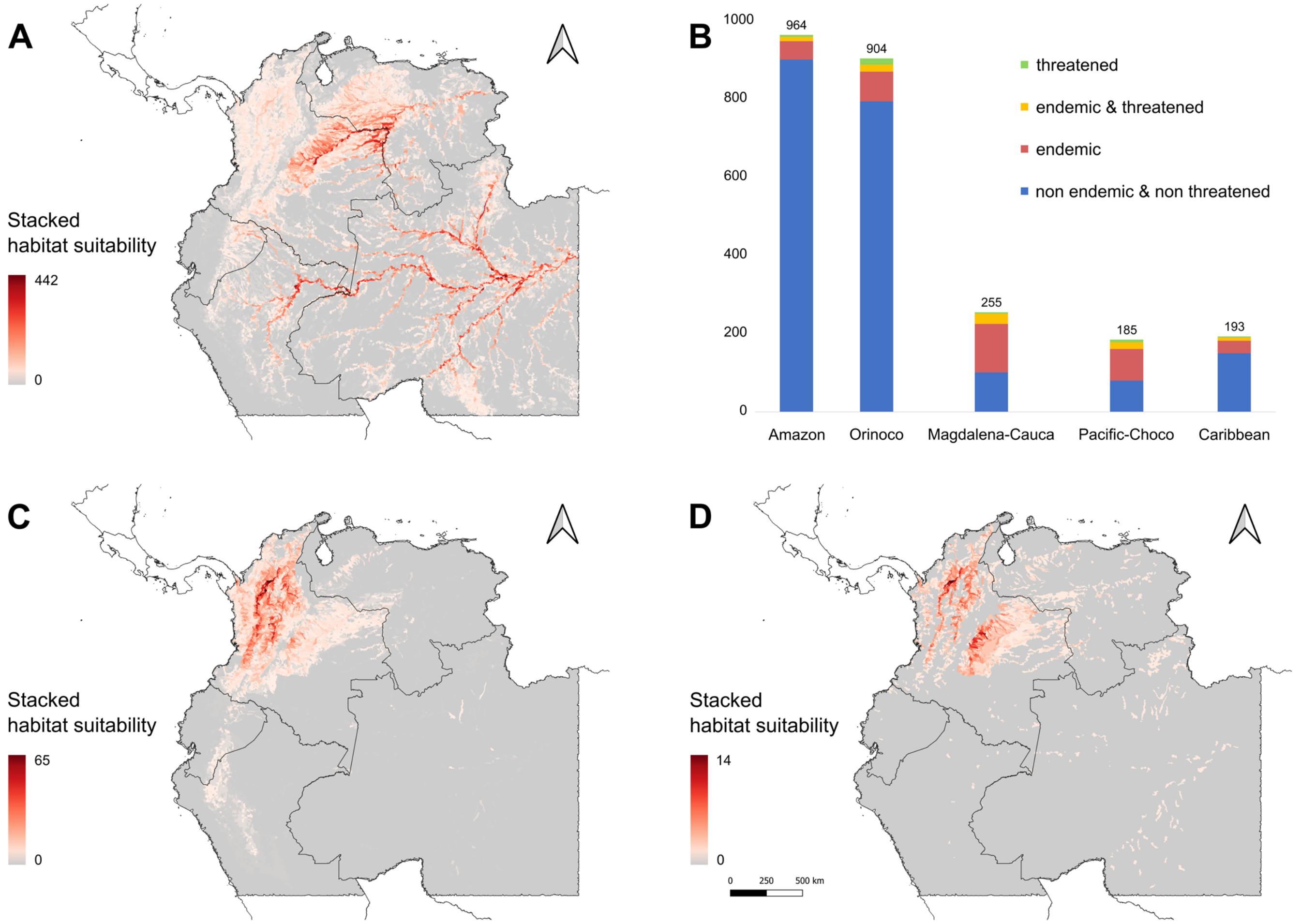

FIGURE 2 | (A–D): (A) Stacked habitat suitability maps of all 1313 freshwater fish species in the larger modelling domain. Colours refer to the amount of species suitable habitat within a sub-catchment; (B) number of species grouped by their endemism and threat status per drainage basin; (C) endemic species stacked habitat suitability map; (D) stacked habitat suitability of threatened species. For online, interactive maps, please see https://glowabio.org/project/colombia_conservation. All maps are projected in the WGS 84 coordinate reference system.

3 | Results

3.1 | Model Evaluation Scores

The evaluation scores of the SDMs ranged between 0.668 and 1 for the TSS scores (0.929 ± 0.061; mean ± standard deviation) and 0.921–1 for the Receiver Operating Characteristics (ROC) curve (0.987 ± 0.012), suggesting overall high model accuracy.

3.2 | Fish Habitat Suitability Predictions

The fraction of the Amazon basin within our study area has the highest number of species with projected suitable habitats. Of all species, 73% (964) have one or more sub-catchments with suitable habitat in the Amazon basin (Figure 2A). This is followed by the Orinoco basin, which holds environmentally suitable habitat for 69% species (904), including also the single sub-catchment with the highest number of species with projected suitable habitat (437 species; Figure 2B). The spatial pattern of higher numbers of suitable habitat per sub-catchment follows the Orinoco river and its larger tributaries, for instance the Meta river. We observe this pattern also in the Amazon basin, which has the highest stacked suitability at the Amazon river and at the confluences with the Rio Negro and Rio Madeira. The Magdalena-Cauca, those parts of the Pacific-Choco and Caribbean basins within our study area have a lower total number of species stacked habitat suitability with 255, 185 and 193 species, respectively.

The Magdalena-Cauca and Pacific-Choco basins contain the highest number of endemic species suitable habitats. Of the total 237 endemic species used in the study, 63% (150) and 41% (98) are projected to have suitable habitats in these two drainage basins, respectively. The areas with the highest amount of endemic suitable habitat can be found along the Magdalena and Cauca rivers (Figure 2C). We observe the highest number of stacked habitat suitability of 34 threatened fish species in the Orinoco basin in the headwater streams of the Meta river (Figure 2D). Another area where threatened species suitable habitats stand out, similarly to the endemic freshwater fish species, is located in the Magdalena-Cauca and Pacific-Choco basins. Those parts of the Amazon basin that overlap with our study area contain lower numbers of endemic and threatened species in comparison to the total number of species. In total only 7% of the suitable habitats in those parts of the Amazon can be attributed to endemic species and 0.6% to threatened freshwater fish species. In the Caribbean basins, we observe

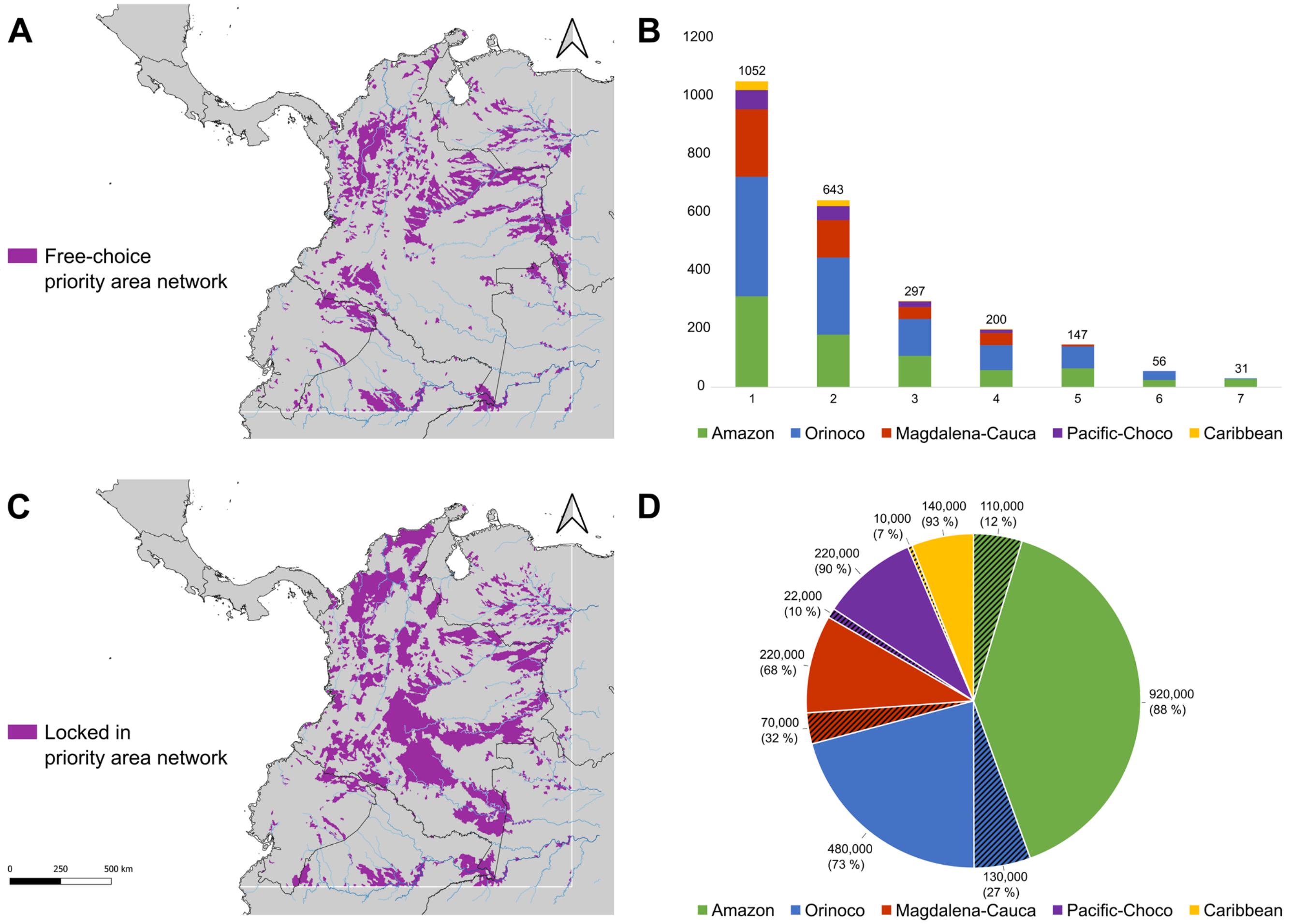

FIGURE 3 | (A–D): (A) Newly-delineated priority areas under the free-choice scenario using a 30% conservation target. Colours refer to sub-catchments included in the newly-delineated priority areas; (B) Strahler order of the newly-delineated priority areas, that is, sub-catchments grouped by their drainage basins; (C) newly-delineated priority areas under the locked-in scenario with a 30% conservation target. Colours refer to sub-catchments included in the priority area network; (D) Drainage basins area in km^2 within our study area; for example, green represents the fraction of the Amazon basin within our study area with shaded green showing the prioritised area in km^2 and the percentage of the Amazon drainage basin area in brackets. Light green represents the non-prioritised area and the percentage of the total Amazon drainage basin area in brackets. All maps are projected in the WGS 84 coordinate reference system.

the lowest amount of stacked suitable habitat of endemic and threatened Colombian freshwater fish species. It contains suitable habitat for 193 species, of which 17% are endemic and 3% are threatened species.

3.3 | Spatial Prioritisation

The resulting priority areas targeting 30% of each species' suitable habitat comprise 2426 sub-catchments distributed throughout the study area, corresponding to a total area of 336,167 km^2 (or 14.4% of the study area; Figure 3). We found that within the territory of Colombia, 1532 sub-catchments are selected as newly-delineated priority area, corresponding to 214,943 km^2 in size or 18.8% of Colombia's territory. The remaining 894 sub-catchments with a size of 121,596 km^2 are located in the neighbouring countries of Brazil, Peru, Venezuela and Ecuador.

The majority of the sub-catchments within the newly-delineated priority areas belong to the Strahler stream order 1 and 2 (Figure 3B). They make up around 43% and 27% respectively of the newly-delineated priority areas. Larger stream segments of Strahler order 6 and 7 constitute around 2% and 1%, respectively, and are solely selected in the Orinoco and Amazon basins. The largest share of stream segments of the Strahler order 1–6 was selected from the Orinoco basin. For Strahler order 7, the majority (28 of the 31) of prioritised sub-catchments belong to the Amazon basin.

For the locked-in run with the existing protected areas of Colombia, we found that compared to the free-choice run, an additional area of 191,152 km^2 would be required to achieve the 30% conservation target. In total, the newly-delineated priority areas extend over 527,319 km^2 of which 119,927 km^2 constitute the prior locked-in existing protected areas. Notable additional patches of priority areas were needed in the headwater streams of the Orinoco tributaries, for instance, of the Meta and Inirida rivers, as well as the Cauca river in the Magdalena-Cauca basin to fulfil the conservation target. Furthermore, the locked-in run added larger priority areas in Venezuela, Peru and Ecuador.

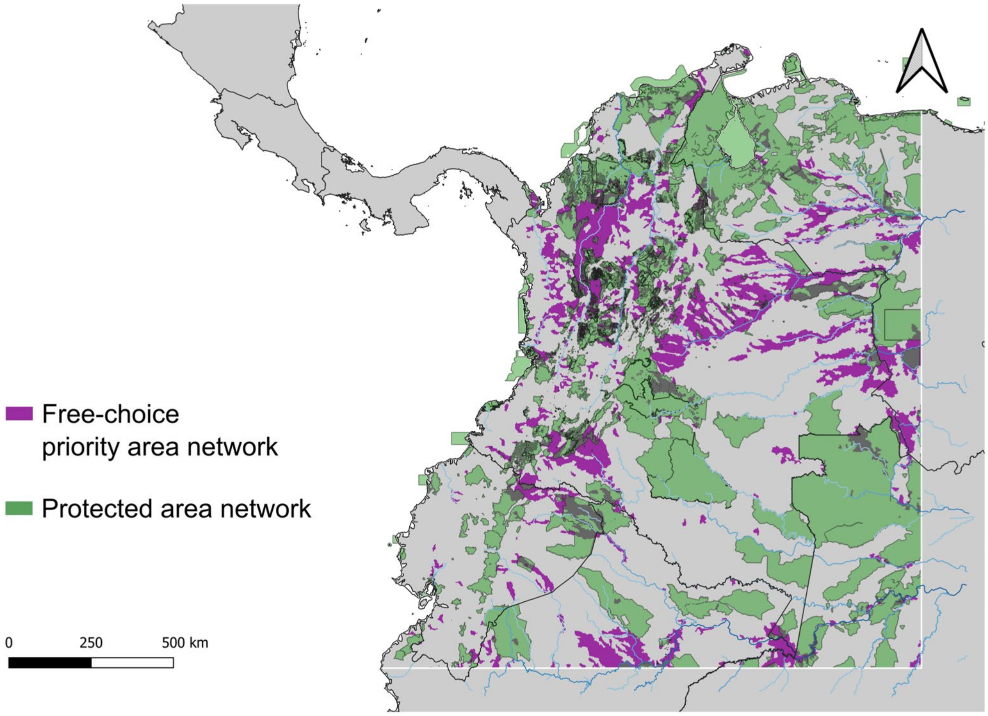

FIGURE 4 | Overlay analysis between existing protected areas and the newly-delineated priority areas derived from the free-choice scenario and the 30% conservation target. Purple colours refer to the newly-delineated priority areas, green colours refer to existing protected areas derived from the World Database of Protected Areas (Protected Planet 2024). Map projection in WGS 84.

3.4 | Comparison With the Existing Protected Areas

The spatial overlap between the existing protected areas and the newly-delineated priority areas shows an overlap of 25.2%. In total, 84,688 km^2 (51,604 km^2 within Colombia) of prioritised sub-catchments located within the study area overlay with the existing protected area network (Figure 4).

4 | Discussion

Our study assessed the spatial distribution of 1313 Colombian freshwater fish suitable habitats, which followed the known core-periphery species richness patterns of the neotropical region (Albert et al. 2020; Boschman et al. 2023). The results support our hypotheses, and we (i) observed that the highest number of species suitable habitats are found in sub-catchments of the major streams of the Orinoco and Amazon rivers and their largest tributaries. They are located closer to the core of the South American continent and its highest freshwater fish species richness (Dagosta et al. 2021). Moreover, we found that (ii) achieving a 30% target in protecting individual species distributions would require 14.4% of the study area, and that the newly-delineated priority areas overlap only by 25.2% with the existing protected areas. In addition, (iii) we found that endemic and threatened species are of special importance for the delineation of the newly-delineated priority areas, given that these species occupy unique habitats within restricted geographical locations (Barletta et al. 2010). Strikingly, our study indicates that the required amount of area to protect the Colombian ichthyofauna is close to what the existing protected areas already cover, however the spatial distribution of these existing protected areas cover only a fraction of the fish species suitable habitats. Hence, this questions the efficiency of the existing protected areas towards freshwater fish conservation. The advantage of our modelling approach hereby lies in its comprehensiveness including the majority of Colombian freshwater fish biodiversity, while exclusively favouring endemic and threatened species with small distribution ranges. Additionally, it buffers uncertainties about the threat status of data deficient species or potential shifts of suitable habitat in light of climate change or other increased anthropogenic impacts since it targets all species through a connected set of priority areas (Dinerstein et al. 2017). Our study indicates the ineffectiveness of the so-called “umbrella concept” in Colombia towards safeguarding biodiversity in its entirety, meaning that by focusing conservation efforts on a flagship species or particular types of ecosystems it confers protection to a larger number of co-existing species (Roberge and Angelstam 2004). By integrating stream connectivity and socio-economic considerations through the use of the HFI we are able to identify relevant areas for freshwater fish conservation on the national scale of Colombia.

4.1 | Distribution of the Newly-Delineated Priority Areas

Our results showed that those sub-catchments that would be needed to fulfil the 30% conservation target are distributed across all drainage basins (Figure 1). The Orinoco basin contains the highest amount of the newly-delineated priority area patches (908), which reflects the high number of species and high number of endemic species found in the basin. In general, the high share of endemics in this basin is due to its unique biogeographic history given the habitat fragmentation and isolation caused by the uplift of the Northern Andes during the Late Miocene and Pliocene (c. 10–4.5 Ma) and general core-periphery characteristics (Cassemiro et al. 2023), such that these endemic species have evolved occupying different niches and structurally different habitat types. The newly-delineated priority areas need to cover those spatially diverse habitats and thereby integrate a higher number of sub-catchments for endemic species into the network. This is in contrast to either generalised species tolerating wider environmental factors or species occupying habitats of similar environmental conditions, where the complementarity regarding all fish species can be reached with a limited set of habitat suitability patches.

We observe this trend in the part of the Amazon basin within our study area, which has an equally high species richness (964 number of all species) as those parts of the Orinoco basin, yet a smaller share of endemic species (47 endemic species) and in total contains fewer prioritised sub-catchments (744). In the Amazon basin, species occupy habitats with similar environmental conditions in the newly-delineated priority areas, mainly clustered around the main stem of the Amazon river (Bogotá-Gregory et al. 2020). More strikingly, only 12% of the area in the Amazon basin, which is within our study area, is part of the newly-delineated priority areas (Figure 3D). In comparison, the Magdalena-Cauca basin, which contains just 255 freshwater species, requires 32% of the drainage basin to be delineated as priority areas. The Magdalena-Cauca basin in turn shows a high degree of endemic and threatened species, again resulting in a larger share of newly-delineated priority areas compared to the total number of sub-catchments. The Caribbean drainage basin, with the smallest species richness and low endemism, reveals the lowest number of all priority areas.

Around 70% of the newly-delineated priority areas fall into 1st and 2nd Strahler order streams. This indicates that headwaters and small streams are a cornerstone in providing suitable habitat to most of the species in the study area (Maire et al. 2017). The diversity of headwater streams, in terms of their water flow, structural elements and chemical composition results in various unique habitats (Richardson 2019). Furthermore, this structural diversity in habitats facilitates evolutionary adaptations in fish species, observable in the higher rates of endemism found in headwater streams in Colombia (Albert and Carvalho 2011; Tognelli et al. 2016). Headwater streams are not only important habitats for endemic and specialised species but impact the ecological processes and fisheries of downstream rivers as well, for instance by constituting important spawning sites for migratory species in Colombia (Colvin et al. 2019; Lasso et al. 2016). Additionally, priority areas of smaller streams in the vicinity of larger ones, such as the Amazon river, are important to the latter especially during flood periods, in which they form lateral connections with a mosaic of different habitats (Stegmann et al. 2019). With their smaller water volume, headwater streams are more vulnerable to structural and environmental changes (Swan and Brown 2017) and their biodiversity faces a higher risk of extinction (Tagliacollo et al. 2021).

4.2 | Overlap With the Existing Protected Area Network

The locked-in solution required an additional area of 191,152 km^2 compared to the free-choice run, indicating a high share of fish suitable habitats outside the existing protected areas, which the model needed to select to fulfil the 30% conservation target. The lack of coverage between Colombia's protected areas and key biodiversity features such as threatened species has been well reported for other organism groups such as mammals, birds, amphibians and reptiles (Albornoz-Espinel et al. 2017; Bax and Francesconi 2019; Forero-Medina et al. 2014). The priority areas identified outside of the existing protected areas offer a range of possibilities to implement conservation strategies for fish diversity in Colombia. In general, any initiative to implement areas for conservation in Colombia, from the highest level of National Protected Areas to the local reserves, can greatly benefit from the areas defined here, by overlapping different areas of interest and making sure that fish diversity is also included. Moreover, the newly-delineated priority areas can further promote the creation of distinct fish-focused protected areas: similar as the Important Bird and Biodiversity Areas (IBAs; Donald et al. 2019) identified as being internationally significant for the conservation of birds and other biodiversity, our newly-delineated priority areas can also be used by local institutions or NGO's to create new forms of Important Fish and Biodiversity Areas (IFAs). The inclusion of the Rio Bita catchment area as a priority area in both free-choice and locked-in solution suggests that the Rio Bita could be considered as a prime example to address freshwater biodiversity in protected areas (Suárez et al. 2021). It thus represents a promising path in Colombian freshwater conservation since it focuses on the entire catchment area instead of viewing rivers merely as borders to outline protected areas. Our results have the potential to facilitate decisions regarding new protected areas, with a focus on freshwater biodiversity, in contrast to the terrestrial-focused approach. Beyond the identification of non-protected important areas for fish diversity, a key contribution of this study is the map of habitat ranges for the fish species. Colombia has a very robust system in place to visualise the state-of-the-art knowledge of biodiversity, for example with distribution range maps (https://biomodelos.humboldt.org.co/), yet missing distribution maps of fishes. The outputs of this study could feed such tools and start the process of involving expert knowledge to improve the location of fish habitats.

4.3 | The Newly-Delineated Priority Areas Covering Biodiversity Hotspots

The newly-delineated priority areas overlap with several important freshwater biodiversity sites (hotspots) in Colombia (Henao et al. 2020; Lasso et al. 2016; Suárez et al. 2021). For instance, the Rio Bita freshwater biodiversity hotspot is situated in the north-east of Colombia at the border to Venezuela, and its catchment was officially designated as a protected area in 2018 (Andrade et al. 2018). In our free-choice scenario, the Rio Bita is also included in its majority within the newly-delineated priority areas. The overlap between the existing protected areas of the Bita river and the newly-delineated priority areas constitutes 72%. The high coverage contrasts the otherwise poor overlap between protected and priority areas and indicates the improvements to freshwater biodiversity conservation in Colombia when focusing on entire river catchments. Other biodiversity hotspots of the Orinoco basin represented in our priority areas are the Ramsar site of the fluvial star of Inirida, the majority of the Meta river, as well as the Ariari river (Lasso et al. 2016). Noteworthy for its ecological uniqueness and high freshwater biodiversity in the Amazon region and included in our priority areas is the Yahuarcaca lake system (Henao et al. 2020; Portocarrero-Aya and Cowx 2016). It is situated in the most southern part of Colombia at the border to Peru and Brazil. At this location the Amazon river forms an interconnected system with four lakes (Henao et al. 2020). Part of it in Colombia is designated as a Ramsar site (Protected Planet 2024). Our priority areas fully include the Ramsar site and extends further the entire Colombian Peruvian border into Peru.

For Colombia our findings agree with the general pattern found by Tognelli et al. (2019) and Miqueleiz et al. (2023) who reported a low overlap between protected areas and freshwater fish species on larger scales (e.g., average sub-catchment of 1000 km^2 for Tognelli et al. (2019)). However, large spatial domains are prone to the modifiable area unit problem (MAUP; Jelinski and Wu (1996)), resulting in different spatial patterns for larger scales through the aggregation of data (Friedrichs-Manthey et al. 2020) and which are likely to increase the underlying uncertainty of the spatial prioritisation (Hermoso and Kennard 2012). For instance, Nogales et al. (2023) reports for a single river sub-catchment a high overlap between protected areas and freshwater fish priority areas. Their study, even though being conducted in a remote sub-catchment of the Amazon basin, where large protected areas exist (Nogales et al. 2023), shows the importance of high-resolution data in spatial prioritisation analyses. In this regard, our study strikes a balance between the high-resolution data application and the high computational demands on the national scale. Further research using recent advances in geospatial computing and seamless high resolution hydrological and species data (Amatulli et al. 2022; Schürz et al. 2023) are necessary to identify the potential effects of the MAUP in our results, and how the MAUP possibly cascades in the priority area delineation.

In the broader context, our findings align with previous studies that highlight the protection gaps in freshwater biodiversity in the neotropics. For instance, in a global study Miqueleiz et al. (2023) identified basins in the neotropics requiring freshwater conservation due to their low overlap with current protected areas. Further, Tognelli et al. (2019) and Quenta-Herrera et al. (2022) observed a similar trend for endemic freshwater fish species in the tropical Andean mountain region, while Oliveira et al. (2021) observed this pattern in the Paraná-Paraguay basin in central South America. For the Amazon basin, studies show mixed outcomes regarding freshwater fish spatial prioritisation. On the one hand, Jézéquel et al. (2020b) showed a good representation of freshwater fish habitats; however, using large spatial units of analysis. On the other hand, this is in contrast with Dagosta et al. (2021), who focused on endemic Amazon freshwater fish species, as well as Frederico et al. (2018) and Leal et al. (2020), who observed a mismatch between freshwater fish biodiversity and protected areas; however, using smaller spatial units and at local scale. This exemplifies the importance of addressing spatial scale and resolution, and strengthens the contribution of our study in providing high-resolution outputs on the national scale, limiting the effect of the MAUP (see also Friedrichs-Manthey et al. 2020). Moreover, the inadequate representation of freshwater organisms within protected areas extends beyond just freshwater fish taxa, as also shown by Torres-Cambas et al. (2026) using aquatic insects across the Cuban archipelago, Dias-Silva et al. (2021) using aquatic insects in Brazil, and Nieto et al. (2017) focusing on macroinvertebrates in northern Argentina. In addition, Gonçalves et al. (2018) observed this similar trend in freshwater crustaceans in southern Brazil and Uruguay. Terrestrial protected areas especially fail to address small range, often endemic and threatened, freshwater fish species (Dagosta et al. 2021; Raghavan et al. 2016; Tognelli et al. 2019) which are inherently addressed in the spatial prioritisation of this study.

4.4 | The Effect of Endemic and Threatened Species on the Newly-Delineated Priority Areas

Our newly-delineated priority areas implicitly favour species with small distribution ranges which often coincide with endemic and threatened freshwater fish species. On average, small-ranged species with less than 10 suitable habitat sub-catchments have ca. 60% of their suitable habitats included in the priority areas (see Appendix S1). This high number of suitable habitats of endemic species compared to the conservation target of 30% is achieved through the implicit focus on clumped and longitudinally connected areas in the spatial prioritisation. Sub-catchments in close spatial proximity, and which are longitudinally connected to those sub-catchments which are suitable for endemic species, have a higher chance to be included via the spatial auto-correlation, given that the environmental conditions are also similar. This favours the selection of sub-catchments close to endemic species, as reflected in the higher share of sub-catchments prioritised in the endemic-rich basins of the Magdalena-Cauca and Orinoco basins, and addresses their special importance for conservation given their high vulnerability towards environmental or anthropogenic stressors (Nogueira et al. 2010).

The entire newly-delineated priority areas of the Magdalena-Cauca basin can be considered suitable habitat for endemic fish species. While this would be in contrast to the high human footprint index across the basin, it also means that the spatial prioritisation selected those sub-catchments that can be considered unique regarding their habitat for endemic fish species, which could not be integrated in the solution elsewhere. This is also in line with Tognelli et al. (2019) who reported a high number of endemic fish species in the Andean region, and agrees with the high number of threatened and endemic species in the Magdalena-Cauca basin. This underlines the importance of an increased focus especially on the priority areas within the Magdalena-Cauca basin.

4.5 | Limitations

We identified several limitations in our study: first, the heterogeneous and systematic (taxonomic and spatial) biases of the observed species data, typical for publicly available species occurrence information, may cascade into the SDMs. We addressed this limitation by data cleaning as well as spatially aggregating data across sub-catchments to reduce the impact of sampling biases, as well as to account for network connectivity. In addition, we limited species habitat suitability projections only to those drainages that are connected to the occurrences, further reducing the impacts of model overpredictions. Regarding the connectivity of the network, we have not included any intermittencies such as dams or other barriers in our study which may impact the conservation effectiveness. Given the importance of connectivity on species dispersal, this integration of stream fragmentation into our modelling approach represents a vital avenue of future research. This however requires overcoming the challenges regarding range-wide information on dams and barriers, their attribution to the correct (modelled) stream network segment, their height, size and thus the potential passability of fish, and finally possible legacy effects in case of, for example, recent dam constructions or removals. Although the existing protected areas differ in their status (e.g., National Protected Areas vs. Local Reserves), we note that we treated these equally such that the overlap of 25.2% between the existing and newly-delineated priority areas is likely to be lower when addressing strict conservation areas. The analysis thus constitutes the minimum extent of freshwater conservation, since any filtering, that is, by IUCN categories of different protection statuses would likely decrease the overlap further. In general, the conservation potential of protected areas depends on how they address the local threats that affect fish species and how they are managed and enforced (Edgar et al. 2014). For example, our study does not imply that the chosen protected areas must be strict no-take areas as long as exploitation pressures threatening local fish species are properly addressed through harvest regulations and effort controls. The most important threats to riverine freshwater fishes are usually not exploitation-induced, but related to environmental and land use changes, including damming (Arlinghaus et al. 2002).

We highlight that the size of the sub-catchments bears uncertainties regarding the SDMs as well as the spatial prioritisation, although the average size of the protected areas of 264.5 km^2 exceeds the average size of the sub-catchments (153 km^2). This is because data is aggregated and averaged to these spatial units while not addressing the within-unit heterogeneity. Using such a proxy, in addition to the human footprint index (HFI), can only provide basic information regarding the costs or penalties in selecting areas deemed for protection. For instance, range-wide data on the enforcement capacity, restoration feasibility, or opportunity costs could provide more informed results regarding the on-ground situation and potential for successful protection within a given sub-catchment.

That said, we emphasise that the newly-delineated priority areas should not be used as the only source for biodiversity conservation measures, but can be used to yield a general estimate of the coverage of freshwater biodiversity in protected areas in Colombia and their potential conservation efficacy. In contrast, systematic conservation planning would require taking socio-economic trade-offs and stakeholders into consideration (Ribeiro and Atadeu 2019), which was however beyond the scope of our analysis. Consequently, our study cannot replace, for instance, systematic conservation planning, but rather guide decision makers and conservationists to areas of potential high biological value currently not represented in the existing protected area network, where further analyses can take place.

5 | Conclusions

Freshwater fish biodiversity is currently poorly covered by the existing protected areas in Colombia. We found that 25.2% of the newly-delineated priority areas, targeting 30% of the 1313 individual fish suitable habitats, overlap with the existing protected areas in the study area, emphasising a major gap in present-day freshwater fish protection. The large contribution of range-restricted endemic and threatened species stood out in the priority area delineation, as well as the high prevalence of headwater streams that contribute by 70% to the newly-delineated priority areas. We consider the newly-delineated priority areas a valuable starting point for effective freshwater conservation in Colombia, and call for further analyses on other freshwater taxa groups, also at high spatial resolution, to ultimately close the knowledge and protection gap regarding spatial freshwater biodiversity and conservation. We acknowledge that our work is only one piece of information towards improving conservation in Colombia and entirely disregards socio-economic trade-offs and other values in conservation decision-making. While addressing these is beyond the scope of our work, our study clearly identifies the areas where improved conservation actions would be required, be it through protected areas or other means, to advance freshwater fish conservation.

Author Contributions

Thomas Tomiczek: conceptualization (equal), methodology (equal), formal analysis (lead), visualization (lead), writing – original draft (lead), writing – review and editing (equal). **Jaime García Márquez:** conceptualization (equal), formal analysis (supporting), writing – review and editing (equal). **Robert Arlinghaus:** writing – review and editing (equal). **Sami Domisch:** conceptualization (equal), methodology (equal), formal analysis (supporting), writing – review and editing (equal), supervision (lead).

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data, including the newly-delineated priority areas for multiple targets are available in the IGB Freshwater Research and Environmental Database (FRED) (https://doi.org/10.18728/igb-fred-1074.0) and as a

DRYAD dataset (https://doi.org/10.5061/dryad.ksn02v7fx). An online interactive visualisation of the results is available at https://glowabio.org/project/colombia_conservation. All code for the analyses is available in Github under https://github.com/glowabio/Colombian-fish-prioritisation.

Peer Review

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** All conservation targets. (A–D): (A) Newly-delineated priority areas under the free-choice scenario with a 20% conservation target. Colours refer to sub-catchments included in the newly-delineated priority areas; (B) Newly-delineated priority areas under the free-choice scenario with a 30% conservation target; (C) a 40% conservation target; and (D) a 50% conservation target. **Figure S2:** All locked-in targets. (A–D): (A) Newly-delineated priority areas under the locked-in scenario with a 20% conservation target. Colours refer to sub-catchments included in the newly-delineated priority areas; (B) Newly-delineated priority areas under the locked-in scenario with a 30% conservation target; (C) a 40% conservation target; and (D) a 50% conservation target. **Table S1:** Species list. Table S1 provides the full overview of all 1313 species used in the study including the names, family, endemic and threat status, occurrence per drainage basin, occurrence aggregated per sub-catchment and drainage basin, habitat suitability distance scaled per drainage basin, habitat suitability per drainage basin and occurrence per data provider (GBIF, Species link network, FishNet2, IdigBio).