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Identifying the current and future status of freshwater connectivity corridors in the Amazon Basin

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Abstract

The Amazon Basin features a vast network of healthy, free-flowing rivers, which provides habitat for the most biodiverse freshwater fauna of any basin globally. However, existing and future infrastructure developments, including dams, threaten its integrity by diminishing river connectivity, altering flows, or changing sediment regimes, which can impact freshwater species. In this study, we assess critical rivers that need to be maintained as freshwater

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connectivity corridors (FCCs) for selective freshwater species—long-distance migratory fishes and turtles (both with migrations >500 km) and river dolphins. We define FCCs as river stretches of uninterrupted river connectivity that provide important riverine and floodplain habitat for long-distance migratory and other species and that maintain associated ecosystem functions. We assessed more than 340,000 km of river, beginning with an assessment of the connectivity status of all rivers and then combining river status with models of occurrence of key species to map where FCCs occur and how they could be affected under a scenario of proposed dams. We identified that in 2019, 16 of 26 very long (>1000 km) rivers are free-flowing but only 9 would remain free-flowing if all proposed dams are built. Among long and very long rivers (>500 km), 93 are considered FCCs. Under the future scenario, one-fifth (18) of these long and very long FCCs—those that are of critical importance for long-distance migrants and dolphins—would lose their FCC status, including the Amazon, the Negro, Marañón, Napo, Ucayali, Preto do Igapó Açu, Beni, and Uraricoera rivers. To avoid impacts of poorly sited infrastructure, we advocate for energy and water resources planning at the basin scale that evaluates alternative development options and limits development that will impact on FCCs. The results also highlight where corridors could be designated as protected from future fragmentation.

KEYWORDS
Amazon, connectivity, freshwater biodiversity, rivers

1 | INTRODUCTION

The Amazon Basin is one of the world's ecological treasures because of its high biodiversity and its functional role in the climate and hydrological cycles (Coe et al., 2017; Reis et al., 2016). Over the last few decades, significant resources have been invested in developing a sustainable terrestrial protected area (PA) network across the basin (World Bank, 2018). The Amazon Basin has about 23% (1,984,569 km^2) of its territory under some level of protection within PAs across five countries. The most extensive PA coverage is located in Brazil (1,037,074 km^2), followed by Venezuela (249,109 km^2), and Bolivia (207,227 km^2) (RAISG, 2019). However, freshwater ecosystems have not received dedicated attention, with several studies showing that the current PA system under-represents freshwater species and ecosystems (Fagundes et al., 2015; Frederico et al. 2018; Mosquera-Guerra, Trujillo, Park, et al., 2018; Anderson et al., 2019; Azevedo-Santos et al., 2019; Leal et al., 2020). In addition, existing PAs are threatened by downsizing, downgrading, and degazettement (Mascia et al., 2014), with the construction of hydropower plants having been the most frequent cause of documented changes to PAs in Brazil (Pack et al., 2016).

The hydrological dynamics and the connectivity of rivers in the Amazon Basin are critical for life cycle completion for many freshwater species. For example, dolphins, river turtles, and many fish migrate longitudinally and/or laterally to feed, disperse, or reproduce (Hurd et al., 2016). *Podocnemis* river turtles have temporal and spatial periodicity to both their lateral and longitudinal movements and at least one species (*P. expansa*) has been documented to move over 500 km (Carneiro & Pezzuti, 2015). During flooding, most *Podocnemis* river turtles use lakes, flooded forests, backwaters, and channels to feed. In the dry period, they move towards the rivers where their nesting areas are located (Fachín-Terán et al., 2006). The health of river dolphin populations in the Amazon Basin is strongly influenced by flood pulses and habitat connectivity (Pavanato et al., 2016; Trujillo et al., 2010). River dolphins move between main river channels, tributaries, flooded forests, and lagoons, in response to seasonal water level changes and often following the movements of fish (e.g., Gomez-Salazar et al., 2011; Mosquera-Guerra et al., 2021). Additionally, many terrestrial or semi-aquatic species, such as jaguars (*Panthera onca*), capybaras (*Hydrochoerus hydrochaeris*), otters (*Pteronura brasiliensis*, *Lontra longicaudis*), marsh deer (*Blastocerus dichotomus*), and several monkey species, are highly dependent on lateral connectivity to floodplain habitats (e.g., Groenendijk et al., 2014; Haugaasen & Peres, 2005).

Amazonian migratory fish species can be grouped by the distance and pattern of annual movements. Recent studies show that some Amazonian goliath catfishes (*Brachyplatystoma* spp.) display continental scale migrations (>2000 km) with the most extreme case being the gilded catfish *B. rousseauxii*, migrating up to nearly 6000 km between nursery sites in the lower Amazon and estuary in Brazil and spawning sites in the Andean piedmont of Bolivia, Colombia, Ecuador, and Peru (Barthem et al., 2017; Cañas & Pine III, 2011; Duponchelle et al., 2016). Goliath catfish continental migrations contribute about 23% of annual landings in the basin (Duponchelle et al., 2021). Amazonian migratory Characiformes species perform inter-basin longitudinal and lateral migrations connecting wetlands between nutrient-rich (floodplains) and nutrient-poor rivers (tributaries) over at least 2 million km^2, or about one-third of the Amazon Basin (Goulding et al., 2019). Based on detailed studies of jaraqui (*Semaprochilodus* spp.), annual inter-basin migrations include three complex movements (spawning, trophic, and dispersal) that can extend for 1300 km in Central Amazonia (Ribeiro & Petrere, 1990). Inter-basin migratory large-sized Characiformes (*Colossoma macropomum* and *Piaractus brachypomus*) and small-sized Characiformes (e.g., *Semaprochilodus* spp., *Prochilodus* spp., *Brycon* spp.) are the most important food fishes in Amazonia contributing about 67% of annual fisheries landings in the basin (Duponchelle et al., 2021). Nutrient-poor tributary-restricted fish migrants display annual longitudinal and lateral movements (500–1200 km) that do not include a whitewater mainstem. Many Characiformes and Siluriformes species have been recorded migrating in the lower Rio Tocantins (Mérona et al., 2010), along the middle-upper Rio Araguaia and middle-upper Rio Tocantins (Ribeiro et al., 1995), along the lower-middle Rio Xingu (Hahn et al., 2019), along the lower–middle Rio Tapajós (Nunes et al., 2019) and upper Rio Tapajós (Lopes, 2018). Blackwater tributary-restricted migratory fishes account for about 5% of annual fisheries landings in the basin (Duponchelle et al., 2021).

Short-distance fish migrants and residents (<500 km) form a large group of generally small species (<20 cm) that may be abundant from the mainstem to the upper courses of tributaries (Bogotá-Gregory et al., 2022; Duponchelle et al., 2021) where they overlap somehow with long-distance migratory species or even in small upland forest streams (Beltrão et al., 2019). However, with some local exceptions, their migrations are poorly understood as they are not commonly captured by commercial fishing. Lateral migrations (<100 km) performed by most migratory Characiformes between floodplain lakes and the whitewater mainstem have been recorded (Araújo-Lima & Ruffino, 2003; Diaz-Sarmineto & Alvarez-León, 2003; Cox-Fernandes, 1997; Goulding, 1980). Short-distance longitudinal migrations (<400 km) have also been successfully monitored by indigenous fishermen in Rio Tiquié where copious schools of *Leporinus agassizii*, *Leporinus klausewitzi*, *Cyphocharax multilineatus*, *Chyphocharax spilurus*, *Curimatella alburna* among others move upstream to spawn *and* return to the lower course floodplains to feed (Lima et al., 2005).

Meanwhile, human pressures remain intense on freshwater systems and river connectivity is under threat, particularly from dam development (e.g., Anderson et al., 2018; Flecker et al., 2022; Lees et al., 2016; Winemiller et al., 2016). Healthy and connected rivers provide a suite of ecosystem services within the Amazon Basin, including fisheries, floodplain and recession agriculture, river transport, and carbon sequestration in peat ecosystems (Coomes et al., 2010; Coomes et al., 2016; Ribeiro et al., 2021). Migratory fishes contribute about 93% (range 77%–99%) of the fisheries landings in the basin, amounting to ~US $436 million annually (Duponchelle et al., 2021). Dams present are not only unpassable obstacles for migratory species but also affect the hydrological dynamics and water quality characteristics that can potentially affect a wide range of freshwater organisms (Poff & Zimmerman, 2010). The most significant cumulative hydrological alterations of dams in the Amazon are in the frequency and duration of flow pulses (Timpe & Kaplan, 2017), with large dams in certain subbasins of the Amazon having already altered downstream river flow amplitude by up to 3 orders of magnitude (Chaudhari & Pokhrel, 2022). However, the Amazon still contains many free-flowing rivers (FFR) with a recent study documenting the Amazon River as the longest remaining FFR from source to outlet globally (Grill et al., 2019). The location and characteristics of aquatic infrastructure, especially dams, play a decisive role in the scope and magnitude of impacts, with even small dams potentially delivering significant impacts (Almeida et al., 2019; Couto et al., 2021; Flecker et al., 2022; Timpe & Kaplan, 2017). Recently several studies have been published focusing on the potential loss of biodiversity, fisheries, water and sediment flows, and river connectivity in the face of proposed dam development (e.g., Anderson et al., 2018; Forsberg et al., 2017; Latrubesse et al., 2017; Winemiller et al., 2016). These assessments show that existing dams are concentrated in tributary networks and headwater systems, leaving many mainstem rivers particularly vulnerable to fragmentation by future large dam development. Anderson et al. (2018) emphasize the high alpha and beta diversity of headwater streams and anticipated declines in diversity due to further fragmentation and Couto et al. (2021) emphasize the role that small hydropower plants are anticipated to have in this fragmentation.

In this study, we analyze the current and future status of the Amazon Basin's river connectivity for long-distance migratory fish and turtles and for river dolphins. This study builds on and complements previous connectivity studies in the Amazon Basin by providing a comprehensive analysis of river connectivity impacts (i.e., dams [hydropower and non-hydropower], lateral connectivity disruption due to roads and urban areas, water regulation, and sediment disruption) and combining that with information on long-distance species movements and migrations. We consider the potential consequences, including fragmentation and changes to habitat quality downstream and upstream of barriers, and quantify the cumulative impacts of dams and other pressures on river connectivity. Furthermore, we estimate future impacts in order to support conservation planning, the formulation or improvement of national policies and infrastructure plans, and inputs to implementation of international agreements such as the Amazon Cooperation Treaty (ACT), the Convention on Biological Diversity (CBD), and the Leticia Pact. As a way of classifying which rivers are most important to migratory fish, turtle, and river dolphin species that need large-scale river connectivity to complete their life cycles, we identified freshwater connectivity corridors (FCCs). We define FCCs as river stretches of uninterrupted river connectivity that provide important riverine and floodplain habitat for long-distance migratory and other species and that maintain associated ecosystem functions. Our study has the following objectives: (1) mapping the current and future status of river connectivity following methods from Grill et al. (2019) and updated with data and methodological adjustments specific to the Amazon; (2) identifying FCCs for long-distance migratory fishes, turtle, and river dolphin species considering current river connectivity; and (3) identifying the FCCs most vulnerable to be impacted by planned dams.

2 | METHODS

2.1 | Overview

In this assessment we use a combination of spatial analysis and indicator mapping to identify FCCs. The main steps and components are outlined in Figure 1 and are described in more detail in the respective sections below. First, we followed the methods in Grill et al. (2019) and conducted a "Free-flowing River Assessment" to identify the connectivity status of rivers in the Amazon Basin. For this, we gathered up-to-date information on a set of pressure factors impacting river connectivity using mainly official data provided by national governments or data published in scientific journals (Table 1).

We then conducted a literature review to identify long-distance (>500 km) migratory fishes and turtles, and all river dolphin species in the Amazon Basin (Literature Review S1) and used spatial mapping techniques to identify their range within the river network. Then, we combined the connectivity status with the migratory species ranges and applied a simple algorithm to identify FCCs. To assess future threats and the status of FCCs, we conducted the identification of FCCs for two scenarios: the "current" scenario of connectivity status including operational dams as of 2019 and the "future" scenario representing a hypothetical, worst-case outcome under the assumption that all proposed hydropower projects in the Amazon Basin are built.

2.2 | Hydrographic framework

The river network used in this study is from the global hydrographic data framework of HydroSHEDS (Lehner & Grill, 2013) with a grid resolution of 500 m. The river network includes long-term average discharge values derived from the hydrological model WaterGAP (Döll et al., 2003). Discharge values were used for the calculation of pressure indices, and to focus the analysis on rivers that had a long-term average natural discharge of 10 m^3/s or greater. Our study area covers the entire hydrological Amazon Basin including the Tocantins River as well as several small basins that flow directly into the Atlantic Ocean in the Amapa and Maranhão states in Brazil as these basins are categorized as part of the Brazilian legal Amazon. River reaches were defined as the linear unit between two confluences resulting in 136,866 river reaches (343,237 km total length). Following Grill et al. (2019), a river, as a hydrological unit distinct from river reaches, was defined as all river reaches from source to outlet with an outlet being either the confluence with the next largest river or the ocean, a method first described by Hack (1957). Using this definition, we identified 6291 rivers, which were classified according to their individual length into short (10–100 km); medium (100–500 km); long (500–1000 km); and very long (>1000 km) rivers.

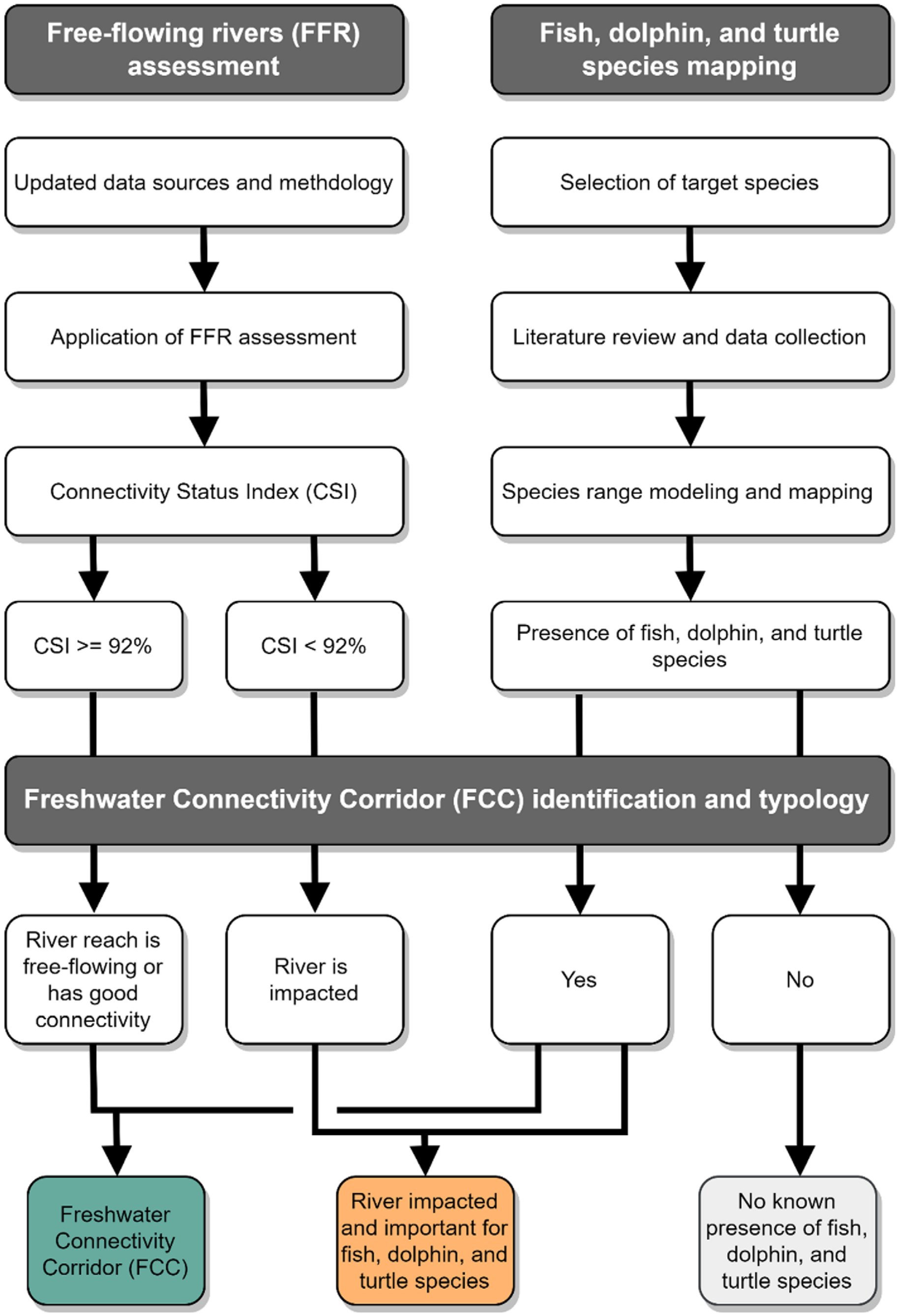

FIGURE 1 Conceptual overview of methodology and steps to determining freshwater connectivity corridors. We first assessed the connectivity status of all Rivers in the study area using the free-flowing Rivers assessment outlined by Grill et al. (2019). We then mapped fish, dolphin, and turtle species using available datasets and species range modeling. We then identified the freshwater connectivity corridors by combining river connectivity status with models of occurrence of key species to map where FCCs occur. FCC, freshwater connectivity corridor

2.3 | River connectivity status

River connectivity is a critical component of the identification of FCCs. We follow a comprehensive definition of river connectivity inclusive of its four dimensions: "fluvial connectivity encompasses longitudinal (river channel), lateral (floodplains), vertical (groundwater and atmosphere), and temporal (intermittency) components" (Grill et al., 2019). The pressure factors that affect different dimensions of river connectivity were previously identified by Grill et al. (2019) and have been included in this study: (a) river fragmentation; (b) flow regulation; (c) sediment trapping; (d) water consumption (surface or groundwater abstractions); and (e) infrastructure development in riparian and floodplain areas (using information from the proxy indicators of road density and nightlight intensity in urban areas). To quantify each pressure factor, we calculated six proxy indicators using data from available local sources, or otherwise used global remote sensing products, other data compilations, or numerical model outputs such as discharge simulations (Table 1).

We introduced four important modifications to Grill et al. (2019) in regard to input data and methodology.

TABLE 1 Connectivity pressure indicators, connectivity aspects affected and data sources used to determine connectivity status index (CSI)

Proxy indices	Description	Main connectivity aspects affected	Data sources
DOF	Degree of fragmentation	Longitudinal	HydroSHEDS (Lehner & Grill, 2013); see Table S1 for list of sources for dams data; HydroFALLS (Lehner et al., 2016)
DOR	Degree of regulation	Longitudinal, lateral, vertical, temporal	HydroSHEDS (Lehner & Grill, 2013); HydroLAKES (Messager et al., 2016); see Table S1 for list of sources for dams data
RDD	Road development	Lateral	IBGE, 2016; IIRSA, 2016; OSM, 2020
URB	Nightlights intensity in urban areas	Lateral	DMSP-OLS v4 (Doll, 2008; Schneider et al., 2009)
USE	Consumptive water use (abstracted from rivers)	Longitudinal, lateral, vertical, temporal	WaterGAP (Döll et al., 2003); HydroSHEDS (Lehner & Grill, 2013)
SED	Sediment trapping	Longitudinal, lateral, vertical	HydroSHEDS (Lehner & Grill, 2013); HydroLAKES (Messager et al., 2016); Global Erosion Map (Borrelli et al., 2017); see Table S1 for list of sources for dams data

First, we replaced the dams, barriers, and waterfall data needed to calculate degree of fragmentation (DOF), degree of regulation (DOR), and sediment trapping (SED) indices with updated data from literature and government sources from multiple countries (Table S1). In total we identified 434 barriers built or under construction and 463 that are proposed (in the early planning phases) in the Amazon Basin (see Table S1 for list of sources) and geo-located the projects to the river network. Note that the list of proposed dams changes from one year to the next as development and economic priorities change. Attributes for proposed dams are typically sparse, including critical information on their reservoir storage volume, which influences our calculations of DOR and SED. We used the storage volume provided in the respective data layers, however for 275 projects, we estimated storage volumes based on a simple linear model that has been derived for observed storage capacity and power generation capacity of planned dams in Asia (Grill et al., 2015). We acknowledge the fact that some run-of-the-river dams have little storage volume, whereas some storage dams are not designed to produce much power. In these cases, the effect of a future dam on the DOR or SED index may be over- or underestimated.

To support the calculation of DOF and account for natural fragmentation from waterfalls and rapids, we identified and geo-located 206 waterfalls and rapids that were considered barriers for at least some of the mapped migratory species (Lehner et al., 2016). Out of these 148 overlapped with species ranges of our mapped migratory species, and include small waterfalls in headwaters, as well as significant rapids on large rivers. During an expert review workshop, these waterfalls were evaluated to act as natural discontinuities for at least some of the mapped migratory species; hence the upstream fragmentation effect of an artificial barrier as calculated by our model did not extend beyond an existing waterfall or rapid.

Second, we replaced the relatively coarse global data used to calculate road density with finer-scale data from multiple sources, including the Brazilian Institute of Geography and Statistics (IBGE) and the GeoBolivia platform, and recalculated the road density (RDD) index. Aside from dam and road data, no other local data could be collected consistently at the regional level to replace global datasets used in Grill et al. (2019).

Third, we applied a weighting model that combines the six proxy indicators to derive the Connectivity Status Index (CSI) for every river reach. The weighting model combines the pressure indices using a simple weighted average, with weighting percentages as suggested by Grill et al. (2019). As such, DOF and DOR were weighted with 30% each, SED and USE, received 15% each, and RDD and URB both received 5%. The CSI ranges from 0% to 100%, the latter indicating full connectivity. Grill et al. (2019) used a threshold of 95% at or above which a river or river reach is defined as free-flowing. In order to set the appropriate threshold within the context of the Amazon Basin, we undertook a benchmarking analysis, which compares the status of known free-flowing rivers (benchmark rivers as defined by local and regional experts; Table S2) with model results from about 100 model simulations using different weights and CSI thresholds. Based on benchmarking analysis results, we determined that 92% was a suitable threshold to generate model results that identify the status of most benchmark rivers correctly. Only river reaches with a CSI of ≥92% were considered as having "good connectivity status" while river reaches below 92% were classified as impacted. Finally, the free-flowing status of a river was defined based on the CSI of its river reaches: if a river is at or above the CSI threshold of 92% over its entire length from source to outlet, then it is considered a free-flowing river. Otherwise, the river is declared not free-flowing, yet it can maintain a mix of reaches with "good connectivity status" (i.e., above 92% threshold) and reaches that are impacted.

2.4 | Freshwater connectivity corridor mapping

2.4.1 | Species selection

We limited the inclusion of species in the analysis to long-distance (>500 km) migratory fishes and turtles, and all river dolphin species in the Amazon Basin for which sufficient information documenting their range and movements were available (see next section and Literature Review S1). We follow Brönmark et al. (2014) and define migratory species as those that undertake movements of individuals or populations from one well-defined habitat to another, usually on a temporally predictable and periodic basis.

In the case of fishes, we included species for which documented migrations of at least 500 km exist, all of which belong to the Siluriformes and Chariciformes orders (see Literature Review S1 for references). Although over a hundred species of fishes have been shown to have short-distance migrations linking floodplains and tributaries to the mainstem habitats (Barthem & Goulding, 2007; García-Dávila et al., 2015; Usma et al., 2009; Van Damme et al., 2011), it is the long-distance migrants that require extensive connected corridors across the basin to complete their life cycles. The importance of these long-distance migratory species is related to their ecological role, their uniqueness of freshwater migration behavior, and as indicators of connectivity, and at the same time, the health status of the basin. Our analysis does not undermine the importance of short distance migrants as they play an essential ecological role at the local scale, nor does it imply that the 500-km threshold used in the selection of species for this analysis would necessarily include all habitat needs of individual species as these are covered in individual species ranges. The focus on the long-distance migratory species provides an understanding of the large-scale connectivity needs across the basin. These species will be particularly affected by loss of large-scale river connectivity (Vasconcelos et al., 2021), as already demonstrated with recent declines in Gilded catfish *B. rousseauxii* within the Madeira Basin (Van Damme et al., 2019). The focus on migratory fish species is additionally justified since they provide a vital food source for local peoples (Goulding et al., 2019). While short-distance migrations are equally important, their movements are poorly understood with some local exceptions and, where they have been documented, short-distance and long-distance migrations overlap along most river stretches (Anderson et al., 2009; Goulding et al., 2003; Miranda-Chumacero et al., 2015). The initial list of species was compiled during a consultation workshop with scientific experts in April 2018, which was then verified by a literature review of gray and published sources to validate that all major documented migration routes were covered (Literature Review S1). In the case of river turtles, we included, *Podocnemis expansa*, the only known turtle species for which migration distances of greater than 500 km have been documented (Carneiro, 2017; Carneiro & Pezzuti, 2015).

River dolphins were also included in the assessment, given their dependence on connectivity of the mainstem to floodplains, some documentation of longitudinal movements and known impacts from fragmentation and flow alterations from dams. South American researchers have published evidence of at least four river dolphin species (Cetartiodactyla): the Delphinid tucuxi *Sotalia fluviatilis* (Gervais 1853), the Iniid pink river dolphin *Inia geoffrensis* (Blainville 1817), the Bolivian river dolphin (*Inia boliviensis*) (Ruiz-Garcia et al., 2008), and the Araguaian river dolphin (*Inia araguaiaensis*) (Hrbek et al., 2014). However, as of 2018, the IUCN and Committee of Taxonomy (2020) of Society of Marine Mammalogy only recognize two species (i.e., *Inia geoffrensis* and *Sotalia fluviatilis*). While all four species are not formally recognized, we included them given that they have been documented in the literature and experienced documented impacts from loss of river connectivity. They have been shown to move hundreds of kilometers (e.g., Martin & da Silva, 2004), with a record maximum of 333 km traveled (Mosquera-Guerra, Trujillo, Da-Costa, et al., 2018).

2.4.2 | Mapping species ranges

Freshwater fishes

Freshwater fish species included only those long-distance migratory species for which we had distribution ranges and some level of evidence of migratory movements >500 km. From the 200 migrating species documented in sources from Colombia, Brazil, Bolivia, and Peru (Barthem & Goulding, 2007; García-Dávila et al., 2015; Usma et al., 2009; Van Damme et al., 2011), we selected 44 species with published indications of migrations >500 km. For five of the species there is direct evidence from telemetry and isotope analysis, while for the others there is medium evidence as provided from country lists of migratory species (see Literature Review S1 for detailed sources on migration). Point location data for these long-distance migratory fishes were compiled from the Global Biodiversity Information Facility, the Brazilian Biodiversity Information Facility Repository (SiBBr), and Amazon Fish (Jézéquel et al., 2020). Species with less than 50 point locations and species with uncertainty around naming convention were not included in the analysis. Twenty-six species had sufficient data to be included in the analysis. In total over 15,000 sample locations were included in the analysis. Following Grill et al. (2014), we used the "minimum spanning tree" method to estimate the ranges for the 26 selected migratory fishes. The "minimum spanning tree method" connects the species point locations in the river network using the shortest distance between each of the point locations. Adjustments to estimate individual species ranges were made based on expert knowledge from field observations.

River turtle

Point data and a species distribution model for *Podocnemis expansa*, the only migratory turtle species in the Amazon Basin that travels >500 km, were collected from existing data sources (Fagundes et al., 2018). Following Grill et al. (2014) we used the "minimum spanning tree" method to estimate *P. expansa*'s range. Adjustments were then made based on expert knowledge and expertise from field observations (Fagundes, pers commun.).

River dolphins

A database with more than 44,000 point locations of dolphin species across the Amazon Basin was recently developed using niche modeling analysis (Mosquera-Guerra, Trujillo, Da-Costa, et al., 2018). This database was the main reference for the four dolphin species included in this analysis. The resulting ranges were improved through a cross-validation process conducted with the support of specialists from Bolivia, Brazil, Colombia, Ecuador, Peru, and Venezuela. For those areas where the presence of river dolphins was not confirmed by experts or found in scientific literature, the range was removed. After the validation, the "minimum spanning tree" method was used to fill small data gaps and to ensure these models were correctly transferred onto the river network.

2.4.3 | Identification of freshwater connectivity corridors

To select FCCs, we combined results from the free-flowing rivers analysis with species range data. If a river reach had at least one of the selected species present and had a connectivity status of free-flowing or good connectivity, then it was considered an FCC (Figure 1). FCCs were mapped for all species and the number of species were split into quartiles that visually represent the diversity of these species across the Amazon Basin.

2.4.4 | Future status of freshwater connectivity corridors

We examined the status of FCCs under two scenarios: the current situation with existing impacts and a future scenario, which includes a set of proposed dams for the region. Our future scenario incorporates the cumulative effects of all 463 proposed dams and as such represents a worst-case scenario, that is unlikely to materialize as is. The results should be seen as an illustrative and hypothetical example, rather than as a prediction of future development, but they provide useful information about the potential magnitude of changes to FCCs in the future.

3 | RESULTS

3.1 | River connectivity status

The first step in identifying FCCs was to conduct a river connectivity assessment, which included the calculation of the CSI (Table 1) and then to identify the existing free-flowing rivers across the Amazon Basin (Figure 3). Most existing dams are located on smaller rivers in the headwaters of the Amazon across the Andes, or in the southern parts of Brazil (Figure 2). Consequently, the impacts on river connectivity from these dams are limited to short- and medium-sized rivers with only small reductions to their CSI values (Figure 3a). However, a small number of hydropower projects on larger rivers cause substantial reductions of connectivity in large and very large rivers over long distances. Notable examples are dams on the Madeira River, the Tapajos, Xingu, and the Tocantins Rivers. Road density (for shorter rivers) and sediment trapping (for longer rivers) are the main pressures for rivers that still maintain good connectivity status (Table S3). DOF is the main pressure for all river categories that are impacted. As a result of substantial connectivity losses in sections of a

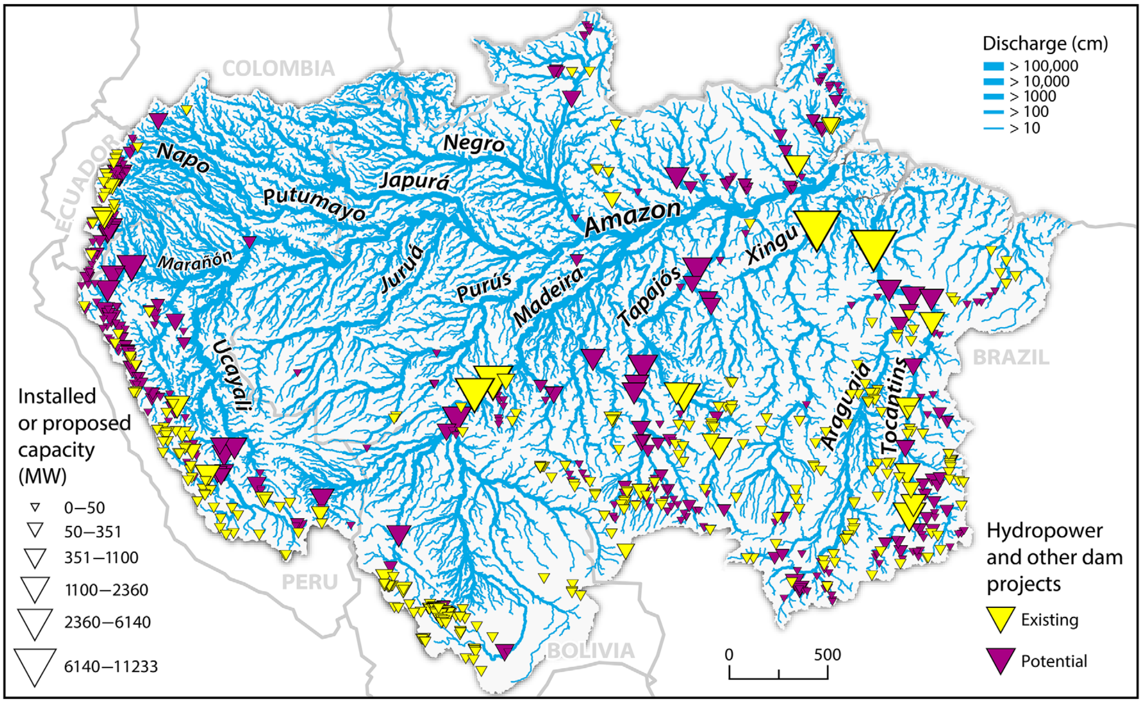

FIGURE 2 Existing and potential dam projects in the Amazon region. Our data included mainly hydropower projects, with a small number of existing dam projects without hydropower production (installed capacity = 0). Dam data was collected from multiple sources listed in Table S1

river, the free-flowing status of the river as an entity is also altered (Figure 3a). Even though the vast majority of short- (10–100 km) and medium-sized (100–500 km) rivers are still considered free-flowing from source to outlet, a larger proportion of longer rivers are affected by dam impacts under the current scenario. By length, only 79% and 63% of long (500–1000 km) and very long (>1000 km) rivers, respectively, are still considered free-flowing (Table 2).

Under the future scenario, a substantial number of potential barriers were identified, with major potential projects in the Marañón, Ucayali, Madeira, Tapajos, and Tocantins rivers (Figure 2). By number, 16 of the 26 very long rivers (>1000 km) are free-flowing as of 2019, but only 9 of them would remain fully free-flowing if all planned dams are built (Figure 3; Table 3). Among those very long rivers that would lose their free-flowing river status are the Amazon, Negro, Marañón, Beni, Ucayali, Uraricoera, and Napo rivers. In addition to the loss of 77 free-flowing rivers, the connectivity status of many additional rivers would also deteriorate (Figure 3b). River fragmentation remains the main pressure for impacted rivers between 10 and 1000 km, whereas for rivers >1000 km sediment trapping becomes more important, with the Amazon River losing its free-flowing status due to the cumulative impact of sediment trapping from dams (Table S3).

3.2 | Freshwater connectivity corridors identification

Migratory freshwater fishes are present in FCCs covering 89,990 km of river length (Figure 4a). The Amazon, Negro, Marañón, and Madeira rivers host 25 migratory species, followed by Putumayo and Nanay (24 species), and Napo, Japurá/Caquetá, Jiparana, and Purus (23 species) (Table S4). River turtles are present in FCCs covering 200,592 km of river length, including the top 10 most diverse rivers (Figure 4b). River dolphins are present in FCCs covering 146,150 km of river length (Figure 4c). There are five rivers near the Amazon estuary that support three different species of river dolphins (Anapu, Camaraipi, Jacundá, Pacajá, Pracuí).

Of the 6291 rivers mapped across the Amazon Basin, featuring a total length of 343,237 km, we found 4644 rivers (260,062 km) whose connectivity is particularly important for migratory fishes, migratory turtle, and/or river dolphin species (Table 4; Figure 5a). Of the rivers that host these species, 4581 rivers (248,341 km) qualify as FCCs, as they also have free-flowing or good connectivity status, whereas 63 rivers (11,721 km) show losses of connectivity that classifies them as impacted (Table 4). We did not identify migratory species or dolphin in about 24% of the analyzed river network representing

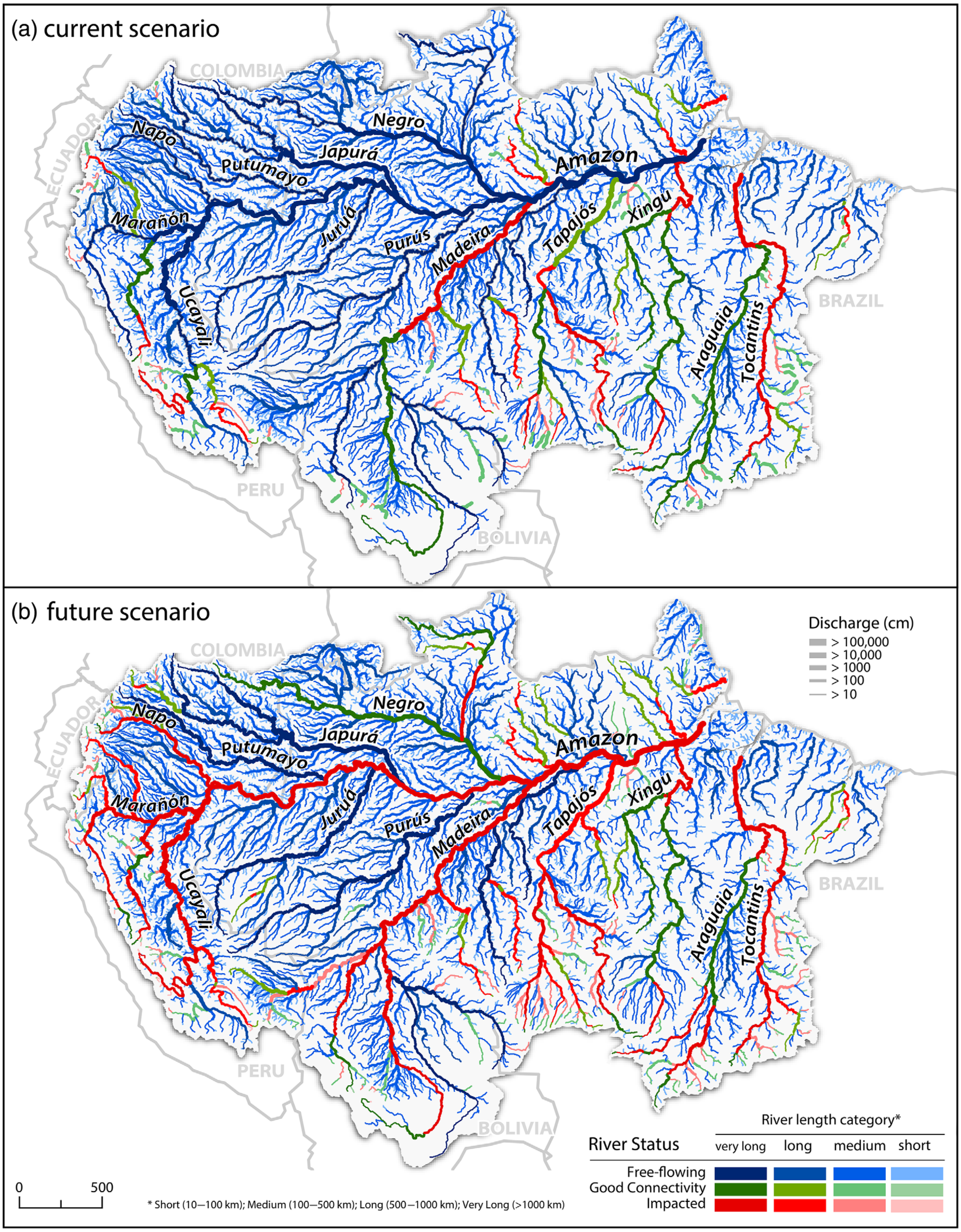

FIGURE 3 Free-flowing river status for current (a) and future (b) scenarios. Discharge is represented by river network thickness, river length is represented by shades of color, and category of colors represent river status

83,175 km. The vast majority (about 88%) of the rivers without migratory species or dolphin is concentrated in short- and medium-length rivers. On the other hand, we found migratory species and dolphins in 86% and 91% of long and very long rivers, respectively, illustrating the importance of these rivers as FCCs (Table 4).

3.3 | Future status of freshwater connectivity corridors

Among rivers >500 km in length, 65% (by river km) are considered FCCs (Table 4). In total, there are currently 93 FCCs >500 km in length that are either free-flowing

TABLE 2 Length of rivers by free-flowing status and river length category for (a) current scenario, (b) future scenario, and (c) difference

River length category[a]	Short	Medium	Long	Very long	Total
(a) Current scenario					
Free-flowing (km)	101,625	142,140	33,791	28,588	306,145
Impacted (km)	1313	9815	8853	17,111	37,092
Total	102,939	151,955	42,644	45,699	343,237
(b) Future scenario					
Free-flowing (km)	101,020	135,019	27,493	15,964	279,495
Impacted (km)	1919	16,936	15,151	29,736	63,742
Total	102,939	151,955	42,644	45,699	343,237
(c) Difference					
Free-flowing (km)	−606	−7122	−6298	−12,625	−26,650

[a]Short (10–100 km); medium (100–500 km); long (500–1000 km); very Long (>1000 km).

TABLE 3 Number of rivers by free-flowing status and river length category for (a) current scenario, (b) future scenario, and (c) difference

River length category[a]	Short	Medium	Long	Very long	Total
(a) Current scenario					
Free-flowing (#)	5067	1029	57	16	6169
Impacted (#)	45	54	13	10	122
Total (#)	5112	1083	70	26	6291
(b) Future scenario					
Free-flowing (#)	5045	992	46	9	6092
Impacted (#)	67	91	24	17	199
Total (#)	5112	1083	70	26	6291
(c) Difference					
Free-flowing (#)	−22	−37	−11	−7	−77

[a]Short (10–100 km); medium (100–500 km); long (500–1000 km); very Long (>1000 km).

(70) or of good connectivity status (23). Under the future scenario, one-fifth (18) of these long and very long FCCs—those that are of critical importance for long-distance migrants and dolphins—would no longer be considered FCCs due to impacts from dams. Among FCC rivers supporting 20 or more species, 8 of them would no longer be considered FCCs (i.e., Amazon, Negro, Marañón, Napo, Ucayali, Preto do Igapó Açu, Beni, and Uraricoera) if all planned dams were built as they would lose their free-flowing status (Figure 5b; Table S4), and 55 FCCs with a total length of 19,419 km would change status (Table 4).

4 | DISCUSSION

Our results indicate where FCCs and important reaches for long-distance migratory fishes, migratory turtle, and dolphins occur across the Amazon Basin, and corroborates the understanding that we should avoid dams on the large rivers that provide migration corridors and pathways for hydrological and sediment flows (Almeida et al., 2019; Anderson et al., 2019; Timpe & Kaplan, 2017). Higher diversity of migratory species in corridors in the central Amazon Basin is expected, this region integrates river flows from many sub-basins (Carvajal-Quintero et al., 2019) and comprises a high heterogeneity of geology and riparian vegetation types (McClain & Naiman, 2008). Our results agree with previously identified turtle conservation priorities based on species richness in the Brazilian Amazon Basin, mostly located in the Amazon River and lower portions of its tributaries and in parts of the Tocantins sub-basin (Fagundes et al., 2018). A congruent pattern is observed for long-distance migratory fishes, where the Amazon River and its major tributaries link reproduction and

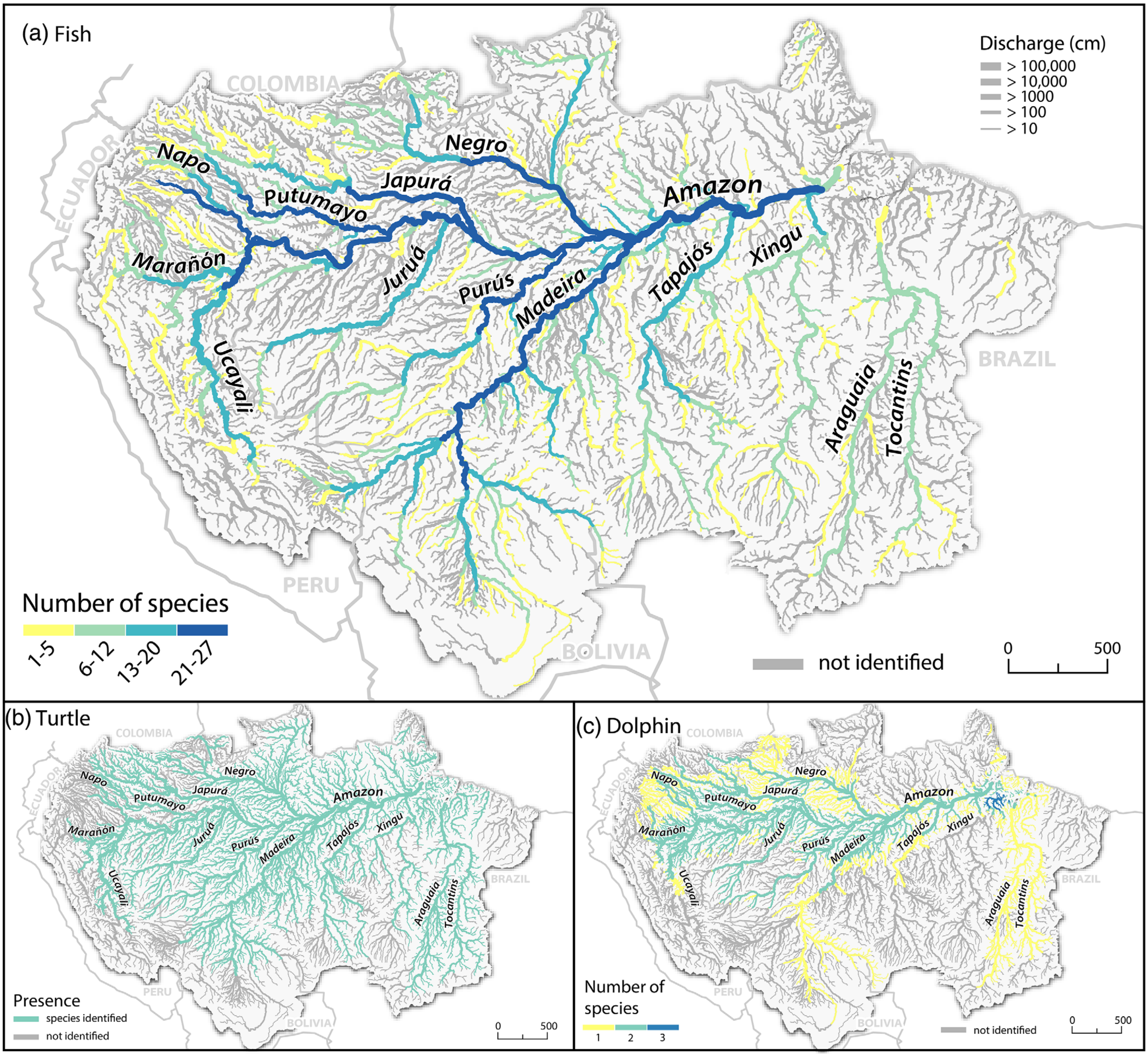

FIGURE 4 Species richness and distribution maps for fish (a), turtle (b), and dolphin (c) species

growth areas and provide irreplaceable migratory corridors (Anderson et al., 2018; Barthem et al., 2017; Ribeiro & Petrere, 1990). A similar pattern is also found for river dolphins, based on recently updated and synthesized information on their distribution patterns in the region, reflecting best available and most up-to-date knowledge (Mosquera-Guerra, Trujillo, Park, et al., 2018; Mosquera-Guerra, Trujillo, Da-Costa, et al., 2018).

While many rivers across the basin maintain high levels of connectivity, significant fragmentation of the major FCCs would occur in a future scenario with planned dams. In particular, the Amazon River, and Negro, Marañón, Napo, Ucayali, Preto do Igapó Açu, Beni, and Uraricoera rivers stand out as critical corridors for large numbers (>20 species) of long-distance migratory fauna and dolphins that are potentially threatened by dam development. Our results largely concur with other recent assessments but add some rivers not identified in prior studies as important corridors (i.e., Preto do Igapó Açu and Uraricoera). For example, Latrubesse et al. (2017), who examined impacts of dams on the alteration of water and sediment flows, similarly concluded that the Tapajós, Marañón, Madeira, and Tocantins-Araguaia are among the most vulnerable sub-basins. Anderson et al. (2018), who focused on Andean-origin rivers, concurred in their conclusion that the Napo, Marañon, Ucayali, Marmoré, and Beni river systems were at risk from proposed hydropower. We did not highlight

TABLE 4 Freshwater connectivity corridors (FCCs) status for current and future planning scenarios

Scenario	Freshwater connectivity corridor status	River length category[a] (km)				Total (km)	Number of rivers
		Short	Medium	Long	Very long		
(a) Current	Freshwater connectivity corridors	68,648	110,602	33,591	35,500	248,341	4581
	Impacted and important for migratory species and dolphins	145	2666	2927	5983	11,721	63
	Sum	68,793	113,268	36,518	41,483	260,062	4644
	No known presence of migratory species or dolphins	34,146	38,687	6126	4216	83,175	1647
	Total	102,939	151,955	42,644	45,699	343,237	6291
(b) Future	Freshwater connectivity corridors	68,578	108,257	29,564	22,524	228,923	4526
	Impacted and important for migratory species and dolphins	215	5011	6954	18,959	31,139	118
	Sum	68,793	113,268	36,518	41,483	260,062	4644
	No known presence of migratory species or dolphins	34,146	38,687	6126	4216	83,175	1647
	Total	102,939	151,955	42,644	45,699	343,237	6291
(c) Difference	Freshwater connectivity corridors status changed (km/number of rivers)	−70	−2345	−4027	−12,976	−19,419	−55

[a]Short (10–100 km); medium (100–500 km); long (500–1000 km); very long (>1000 km).

the Madeira (or the Marmoré, which was classified as part of the Madeira) as at risk as it was already considered to have lost free-flowing status due to the Santo Antônio and Jirau dams. Our assessment builds on earlier studies by providing mapped FCCs and other metrics that can now be explicitly included in basin-wide planning, including informing alternative development pathways and corridors to keep protected from future fragmentation.

The socio-ecological and economic impacts of such fragmentation and alteration of the flow regime can be expected to lead to declines in populations or losses of migratory species, declines in fisheries, changes to floodplain and riverine habitats due to inundation and flow alterations, and loss of sediment flows that feed downstream floodplains and delta habitats (Arantes et al., 2019; Constantine et al., 2014; Prestes et al., 2022). Many indigenous and riverine communities depend on migratory fish as a source of protein and livelihood with recorded consumption rates of freshwater fish by Amazonian riverine communities being among the highest recorded globally (e.g., Isaac et al., 2015). Fragmentation of additional free-flowing corridors would be expected to impact fish populations as has been documented in recent declines in fish populations and associated reductions in catch, particularly for migratory species (Lima et al., 2020; Prestes et al., 2022; Van Damme et al., 2019). An example of community-level impacts comes from the decline in fisheries affecting the livelihoods of fishers in the vicinity of the Belo Monte hydroelectric dam following its construction (Castro-Diaz et al., 2018).

Floodplains and the flows that sustain them also provide critical habitats for fishes, dolphins, and turtles during different parts of their life cycles, and their integrity can be expected to be affected if upstream dams change hydrological or fluvio-geomorphological processes. It is important to note that 7 of the selected migratory fish species only use lotic habitats along their life cycle, being restricted to the main river channels (although their fish prey are floodplain-dependent), whereas the other 37 species use both the river channels and the inundated floodplain and/or oxbow lakes to complete their life cycle. For turtles, changes in hydrology impact the availability of nesting site locations and their exposure time, and consequently, the rate of nesting success (Eisemberg et al., 2016). For example, Norris et al. (2018) verified the decrease of nesting sandbanks due to the construction of a dam in the state of Amapá, in the Brazilian portion of the Amazon Basin. Several rivers of importance to river turtles are already fragmented (such as Xingu River and Tocantins and Araguaia rivers) and the future scenario with planned dams would likely further impact populations since crucial rivers like the Amazon River, Branco River, and Negro River would no longer be free-flowing. Isolation of subpopulations of river dolphins can also cause the extinction of the species at the local level in

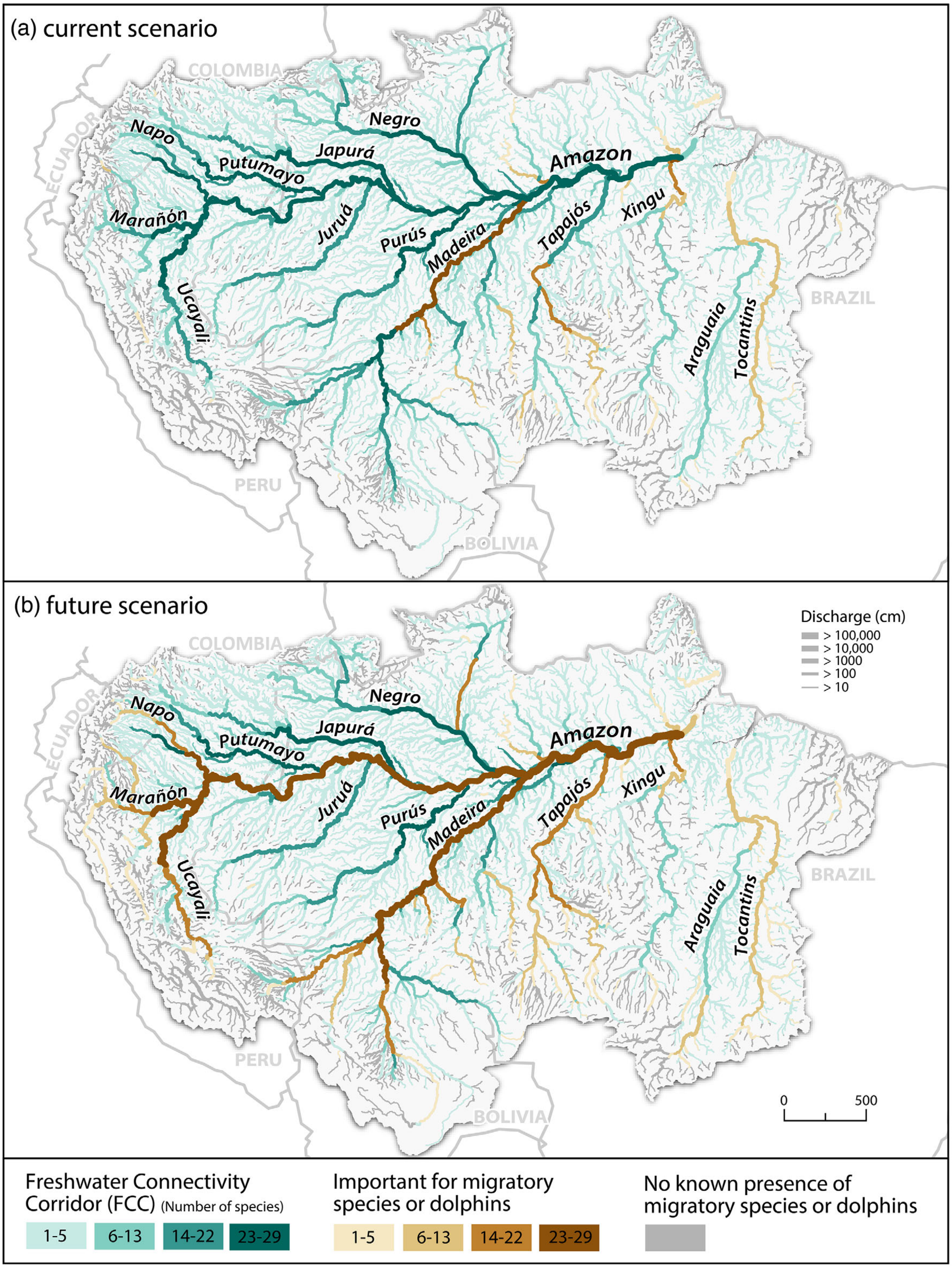

FIGURE 5 Freshwater connectivity corridors (green shades) and important river reaches that still host migratory fish or turtles or dolphin species (brown shades) under current scenario (a) and future scenario, if planned dams are built (b). Color gradations reflect species richness (number of species divided into natural breaks using Jenks' method)

basins affected by dams (e.g., Pavanato et al., 2016) as connectivity across portions of their range is important for genetic exchange (Martin & da Silva, 2004). The connectivity of critical rivers for dolphin species (such as Tocantins, Madeira, and Araguari) is already impacted by dams; for example, the Tucurui Dam isolated the population of *Inia araguaiaensis* within the Araguaia-Tocantins river basin (Araújo & Wang, 2015; da Silva &

Martin, 2010; Paschoalini et al., 2020). Dramatic changes in the distribution and health of river dolphin populations in the Amazon Basin would be expected with additional fragmentation of dolphin ranges.

While many of the FCCs flow through protected areas or border them, there are often not explicit protection mechanisms in place that protect the rivers themselves. In fact, an examination of protected area downgrading, downsizing, and degazettement in Brazil found 28 events that either occurred or were proposed that involved changing protected area status or boundaries to allow dams to be constructed on rivers that flow through them (Pack et al., 2016). Improvement of current policies and the creation of new or innovative mechanisms, such as Other Effective Conservation Area Measures (IUCN, 2019), are needed to ensure that critically important river and floodplain corridors are kept free-flowing or highly connected. In 2021, IUCN adopted a motion at the World Conservation Congress that urges needed actions to protect river corridors in a changing climate (IUCN, 2021). Examples of such mechanisms that could be implemented include river-specific protections that limit loss of connectivity. Anderson et al. (2019) suggest replicating recent policies enacted in Colombia and Costa Rica that restrict hydropower development on certain rivers (Andrade, 2011; MINAE, 2015). For example, long stretches or entire rivers that are FCCs and that are important for multiple species such as the Amazon River and lower reaches of the Tapajós River, could be highlighted as "no-go" zones for future dam development. Prestes et al. (2022) similarly recommend trans-national or interstate agreements for migratory fisheries management across jurisdictions, noting that while all Amazonian countries with the exception of Colombia are signatories to the Convention on Migratory Species, no Amazonian freshwater migratory species are listed within the Convention. Other models include the U.S. Wild and Scenic Rivers designation, Ramsar sites that protect entire free-flowing river catchments (e.g., the Bita River Ramsar site in Colombia), the designation of water reserves that guarantee allocations of river flow for nature and specific human uses (Salinas-Rodríguez et al., 2018), and a recent law that would protect "permanent preservation rivers" ("Rios de preservação permanente") in the state of Minas Gerais in Brazil (Azevedo-Santos et al., 2019). Worthington et al. (2022) recommend the development of a Global Swimways program, similar to the Flyways program for migratory birds, to identify rivers and their associated ecosystems that support the entire migration routes of biologically and/or socio-economically important freshwater fishes. Another recent effort is the Amazon Sacred Headwaters Initiative that is an Indigenous-led effort in Peru and Ecuador to protect headwaters that are considered sacred (Amazon Sacred Headwaters Initiative, 2022). Critical corridors identified in this study would benefit from protection to maintain their free-flowing status and could support countries to meet their commitments under the post-2020 CBD Biodiversity Framework (e.g., goal and targets around area, connectivity and integrity of natural systems). Protection of these corridors would ensure that the critical processes that support the viability of these species and the ecosystem services (e.g., fisheries as food and livelihoods, tourism, river transport routes) that they provide would be maintained. Policies and platforms of particular relevance for these recommendations include the Amazon Cooperation Treaty Organization (ACTO) and its recently initiated Strategic Action Plan, as well as the Leticia Pact. Under the latter, Mandate 8 focuses on connectivity for priority ecosystems and protection mechanisms for the conservation of biodiversity through sustainable use, restoration, and landscape management.

Early upstream planning, which includes socio-ecological and economic information on freshwater species and ecosystems and examines alternative options for meeting energy or water resources needs and sites needed infrastructure in the least harmful locations to ecosystem services delivery, is necessary (Thieme et al., 2021). Two recent studies in the region provide examples of the use of multi-objective optimization techniques to examine alternatives for siting hydropower dams to minimize impacts on five ecosystem services while achieving energy production goals (Flecker et al., 2022) and for siting small hydropower to limit impacts on migratory fish (Couto et al., 2021). Strategic environmental assessments early in the development process that incorporate metrics that examine cumulative impacts within the river and floodplain corridor, such as the CSI (Grill et al., 2019) or locations of FCCs and the Indicators of Hydrologic Alteration (Timpe & Kaplan, 2017), can also be critical to limit impacts across the system (Fortes Westin et al., 2014). State of the art for best practices for dam operations, such as environmental flows (Acreman et al., 2014), can also reduce impacts and modernization of older hydropower plants, to improve their energy efficiency, are also important to maximize energy output of existing dams.

There are several limitations of this current study. First, while more information is collected and available every year, there are still significant gaps in both species distribution and life history for many freshwater Amazonian species. For example, new species of fish are still being described each year and significant gaps remain in sampling across portions of the basin (Jézéquel et al., 2020; Reis, 2013). There is also a severe lack of knowledge about the migratory pathways, timing and frequency of movements, and intraspecies variability in migratory patterns, such that the information provided here is an initial attempt to map where some of the most important corridors are and can be expected to be updated as new information becomes available. Future work should include adding additional migratory species and verifying migration routes of species included in this analysis through tracking or using chemical indicators. Due to the different modeling techniques across groups of species, the resulting FCCs are sensitive to species mapping criteria. For example, fish presence in FCCs is significantly lower than river dolphins. A major difference is the use of point data for fish species, which results in more conservative ranges compared to the modeling method used for river dolphins. The CSI analysis also uses weights that are generic to all species, meaning that they have not been tailored to expected impacts on individual species. For example, all waterfalls included in the analysis are designated as impassable even though certain falls likely have varying degrees of permeability depending on the species. Climate change will also impact river flows and affect river connectivity; future analyses could include scenario modeling of climate change impacts on hydrology (Herrera-R et al., 2020). Finally, the analysis of future scenarios only considered dam development due to limitations in regional datasets for other developments such as planned roads, water-diversion schemes, waterways, and mining.

Our results reinforce the importance of integrated and regional planning for the construction of new dams and other infrastructure across the Amazon Basin. This analysis brings a unique angle by summarizing results by rivers and river reaches and emphasizing that certain rivers that remain intact are crucial for species movement and ecosystem services delivery. Existing conservation and protection mechanisms and OECMs, such as ecological flows or water reserves and national PAs systems are potential avenues for the conservation of FCCs, as well as new mechanisms, such as swimways or dam-free river reaches, which provide opportunities for countries to meet their commitments under a range of regional and international agreements, such as biodiversity goals under the CBD (CBD Secretariat 2021; IUCN-WCPA 2019). The methodology presented here also provides a model that could be applied in other basins around the world to identify FCCs for migratory fauna and can be applied at different scales within the Amazon or other basins (e.g., using shorter-distance migratory species). Decisions on transboundary rivers are particularly difficult where the benefits of dam or other development may accrue in one country while the harm is felt acutely in another. Therefore, it is critical to include this information and debate in regional discussions, such as those through the ACTO, the Leticia Pact, and around development agreements such as the Initiative for Regional Infrastructure Integration in South America.

AUTHOR CONTRIBUTIONS

All authors contributed to the study conception and design. Paul A. Van Damme, Carlos Cañas, C. Fagundes, Nicole Franco-León, E.E. Herrera-Collazos, Céline Jézéquel, Mariana Montoya, Frederico Mosquera-Guerra, Marcelo Oliveira-da-Costa, Mariana Paschoalini, Paulo Petry, Thierry Oberdorff, Fernando Trujillo, Pablo A. Tedesco, and Mauro César Lambert de Brito Ribeiro contributed and reviewed fish, turtle, or dolphin data. Data compilation, cleaning, and analysis were performed by Ricardo Aranha, Guenther Grill, M. Eduarda Coelho, and Natalie Shahbol. The first draft of the manuscript was written by Michele L. Thieme, Bernardo Caldas, Guenther Grill, M. Eduarda Coelho, and Natalie Shahbol and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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CONFLICT OF INTEREST

The authors have no conflict of interest to disclose.

DATA AVAILABILITY STATEMENT

Supporting data and results can be found at: https://doi.org/10.6084/m9.figshare.21267363.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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