



# The effectiveness of protected areas in the Paraná-Paraguay basin in preserving multiple facets of freshwater fish diversity under climate change

Correspondence:  
Anielly Galego de Oliveira  
[anielly\\_oliveira@hotmail.com](mailto:anielly_oliveira@hotmail.com)

Anielly Galego de Oliveira<sup>1</sup>, Oscar Peláez<sup>1</sup> and  
 Angelo Antonio Agostinho<sup>1,2</sup>

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Andrea Bialezki

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Our objective was to evaluate the effectiveness of protected areas (PAs) in the Paraná-Paraguay basin on multiple facets of ichthyofauna, both currently and in future climate change scenarios, based on reaching the 17% of conserved terrestrial and inland water defined by Aichi Target 11. Analyses were carried out vis-à-vis a distribution of 496 native species, modeling for the present and for the future, and in moderate and pessimistic scenarios of greenhouse gases. We calculated species richness, functional richness, and phylogenetic diversity, overlapping the combination of these facets with the PAs. The results indicate that the current PAs of the Paraná-Paraguay basin are not efficient in protecting the richest areas of ichthyofauna in their multiple facets. While there is a larger overlap between PAs and the richest areas in phylogenetic diversity, the values are too low (2.37%). Currently, the overlap between PAs and areas with larger species richness, functional richness, and phylogenetic diversity is only 1.48%. Although this value can increase for future projections, the values of the indices decrease substantially. The relevant aquatic environments, biological communities, and climate change should be considered as part of the systematic planning of PAs that take into consideration the terrestrial environments and their threats.

**Keywords:** Conservation, Functional richness, Ichthyofauna, Phylogenetic diversity, Species distribution modeling.

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<sup>1</sup> Programa de Pós-Graduação em Ecologia de Ambientes Aquáticos Continentais, Universidade Estadual de Maringá, Av. Colombo, 5790, 87020-900 Maringá, PR, Brazil. (AGO) [anielly\\_oliveira@hotmail.com](mailto:anielly_oliveira@hotmail.com) (corresponding author), (OP) [oscar\\_pelaez@hotmail.es](mailto:oscar_pelaez@hotmail.es), (AAA) [agostinhoaa@gmail.com](mailto:agostinhoaa@gmail.com).

<sup>2</sup> Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura, Blocos H90, G80, G90. Universidade Estadual de Maringá, Av. Colombo, 5790, 87020-900 Maringá, PR, Brazil.



Nosso objetivo foi avaliar a efetividade das áreas protegidas da bacia Paraná-Paraguai sobre múltiplas facetas da ictiofauna, atualmente e em cenários futuros de mudanças climáticas baseado em alcançar 17% de áreas protegidas, de acordo com os objetivos de Aichi. Análises foram feitas a partir da distribuição de 496 espécies para o presente e futuro, em diferentes cenários climáticos. Foram calculadas a riqueza de espécies, a riqueza funcional e a diversidade filogenética, sobrepondo a combinação destas facetas com as áreas protegidas. Os resultados indicaram que as áreas protegidas da bacia Paraná-Paraguai não são eficientes em proteger as áreas mais ricas em ictiofauna considerando diversas facetas. A maior sobreposição se dá entre as áreas protegidas e as áreas mais ricas em diversidade filogenética, mas os valores são muito baixos (2,37%). A sobreposição entre as áreas protegidas e os 17% das áreas com maior riqueza de espécies, riqueza funcional e diversidade filogenética é de apenas 1,48%. Para o futuro as projeções indicaram que a sobreposição pode aumentar, mas os valores dos índices caem consideravelmente. Os ambientes aquáticos e as mudanças climáticas são componentes que devem ser considerados no planejamento sistemático de áreas protegidas que consideram essencialmente ambientes terrestres e suas ameaças.

**Palavras-chave:** Conservação, Diversidade filogenética, Ictiofauna, Modelagem de distribuição de espécies, Riqueza funcional.

## INTRODUCTION

Biodiversity can be defined as “the variety of life in all its forms and at all levels of organization” (Hunter Jr., Gibbs, 2007), indicating the diversity of species, genes, functions, biotic interactions, and ecosystems that compose it. All of these distinct facets of diversity are under strong anthropic pressure, which are driving changes in biodiversity patterns and species abundance and occurrence (Naeem *et al.*, 2012), resulting in a fast and marked loss of biodiversity (Barnosky *et al.*, 2011). This loss also implies the loss of ecosystem services and, therefore, the benefits provided by nature to human welfare, without which human society could not persist (Balmford, Bond, 2005). Even so, the evolutionary history that reflects the uniqueness of ancestry over time and potential future diversification (Faith, 1992) is neglected in many studies and decision making related to biodiversity. A similar neglect is observed with respect to the functional role of species, which is inseparable from ecosystem function and services (Woodward, Perkins, 2015).

One of the keystones in global efforts to protect biodiversity is the establishment of protected areas (PAs; Rodrigues *et al.*, 2004). PAs act as refuges for native species and can serve — as one objective among others — the protection of clusters of ecosystems that are representative of the ecological diversity and thus are likely to contain a large portion of the regional species or even target species (Hunter Jr., Gibbs, 2007). These areas can also help the concerned species and communities adapt to climate change over time (Mawdsley *et al.*, 2009), since they provide suitable microhabitats and limit habitat loss and environmental degradation (Hole *et al.*, 2009; Azevedo-Santos *et al.*, 2019; Elsen *et al.*, 2020).



Usually, areas of conservation priority and PAs are founded on the taxonomic dimensions of biodiversity, such as species richness, geographic distribution, and endemism degree (Brum *et al.*, 2017). Despite its importance in the identification of key areas for biodiversity, area selection based solely on species richness cannot be the best conservation strategy. This is because they might underrepresent ecological, morphological, physiological, and evolutionary information (*i.e.*, lineages through time) (Brum *et al.*, 2017). In addition, the taxonomic dimension itself does not reflect complementarity, and can give priority to areas with a similar composition instead of protecting unique assemblages (Brown *et al.*, 2015) and their multiple facets (*e.g.*, functional and phylogenetic). Since the relationship between these complementary dimensions of diversity is poorly understood, little is known about the effectiveness of protected areas that embrace different biodiversity dimensions besides the taxonomic. New insights may be gained through studies mapping where the taxonomic facet overlaps with other biodiversity components. This would allow us to identify which areas feature in the major overlap between these dimensions, and which should therefore be prioritized for management and, at the same time, optimal resource investment (Margules, Pressey, 2000).

Freshwater ecosystems are the most diverse per unit habitat volume on Earth (Albert *et al.*, 2020), but despite being among the most threatened worldwide (Vörösmarty *et al.*, 2010), they are still neglected during conservation area proposals (Saunders *et al.*, 2002; Dudgeon *et al.*, 2006; Azevedo-Santos *et al.*, 2019). They are only incidentally protected by their partial inclusion within terrestrial reserves (Lake, 1980; Skelton *et al.*, 1995), which does not guarantee real protection (Abell *et al.*, 2017). Terrestrial protected areas usually fail to embrace important aquatic issues, such as basin integrity, hydrology, and the introductions of non-native species (Lake, 1980; Skelton *et al.*, 1995). Actions that threaten the freshwater ecosystems — such as dam construction, the removal of water for irrigation, pollution, deforestation, the introduction of non-native species, and mining (Albert *et al.*, 2020; Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services – IPBES, 2019) — can occur outside preserved areas and still affect habitats and biota inside the reserves (Saunders *et al.*, 2002; Johnson, Host, 2010; Abell *et al.*, 2017).

Thus, freshwater species are often unprotected and in danger of disappearing (Dias *et al.*, 2017). Extinction rates of freshwater animals are expected to be almost five times higher than those of terrestrial animals (Ricciardi, Rasmussen, 1999; Turak *et al.*, 2017). We can relate this to the fact that freshwater fish are among the most threatened vertebrate groups in the world, with approximately 35% of all species facing some degree of threat (International Union for Conservation of Nature – IUCN, 2021), behind only amphibians. Freshwater fish are important mediators of ecosystem functions in aquatic environments (Villéger *et al.*, 2017), participating in food webs and the cycling and transport of nutrients, in addition to their regulatory roles impacting a variety of other ecosystem properties (Wootton, Power, 1993; Villéger *et al.*, 2017).

Studies quantifying changes in ichthyofauna along environmental gradients, relating biogeographic patterns to changes in climatic conditions, generally focus on the distribution of individual species and the determination of patterns of richness — and these alone. The species are treated as equivalent units, with their functional role (McMahon *et al.*, 2011) and the ancestral relationships between species (Edwards *et*



*al.*, 2007; Cadotte *et al.*, 2008) being given little consideration. There is thus a great difficulty in assessing how changes in community composition in response to climate changes will translate into changes in functional and phylogenetic diversity (Tilman *et al.*, 2001; Prather *et al.*, 2012; Cadotte *et al.*, 2017), and even in taxonomic diversity. The difficulty of this issue is exacerbated by a great shortfall in the knowledge of the geographical distribution of species and how these species would be supported by protected areas, given that this information is scarce.

Under the agenda of the Convention on Biological Diversity, the Strategic Plan for Biodiversity included the Aichi Biodiversity Targets (CBD, 2020). Target 11 proposes, among other goals, that:

*“by 2020, 17 per cent of terrestrial and inland water areas, especially of particular importance for biodiversity and ecosystem services, are conserved through effectively and equitably managed, ecologically representative and well-connected systems of protected areas and other effective area-based conservation measures, and integrated into the wider landscapes and seascapes.”*

In this context, it is important to evaluate the effectiveness of current PAs on different perspectives of fish diversity, considering a wide range of river basins and also in anticipation of future climate change scenarios, especially for tropical regions of the southern hemisphere, where there is a rich and unique biodiversity, little available information, and more developing countries (CBD, 2007). The mapping of diversity patterns is an essential tool for implementing conservation strategies, although it is only an initial step and one of several important aspects to be considered when planning PAs.

This work evaluates the efficiency of the currently existing PAs in protecting the 17% of areas with the highest values of a combination of different freshwater fish diversity facets in the Paraná-Paraguay basin, a water system distributed across four countries in South America. We linked *in-situ* data recorded in the biological collections to environmental and climate modeling data, functional traits, and phylogenetic information. We expect to find low protection efficiency, since the currently protected areas in the basin have been defined without consideration of the spatial distribution of aquatic organisms. By incorporating a multi-faceted approach to fish fauna, we expect to increase conservation action efficiency, making the basin more resilient to the anthropic actions responsible for the ongoing massive biodiversity loss.

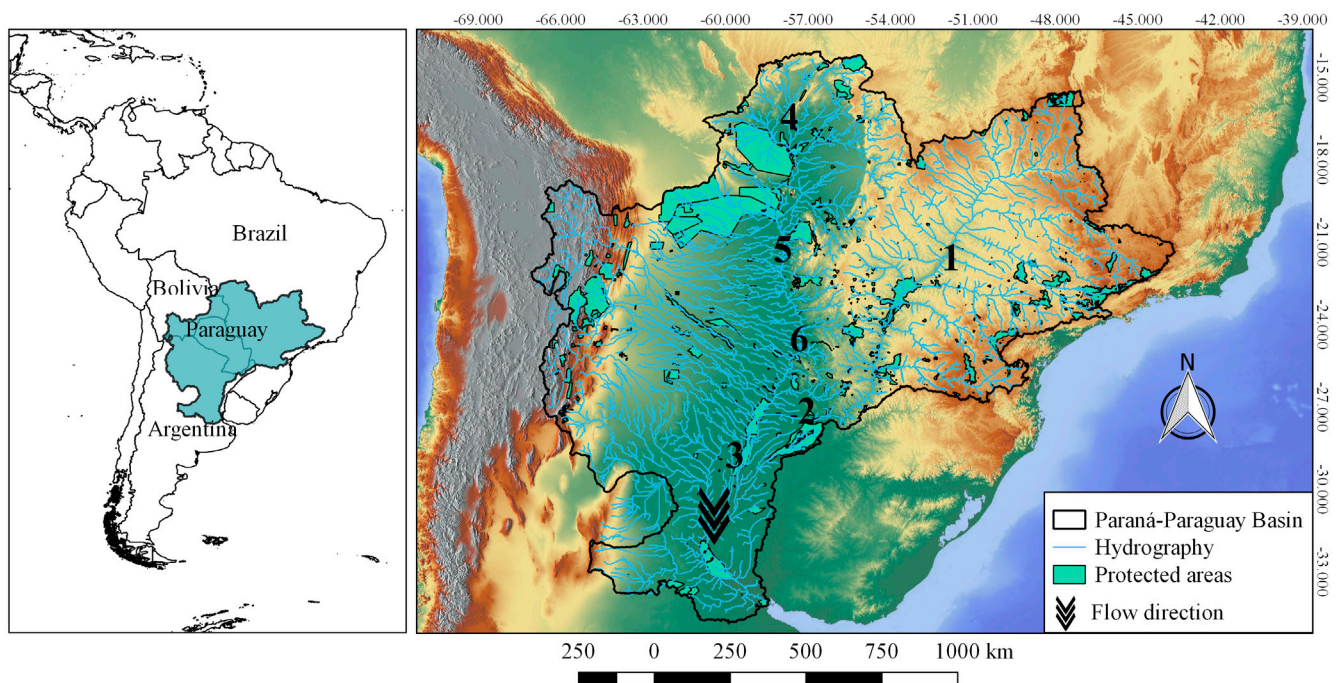
## MATERIAL AND METHODS

**Study area.** The Paraná-Paraguay basin drains about 2,800,000 km<sup>2</sup> of South American territory. Besides occupying a great part of southwestern and southeastern of Brazil, it covers part of the Argentina, eastern Bolivia, and Paraguay territories (Fig. 1). The basin has 1,358 hydroelectric projects in Brazilian territory, from small to large size, including those from inventories, under construction, and in operation (ANEEL, 2018). The northern region of the Paraná-Paraguay basin is characterized by a tropical climate, with marked seasonality, rainy summers, and dry winters. The southern region has a temperate subtropical climate, with rainfall distributed throughout the year (Berbery, Barros, 2002). The Paraná River is formed by the confluence of the Grande and Paranaíba rivers, and is the second-largest river in South America (4,695 km long) and the tenth in the world in water discharge (Agostinho *et al.*, 2008), which corresponds to



12,378 m<sup>3</sup>/s<sup>-1</sup> upstream the confluence with the Paraguay River (IPH, 2015). The Paraná River basin can be divided into upper Paraná, historically separated from the rest of the basin by the “Sete Quedas” falls, which was flooded by the Itaipu reservoir, resulting in the union of two distinct ichthyofaunistic provinces. Currently, it is considered the upper Paraná basin until it reaches the Posadas region in Argentina. The middle Paraná extends to downstream Corrientes, also in Argentina, and the lower Paraná until the Prata River (Berbery, Barros, 2002).

The Paraguay River is the fifth largest in South America (2,550 km long). It originates in the Chapada dos Parecis, receives large rivers such as Cuiabá, São Lourenço, Pilcomayo, and Bermejo, and is the main tributary of the right bank of the Paraná River (Resende, 2003), with an average discharge of 3,899 m<sup>3</sup>/s<sup>-1</sup>. Except for small upper stretches, the Paraguay River is characterized by a low and uniform slope (Berbery, Barros, 2002). The flooded areas of this basin house the Chaco-Pantanal biome, an extensive alluvial plain located in the center of South America (Paranhos Filho *et al.*, 2013) that is both a common destination for ecotourists and home to indigenous people (Mega, 2020). This biome is formed by a complex hydrological system, including different aquatic habitats, such as rivers, lagoons, swamps, and bays. The Pantanal is one of the largest wetlands in the world, sheltering exuberant biodiversity, and is considered a UNESCO-World Heritage Site (Paranhos Filho *et al.*, 2013). Since 2020, this biome has been suffering from unprecedented fires (Mega, 2020).



**FIGURE 1** | Paraná-Paraguay basin showing countries' boundaries, topography, hydrographic features, and protected areas. 1. Upper Paraná River basin; 2. Middle Paraná River basin; 3. Lower Paraná basin; 4. Upper Paraguay basin; 5. Middle Paraguay basin; 6. Lower Paraguay basin.



**Species distribution modeling.** The species occurrence records were compiled from the databases FishNet2 (<http://fishnet2.net/>), SpeciesLink (<http://www.specieslink.net/>), Global Biodiversity Information Facility – GBIF (<http://www.gbif.org/>), and Base de Datos de Peces de Águas Continentales de Argentina (<http://www.pecesargentina.com/>) Eschmeyer's Catalog of Fishes (Fricke *et al.*, 2020). These data were distributed along a regular grid on the Paraná-Paraguay basin, with cells in a spatial resolution of 10 km on each side (11,752 grid cells; EPGS 5880; datum SIRGAS 2000; polyconic projection to keep the area constant). We built a binary matrix of presence (1) and pseudo-absence (0) for each species, composing the biotic component of the analysis. In order to ensure better precision for our predictive models, rare species (species occupying < 4 grid cells) were excluded, as were all non-native species.

Through the species distribution modeling (SDM) technique, the occurrence was extended according to the habitat suitability generated from the climatic/abiotic conditions in sample locations. The bioclimatic predictor variables used were maximum temperature in the hottest month (TMAX; °C), minimum temperature in the coldest month (TMIN; °C), precipitation of the wettest month (PMAX; mm), and precipitation of the driest month (PMIN; mm), all obtained from the WORLDCLIM database (<https://www.worldclim.org/>) for the present and from CCAFS for the future (<http://ccafs-climate.org/>; Research program on Climate Change, Agriculture and Food security). We also used the catchment topographic variable stream elevation (m; SELE, the highest elevation value of the stream segment) and upstream flow length (m; UPFL, the distance to the headwater source from the node) obtained from a digital elevation map (<http://eros.usgs.gov/>) rescaled to our grid. The choice of these variables consisted in searching for a set of ecologically relevant and minimally redundant environmental attributes for the SDM, which would then represent the main parameters determining the organisms' distributions on Earth (Barbet-Massin, Jetz, 2015; Petitpierre *et al.*, 2017).

For the future, we chose a time in the middle of the century (2050) and another at the end of the century (2080) in order to predict the effect of climate change on the fish distribution, according to the International Panel on Climate Change, Fifth Assessment Report (IPCC-AR5) (International Panel on Climate Change – IPCC, 2014). Our predictions involved three Atmosphere–Ocean General Circulation Models (AOGCMs): CSIRO (Australia's Commonwealth Scientific and Industrial Research), MRI (Meteorological Research Institute), and NCAR (National Center for Atmospheric Research). The greenhouse gas concentration trajectory for each AOGCM was based on the Representative Concentration Pathways (RCP), of moderate (RCP 4.5 *stabilization*) and pessimistic (RCP 8.5 *business-as-usual*) scenarios of future carbon emission.

For the SDM we used six models, conceptually and statistically different for the environmental suitability predictions and species distribution area. Specifically, these models were BIOCLIM (Busby, 1991); Euclidian Distance (Carpenter *et al.*, 1993); Gower Distance (Gower, 1971; Carpenter *et al.*, 1993); Ecological Niche Factor Analysis (Hirzel *et al.*, 2002), based on the presence-only data (observed presences to adjust their functions); Maximum Entropy (Phillips *et al.*, 2006); and Genetic Algorithm for Rule-set Production (Stockwell, 1999), based on the presence and pseudo-absence data, with the locations that correspond to pseudo-absences being randomly selected within the study area and used as support for the construction of functions (Ruaro *et al.*, 2019).



To overcome uncertainty about which model is the best for representing environmental suitability — since each model has conceptual and statistical particularities and a range of predictions can be generated — we applied an ensemble forecasting approach as a way to derive the consensus result among six SDM approaches (CONS, Araújo, New, 2007). The main principle in using a consensus approach is that different sources of error affect each niche model in different ways, and the combination of its predictions tends to minimize errors and generate more robust predictions (Diniz-Filho *et al.*, 2009). Only the results of the consensus models were retained for interpretation since it generated a wide variation in predictions. If a model did not have a good performance according to the evaluation and validation methods described below, it was not included in the final model.

The suitability matrices range from 0 to 1, in which values that equal 1 correspond to ideal habitat conditions, and values that equal 0 correspond to suboptimal habitat conditions for the species (Peterson *et al.*, 2011). For each SDM, the continuous suitability predictions were converted into binary vector (1/0) using a threshold that maximizes the sensitivity and specificity values in the Receiver Operating Characteristic curve (ROC curve; see Fielding, Bell, 1997). The ROC curve is generated by plotting the fraction of true positives versus the fraction of false positives, at various threshold settings. The use of all possible thresholds avoids the need for a selection of a single threshold, which is often arbitrary. The area under the ROC curve (AUC) is often used as a single threshold-independent measure for model performance (Allouche *et al.*, 2006).

The species occurrence dataset was randomly divided into subgroups: 75% of the data was used for calibration (training data), and 25% for validation/evaluation (test data). This procedure was performed 50 times in order to avoid biases in the calibration and evaluation data subgroups (Ruaro *et al.*, 2019; Bailly *et al.*, 2021).

Each model was performed with 50 randomizations, and thus we generated 900 predictions (6 SDMs  $\times$  50 randomizations  $\times$  3 AOGCMs) for each future time and carbon emission scenario, totaling 3,600 future predictions. This frequency of projections was weighted by True Skill Statistics (TSS), where better models will have more weight in our consensus projections. The TSS varies from -1 to +1, where values equal to +1 are a perfect prediction, and values equal to or less than 0 are no better than random ones (Allouche *et al.*, 2006). We used the majority consensus rule to obtain the final consensus model for each species, in which the species are considered present only in cells where at least 50% of the models are retained in the ensemble. The SDMs were performed in the BioEnsembles computational platform (Diniz-Filho *et al.*, 2009). After the SDMs, the modeling was restricted according to the geographic barrier to the dispersion of fish species imposed by the Iguaçu Falls, in order to obtain the final species distributions. We also considered the origin and endemism of the species (1 = endemic species of Iguaçu River basin; 2 = species which do not occur in the Iguaçu River basin; 3 = species occurring upstream and downstream from the falls). Finally, this algorithm was performed in the R environment (R Core Development Team, 2019).

**Biodiversity facets.** *Species richness.* To determine the species richness (SR) based on the modeling after the restriction by the Iguaçu Falls, we used the strategy of “*predict first, assemble later*” (*sensu* Overton *et al.*, 2002), in which the distributions of each species



in the present and future scenarios were overlapped to obtain the species number in each grid cell.

**Functional diversity.** We built a functional traits matrix to characterize the species of the Paraná-Paraguay basin. The ecological characteristics chosen were trophic guild, habitat use, presence of long-distance migrations, parental care, internal fertilization, mouth position, and maximum standard length. This information was obtained from articles, books, reports, online databases (*e.g.*, FishBase), and sometimes personal correspondence with experts. When some trait was not available from a species, we used the information for the genera. These data are summarized in the Tab. S1.

From the presence and pseudo-absence matrix resulting from each modeling scenario combined with the trait matrix (matrix T, traits per grid cell), we calculated the functional richness (FRic) (Villéger *et al.*, 2008). The functional richness represents the quantity of multidimensional space occupied by the community, and does not consider species abundance. FRic was calculated in the R environment (R Development Core Team, 2019) using the package FD, function “dbFD” (distance based functional diversity) (Laliberté *et al.*, 2014).

**Phylogenetic diversity (PD).** A molecular fossil-calibrated phylogeny for ray-finned fishes (Chang *et al.*, 2019) was used as the backbone for reconstructing the evolutionary relationships of the 496 fish species from the Paraná-Paraguay basin. At first, the original phylogeny contained only 69% of the species in our occurrence matrix. Missing species were inserted “by hand” in the phylogeny. Species outside Teleostei (Myliobatiformes, Ceratodontiformes) were located in the phylogeny following Betancur-R. *et al.* (2013). Using the functions “add.species.to.genus” and “bind.tip” from the phytools R package (Revell, 2012), the missing Teleostei species were inserted randomly into the roots of genera or families as polytomies. A polytomy resolver following a birth-death model was employed to sample from branch lengths and topologies distributions within the polytomies (Kuhn *et al.*, 2011). The inputs of the birth-death model are the partially resolved phylogeny (constraining by topology), and a uniform prior based on the node ages that determine the range of time where the relationships are to be solved. The Markov Chain Monte Carlo search algorithm of the BEAST software (Suchard *et al.*, 2018) is used to estimate the parameters of growth rate and death rate, based on the uniform distribution of the constrained nodes, and to generate the phylogenetic trees. We sampled 1,000 phylogenies and retained the consensus tree for computing diversity indices.

Phylogenetic diversity was calculated as the sum of the branch lengths (PD; *sensu* Faith, 1992) of the species occurring in each grid cell. For this, we used the “pd” function of the package “picante” (Kembel *et al.*, 2010). Since the phylogeny is dated, the PD index is measured here in millions of years.

**Protected areas and the overlap between the fish diversity facets.** The georeferenced spatial data of the currently protected areas of the Paraná-Paraguay Basin were obtained from the World Database on Protected Areas (WDPA) (UN Environment Programme World Conservation Monitoring Centre; [www.protectedplanet.net](http://www.protectedplanet.net)).

In order to estimate the effectiveness of the currently protected areas, a spatial overlap was carried out between the grid cells in which PAs are located and the 17% of the cells (1,998 cells from 11,752 of total in the grid) with higher values of species



richness, functional richness, and phylogenetic diversity, for both present and future climate change scenarios. We performed these analyses in the free and open source QGIS software (QGIS Development Team, 2020) by using the tool “intersection” and counting the number of cells.

## RESULTS

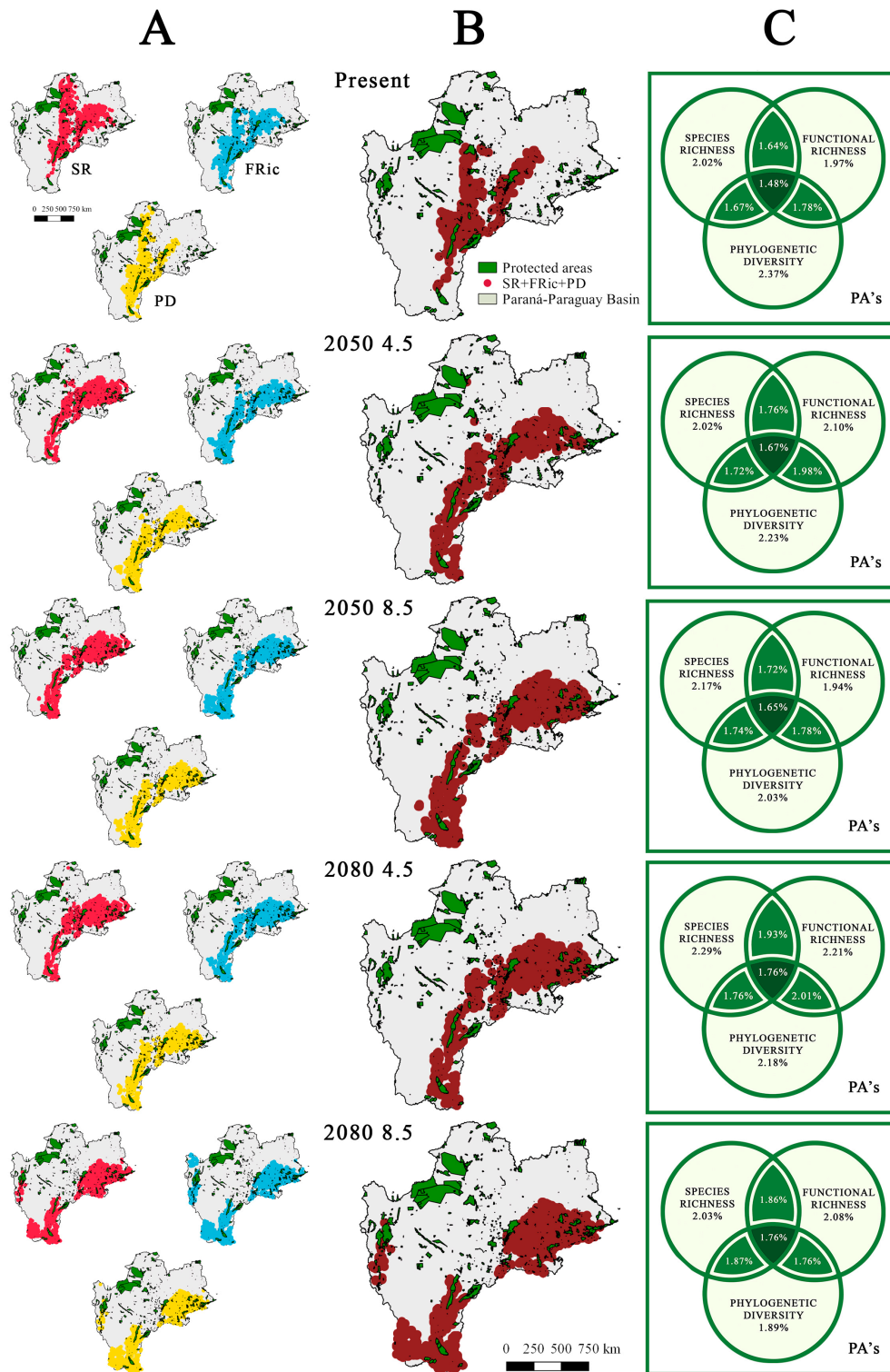
We used 496 species from the fish fauna of Paraná-Paraguay basin, suitable to the SDMs (at least 4 records in different grid cells), belonging to 12 orders and 46 families (Tab. S1).

The distribution of the 17% of the grid cells (1,998 cells) with the highest values of each component analyzed (*i.e.*, SR, FRic, and PD) are illustrated in Fig. 2A. For the present day scenario, the species richness in these cells ranged from 150 to 245 species, with the upper Paraná River, middle Paraná, and lower Paraguay River exhibiting the highest values. The functional richness ranged from 2.06 to 2.23. The highest values are widely spread to the upper Paraná River, middle and lower Paraguay, and lower Paraná. The highest values of phylogenetic diversity (from 1,461.22 to 2,104.26) were found in the main channel of the Paraná and Paraguay rivers, since the upper stretches to the lower, including the tributaries from the west margin, within the Paraguay and Argentina regions.

For the future scenario, the highest values of SR, FRic, and PD present in the 17% of the grid cells diminished considerably due to species that lose 100% of areas climatically suitable. The tributaries from the eastern margin of the upper Paraná River are identified as climatic refugees when considering species richness, which ranged from 64 to 205 species and from 35 to 191 species in the scenarios 2050 4.5 and 2050 8.5, respectively. For 2080, the range of species richness was from 36 to 200 species and from only 6 to 157 species. The uppermost and lower stretches of the Paraná River are identified as keeping the highest values of functional richness, even in the pessimistic scenario of 2080. The range in 2050 ran from 1.76 to 2.17 and from 1.58 to 2.15. In 2080, the values of functional richness ranged from 1.60 to 2.15 and 0.6 to 2.06 in the RCPs 4.5 and 8.5, respectively. The trend for the phylogenetic diversity consists in the highest values found toward the south of the basin, specially the Paraná River mouth, and the ranges of PD ran from 1,015.43 to 1,992.10 and from 878.49 to 2050 in the RCPs 4.5 and 8.5, respectively, and for 2080 the range ran from 877.01 to 1,937.81 and from 454.40 to 1,815.54.

Thus, there is a high congruence between a high species richness, high functional richness, and high phylogenetic diversity. However, this is not always true, as we can see a decoupling of species richness from phylogenetic diversity with the functional richness in the upper Paraguay basin. It was an interesting pattern to observe, since the limitation imposed by SR to FRic and PD in the intersection shows that to preserve SR alone does not take into consideration other places with high values of FRic and PD. Depending on the objectives of a protected area, we can, for example, leave entire lineages unprotected, preserving merely a high species richness and ignoring the composition of the assemblages. The overlap between the three components and the protected areas seems to increase over time (Fig. 2B), but the values of combination decrease, as described above in the range of the components by year and RCP. This





**FIGURE 2** | Paraná-Paraguay basin and the 17% of the area with the highest values of species richness (SR), functional richness (FRic), and phylogenetic diversity (PD), as well as the protected areas (PA's). **A**. SR, FRic, and PD, as well as their individual distribution for the current and future scenarios of climate change; **B**. the overlap between SR, FRic, and PD, as well as the protected areas in the Paraná-Paraguay basin, for the current and future scenarios of climate change **C**. The Venn diagrams showing the percentage of overlap between the components of fish diversity and the protected areas currently in the basin.



means that, despite the values of overlapping between the biodiversity components and PAs in the future scenarios being slightly higher, the species which remain exhibit similar ecosystem functions and belong to close lineages.

Of the 11,752 cells in the grid, 1,576 are currently inserted in protected areas, which corresponds to 13.41% and an area of 157,600 km<sup>2</sup>. Cells inside PAs and also within the 17% of cells harboring the highest values of the three components of fish fauna diversity (species richness, functional richness, and phylogenetic diversity) overlapped with only 174 cells, or 1.48%, in the present (Fig. 2C). The highest overlap between PAs and the individual components was with PD in the present, but it varied depending on the scenario analyzed (Fig. 2C) due to niche tracking by species.

In the west of the basin, particularly in the Paraguay River tributaries (an insufficiently sampled area), there are few cells with the highest values of fish diversity inside the protected areas, especially in Paraguayan territory. But, in the most pessimistic scenario (*i.e.*, 2080 8.5), these cells reappear, in keeping with the loss, in the other portions of the basin, of species with 100% of areas climatically suitable.

## DISCUSSION

The effectiveness of protected areas in the Paraná-Paraguay basin for fish fauna protection is currently low, and tends to be low in projected scenarios of global climate change. We found a small proportion of PAs overlapping with the facets of fish diversity analyzed both individually or in combination (maximum of 1.48% overlap in the present). It means that areas with a large number of species, containing fishes with diverse characteristics and functions and with important evolutionary history, are currently unprotected and will continue to be in the future because the climate and habitats are changing rapidly. The projections indicated a mere 1.76% overlap between PAs and the three ichthyofauna features in the most pessimistic scenario at the end of the century, but with values of the components very reduced. Since fish play essential ecological roles and services for the conservation of aquatic systems, and given the potential to assist future diversification that the currently existing groups have, it is indispensable that these organisms be protected.

The “phylogenetic gambit” hypothesis postulates that if species traits reflect their shared evolutionary history, then the pattern of that evolutionary history should serve as a useful surrogate for unmeasured and unmeasurable traits. It implies that maximizing PD will ensure that a wide variety of forms and functions will be present within a species set (Mazel *et al.*, 2018). Our results from mapping the distribution of both components of the ichthyofauna (FRic and PD) agree only partially with this, since we could identify different areas sheltering the highest values of FRic and PD. More specifically, we could identify a different distribution for the highest values of these components in the basin, with FRic in the upper Paraná basin and PD in the upper Paraguay, uncoupling this correlation, and corroborating Mazel *et al.* (2018), who called unreliable the idea that prioritizing PD would capture functional diversity. Other studies with birds and mammals on a global scale also found a poor congruency between taxonomic, phylogenetic, and functional features (Devictor *et al.*, 2010; Brum *et al.*, 2017).



Therefore, PA planning based in one lone dimension could result in the underrepresentation of important facets of diversity. It seems likely that by considering biodiversity features other than taxonomy, ecological differences may be better reflected in the protected areas. Measures of functional diversity, for example, have been better able to predict the productivity and vulnerability of ecosystems than traditional species diversity measures (Hooper *et al.*, 2005). This can be important for systems facing the effects of extreme or rapid environmental change, because the higher the biodiversity, the higher can be the resiliency of a system and thus the capacity of an ecosystem to respond to external events, such as climate change, likely preventing the loss of ecosystem services (Oliver *et al.*, 2015).

We found that a change in the 17% of the grid cells (which corresponds to 1998 cells) with the highest values of SR, FRic, and PD, through the east and south of the Paraná-Paraguay basin, occurred in response to the better climatic conditions expected from the tropics to the poles in front of climate change. The responses of the species to climate change can proceed in different and still unknown ways (Parmesan *et al.*, 2005), changing or not changing completely the composition of an ecosystem. The species can search for suitable climate areas by expanding or retracting their range (Parmesan, 2006; Comte *et al.*, 2014). They might not exhibit adaptations, and their populations can become smaller and smaller until finally they disappear. The species can also have its phenology altered, thus disrupting important ecological interactions such as co-evolutionary interspecific relationships (Parmesan, 2006; Nelles, Serrer, 2020; Weiskopf *et al.*, 2020). In this search, it is important that the species reach protected climatic refuges in order to maintain viable populations and avoid significant extinction risks.

Protected areas are undoubtedly one of the best strategies to ensure biodiversity conservation, and aquatic protected areas may be an appropriate preservation measure in the face of anthropogenic impacts (van Klink *et al.*, 2020). Thus, Target 11 of the Aichi Biodiversity Targets (<https://www.cbd.int/convention/>) planned to extend conserved terrestrial areas (including inland water) to 17%. However, as they are based mainly on terrestrial species and ecosystems, as well as their threats, their efficiencies are limited with respect to aquatic biodiversity conservation (Fagundes *et al.*, 2016; Frederico *et al.*, 2018). As our results also show, despite the protected area in the Paraná-Paraguay basin being 13.41%, it poorly protects the multiple dimensions of fish diversity. In the Amazonian basin, the decline of the large migratory fish indicates that 60 million hectares of PAs are not enough to maintain the population dynamics and fisheries stocks (Petrere Jr. *et al.*, 2004; Castello *et al.*, 2013; Correa *et al.*, 2015).

As a consequence of the terrestrial focus, most PAs embrace only stretches of the river basin, neglecting the importance of spatial connectivity (Hermoso *et al.*, 2018) and without guarantee of the integrity even on those stretches, since the effects of human activity at a point of the basin — such as mining, pollution, overfishing, and damming — can spread among the entire system (Azevedo-Santos *et al.*, 2019). On the other hand, spatially planned PAs with restricted use (*e.g.*, closed for visitation) often export clean air and water and are a source of individual organisms that can bolster small populations outside the area. Fishing outside of PAs is improved because of how breeding stocks in the PAs produce offspring that are caught outside the area (Palumbi, 2004; Roberts *et al.*, 2005). Unfortunately, the actual track record for



maintaining healthy seminatural aquatic ecosystems (e.g., PAs of sustainable use) is poor, highlighting the need for many more aquatic reserves closed to fishing (Edgar *et al.*, 2014).

As concerns spatial connectivity in the rivers, our species distribution modeling assumes no constraints on species dispersal, disregarding natural or artificial obstacles, with an exception granted to the Iguaçu Falls, which we have taken into consideration. We still cannot account for the presence of the numerous dams blocking fish movement and migratory routes (Agostinho *et al.*, 2007; Pelicice *et al.*, 2015; Oliveira *et al.*, 2018). The inclusion of these barriers can make the scenarios under climate change even worse by preventing species from reaching climatically suitable areas, bringing the accessibility issue to the fore (Barve *et al.*, 2011). When planning protected areas, information about the connectivity of the fluvial networks, water flow, and the presence of corridors should be considered (Hunter Jr., Gibbs, 2007; Azevedo-Santos *et al.*, 2019). It is also necessary to consider daily movements, annual migrations (particularly important for potamodromous fish), dispersal movements, and range shifts that species make in response to climate change (“niche tracking”) (Tingley *et al.*, 2009).

In this context, the protection of some unique natural ecosystems is not enough. We must look beyond the boundaries of PAs and to the ecosystems that form the larger matrix, in which they are embedded, especially those seminatural ecosystems in which we can integrate the management of biodiversity and the management of commodities such as timber, livestock, and fisheries. Integrating biodiversity maintenance with natural resource management in seminatural ecosystems offers vast expanses of land and water; they may never be pristine ecosystems, but they can support a multitude of species (Hunter Jr., Gibbs, 2007).

We cannot maintain genetic diversity without maintaining species diversity, and we cannot maintain species diversity without maintaining ecosystem diversity. Moreover, ecosystem maintenance depends on functional biodiversity. Here, we have provided a mapping of each of the biodiversity components (SR, FRic, and PD) — using several layers of information, biotic and physical, and with the help of georeferenced information system (GIS) — that open doors to various quantitative techniques for selecting reserves and evaluations of their effectiveness over several organism groups (Hunter Jr., Gibbs, 2007). In front of the rapid expansion of unsustainable anthropic activities and biodiversity losses, it is urgent that the creation of new PAs, or the remodeling of existing PAs, be sought, with a focus on freshwater biodiversity (Azevedo-Santos *et al.*, 2019).

Conservationists rarely have the opportunity to create a system of PAs from scratch. Usually, there is an existing set of PAs, and they must undertake a process called “gap analysis” in order to identify holes in the existing network, which is often unbalanced and incomplete from the perspective of biodiversity conservation (Hunter Jr., Gibbs, 2007). Based on our results, we reinforce the idea that the PAs for freshwater environments need systematic planning and a careful prioritization analysis. Some aspects to be considered for the entire watershed and when choosing an area are the composition of species, their functional traits and life history, rarity, endemism, and complementarity, all for an optimal allocation of the limited conservation resources that incorporates multiple components of biodiversity (Strecker *et al.*, 2011; Brum *et al.*, 2017).



Besides the creation of new PAs, the management of those currently existing should pay special attention to the aquatic systems — also taking into consideration social, political, and economic aspects, which are very important to the management of a reserve — and try to change them so that they are made more compatible with all life on Earth. Since the planning and creation of a new PA is hard work, other strategies for fish conservation should be applied, such as surveillance concerning water pollution, loss of wetlands, dam construction, and non-native species introduction (Hunter Jr., Gibbs, 2007), as well as the prevention of events such as the recent apocalyptic fires in the Pantanal biome, especially in the Paraná-Paraguay basin (Mega, 2020).

In addition to the biotic characterization we have provided, and to our pointing out the threats to which the Paraná-Paraguay basin is subject, we highlight that it is a transboundary basin. Thus, environmental policies for their conservation also need to take on this cross-border character, and do so through joint systematic planning between countries, specifically by means of international agreements, as proposed in the Aichi Biodiversity Targets of the Convention on Biological Diversity (Leadley *et al.*, 2010).

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**AUTHORS' CONTRIBUTION**

**Anielly Galego de Oliveira:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Validation, Visualization, Writing-original draft, Writing-review and editing.

**Oscar Peláez:** Data curation, Formal analysis, Funding acquisition, Methodology, Writing-review and editing.

**Angelo Antonio Agostinho:** Supervision, Writing-review and editing.

**ETHICAL STATEMENT**

This manuscript does not require approval from the Ethical Committee for Animal Use in Experiments, since the data is obtained from databases available online.

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The authors declare no competing interests.

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