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Fish diversity in the Upper Paraguay River Basin: implications for fish conservation and fishing sustainability

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Índice

Chapter 3

General Abstract

This study addresses the current gaps in understanding fish richness and composition patterns within the Upper Paraguay River Basin (UPRB) and explores the primary drivers influencing these patterns. Additionally, it conducts a comprehensive review of fishing activities in the basin, particularly focusing on the Pantanal wetland. The findings highlight the role of area in shaping freshwater fish richness at the sub-basin scale due to the environmental heterogeneity. Along the altitudinal gradient, fish richness decreases. Regarding the composition, the UPRB displays high β diversity, primarily driven by species turnover. The Paraguay River serves as a crucial connector among sub-basins, while upland areas contribute significantly to the overall diversity of fish species. There are high negative impact projects implemented and planned to be installed in the Upper Paraguay river basin that put at risk one of the greatest fish diversities in the world and are ignored by decision makers in fisheries management in the region. Therefore, to safeguard fish diversity and ensure fisheries sustainability in the UPRB, we recommend based on the results obtained: (i) increased representation of Conservation Units focused on aquatic ecosystems in upland areas; (ii) providing greater incentives for ichthyological research, given the substantial ecological and economic value of fish to the region, alongside studies aimed at comprehending fisheries and socio-ecological dynamics; and (iii) the integration of scientific insights and active involvement of fishers in fisheries management processes.

Resumo Geral

Este estudo aborda as lacunas atuais na compreensão dos padrões de riqueza e composição de peixes na Bacia do Alto Rio Paraguai (BAP) e explora os principais fatores que influenciam esses padrões. Além disso, realiza uma revisão abrangente das atividades pesqueiras na bacia, com foco especial no Pantanal. Os resultados destacam o papel da área na riqueza de peixes à escala da sub-bacia devido à heterogeneidade ambiental. Ao longo do gradiente altitudinal, a riqueza de peixes diminui e o planalto apresenta menor diversidade de espécies. Com relação a composição, a UPRB apresenta alta diversidade β, impulsionada principalmente pela substituição de espécies. O Rio Paraguai serve como um corredor ecológico aquático crucial entre as sub-bacias, enquanto o planalto contribui significativamente para a diversidade geral de espécies de peixes. Existem projetos de alto impacto negativo implementados e planejados para a BAP que colocam em risco uma das maiores diversidades de peixes do mundo e são ignorados pelos tomadores de decisão na gestão pesqueira da região. Portanto, para salvaguardar a diversidade de peixes e garantir a sustentabilidade da pesca na BAP, recomendamos: (i) aumento da representação de Unidades de Conservação focadas em ecossistemas aquáticos no planalto; (ii) maiores incentivos aos estudos ictiológicos, devido a importância ecológica e econômica dos peixes, juntamente com estudos que examinem a pesca e a dinâmica socioecológica da atividade; e (iii) a integração de conhecimentos científicos e o envolvimento ativo dos pescadores nos processos de gestão da pesca.

General Introduction

The Upper Paraguay River Basin (UPRB) stands as one of South America's largest river basins, spanning over 360,000 km², and harboring one of the most remarkable fish diversities globally (Tomas et al. 2019, Gimênes Junior & Rech 2022). With 386 fish species inhabiting the Amazon, Atlantic Forest, Cerrado, and Pantanal biomes within its confines (Gimênes Junior & Rech 2022), the UPRB holds significant ecological importance. However, the comprehensive understanding of fish richness and composition patterns in the UPRB at the basin scale, as well as the underlying drivers shaping these patterns remains poorly understood.

Beta (β) diversity, defined as the variation in species composition among sites, can be partitioned into nestedness and spatial turnover components (Baselga 2010). It is fundamental to quantify the contribution of each component of β diversity, as this information is crucial for devising effective conservation strategies (Baselga 2010, Gutiérrez-Cánovas et al. 2013). In environments characterized by substantial environmental dissimilarity, is expected a correspondingly high level of species dissimilarity owing to the heterogeneity of environmental conditions. In situations characterized by nested dissimilarity, wherein species composition in certain areas represents a subset of those with higher richness, prioritizing areas of greater richness is considered most appropriate, as they offer a more comprehensive representation of diversity (Baselga 2010, Leprieur et al. 2011, Si et al. 2015). On the other hand, in sites where the spatial turnover component predominates, there occurs a substitution of species from one location to another. In such cases, a broad spectrum of locations is most appropriate to ensure the conservation of the majority of species (Wiersma & Urban 2005, Baselga 2010, Leprieur et al. 2011, Angeler 2013, Si et al. 2015).

Within the Upper Paraguay River Basin (UPRB), the extensive fish diversity serves as a crucial resource for numerous Indigenous Peoples and Local Communities (IPLC). Similar to scenarios in developing countries across Africa, Asia, and South America, fisheries play a significant role in promoting employment and food security (Funge-Smith & Bennett 2019, ANA 2020a). However, the global freshwater biodiversity, and consequently, the livelihoods of millions of small-scale fishers, face imminent threats (Darwall et al. 2018). Currently, the rate of wetland loss is three times faster than forest loss, attributable to alterations in water quality, habitat degradation, pollution, and climate change (Gardner & Finlayson 2018). In the UPRB, additional challenges such as significant forest fires, the introduction of exotic species, and silting up of rivers exacerbate the situation. Furthermore, numerous transportation and energy sector projects throughout the basin pose further detriment to river health, to fish populations, and fisheries (Agostinho et al. 2007, Fantin-Cruz et al. 2020, Peluso et al. 2022).

This thesis investigates the patterns of fish richness and β diversity within the Upper Paraguay River Basin (UPRB), elucidating the primary factors influencing this diversity across different spatial scales. Given the significant social and economic importance of these organisms for the region, we also conduct a comprehensive review of the current state of fishing activities in the basin, with a specific focus on the Pantanal wetland, designated as a Biosphere Reserve and World Heritage site by UNESCO. The first chapter, titled "Patterns of richness and β diversity among sub-basins of the Upper Paraguay River Basin," adopts a broad approach, examining diversity patterns at the sub-basin scale. The second chapter, titled "Fish distribution across altitudinal gradients in the Upper Paraguay River Basin: implications for conservation in the Pantanal region," employs a more focused perspective, investigating the altitudinal gradient within the basin. The third chapter, titled "Threats, conflicts, and the future of small-scale fisheries in the Pantanal Wetland, Brazil," addresses scientific insights into Pantanal fisheries, emphasizing the environmental ramifications of the main threats. Additionally, we conduct a historical assessment of fishing policies and social conflicts in the region, exploring their potential impacts.

Chapter 1. Patterns of richness and β diversity among the sub-basins of the Upper Paraguay River Basin

Abstract

Various theoretical frameworks have been proposed to elucidate the patterns of diversity across environmental gradients. Regarding species richness, a fundamental premise posits a positive correlation with area and the total energy available within a system. Beyond species count, understanding the differences in species composition between environments is crucial for formulating effective conservation strategies. These differences, termed β diversity, may arise from either nestedness or spatial turnover processes. In this study, we evaluate the influence of area, energy availability, and habitat heterogeneity on fish species richness, the occurrence of rare species, and β diversity across 10 sub-basins within the Upper Paraguay River Basin (UPRB) in Brazil. We utilize occurrence data encompassing 358 fish species within the UPRB, derived from primary sources and supplemented by a comprehensive database. Notably, only richness demonstrates a positive correlation with sub-basin area. Weight of species with low occurrence positively correlates with richness and the percentage of upland area, while altitude exhibits a negative correlation. Additionally, a notable similarity in fish composition is observed between the western and northern sub-basins. However, despite this similarity, the UPRB exhibits high β diversity primarily attributed to turnover processes, influenced significantly by mean altitude and the proportion of upland area within the sub-basin. These findings underscore the urgency of addressing current threats, such as the dredging of the Paraguay River , the primary aquatic ecological corridor in the basin, and the construction of dams in upland areas critical for the fish diversity of the UPRB.

Resumo

Teorias complementares foram propostas para explicar os padrões de diversidade ao longo dos gradientes ambientais. Em relação à riqueza de espécies, uma premissa fundamental postula uma correlação positiva com a área e a energia total disponível dentro de um sistema. Além da riqueza, compreender as diferenças na composição de espécies entre ambientes é crucial para a formulação de estratégias de conservação eficazes. Essas diferenças, denominadas diversidade β, podem surgir de processos de aninhamento ou de substituição de espécies. Neste estudo, avaliamos a influência da área, disponibilidade de energia e heterogeneidade de habitat na riqueza de espécies de peixes, na ocorrência de espécies raras e na diversidade β em 10 sub-bacias da Bacia do Alto Rio Paraguai (BAP) no Brasil. Utilizamos dados de ocorrência abrangendo 358 espécies de peixes da BAP, derivados de fontes primárias e complementados por um banco de dados abrangente. Apenas a riqueza demonstrou uma correlação positiva com a área da sub-bacia. O peso das espécies com baixa ocorrência correlacionou-se positivamente com a riqueza e a porcentagem de área de planalto, enquanto a altitude apresentou uma correlação negativa. Além disso, observamos uma notável similaridade na composição dos peixes entre as sub-bacias das regiões oeste e norte. No entanto, apesar desta similaridade, a BAP apresentou elevada diversidade β atribuída principalmente a substituição de espécies, influenciada significativamente pela altitude média e pela proporção de área de planalto dentro da sub-bacia. Esses resultados reforçam o alerta sobre as atuais ameaças, como a dragagem do Rio Paraguai, principal corredor ecológico aquático da bacia, e a implementação de barragens em áreas do planalto, importantes para a ictiofauna da BAP.

1. Introduction

Understanding patterns of diversity along environmental gradients is crucial for the development of effective conservation strategies. To elucidate these patterns, several theoretical frameworks have been proposed. Regarding the variation in species richness, the island biogeography theory (IBT) stands as a prominent explanatory model. IBT posits that the size of a habitat patch influences species richness, with larger patches supporting greater species diversity through increased immigration rates and the maintenance of larger, more stable populations less susceptible to local extinction due to demographic processes (MacArthur & Wilson 1967).

Species-energy (SET) and niche (NT) theories are regarded as complementary to IBT, postulating that population sizes and speciation rates are influenced by the total energy available within a system, thereby demonstrating a positive correlation between species richness and energy (Wright 1983, Guégan et al. 1998). These species can coexist due to the greater opportunities for niche differentiation afforded by habitat heterogeneity in these patches (MacArthur 1969, Chesson & Kuang 2008). For riverine fish species, both area and energy availability emerge as principal drivers of richness patterns globally (Hugueny et al. 2010, Oberdorff et al. 2019). At smaller spatial scales, geographical barriers resulting in the formation of river basins can effectively be viewed as biogeographical islands (Hugueny et al. 2010).

An additional crucial aspect to explore, aiding in the comprehension of diversity patterns, is the variation in species composition across different environments (Legendre & De Cáceres 2013, López-Delgado et al. 2020). This variance, defined as β diversity, can arise from two distinct processes: nestedness or spatial turnover (Harrison et al. 1992, Baselga et al. 2010). Nestedness occurs when communities with fewer species constitute subsets of richer communities (Baselga 2010, Legendre 2013). Such dissimilarities reflect differences in niche diversity, as observed along a gradient of spatial extent, where species are lost from larger to smaller spatial scales, often manifesting as nested patterns wherein the species composition of smaller areas is a subset of those found in more extensive samples. Conversely, spatial turnover involves the replacement of certain species by others from site to site, resulting in pronounced dissimilarities between environments (Gaston & Blackburn 2000, Baselga 2012). This phenomenon may be attributed to a history of environmental constraints along a gradient of physical structure (Qian & Ricklefs 2012).

In this study, we evaluate the influence of area, energy and habitat heterogeneity on fish species richness, occurrence of rare species, and β diversity in 10 sub-basins of the Upper Paraguay River Basin (UPRB), in Brazil. In the lower regions of the UPRB, particular emphasis is placed on the Pantanal wetland, where the primary biological driver is the flood pulse, facilitating connectivity between rivers and isolated areas such as lakes and flooded lands. Within this dynamic, the expansion of aquatic environments enhances niche availability and environmental connectivity, promoting species dispersal and consequent homogenization of species composition (Thomaz et al. 2007). Conversely, in the upland areas surrounding the Pantanal wetland, headwater streams and rivers of varying orders are prevalent, and the presence of geographic barriers. Headwater regions represent relatively isolated environments with limited migration, thereby increasing the likelihood of encountering rare species (López-Delgado et al. 2020).

Given the environmental differences within the basin, we hypothesize that fish species richness within sub-basins exhibits a positive correlation with area and net primary productivity. Moreover, richness will favor the number of species with low occurrence, alongside variables associated with isolation, habitat variability, and colonization challenges (e.g., altitude, upland area, slope). Additionally, we expect turnover to constitute the principal component of β diversity, particularly attributable to environmental variations in the upland regions.

2. Methods

2.1. Study area

The Upper Paraguay River Basin (UPRB) in Brazil encompasses approximately 362,000 km² and exhibits an altitudinal gradient ranging from the floodplain (Pantanal) to the surrounding upland areas (elevations exceeding 200 meters) (see Figure 1). The upland predominantly harbors Cerrado vegetation, yet over 60% of the original vegetation cover has been lost (Roque et al. 2016, Tomas et al. 2019, Guerra et al. 2020). The headwaters of all rivers draining the Pantanal wetland and ultimately converging into the Paraguay River are situated within these upland regions. Spanning approximately 179,000 km², the Pantanal sustains nearly 80% of its native vegetation (Roque et al. 2016, Tomas et al. 2019). This biome is characterized by its seasonal flood pulse (Junk 1989, Junk & Wantzen 2004, Junk et al. 2014) a phenomenon driven by local precipitation patterns and the limited capacity to channel water from the uplands owing to a very low slope (Thielen et al. 2020). The propagation of the flood wave occurs gradually, extending in both north/south and east/west directions, with regional variations leading to delays of up to 4 months. On average, approximately 35,000 km² of seasonally inundated areas interconnect rivers, lakes, and other aquatic bodies (Hamilton et al. 1996).

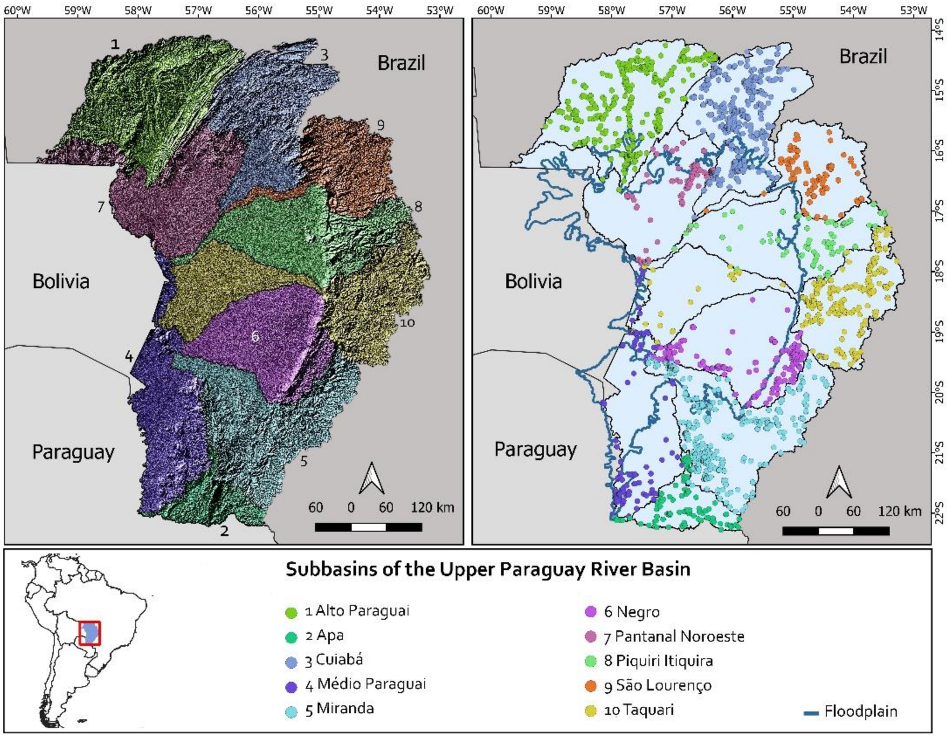

Figure 1. Fish occurrence points on each sub-basin of the Upper Paraguay River Basin and altitude.

2.2. Obtaining the data

We used fish occurrence data on Upper Paraguay River Basin (UPRB) obtained from primary data and complemented by a fish database (Tonella et al. 2023). For the primary data, we collect the fishes with different equipment, adapting the methods on the different environments. We used rectangular sieves (80x120), seine nets with mesh (2 mm), trawls, casting net and electric fishing. In the laboratory, we fixed all sampled fishes in 10% formaldehyde and stored them in 70% alcohol. To obtain the occurrence data, we used GBIF, FishNet, SpeciesLink and data papers of Neotropical fish. We select only species whose occurrences were confirmed by specialists. After this, we made a detailed conference, removing incomplete data and species that do not occur in the basin, and updating scientific names. For this step, we used the books of Britski, Silimon & Lopes (2007) and Gimênes Junior & Rech (2022). In total, we recorded 4281 fish occurrence points.

We obtained the limits of all 10 sub-basin of the UPRB on the Agência Nacional de Águas (ANA, Brazil). We calculated total sub-basin area (km^2), percentage of the floodplain and upland area, drainage (km) and from HydroSHEDS (Lehner & Grill 2013) we obtained the average order of water bodies. The average altitude and declivity were obtained from the SRTM (Shuttle Radar Topography Mission), the average temperature and precipitation from the WordClean dataset (Fick & Hijmans 2017) and the average net primary productivity from Modis Satellites (Running & Zhao 2021).

2.3. Data analysis

We tested the correlation between all variables with the PerformanceAnalytics package in R, and selected the four variables that we used in our models. We calculated the species richness and the weight of species with low occurrence of each sub-basin. For this last one, we divided 1 by the number of sub-basin that the specific species occur in. Then, we have 1 for a species that occurs in one sub-basin and 0.1 for a species that occurs in all the 10 sub-basins. After this, for each sub-basin, we sum the weight values of the species that occur in it. Thus, the high values represent sub-basins with high occurrences of relatively rare species.

We used Structural Equation Modeling (SEM) to test the hypothesis (Figure 2). To compare the pattern of the field data and our model, we used the chi-square value, the associated *p* value (we consider $p>0.05$ a fit model) and the CFI value. For the species composition we performed a PCoA with Jaccard distance using the “vegdist” and “cmdscale” functions of the vegan package in R.

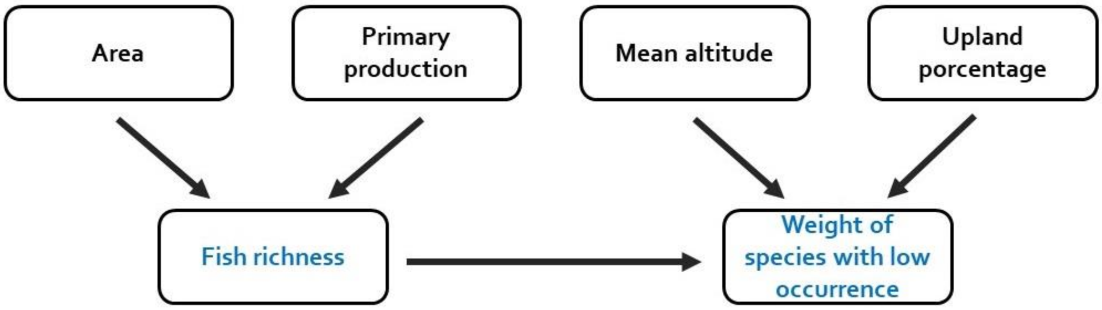

Figure 2. Hypothesis scheme of how environmental variables can influence fish richness and weight of species with low occurrence in the Upper Paraguay River Basin.

2.3.1. *β diversity*

We calculated the β diversity and its components, turnover and nestedness, with the "β.multi" function and we accessed the distances matrixes (Jaccard distance) with the "β.pair" function of the βpart package. To analyze the influence of the environmental variables we performed a Distance Based Redundance Analysis (db-RDA) with each matrix obtained, using the "capscale" function. The first step was to test the global model and exclude the variables with high multicollinearity (sqrt of VIF>2) using "vif.cca" function. With these variables and the three matrix we perform a Partition of Variation with "varpart" function. For each fractions combination we test the dbRDA by performing ANOVA. To compare the differences between the subbasin we constructed a matrix with the pair distance values obtained to the β diversity matrix. We calculated the local contribution of β diversity (LCBD) of each sub-basin with "β.div" funtion and test a linear regression with the area.

3. Results

We recorded 325 fish species (attachment 1) and this richness ranged from 137 in Apa to 290 in Cuiabá sub-basin. For the weight of species with low occurrence, Apa sub-basin still presented the lowest value (21.18) and Miranda presented the highest value (53.42). The SEM showed that fish species richness is positively correlated with area (Figure 3). No significant relationship was found for richness and net primary productivity. Weight of species with low occurrence is positively correlated with richness and percentage of upland, while the altitude presents a negative correlation. We can see the strong relationship between richness and weight of species with low occurrence reflected in the maps which presented a very similar pattern.

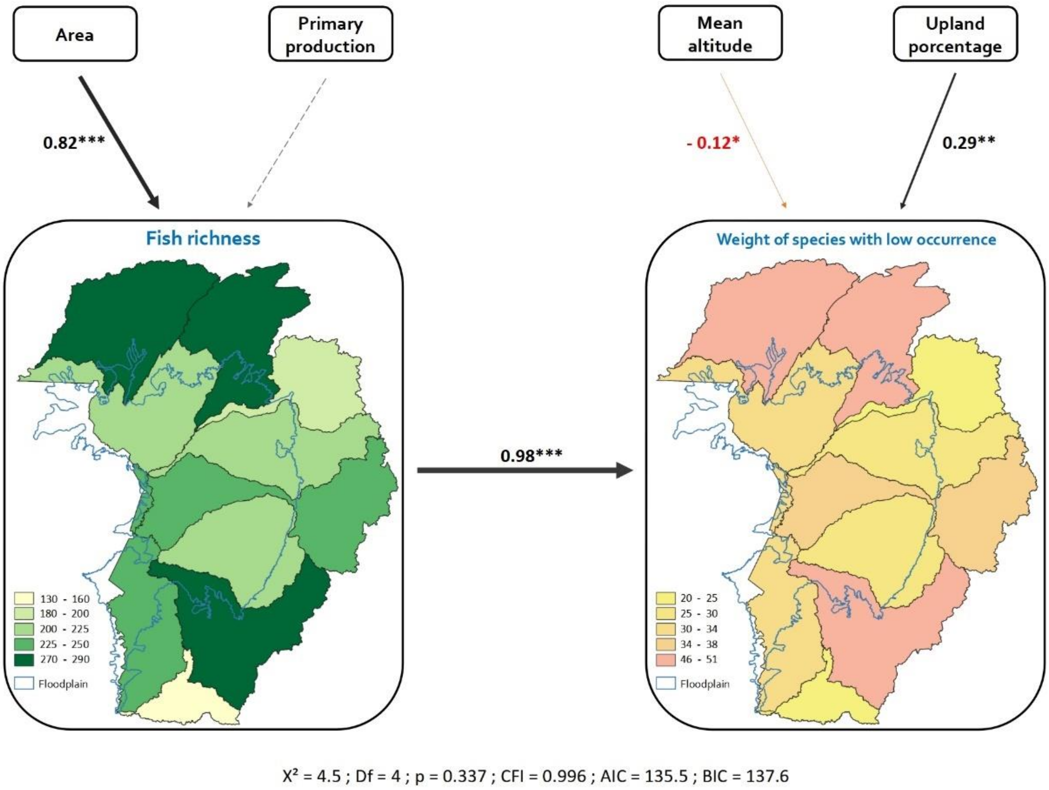

Figure 3. Structural equation model of how environmental variables influence fish richness and weight of species with low occurrence in the Upper Paraguay River Basin.

There is a similarity of fish composition between subbasins in the west part of the UPRB including Alto Paraguai, Cuiabá, Pantanal Noroeste and Médio Paraguai (Figure 4). In the east side, the fish composition is different between the west side and each other. The sub-basins with the biggest portion of floodplain are more similar than the sub-basins with the smaller portion of floodplain like Apa and São Lourenço. This dissimilarity is reflected in the β diversity of subbasin pairs (Figure 5). Apa and São Lourenço presented the highest values. The dbRDA showed that area and area with mean altitude and upland percentage influenced the total β diversity (Figure 5A - Total). We can see the area influence when we compare small and big subbasins (Apa and São Lourenço with Alto Paraguai, Cuiabá and Miranda) (Figure 5B - Total). At the same time, we can see the influence of altitude and upland when we compare high and low mean altitude subbasin (São Lourenço with Pantanal Noroeste) and sub-basins with high and low upland percentage (Apa with Piquiri Itiquira) (Figure 5B - Total).

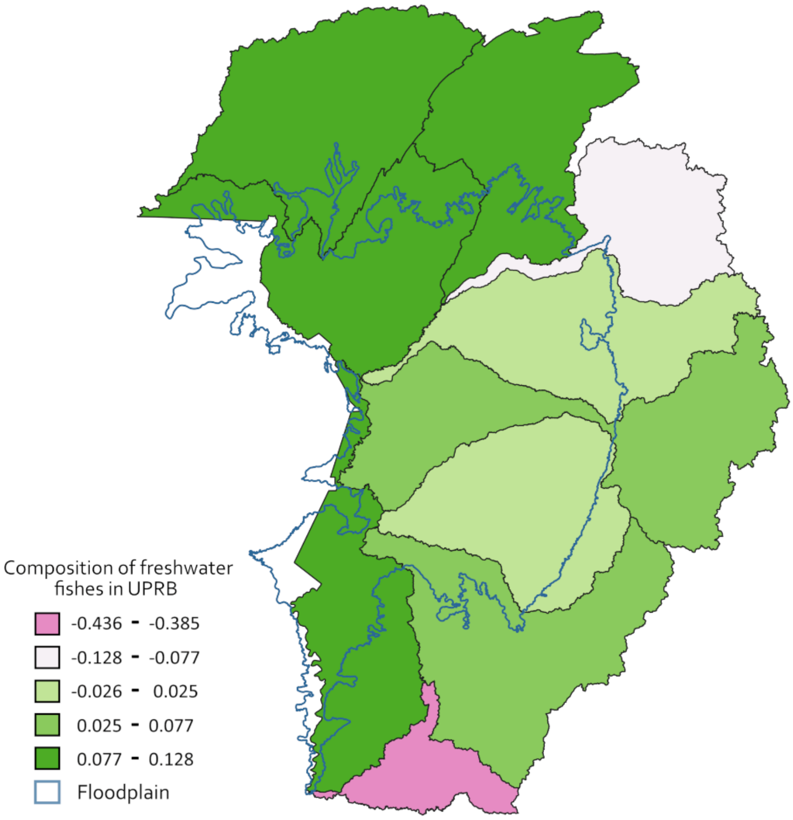

Figure 4. Composition of fish species in the Upper Paraguay River Basin, resulting from PCoA.

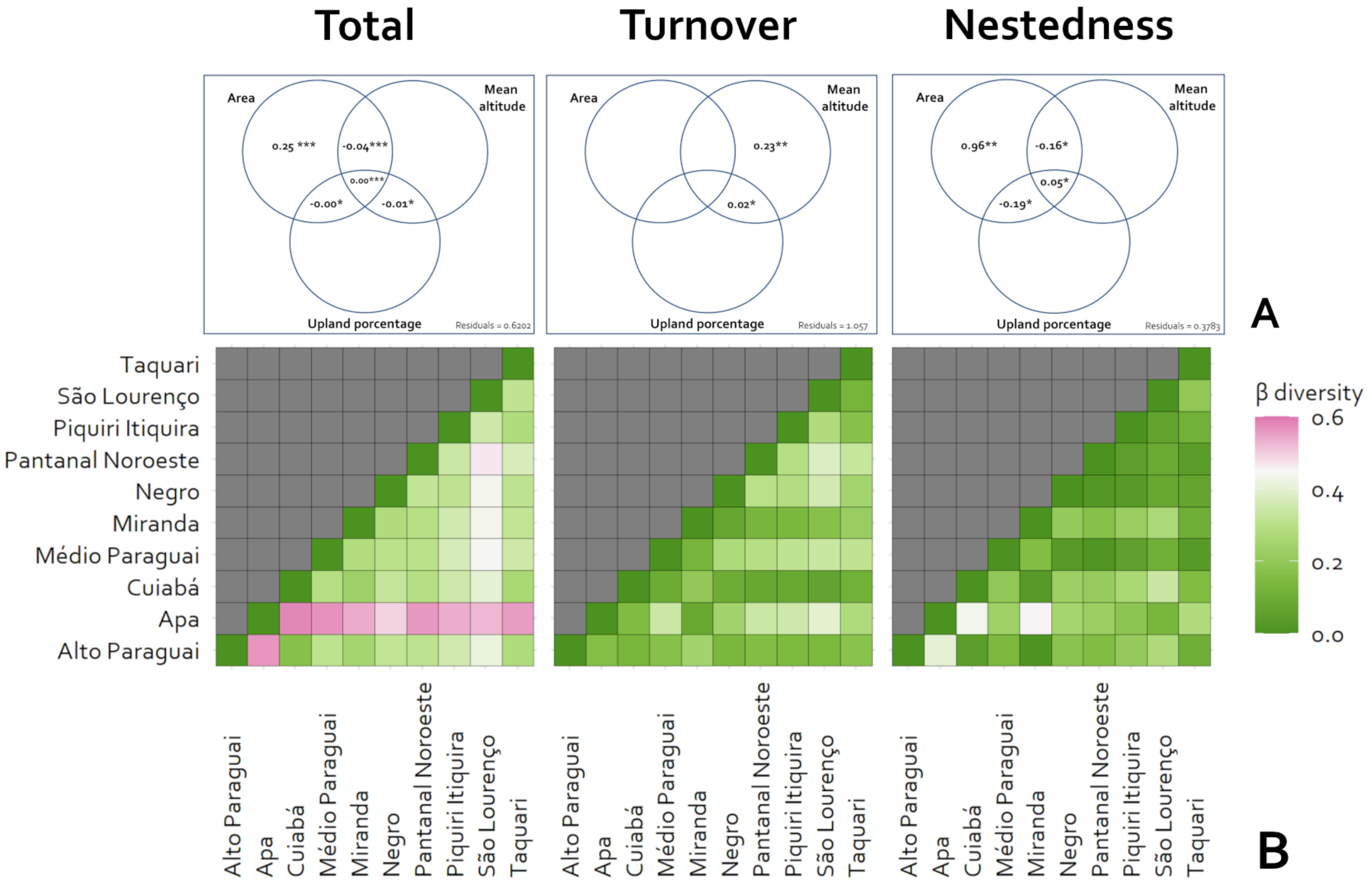

Figure 5. Distance Based Redundance Analysis (db-RDA) and variance partitioning (A) and β diversity of subbasin pairs (B).

The turnover was responsible for 71% of the difference of species composition and 29% of nestedness. For the turnover component, mean altitude and mean altitude with upland percentage showed a significant effect (Figure 5A - Turnover). Analyzing the turnover matrix (Figure 5B - Turnover), we can see that, sub-basins with low (Pantanal Noroeste) and high (São Lourenço) values of altitude and upland percentage, presented high values of β diversity (Figure 5B - Turnover). For nestedness component, area and area with upland percentage and mean altitude showed a significant effect (Figure 5A - Nestedness). Analyzing the nestedness matrix (Figure 5B - Nestedness), we can see that the big sub-basins as Alto Paraguai, Cuiabá and Miranda presented high values of nested β diversity. When we compare these sub-basins with Apa, the smaller subbasin, we can see the highest value (Figure 5A - Nestedness). Apa is the subbasin with more contribution to β diversity and Cuiabá has the least contribution (Figure 6A). LCBD was negatively correlated with area (Figure 6B).

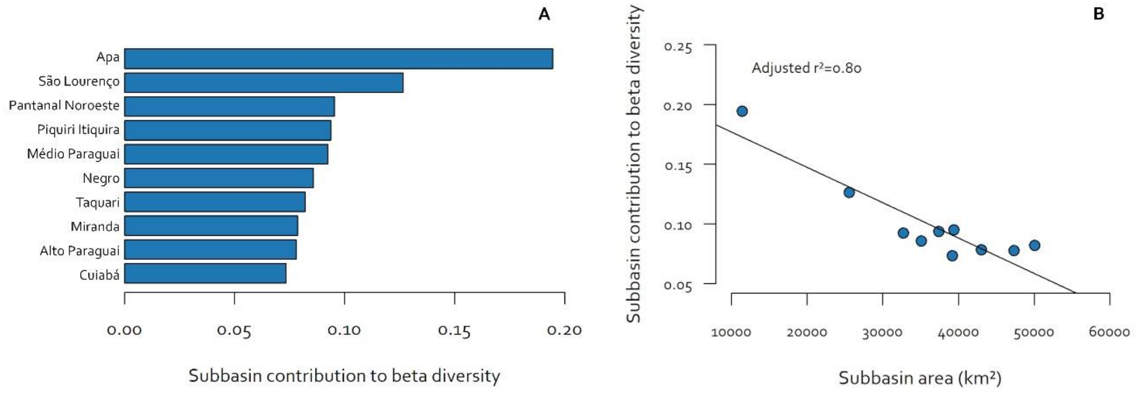

Figure 6. Contribution of each subbasin to fish β diversity of the Upper Paraguay River Basin (A) and their correlation with area (B).

4. Discussion

Larger sub-basins have greater fish richness, and the upland is home to "rare species"

Richness was positively correlated with sub-basin area, a relationship that is extensively documented in various regions (Oberdorff et al. 2019). This phenomenon can be attributed to the capacity of larger areas to accommodate diverse environmental conditions, thereby exposing species to a heightened ecological heterogeneity and potential geographical barriers that enhancing speciation probabilities, and facilitates species coexistence (Hugueny et al. 2011, Dias et al. 2014, Oberdorff et al. 2019).

The environmental conditions within the UPRB exhibit considerable heterogeneity. The most pronounced dissimilarities occur between the upland and floodplain areas, with larger sub-basins often encompassing these environmental variations. Upland regions there are streams, rivers, and geographical barriers, while floodplain areas lack such barriers, facilitating species movement, particularly during the flood season when aquatic environments expand, allowing fish fauna to access flooded terrestrial areas and isolated lagoons (Welcomme, 2001; Thomaz et al., 2007; Mateus et al., 2011). The contrasting environments represented by these two extremes expose fish populations to diverse conditions and ecological niches. The increased availability of niches, stemming from greater ecological heterogeneity, promotes the coexistence of a wider array of species. Moreover, the presence of multiple environmental types within a single basin suggests that primary productivity is not necessarily correlated with species richness.

Richness patterns are predominantly influenced by three factors: environmental conditions, energy availability, and natural history dynamics (Oberdorff et al. 2019).

Therefore, it is noteworthy that the sub-basin exhibiting the highest species richness within the UPRB borders the Amazon basin. It is plausible that the proximity of these adjacent Amazonian sub-basins has contributed to the observed richness through species migration. Ribeiro et al. (2013) have highlighted the existence of significant fish migration routes from the Tapajós River, located within the Amazon basin, to the Cuiabá sub-basin. It is possible that numerous other migration routes within this region connect the world's largest basin to the UPRB.

Sub-basins with high fish richness has a great number of species with low occurrence. The Structural Equation Model (SEM) further revealed an indirect influence of area on this variable, thereby reinforcing the hypothesis of environmental heterogeneity. Such sub-basins host a diverse array of species occupying various ecological niches, which may support the presence of relatively rare species. Additionally, the presence of geographical barriers in upland areas serves to isolate fish populations. Consequently, the larger size of these sub-basins, and the presence of geographical barriers in the upland regions, impedes access to other areas, resulting in the occurrence of these species in only a few sub-basins. We noted a weak negative correlation with altitude, which may be influenced by the strong relationship with species richness, as richness and altitude typically exhibit a negative correlation (Lomolino, 2001). Hence, the elevated average altitude of certain sub-basins may hinder the access and establishment of species, particularly those with low occurrence.

Paraguay River as an important ecological corridor for fish

The (PCoA) results, represented on the map of the UPRB, reveal a notable similarity in fish composition between the western and northern sub-basins, indicative of a region conducive to unhindered fish movement. Within these areas, the Paraguay River, the largest river within the basin, originates from the upland of the Alto Paraguay sub-basin and traverses the plain, serving as a crucial ecological corridor for fish species. The lack of geographical barriers, coupled with the influence of the flood pulse, facilitates both longitudinal and lateral connectivity, thereby fostering similarities in composition among basins characterized by substantial floodplain areas (Thomaz et al. 2007). This contrasts with the Apa and São Lourenço sub-basins, which exhibit distinct compositions of fish species compared to the others.

Large rivers represent important connectors facilitating the movement of fishes between basins, enabling crucial ecological processes such as dispersal and migration (Shao et al. 2019). Within the UPRB, the connectivity between the floodplain and upland areas plays a fundamental role for the ichthyofauna. Annually, migratory fish species leave the floodplain and migrate to surround upland areas for reproduction (Ziober et al., 2012; Souza et al., 2023). In this migration, known as "Piracema," certain species travel hundreds of kilometers upstream to reach their spawning grounds. Following reproduction, both adults and juveniles return to the floodplains, where they encounter favorable habitats providing shelter from predators, opportunities for feeding, and conditions conducive to growth (Resende, 2003; Souza et al., 2023).

β *diversity is influenced by species replacement*

We observed that turnover, which constitutes the most significant component of β diversity, is primarily influenced by altitude and the extent of upland areas. High turnover values are evident when contrasting the São Lourenço sub-basin, characterized by high average altitude and a substantial proportion of upland area, with sub-basins exhibiting contrasting characteristics, such as Pantanal Noroeste, Negro, and Médio Paraguai. While the Pantanal plain demonstrates a homogenization of species composition, taxonomic differentiation between sub-basins arises from regions characterized by greater environmental harshness, variability, and instability. Factors contributing to this differentiation include the presence of geographical barriers, diverse water bodies of varying orders, variability in slopes, among others. Within these heterogeneous environments, the likelihood of speciation increases, resulting in the occurrence of distinct species across different sub-basins.

We observed that 29% of β diversity is influenced by nestedness. In this case, some larger sub-basins exhibit a greater diversity of species, while smaller ones harbor a subset of species found in the larger sub-basins. The reduced species richness in smaller sub-basins is primarily influenced by their smaller area, as evidenced by the Structural Equation Model (SEM) results. This pattern is evident when comparing large sub-basins such as Cuiabá, Alto Paraguai, and Miranda with smaller ones like Apa. Apa and São Lourenço stand out for their significant contribution to β diversity, primarily driven by their unique characteristics, with area emerging as a dominant factor influencing fish diversity in these basins.

Currently, numerous threats jeopardize the health of rivers and ichthyofauna within the UPRB. Apart from global-scale challenges like climate change, regional factors such as deforestation in the Amazon contribute to diminished rainfall, affecting the headwaters of Pantanal rivers (Bergier et al. 2018). However, it is the local-scale threats that demand urgent attention. With over 130 hydroelectric projects planned for headwater rivers in upland areas, there is significant concern regarding their detrimental impact on the reproduction of migratory fish. Moreover, a project is underway involving the dredging of the Paraguay River to deepen and widen the navigation channel, aimed at facilitating the transportation of soybeans through the Pantanal (Coelho-Junior et al., 2022). The implementation of these projects presents significant risks to fish communities, particularly migratory species, as these organisms rely on the entire basin throughout their life cycle (Resende et al. 2003). The construction of dams on the upland areas and alterations to the depth and width of the Paraguay River could disrupt sediment and nutrient flows, thereby impacting water quality and the hydrological regime of the Pantanal (Ely et al., 2020; Oliveira et al., 2020).

5. Conclusion

Our findings provide a comprehensive understanding of the organization of fish diversity within the UPRB at the sub-basin level. The ichthyofauna of the UPRB ranks among the most diverse globally, with Gimênes Junior & Rech (2022) documenting 386 fish species in this basin. In our study, we accessed 85% of the fish richness within the UPRB. Our results underscore the significant role of area in shaping patterns of freshwater fish richness, attributed to the environmental heterogeneity inherent in larger areas. The UPRB exhibits high β diversity, primarily driven by species turnover. We emphasize the important role of the Paraguay River in facilitating connectivity among sub-basins, as well as the contribution of upland areas to the enhanced diversity of fish species.

Hence, to ensure the conservation of fish diversity within the UPRB, it is necessary to prioritize conservation areas that account for the substantial dissimilarity in fish species composition, particularly in upland regions, encompassing a diverse hydrological network with varied environments. While large sub-basins like Cuiabá and Miranda exhibit higher richness and serve as representatives of basin-wide fish diversity, it is crucial to also consider sub-basins such as Apa and São Lourenço due to their marked contribution to dissimilarity in species composition.

These findings underscore the urgency of addressing ongoing threats within the basin, such as the dredging of the Paraguay River— the primary aquatic ecological corridor in the basin— and the construction of dams in upland areas critical for the fish diversity of the UPRB.

Chapter 2. Fish distribution across altitudinal gradients in the Upper Paraguay River Basin: implications for conservation in the Pantanal region

Abstract

Lack of sufficient knowledge of biological diversity is the first barrier to promoting scientifically-based conservation policies in Neotropical regions, where high diversity and limited sampling remains a challenge. We compiled fish occurrences data from the whole Upper Paraguay River basin (UPRB) and evaluated the altitudinal variation in species richness, local contribution to β diversity (LCBD) and composition. We also evaluate the influence of other environmental variables on species richness. Occurrence of a total of 354 native and five exotic fish species were recorded. Fish species richness was higher in lower portions of the basin, with a clear decrease from 400 m.a.s.l. Richness was negatively correlated with altitude, and positively correlated with net primary productivity and slope. The LCBD presented higher values on floodplain and in headwaters. Intermediate classes presented greater relative importance, as they present greater relative richness in a small relative area in the basin. We observed a partial overlap in species composition along altitude classes. Three species classified in some category of threat according to the conservation status of ichthyofauna in Brazil have a limited spatial extent of occurrence, restricted within the Serra da Bodoquena plateau. The obtained results highlight the unique diversity in the floodplain-plateau continuum, therefore, choosing protected areas must consider altitude gradients in the UPRB. Given the small area of the conservation units in the basin, the important role of higher altitude streams in regional fish species diversity and the several threats in the plateau, we conclude that an increase in conservation effort is needed in the plateau portion of the Upper Paraguay River basin.

Resumo

A falta de conhecimento da diversidade biológica é a primeira barreira para a promoção de políticas de conservação com base científica nas regiões neotropicais, onde a alta diversidade e a amostragem limitada continuam a ser um desafio. Compilamos dados de ocorrências de peixes de toda a bacia do Alto Rio Paraguai (BAP) e avaliamos a variação altitudinal na riqueza de espécies, contribuição local para a diversidade β (LCBD) e composição. Também avaliamos a influência de outras variáveis ambientais na riqueza de espécies. Foi registrada a ocorrência de um total de 354 espécies de peixes nativos e cinco exóticos. A riqueza de espécies de peixes foi maior nas porções mais baixas da bacia, com uma clara diminuição a partir dos 400 m.a.s.l. A riqueza foi correlacionada negativamente com a altitude e positivamente correlacionada com a produtividade primária líquida e declividade. A LCBD apresentou maiores valores na planície de inundação e nas cabeceiras. As classes intermediárias apresentaram maior importância relativa, pois apresentam maior riqueza relativa em uma área relativamente pequena na bacia. Observamos uma sobreposição parcial na composição de espécies ao longo das classes de altitude. Três espécies classificadas em alguma categoria de ameaça de acordo com o estado de conservação da ictiofauna no Brasil possuem extensão espacial de ocorrência limitada, restrita ao planalto da Serra da Bodoquena. Os resultados obtidos destacam a diversidade única no continuum várzea-planalto, portanto, a escolha de áreas protegidas deve considerar gradientes de altitude na UPRB. Dada a pequena área das unidades de conservação na bacia, o importante papel dos riachos de maior altitude na diversidade regional de espécies de peixes e as diversas ameaças no planalto, concluímos que é necessário um aumento no esforço de conservação na porção do planalto BAP.

1. Introduction

Altitudinal variation is one of the most important ecological gradients and is often related to changes in fish diversity (Lomolino, 2001). Generally, fish diversity and altitude have a negative relationship, with diversity increasing with decreasing altitude (Lomolino, 2001). The low diversity of fish at high altitudes can be attributed to large variations in environmental conditions, limiting the presence of species with low tolerance to adverse conditions. In addition, there is difficulty in colonization and the reduction in the area of available habitat (Cheng et al., 2019; Huston, 1994; Jacobsen, 2008; Janzen, 1967). As the altitude decreases, stream order increases, as does the area of available habitat and primary productivity due to greater light input (Vannote et al., 1980). Less environmental variability also facilitates colonization of these habitats that increases the migration rate and fish diversity (Cheng et al., 2019; Huston, 1994; Taylor & Warren Jr, 2001).

Despite the importance of the altitudinal gradients in biogeography and conservation, few studies have evaluated or quickly mentioned how this variable affects the fish assemblages in the Neotropical region. Generally addressing biogeographic patterns and finding a negative correlation between altitude and richness and abundance (e.g., Albert, Tagliacollo and Dagosta, 2020; Albert & Reis, 2011; Jaramillo-Villa, Maldonado-Ocampo and Escobar, 2010; Lorion, Kennedy and Braatne, 2011; Loyola-Bartra, Landeiro, Dala-Corte and Penha, 2022). The Neotropical region encompasses the greatest fish richness in the world (Albert et al., 2020). The La Plata basin, which drains areas of Argentina, Bolivia, Brazil, Paraguay and Uruguay, is the third most diverse basin in South America with 924 species (Reis et al., 2016).

In the La Plata basin, the lower portion of Upper Paraguay River basin (UPRB) contains the Pantanal, the largest floodplain wetland in the world, where many animals threatened in other Brazilian regions are considered relatively well preserved. The

Paraguay River has its headwaters in Mato Grosso and flows for about 2,700 km to its mouth in the Paraná River in Argentina. Due to the absence of barriers to dispersion, the fish species in this region are more homogeneous, and it is possible to find in a short stretch of the river a complete representation of the richness of fish species recorded in the basin (Severo-Neto, Tencatt, Costa-Pereira and Tavares, 2015; Súarez, Ferreira, Tondato and Fialho, 2013). Nevertheless, in the headwaters, species composition varies among sub-basins and in response to differences in altitude (Súarez, Valério, Tondato, Ximenes and Felipe, 2007; Tondato & Súarez, 2010; Valério, Súarez, Felipe, Tondato and Ximenes, 2007).

Sustaining fish assemblages in the region requires more information on how relatively small differences in altitude can determine differences in the composition, diversity and distribution of fish species in the Upper Paraguay basin. Because altitude also has a strong effect on land use in the UPRB, with the plateau portion being intensively more used than the lower portion (Roque et al., 2016), our results can help to determine where fish are at higher risk and can lead to developing effective conservation action toward freshwater biodiversity conservation.

2. Methods

2.1. Obtaining the Data

We obtained fish occurrence from primary data on the entire Upper Paraguay River basin and complemented by GBIF, FishNet, SpeciesLink and data paper of Neotropical fish (Tonella et al., 2023). We included only species whose occurrences were confirmed by specialists. We based the distribution points from recently described species (up to October 2022) on the original descriptions. Taxonomic positions and valid scientific names follow Fricke, Eschmeyer and Fong (2022). After this detailed conference and standardization of the data (scientific names actualization, removal of incomplete data or assessment of species that do not occur in the basin) on occurrence distribution, we analyzed a total of 75,581 individual fish records from the Upper Paraguay River basin. We obtained environmental data from Modis Satellites (Running & Zhao, 2021) and calculated the mean Net Primary Productivity (2000-2023). In HydroSHEDS (Lehner & Grill, 2013) we obtain the mean rivers order and slope (2001-2022). For mean temperature and precipitation, we use the WorldClim dataset (Fick & Hijmans, 2017).

Using the book of Britski, Silimon and Lopes (2007) as a historical landmark on the knowledge of the Upper Paraguay River basin ichthyofauna, we compiled all the publications that described new fish species with the type-locality located in the basin to compile the comprehensive data of the altitudinal quotes of these species.

2.2. Data analysis

We generated a grid of 0.5x0.5 degrees of latitude/longitude for the whole UPRB (~55x55km; Figure 1) from what we extracted species occurrence and mean altitude (m.a.s.l.) using a srtm file (Spatial Resolution = 30x30m) available on the United States Geological Survey (USGS). We generated altitude classes using the "*group_var*" function at "*sjmisc*" package (Lüdecke, 2018) to control for differences in sampling effort. The altitude gradient in the UPRB can be considered low amplitude compared to other gradients in Brazil and South America. Therefore, we divide the altitude classes in such a way as to obtain a reasonable number of classes. For example, at 100m intervals we would only get 6 classes. Below 50m we would not be able to control for differences in sampling effort.

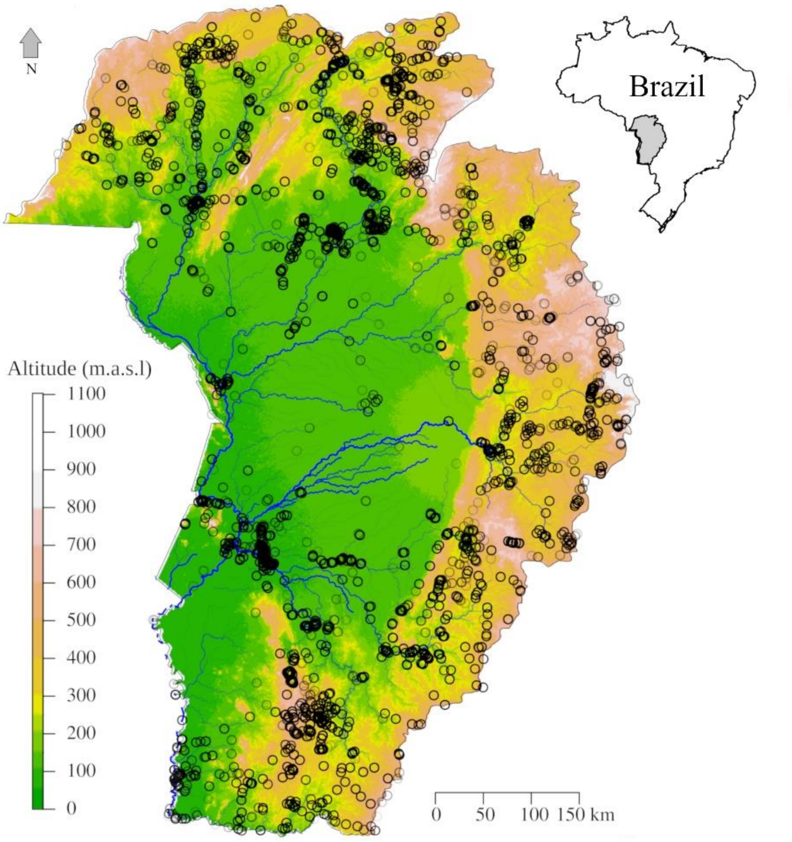

Figure 1. Location of Upper Paraguay River basin in Brazil with altitudinal variation and fish data occurrences.

We calculated the accumulated richness by altitude class using "*specpool*" function in "*vegan*" package (Oksanen et al., 2022). As sampling effort affects species richness, making it difficult to compare results, we made some complementary procedures that we have available in the attachments. We standardized the accumulated richness with the same number of grid cells in all altitude classes. To do this, we use the minimum number of grid cells recorded in an altitude class. We then generated a species accumulation curve based on the number of grid cells and obtained the accumulated richness with three grid cells for all altitude classes, as well as the standard deviation (attachment 2). For this complementary procedure we used the "*specaccum*" function in the "*vegan*" package.

To estimate the relative importance of an altitude class with respect to its richness and area, we divide the relative richness (altitude class accumulated richness/total basin richness) by the relative area (altitude class area/total basin area) of each altitude class. To evaluate the influence of environmental variables (altitude, river order, slope, net primary productivity, precipitation, and temperature) on species richness we used the negative binomial Generalized Linear Model (GLM-nb) from the *"MASS"* package.

Aiming to evaluate differences in fish species composition along the altitudinal gradient we calculate for each local (each grid cell) the Local Contribution to β Diversity (LCBD) (Legendre & De Cáceres, 2013). For this estimate we used the "β.div" function (also from the "vegan" package) with Sorensen dissimilarity coefficient, estimated by the "ecodist" package (Goslee & Urban, 2007). Considering the absence of normal distribution, we used the Kruskall-Wallis' test and Dunn test (function "dunn.test") using the "dunn.test" package (Dinno, 2017) to quantify differences in LCBD (response variable) for altitude classes (factor) to regional fish diversity.

To evaluate the variation in species composition (Sorensen coefficient) among altitude classes, we used a distance-based multivariate permutational analysis of variance (permanova), proposed by Anderson (2001), using the "*adonis2*" function after PERMDisp procedure using "βdisper" function available in the "*vegan*" package. The significance in observed differences was estimated using 999 permutations. Also using Sorensen distance we run a Principal Coordinates Analysis (PCoA) using the "*cmdscale*" function to obtain an ordination of cell grids with species distribution along altitude classes for the whole basin.

We used species with at least ten occurrences to estimate a threshold indicator taxa analysis (TITAN), as proposed by Baker & King (2010). This method identifies groups of species that increase or decrease their occurrence along an environmental gradient (e.g., mean altitude of each cell) and identifies where on that gradient the increase or decrease occurred. For that purpose, we used the function "titan" available in the "TITAN2" package (Baker, King and Kahle, 2022). Given the large number of evaluated species, we used high purity and reliability (=0.99) including in the analysis only species with a clear response to altitudinal gradient.

According to the conservation status of ichthyofauna in Brazil from Ministry of the Environment Ordinance No. 148 (MMA, 2022), five species present in the UPRB are included in the threat category. We selected these species and estimated the extent of occurrence in the UPRB using the "rangemap_boundaries" function from the "rangemap" package (Cobos, Barve, Barve, Jimenez-Valverde and Nuñez-Penichet, 2021).

3. Results

Data compilation resulted in 75,581 records. After the data filtering, we removed 30% of the compiled fish species due inconsistencies with the currently known ichthyofauna in UPRB (e.g., species restricted to other South American basins). This procedure resulted in a reduction of 16% of the total records. In total, we gathered data on 354 native fish species from the entire Upper Paraguay River basin. All known orders from this drainage were represented in the final dataset, including 148 Siluriformes; 131 Characiformes; 22 Cichliformes; 21 Gymnotiformes; 19 Cyprinodontiformes; 8 Myliobatiformes; 2 Beloniformes, 2 Clupeiformes, 2 Perciformes and 2 Synbranchiformes; and one species in the Ceratodontiformes and Pleuronectiformes each. Forty-three families were represented. The five richest families contributed to 52.7% (N=187) of the total richness: Characidae (72), Loricariidae (58), Cichlidae (21), Callichthyidae (18) and Pimelodidae (16). Five introduced fish species were represented as four Cichlidae - the peacock bass (*Cichla piquiti*, *C. kelberi*), the redbreast tilapia and nile tilapia (*Coptodon rendalli*, *Oreochromis niloticus*) - and one Poeciliidae, the guppy (*Poecilia reticulata*).

Fish species richness along the altitudinal gradient was higher in lower portions of basin, from ~100 to 400 m.a.s.l. (Figure 2-A). A clear decrease occurred from 400m of altitude upwards, where the cumulative richness decreases from about 250 species per altitude class to nearly 100 species per altitude class. Despite this decrease, local contributions to the β diversity showed larger values in lower and higher portions of the basin, with smaller mean values in intermediate altitude classes (KW=31.189; p<0.001) (Figure 2-B). We observed differences in LCBD among altitude classes (KW=31.25; p=0.001). The first two altitude classes (<100m and 100-150m) are statistically equal in LCBD, however, these classes were statistically different from the five next altitude classes (from 150 to 400m). Higher altitudes (>600m) differ from 200 to 400 m.a.s.l.

Finally, 500-550 m.a.s.l. also differ from 150-400 m.a.s.l. Thus, lower and higher altitude classes commonly differ from intermediate altitude classes in the local contribution to β diversity (LCBD) along the Upper Paraguay River basin.

Our results also showed that at least 60% of all species richness of the basin is represented in its lower portion up to 400m.a.sl., and above 400m the relative richness represents nearly 30% of total species richness. We also observed that the relative importance of altitude classes (Relative Richness/Relative area) was different from the pattern presented by the accumulated richness. The lower altitude classes have less relative importance and the intermediate classes presented greater relative importance, as they present greater relative richness in a small relative area in the basin (Figure 2-C). We observed a negative correlation between richness and altitude ($p<0.001$) (Figure 2-D). For net primary productivity ($p=0.02$) and slope ($p=0.009$) we found a positive correlation with richness (Figure 2-E-F).

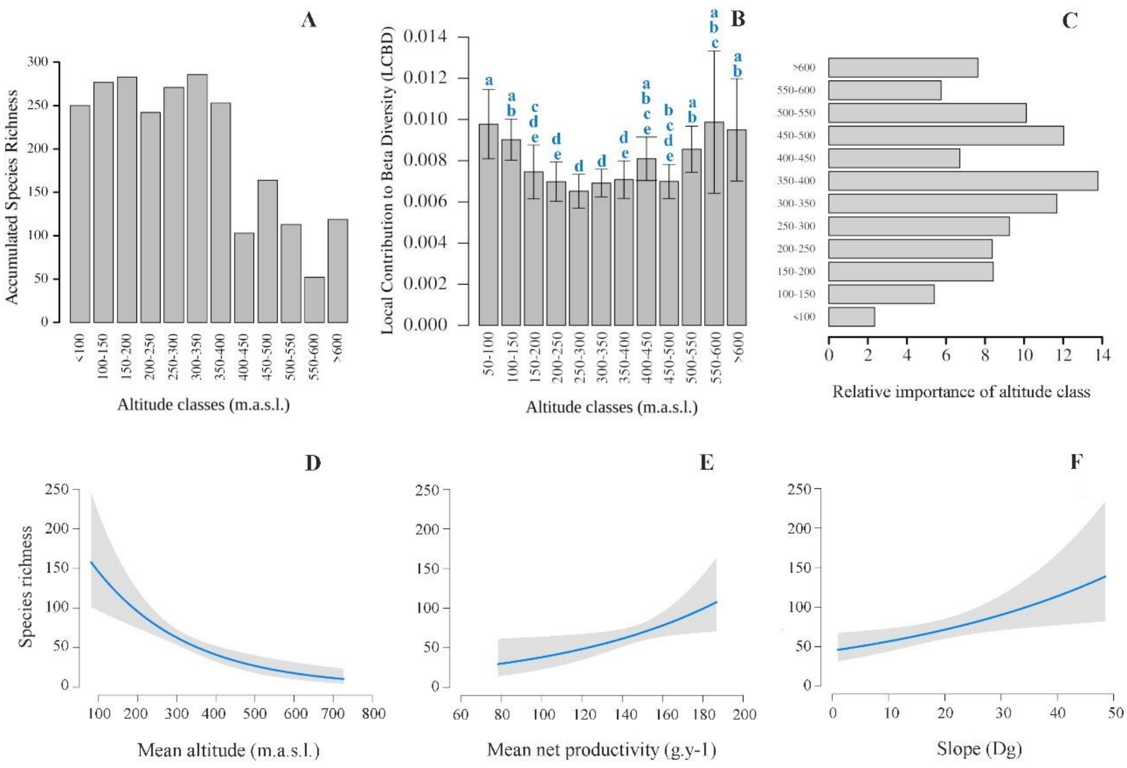

Figure 2. Accumulated fish species richness along altitude classes in the Upper Paraguay River Basin (A), cell grid contribution to β diversity (± confidence interval and pairwise comparisons) (B) and relative importance of altitude classes (C). Correlation **(**GLM-nb) of fish species richness with mean altitude (D), net primary productivity (E) and slope (F) in the Upper Paraguay River Basin.

Principal Coordinates Analysis and distance based permutational Analysis of Variance (permanova pseudo F=8.97; p<0.001) showed differences in species composition along the altitudinal gradient of the Upper Paraguay River basin (Figure 3). We observed that the lower altitudes, in the plain region (up to 200m), present a similar species composition. At intermediate altitudes the species composition changes and becomes more similar to the species composition at higher altitudes. However, we can observe that the species composition at altitudes above 600m is also similar to lower altitudes.

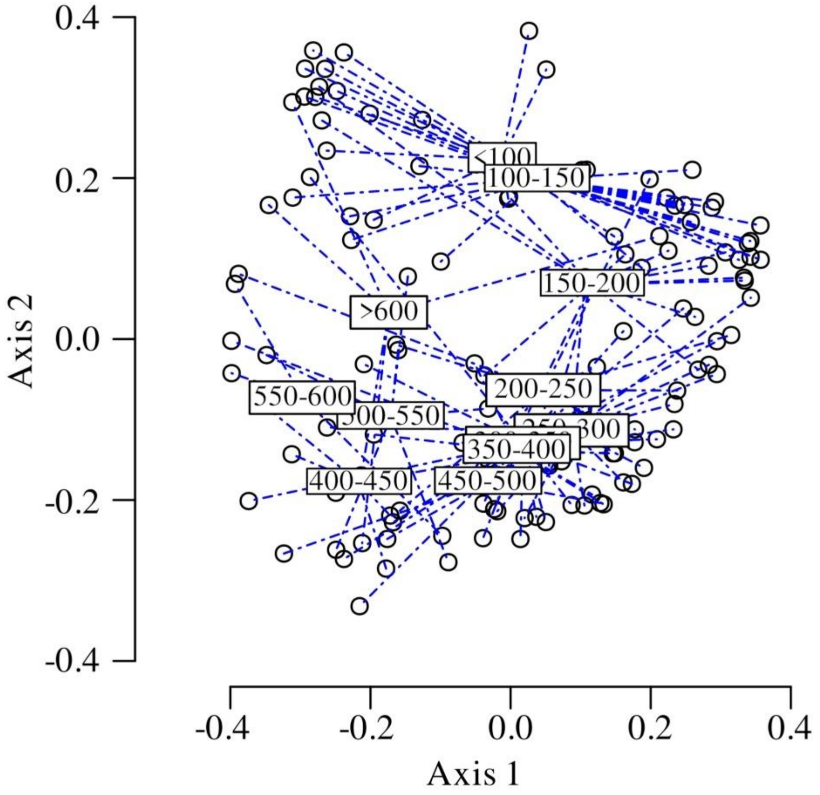

Figure 3. Ordination of Principal Coordinates Analysis (PCoA) of fish species composition along the altitudinal gradient in the Upper Paraguay River Basin.

We also observed that at 163.3m altitude there is an increase in the occurrence of certain species (z+) and at 179.9m there is a reduction in the occurrence of other species (z-) (Figure 4-A). Thirteen fish species increased their occurrence along the altitude gradient and *Astyanax lineatus* is the most associated species with the plateau portion of the basin, followed by *Parodon nasus*, *Hypostomus cochliodon*, *H. khimaera*, *Piabarchus torrenticola* and *Rineloricaria lanceolata* (Figure 4-B). In contrast, 41 species decreased their occurrence along the altitude gradient, with *Astronotus crassipinnis*, *Mesonauta festivus*, *Markiana nigripinnis*, *Apistogramma commbrae* and *Chaetobranchopsis australis* presenting the strongest associations (Figure 4-C).

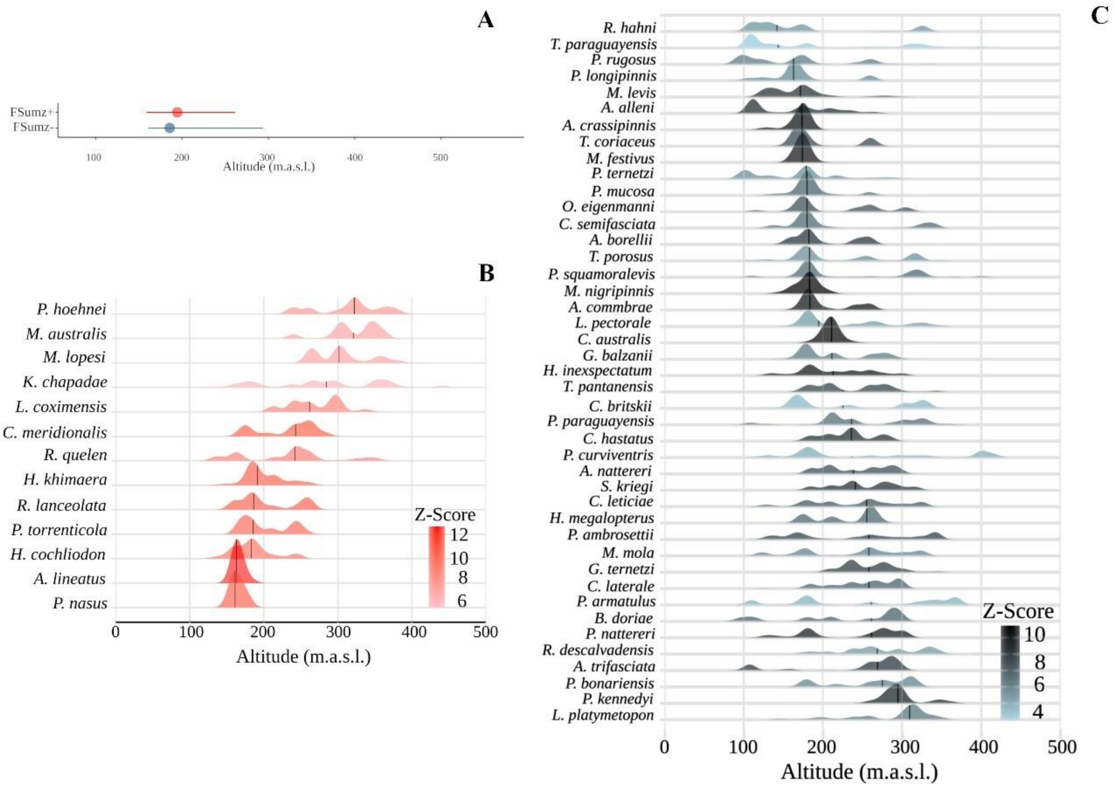

Figure 4. Change points for fish species that decrease (Z-) or increase (Z+) its occurrence. Density plot of fish species that increase (B) and decrease (C) its frequency along the altitudinal gradient in the Upper Paraguay River basin.

Five fish species (1.4% of total richness) are classified in a category of threat: *Ancistrus formoso*, *Trichomycterus dali* and *Pseudoplatystoma corruscans* (Vulnerable), *Austrolebias ephemerus* (Endangered) and *Loricaria coximensis* (Critically Endangered). Three of these species (*A. formoso*, *A. ephemerus* and *T. dali*) present smaller extension of occurrence areas in the UPRB, being 0.37, 44.7 and 3,381.9 km^2, respectively, while *L. coximensis* and *P. corruscans* have 94,182.9 and 240,802 km^2, respectively (Figure 5-A). One fish species (*P. corruscans*) occurred predominantly in the lower portion of the basin while others, even though they occurred in portions with low altitude, as *A. ephemerus,* did not occur in the floodplain portion of the basin (Pantanal).

3.1. Recent state-of-art on the altitudinal landscape perspective

Since the work of Britski, Silimon and Lopes (2007), 39 new fish species have been described from the UPRB. Loricariidae was the family with the highest number of new taxa, with 10 new species; followed by Characidae (9) and Rivulidae (6). These three families had new representatives in a broad altitudinal range, from 100 to 600 m.a.s.l. Peaks of new species occurred between 100 to 200 m.a.s.l. and 400 to 500 m.a.s.l (Figure 5-B). From the 39 new species, four were described within conservation unit boundaries: *Hypostomus froehlichi*, *H. perdido*, *Oligosarcus perdido* and *Trichomycterus dali*. All of them were within the Parque Nacional da Serra da Bodoquena boundaries. Only two species (*Hemigrammus machadoi* and *Potamotrygon amandae*) occur in more than one basin and the 37 others are exclusive to the UPRB up to this date.

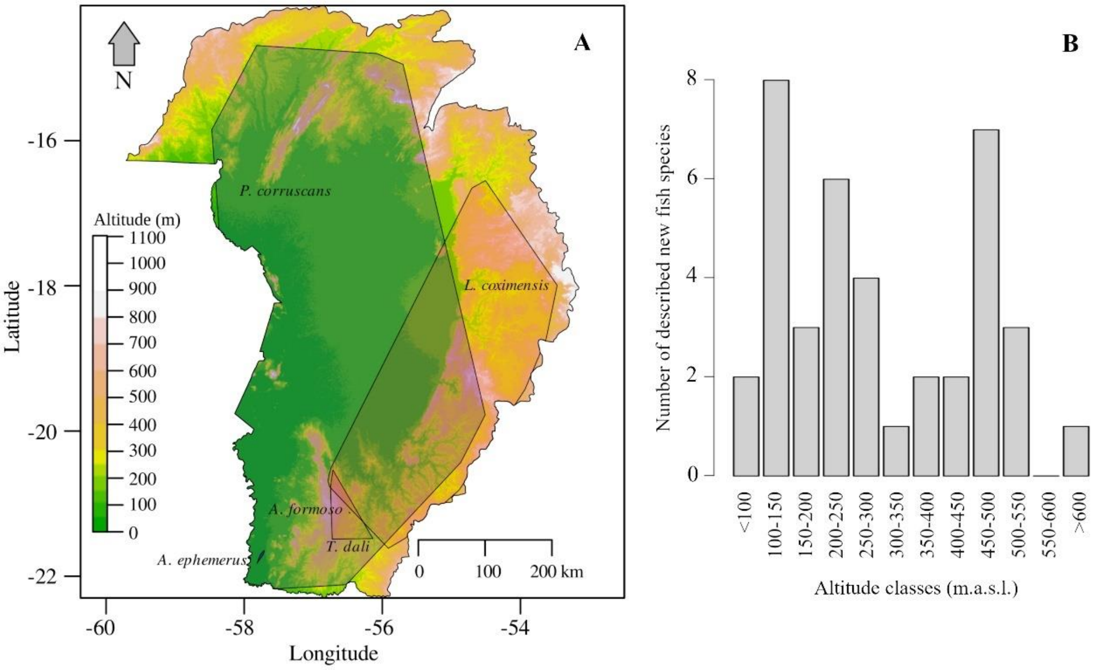

Figure 5. Area of extent of occurrence of fish species with any threat level in the Upper Paraguay River basin (A). Number of fish species described from 2007 by altitude classes in the Upper Paraguay River basin (B).

4. Discussion

Our study found a negative correlation between altitude and richness. We observed a greater richness of fish species in the lower portions of the basin in relation to the headwaters. In the lowland portion up to 400 m.a.s.l. richness is greater with a clear decrease above this altitude class. This high richness in lower portions of the basin was also observed in other studies in the Pantanal floodplain in which many fish species were found in small study areas (e.g., Baginski, Florentino, Fernandes, Penha and Mateus, 2007; Pacheco & Silva, 2009; Súarez et al., 2013; Severo-Neto et al., 2015). Several possible explanations are proposed for the widely reported gradient of lower species richness at higher altitudes. MacArthur (1972) proposed that smaller areas and isolation can be used to explain the influence of altitude on this gradient, like the species-area relationships in island biogeography. Consequently, the lower fish species richness at higher altitudes may reflect difficulty in colonization and persistence in these portions of the basin associated with smaller streams orders (less available habitat area) registered in headwaters portions, which are commonly subject to large hydrological variations (Poff & Allan, 1995).

In the Upper Paraguay River Basin, studies on fish diversity have listed 267 species for the Pantanal floodplain (Britski, Silimon and Lopes, 2007) and 336 valid species for the entire UPRB (Gimênes Junior et al., 2022). Our study increased the richness of 20 described or recorded species, representing a 6% increase in species richness. Notwithstanding, a compilation of the undescribed species is still necessary, with at least 60 species in this situation. Many portions of the UPRB have intermittent streams (in the lower parts and in the headwaters) creating conditions for the existence of other unrecorded (and undescribed) fish species. However, when considering the existence of sampling gaps, it is necessary to sample a larger area in the basin to reduce the Linnean and Wallacean deficit, to obtain more information for better conservation planning of the aquatic assemblages in the UPRB.

We also observed that primary productivity and slope are positively correlated with richness. These variables are related to the availability and heterogeneity of habitat, quantity of resources, presence of geographic barriers to dispersal, and these factors directly influence species richness (Camana et al. 2016; Vannote et al., 1980, Waide et al., 1999). Theories more focused on aquatic habitats (as River Continuum Concept – Vannote et al., 1980) proposals that larger rivers in lower portions of the basin present usually higher species diversity by high primary productivity and more resources availability and heterogeneity. In this study, we observed an expected pattern for primary productivity (positively correlated with richness) in which high primary productivity can sustain primary consumers, increasing the species richness of the site (Waide et al., 1999). For the intermediate altitudes (classes from 150 to 400 m.a.s.l.), species richness was higher than expected by the representativeness in the relative area of the basin, with great relative importance. The positive correlation between richness and slope may be related to this high richness at intermediate altitudes. These areas have greater variability in slope compared to high altitude areas, due to the transition for the floodplain areas, and greater variability in slope can increase species richness due to greater habitat diversity (Camana et al. 2016).

For the Local Contribution to β Diversity, high and low altitude classes presented high values. In the PCoA, we observe that these altitude classes presented a different fish composition (except for the >600 m.a.s.l altitude class). These results suggest that floodplains and high headwaters differ in species composition and that intermediate altitude portions of the basin may have overlap in the species distribution area. This may also explain the higher species richness recorded at intermediate altitudes than expected due to their relative importance. Thus, regions with intermediate altitudes act as an ecotone between fish assemblages from lower and higher areas in the basin. Complementarily, the greater local contribution to β diversity (LCDB) may partially corroborate the results of Carvajal-Quintero et al. (2015) because fish species with limited distribution in the headwaters of the basin boost the uniqueness of this portion of the basin.

Flood Pulse concept (Junk et al., 1989) suggest that variation in river level in floodplain rivers are the main determinant of aquatic assemblages, increasing habitat heterogeneity due to the extension of the aquatic environment to the terrestrial environment, making available new niches and increasing fish diversity. The Pantanal is an area with few geographical barriers and the flood pulse is a strong connecting factor. In addition, this region has large rivers, lagoons, flooded areas, and channels, in contrast to the higher areas of the plateau, which have mainly streams and lower-order rivers. This hypothesis can explain higher fish species richness in the floodplain portion and differences in the composition.

The PCoA showed a similarity in species composition between the lower altitude classes and the >600 m.a.s.l. altitude class. Two hypotheses can explain this result. Not all the lower part of the basin is floodable and almost 40% of the basin is composed of non-flooded areas (Pereira et al. 2021). In the southern portion, mainly from the Nabileque to the Apa rivers, the floodplain of the rivers is smaller, narrower or almost non-existent. This hydrogeomorphology creates a pattern in which species generally associated with headwaters (such as *Ancistrus* spp. and *Astyanax lineatus*) occur frequently in this region. Furthermore, more than ten species of fish in the UPRB are migratory (Resende, 2003), including the *P. corruscans*, which has a large extension of occurrence (240,802 km^2). These fishes migrate hundreds of kilometers from the floodplain to the plateau to spawn. After reproduction, these species return to the plains where they find favorable habitats for shelter from predators, feeding, and growth (Resende, 2003). This observed pattern highlights the unique β diversity in the plateau-floodplain continuum.

The hypothesis that species occurring at higher altitudes may have greater environmental niche breadth (Stevens, 1992) assumes that these species can migrate along this high-altitudinal gradient to find suitable environmental conditions in different seasons. Thus, fish assemblages can be nested along the basin's entire gradient, with many fish species occurring in lower regions of the basin (in our case floodplain) and few species reaching higher regions (when there are no impassable barriers). However, in many situations, headwater assemblages are not a set of species with greater capacity for dispersal (not occurring along the entire altitude gradient) and are isolated by barriers such as rapids and waterfalls, forming exclusive assemblages. In this case, the fish distribution is defined by biogeographic history during basin formation and the vicariance process, along with their relationships in neighboring hydrographic basins by headwater capture. Then, an assessment of tolerance to environmental variations must be carried out to verify the relationship between environmental tolerance and altitude distribution to better understand the altitude-species relationships we describe to the UPRB.

The UPRB has one of the greatest fish diversities in the world, which is currently threatened by several anthropogenic activities. Deforestation projections for the year 2050 are three times higher in the plateau than in the floodplain and could strongly affect stream fish assemblages (Dala-Corte et al., 2020; Guerra et al., 2020). Considering that the Conservation Units and Indigenous Reserves represent less than 8.3% of the basin area (1.9% in the floodplain and 6.4% in the plateau), the predicted increased deforestation could have a more intense impact on a group of species with occurrence more restricted to the upper portion of the Basin. The intense habitat loss and the overlap of species at intermediate altitudes suggests an ideal region for creating conservation units.

Scientists have documented the crisis of global freshwater biodiversity loss and recommended that freshwater ecosystems be ranked among humanity’s highest priorities (Albert et al., 2021). In addition to deforestation, other human impacts that affect headwaters can generally lead to a decrease in the functional and taxonomic diversity of fish in the basin (Brejão et al., 2018; Freitas et al., 2021). Currently, in the UPRB, there are negligent projects implemented and planned that put fish communities at risk. In the portion of the UPRB plateau there are several proposals for the implementation of small hydroelectric power plants with the possibility of building more than 130 barriers proposed in different licensing stages (Zanatta & Maciel, 2020). In addition, a harmful project is underway that foresees the dredging of the Paraguay River to deepen and widen the navigation channel to facilitate the passage of soybeans through the Pantanal (Coelho Jr. et al., 2022).

In this way, hydrological connectivity can be severely reduced, decreasing chances for recolonization if there is any local extinction of species and thereby altering the ecological functioning of rivers and the patterns of occurrence and abundance of species distribution throughout the basin (the functional connectivity). Some of these proposals can alter water quality and create barriers limiting the reproductive migration of economically important fish species (Campos et al., 2020; Cruz et al., 2021). In the UPRB, fish are an important complement for the family's diet, contributing not only to food security, but also to the accessibility of animal protein and other essential nutrients. In addition, fisheries are a traditional activity that provides employment and gender empowerment to people.

Five species of fish are included in threat categories. Three of them have a smaller extent of occurrence in the basin *(Ancistrus formoso*, *Austrolebias ephemerus* and *Trichomycterus dali*) and *A. ephemerus* is an annual species occurring in the portion with the sample gap. *Ancistrus formoso* and *T. dali* occur exclusively in caves in the eastern region of Serra da Bodoquena. In the western portion, there are few samples, with intermittent streams, creating temporary isolation from other portions of watersheds. These types of species distributions require more effort to manage and to conserve.

Two introduced predatory species (*Cichla piquiti* and *C. kelberi*) in the Pantanal floodplain represent yet another threat to native species. The introduction of predatory species can lead to decreased species diversity and changes in ecosystem services (Leal et al., 2021; Petry, Gomes, Piana and Agostinho, 2010). Similarly, introduced competitors such as *Coptodon rendalli, O. niloticus* and *P. reticulata* that are now present only in the plateau portion and despite their different feeding habits (*C. rendalli/O. niloticus* = Omnivory with a tendency to herbivory and *P. reticulata* = planktophagous/insectivore) can compete with native species and alter the functioning of the ecosystem. In both cases, these introductions occurred in response to anthropogenic impacts (aquaculture and aquarium release). Currently, all these threats are ignored by decision makers. Other threats such as large forest fires and domestic and industrial pollution are also present and must be considered in initiatives aimed at conservation.

5. Conclusion

Our study area shows a relatively small variation in altitude gradient, compared to other studies in more mountainous regions, with a floodplain of about 150 to 70 m.a.s.l. and a plateau to close to 700 m.a.s.l., (e.g., Bhatt et al., 2012 or Carvajal-Quintero et al., 2015). Nonetheless, the effects of the altitude gradient on the segregation of fish assemblages can create some significant differences between floodplain and non-floodable regions in the UPRB. Our results showed differences in species richness, uniqueness, and greater importance to headwaters to maintain a large regional diversity of species. Therefore, choosing protected areas must take into account altitude gradients. Another important result is the number of species recently described in the UPRB (39 species) with 33.3% above 400 m.a.s.l. Considering that other undescribed species occur mainly in headwater portions (increasing this representation in regional fish diversity), we reinforce the importance of these portions of the basin in their higher contribution to regional diversity. Noteworthy, the lower representation of Conservation Units and the higher rate of deforestation may affect the mid-term and long-term need for more conservation effort to sustain the ecosystem functioning of the aquatic assemblages in the Upper Paraguay River basin.

Chapter 3. Threats, conflicts, and the future of small-scale fisheries in the Pantanal wetland, Brazil

Abstract

Small-scale fisheries (SSF) play a major role in the well-being and livelihood security of millions of Indigenous Peoples and Local Communities (IPLCs). In the Brazilian Pantanal wetland, thousands of fishers are under threat. Local policies aiming to forbid commercial fishing in the region are currently forcing the economic displacement of IPLCs. In this paper we explore the current situation in the 179,300 Km² Pantanal wetland fisheries and the urgent threats that are putting their existence in the region in jeopardy. Understanding the current situation is fundamental to promote the sustainable development of the Pantanal fisheries. Over the last few decades, the commercial fishing policy has shifted from an incentive policy to a restrictive policy. What makes this scenario worse is that these initiatives are justified based on a scientifically unsupported assumption of a collapse of the local fish populations. On the other hand, there are high negative impact projects implemented and planned to be installed in the Upper Paraguay River Basin that put at risk one of the greatest fish diversities in the world, which are ignored by decision makers in fisheries management. Current policies treat the different fishing categories as incompatible, with a clear disadvantage to already marginalized groups. Therefore, to overcome this negative scenario, we are arguing ten urgent measures to guarantee the sustainability of the Pantanal fisheries and its peoples. A focus on shared, participatory management, with full involvement of fishers, can increase governance helping attain sustainable use and co-responsible management of the Pantanal fisheries resources.

Resumo

A pesca de pequena escala (PPE) desempenha um papel importante no bem-estar e na segurança dos meios de subsistência de milhões de Povos Indígenas e Comunidades Locais (PICLs). No Pantanal brasileiro, milhares de pescadores estão ameaçados. As políticas locais que visam proibir a pesca comercial na região estão atualmente forçando o deslocamento econômico dos PICLs. Neste artigo, exploramos a situação atual dos 179.300 km² da área pesqueira do Pantanal e as ameaças urgentes que estão colocando em risco sua existência na região. Compreender a situação atual é fundamental para promover o desenvolvimento sustentável da pesca pantaneira. Nas últimas décadas, a política de pesca comercial passou de uma política de incentivos para uma política restritiva. O que piora este cenário é que estas iniciativas são justificadas com base numa suposição cientificamente não apoiada de um colapso das populações de peixes locais. Por outro lado, existem projetos de alto impacto negativo implementados e previstos para serem instalados na Bacia do Alto Rio Paraguai que colocam em risco uma das maiores diversidades pesqueiras do mundo, que são ignoradas pelos tomadores de decisão na gestão pesqueira. As políticas atuais tratam as diferentes categorias de pesca como incompatíveis, com uma clara desvantagem para grupos já marginalizados. Portanto, para superar esse cenário negativo, defendemos dez medidas urgentes para garantir a sustentabilidade da pesca pantaneira e de seus povos. O foco na gestão compartilhada e participativa, com total envolvimento dos pescadores, pode melhorar a governança, ajudando a alcançar o uso sustentável e a gestão corresponsável dos recursos pesqueiros do Pantanal.

Introduction

Small-scale fisheries (SSF) play a critical role to the well-being and livelihood security of millions of people worldwide (Béné et al., 2016; FAO, 2022). Around 500 million people directly depend on SSF (FAO, 2023). At least 40 percent of the world's total fishery catch and nearly two-thirds of the fish that goes directly to human consumption are from SSF (FAO, 2015). Furthermore, SSF provides employment to approximately 61 million people (FAO, 2022), with an economic value of over US$ 4.5 billion / per year (FAO, 2023).

Albeit its economic importance, SSF are generally marginalized in environment and development policies. In fact, many are under constant pressure of physical or economic displacements to open space for more industrialized economic activities (Cohen et al., 2019), or to conservation initiatives (Chiaravalotti, 2019). SSF frequently have low/no political voice, with unequal power relations (FAO, 2015). SSF are also many times considered inefficient and their benefits are ignored. Although SSF are considered among the most adaptable systems to environmental changes, particularly in areas with significant resource fluctuations, such as flood-pulsed wetlands (Valdez-Rojas et al., 2022), policy makers and practitioners tend to accuse SSF of impacts that are rather natural changes or a consequence of other groups' use.

In this paper we bring the case of the Pantanal wetland fisheries. Although Pantanal fisheries play an important role for local economy and sustainability, they are on the verge of being virtually displaced from the region (Chiaravalloti, 2019). We show the evidence of fishers' economic, social, and environmental importance for the region and the urgent need to review the local policies focused on pushing people out of fishing activities.

The Pantanal fisheries context

The Pantanal and its ichthyofauna

The Pantanal is a large floodplain inserted in the Upper Paraguay River Basin (UPRB), with a variation in altitude between the floodplain and its surrounding plateau of up to 200m (Figure 1). The connection between these two areas is fundamental for the ichthyofauna of the Pantanal. Annually, migratory fish species leave the floodplain and occupy the surrounding plateau for reproduction (Ziober et al., 2012; Souza et al., 2023). During this period called “Piracema”, some species travel hundreds of kilometers upstream to the spawning grounds. After reproduction, adults and juveniles return to the floodplains where they find favorable habitats for shelter from predators, feeding, and growth (Resende, 2003; Souza et al., 2023).

The ecological dynamics of the floodplain is dictated by a flood pulse. First, the extent of the water in the system will dictate the abundance of fish in the following year (Welcomme, 2001). Therefore, interannual variations in the flood pulse (Galdino & Clarke, 1995; Hamilton et al., 1996), which can vary from covering from 10% to 80% of the floodplain depending on the year (Hamilton et al., 1996), will have a direct consequence on the quantity and distribution of fish in the system (Mateus et al., 2011). Second, due to changes in altitude and rainfall in the surrounding areas of the Pantanal, the flood pulse slowly moves in the north/south and east/west directions. It takes around three months for the flood pulse to cross the Pantanal. As a consequence, windows of protection from predators, feeding, and growth are shifted in space and extended in time, increasing fish recruitment. Therefore, flood pulse dynamics creates a complex spatial pattern of flooding that directly influences availability for fish.

Fishers in the Pantanal

Nowadays, in the Pantanal wetland, there are artisanal and recreational fishing categories. Artisanal fishing is divided into commercial fishing, subsistence fishing and bait gathering. This category is carried out exclusively by small-scale and fishers exhibit a limited educational attainment. Subsistence fishing has been part of Pantaneiros' livelihoods since the first dwellers in the region. Archaeological records show that fishing nets have been used in the Pantanal for at least 5 thousand years (Peixoto, 2003). Also, indigenous mounds found throughout the floodplain see a large amount of fish bones and fish artifacts, showing that man's close relationship with fish is ancient (Silva, 2004).

Commercial fishing in the Pantanal is a formal category of work, in which 90% of riverside residents of the communities are registered (Chiaravalloti, 2019; Chiaravalloti et al., 2022). Fishers are only allowed to use fishing rods; and no fishing nets or other fishing instruments are permitted (Chiaravalloti, 2017). Their primary mode of social organization being represented by what are commonly referred to as "Fishing Colonies" (Figure 1). Commercial fishing activities developed mainly after the 1970s. During this period, a combination of years with large floods (Mateus et al., 2011; Chiaravalloti et al., 2022), the adoption of new fish storage technologies (ice boxes and freezers), and the establishment of fish processing companies in the region allowed fishers and middlemen to expand their activities in the region (Mateus et al., 2011; Chiaravalloti et al., 2022). It is estimated that in the Upper Paraguay River Basin (UPRB), where the Pantanal is inserted, there are a total of 7.667 active commercial fishers generating an annual income of over R$ 70 millions (US$ 14 millions) (ANA, 2020a). In 2018, 5,000 tons of fish were caught by commercial fishers, and 90% of it was from long-distance migratory species (above 100 km) such as spotted sorubim/pintado (*Pseudoplatystoma* *corruscans*), pacu (*Piaractus mesopotamicus*), piavuçu (*Megaleporinus macrocephalus*) and jau catfish (*Zungaro jahu*) (ANA, 2020a; de Campos et al., 2019).

The same technological advances and changes in flood extent, as well as the expansion of the transportation networks (i.e., highways and airports) in the 1970s, led to the emergence of recreational fishing activities. The number of tourists coming to fish in the Pantanal has reached its peak in the 1990s, with over 100,000 tourists coming every year). Currently, recreational fishers have largely dropped, however, it still plays an important role in the local economy, with at least 30,000 tourists coming to fish every year. The growth of recreational fishing has led to an increase in the demand for live bait and many of the local families specialized themselves in capturing small species such as Tuvira (*Gymnotus* spp.) and Pantanal crabs to sell as baits for tourists (Costa & Lucato, 2000; Moraes & Espinoza, 2001). It is important to understand that local people's strategies regarding fishing activities constantly change and adapt according to social, environmental, and economic drivers. People may switch between commercial fishing, bait gathering and working for tourists as guides depending on the demand and personal needs.

Recently researchers have pointed out another type of fishing in a "fuzzy border" that may exist between subsistence and recreational fishing (Nyboer et al., 2022). These recreational fisheries are generally shore-based, or based on wooden platforms fixed along shores, and not linked to tourism (e.g., Massaroli et al., 2021). These are generally cheaper and faster fisheries in which the fish caught is frequently consumed and can contribute to human nutrition (ANA, 2020b).

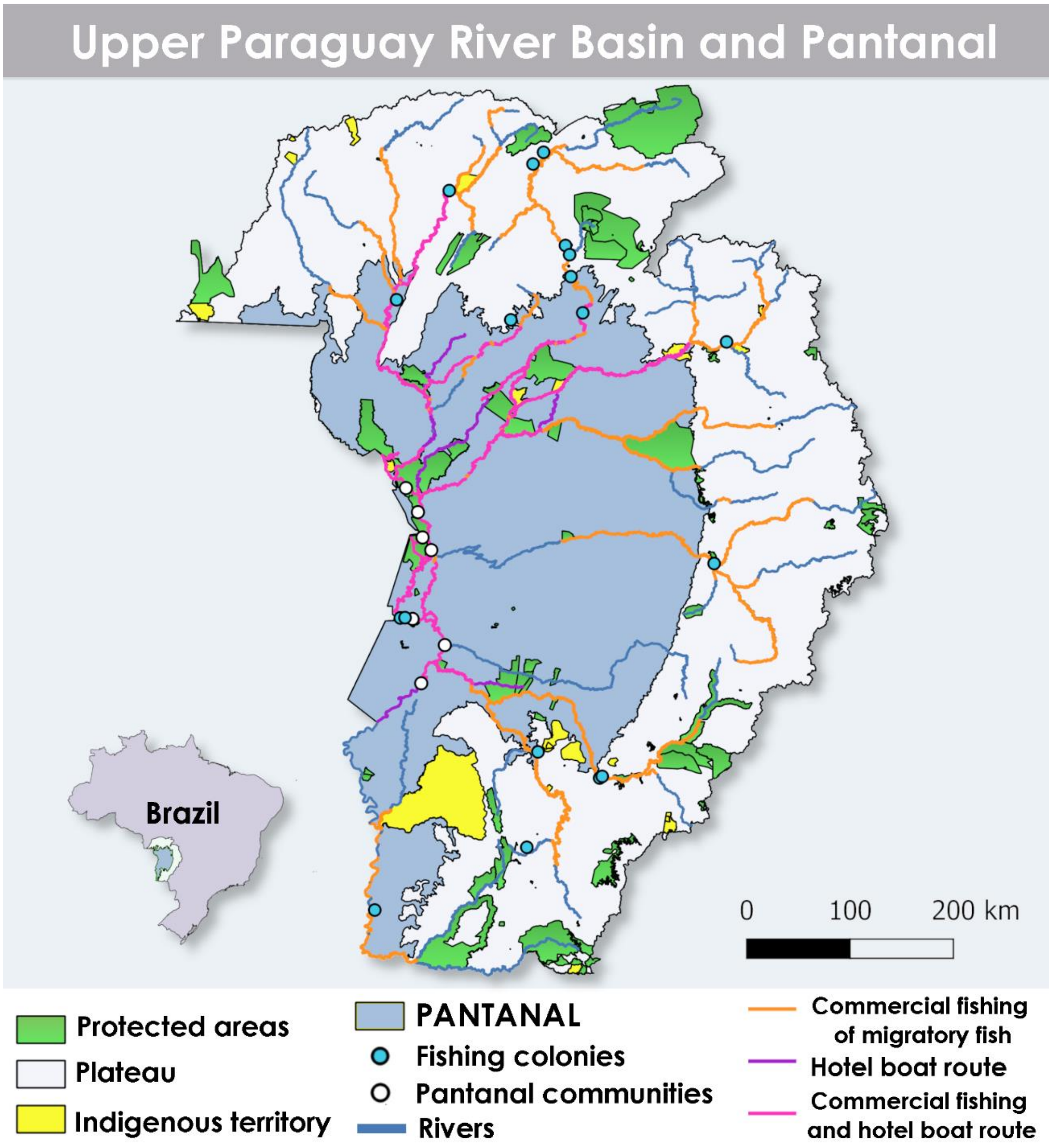

Figure 1. Different uses in the Upper Paraguay River Basin and Pantanal by Indigenous Peoples and Local Communities and other activities linked to fishing. Data source for the map: (ANA, 2021).

Main threats to Pantanal fish population

Infrastructure projects that change the flood dynamics in the Pantanal pose the biggest threat to the fish population. On the one hand, several small-hydroelectric dams have been built (and there are more proposed to be built) in the region. In the last 20 years, the number of small-hydroelectric dams in the surrounding of the Pantanal has more than doubled (Ely et al., 2020). By 2017, there were 47 dams in operation and another 133 have been proposed (Zanatta & Maciel, 2020). At the same time, a new waterway crossing the whole Pantanal aiming to expand transportation through the river is already under construction (Wantzen et al., 2024). The project aims to deepen and widen the Paraguay River (the most important river in the Pantanal) allowing the passage and transportation of agricultural products (e.g. soybean) and other commodities (e.g., metals) through the Pantanal (Figure 2) (Coelho Jr. et al., 2022). Dams and the waterway will have an impact on the time and extent of the flood cycle, deeply affecting fish population, especially migratory fish species who move throughout the Pantanal during their life cycle. For instance, recent study has shown that 30% of dams proposed for the surrounding region of the Pantanal are located on the main migratory routes of fish (Figure 2) (ANA, 2020c; Medinas de Campos et al., 2020). There is also evidence that changes in the river wide, and depth could affect the flow of sediments and nutrients in the Pantanal, with widespread impacts to the entire biome (Ely et al., 2020; Oliveira et al., 2020).

In fact, similar changes in hydrological regimes have shown to cause severe impact in similar ecosystems elsewhere (Halls & Hortle, 2021; Sor et al., 2023). For instance, large parts of the Mekong River and its tributaries have been dammed, disrupting its flow regime and flood pulse (Sor et al., 2023; Ziv et al., 2012). The impacts ranged from changes in basic ecological productivity functions to impacts on fish migratory routes (Stone, 2016; Ziv et al., 2012). Studies have already shown a decline in the capture of larger fish species with no sign of link to possible overfishing, but rather the changes in hydrological patterns and climate change (Halls & Hortle, 2021; Sor et al., 2023).

The presence of invasive species is another important threat to the Pantanal fishery. At least ten invasive species of fish, three of which used in recreational fisheries, as the peacock bass (*Cichla piquiti*) (Figure 2), the pirarara (*Phractocephalus hemiliopterus*) and the tambaquí (*Colossoma macropomum*) have been found in the Pantanal. The presence of these species can represent a serious threat to the native fishes, with impacts on competition for resources, predation and introduction of parasites or pathogens in the environment (Lymbery et al., 2014). Climate change is also impacting local fisheries in the Pantanal. The frequency and intensity of extreme climate events in the region has worsened in the last few years. For instance, in 2019 the Pantanal saw one of the driest years on record with forest fires destroying around 30% of the Pantanal. Although fish themselves were not directly affected, the destruction of a large part of the riverside forest has impacted many frugivorous species in the region. Climate predictions point to a reduction of the flood extent and changes in hydrology for the Pantanal (Marengo et al. 2015), and negative impacts on fishes (Peluso et al. 2023) and fisheries (Peluso et al., 2022).

Although the Pantanal itself does not support large-scale agriculture, the surrounding plateau is an area of intense agricultural activity aimed at exporting commodities. As a result, there has been a high loss of vegetation cover on the plateaus in recent years (Guerra et al. 2020), increasing sediment loads and carrying excess fertilizers and pesticides into the rivers that cross the Pantanal (e.g., Viana et al. 2023).

Loss of vegetation cover is also occurring in the Pantanal, but to a lesser extent. Recently, some studies have shown that the loss of floodplain forests negatively affects fish catches and fishery yield (e.g., Castello et al., 2018; Barros et al., 2020).

Other threats such as domestic and industrial pollution, pesticides, nutrient overload from agriculture (fertilizer and cattle feces) and silting up of rivers are also present. Although individually they may not seem to bring a large impact, the combination of them, in addition to climatic change, the changes hydrology and invasive species can seriously affect fish stocks and harm fisheries in the Pantanal (Agostinho et al., 2007; Barletta et al., 2015; Fantin-Cruz et al., 2020; Peluso et al., 2022).

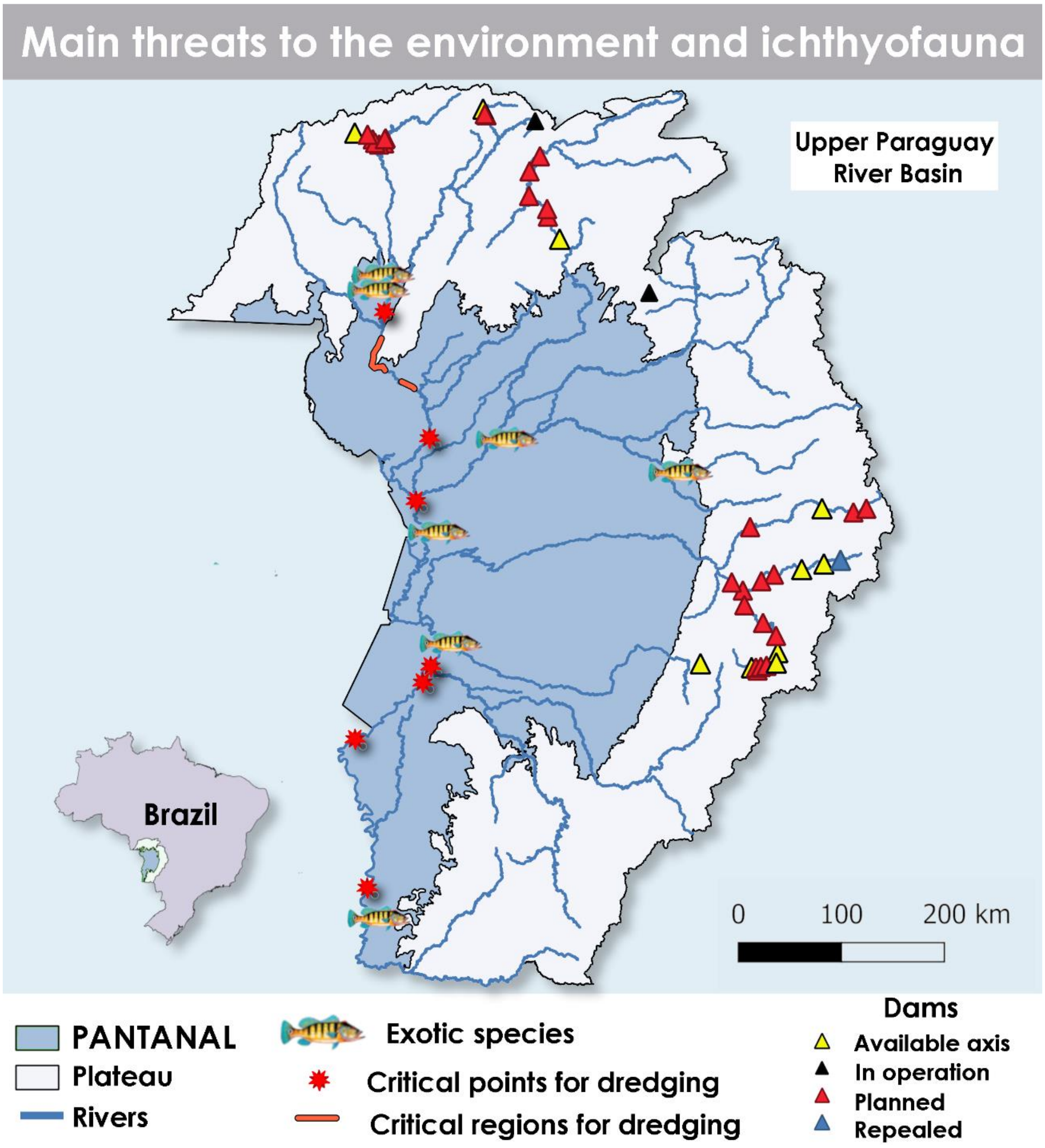

Figure 2. Main threats to the environment and ichthyofauna in the Upper Paraguay River Basin and Pantanal. Triangles represent the 30% of the dams in conflict-of-use zones located on fish migration routes and regions used by commercial fishing. Critical points and regions that would require frequent dredging and in some cases removal of rocks for the Paraguay-Paraná Waterway. Occurrence points of *Cichla kelberi* and *Cichla piquiti* throughout the Pantanal. Data source for the map: (ANA, 2021; EVTEA, 2015; GBIF, 2023ab).

Blaming the wrong one

Despite the clear evidence of the impacts on fish from infrastructure projects, land cover change, climate change, invasive species and other external drivers, there is a narrative in the Pantanal around overfishing from commercial fisheries (Chiaravalloti, 2017). They are blamed for a claimed collapse of the local fish populations, and public policies are implemented based on this scientifically unsupported assumption.

Over the last few decades, the commercial fishing policy has shifted from an incentive policy to a restrictive policy (Catella, 2003; Chiaravalloti et al., 2019). In the 1980s, while recreational fishing started to grow in the region, most policies have shifted to start to support this group instead of commercial fishing. Commercial fishing was seen as a threat to recreational fishing in the region. Tourist operators started to pressure policy makers to reduce the catch quota and transport of fish from commercial fishing (Catella, 2003; Franco et al., 2013). Between 1983 and 1994 different laws were passed forbidding the use of all fishing nets in the region. In 2014, a tool called "branch hook" (fishermen set several fishing gears at the same time) was banned throughout the Pantanal by the Supremo Tribunal Federal (Brazilian Federal Supreme Court). Currently, fishers are only allowed to use a limited number of rods, except for specific live-bait fishing equipment and ornamental fishes.

Most recently a new legislation has been approved that forbids the transport, storage, and sale of fish in the Northern Pantanal for 5 years starting in January 2024 (law nº 1364/2023) (state of Mato Grosso). Following public pressure, this law was amended to prohibit the catch and transport of twelve species, which together accounted for 90% of the commercial catch in 2018. (ANA 2020a). The new law only allows "capture and release" fishing practices, and consumption of fish in places like along riverbanks and hotelboats. This virtually forbides commercial fishing in ⅓ of Pantanal. This is already having a widespread social impact in the entire region. First, the law directly affects thousands of commercial fishers that have fishing in the Northern Pantanal as their main livelihood. Second, the law is impacting fishers from the Southern Pantanal which commonly move to the Northern Pantanal during the early flood period to increase their catch (Chiaravalloti, 2019). Finally, there are over 183,000 people that rely on sporadic fishing from the Pantanal for food purpose and income (ANA, 2020a). Unfortunately, the Southern Pantanal (state of Mato Grosso do Sul) is currently discussing a similar legislation.

The law has triggered an important social movement in favor of commercial fishing in the Pantanal. Yet, local policy makers have approved it anyway. Currently, federal institutions such as the Ministério Público (Public Prosecutors Ministry) and the Defensoria Pública da União (Union Public Defender's Office) argue that the law goes against the Brazilian constitution and violates human rights and are aiming to reverse the law. Recently, in April 2024, a conciliation hearing was held at the Supremo Tribunal Federal (Federal Supreme Court) on the validity of the law that ended without an agreement. At the moment, the minister reporting the actions is awaiting a new opinion from the Procuradoria-Geral da República (Attorney General's Office) to define the decision.

Interestingly, the law to virtually forbid fishing in the Northern Pantanal was proposed soon after the Agência Nacional de Águas e Saneamento Básico (National Agency of Waters and Basic Sanitation) forbade the expansion of new small-hydroelectric dams in the surrounding of the Pantanal. The decision was based on the National Water Resources Policy in Brazil (law nº 9433/1997), which defines that management of the water should consider the different stakeholders using the resource. The agency argued that the dams would impact fish migratory routes and therefore local fishers (ANA, 2020c). The new legislation could, in principle, open space for the construction of the proposed small-hydroelectric dams. In this way, the conflict between users of fishing resources in the Pantanal becomes secondary, because the conflict ignores the external factors that truly endanger the health of rivers and consequently fishing, regardless of the fishing category (Figure 3).

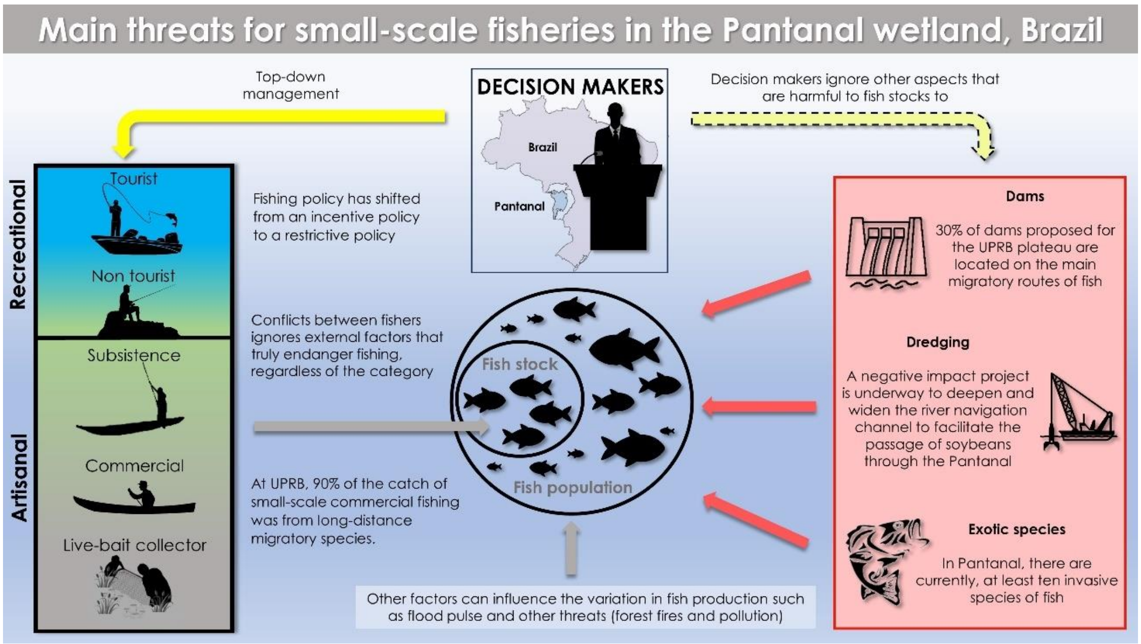

Figure 3. “Snapshot” of the main threats for small-scale fisheries in the Pantanal wetland, Brazil. The figure highlights the importance to consider all factors that can influence the variation in fish production in fisheries management in the Upper Paraguay River Basin (UPRB).

Is there overfishing in the Pantanal?

Several studies were carried out aiming to assess stock exploitation levels of the main species in the Pantanal region (UPRB) in the 1990s and early 2000s (Chiaravalloti et al., 2022). The results indicated over-exploitation only for the most captured species, pacu (*P. mesopotamicus*), and protective measures were adopted. More recently, based on records of the Sistema de Controle de Pesca de Mato grosso do Sul/ SCPESCA/MS (Fisheries Control System of Mato Grosso do Sul State) from 2004 to 2016, Araujo et al. (2019) found stability in the monthly median catch per unit effort (kg per fisherman per day) of commercial fishers in the period; and that the annual landing of migratory species remained constant. They concluded that these indicators signal that the conservative fisheries management measures adopted in the UPRB in Mato Grosso do Sul state (MS) (which includes ⅔ of the Pantanal), have contributed to ensuring the sustainable production of fishing stocks and promoted the economic and social well-being of users. Metrics for biotic integrity indices in fish communities in the Pantanal Matogrossense National Park were also evaluated (Polaz et al., 2017). The surrounding area of the Park is heavily used as a fishing area by commercial and recreational fishers (i.e., tourists). Yet, the indices showed high levels of biological integrity for the fish assemblages, most of which were classified as excellent.

Apart from the ecological evaluations of fish population, researchers have also been looking at the possible presence of governance structures that may protect fish from overfishing. For instance, fishers from a community in the Southern Pantanal rotate the use of fishing areas, allowing the unexplored areas to re-establish themselves. Thus, this mobile exploration avoids the depletion of fishing resources (Wilson et al., 2013; Chiaravalloti, 2017). In the North Pantanal, in Mato Grosso state (MT), the fishers of one community establish territories for each family along the river, which protect from possible free riders and overexploitation (Catella et al., 1997).

Fishery shared management

Fishery sustainability requires the participation of all stakeholders in the landscape. Commercial fishers in the Pantanal have to be heard and their views and needs considered in any fishing policy in the region. They should be part of the discussion on management objectives, data collection, fishing assessment and management measures in order to guarantee the success of the local fishery (Dowling et al., 2023). Fishers have the knowledge, experience and understanding of the social, economic, and ecological dynamics of the region. Only by mixing traditional / local knowledge with scientific evidence can we achieve sustainability (Castelo, 2023). Local knowledge has been increasingly valued and used to fill data gaps in fisheries worldwide, and the Pantanal should seek a similar approach (McElwee et al., 2020; Castello et al., 2023).

There are indeed some possible positive aspects in fishery policies in the Pantanal. A new policy in the state of Mato Grosso Sul state has started a process to reactivate a fishery council (CONPESCA/MS). The council was created in 1999 to draw up fishing guidelines with decision makers, scientists, representatives of all fisheries sectors and civil society. However, the last council meeting was held in 2006. Through the deliberation by the Conselho Estadual de Controle Ambiental/CECA (State Environmental Control Council) (nº 048/2023), in 2023, a working group was formed to define a new composition and regulations for CONPESCA/MS. This should work with the fishing and aquaculture sectors, aiming to "reorganize governance with sustainability and social participation". In principle, the council blocks top-down management with impositions, allows transparency, credibility, and co-responsibility for the management of resources. Although promising, the Mato Grosso state (Northern Pantanal) has a similar fishery council (CEPESCA/MT) created in 2009 and active since about 2014, yet, it did not avoid the new legislation.

Conclusion

The Pantanal is among the largest and most conserved wetlands on the planet. Thousands of people directly depend their livelihoods on commercial fishing in the region and hundreds of thousands indirectly depend on it. Fishery in the Pantanal also plays an important sustainability role, as governance structures and rotational fishing strategies have been protecting the system from overfishing. However, public policies have mostly disregarded its importance. Rather, for many years, they have imposed several intake and out-take fishing restrictions underpinned by a claimed overfishing. Most recently, a new policy virtually forbade commercial fishing in ⅓ of the Pantanal. While nothing has been done to tackle the drivers of real change in the region, such as new infrastructure projects, invasive species, climate change, among others. Rather, in some cases they are celebrated as a positive intervention. Current policies treat the different fishing categories as incompatible, with a clear disadvantage to already marginalized groups.

We are arguing that to guarantee sustainability of the Pantanal fisheries and its peoples it is urgent to 1) Cancel the legislation that virtually forbid fishing in the Northern Pantanal; 2) Implement a robust monitoring protocol that allow a better understanding of the fish population trends; 3) Set aside Sustainable Use Protected Areas that allow fishers to guarantee tenure rights of their fishing grounds and avoid physical and economic displacements; 4) Strengthen spaces for debate and negotiation of the fishing policies where fishers a voice; 5) Create fishing agreement between the different stakeholders in the region in a way that allow the different groups to equally weight their needs; 6) Stop the construction infrastructure projects that may change the hydrology of the region, affecting both local people and biodiversity; 7) Monitor the presence and impact of invasive species in the Pantanal rivers; 8) Support fishers adaptation to climate change and especially extreme climate events in the region; 9) Evaluate the presence and impact of pesticides and mercury in the rivers of the Pantanal; 10) Support and celebrate local fishers associations aiming to give fishers' voice in public policies and conservation interventions in the region.

General Conclusions

This thesis presents a comprehensive examination of the patterns of fish richness and composition within the Upper Paraguay River Basin (UPRB), elucidating the primary drivers that shapes this diversity at different spatial scales. Our findings underscore the significance of sub-basin area and altitude gradients, particularly within intermediate altitudes, in shaping richness patterns. We emphasize the significant role of upland areas in fostering fish diversity throughout the region.

In summary, we contend that to safeguarding fish diversity and ensuring fisheries sustainability in the UPRB it is necessary: (i) increase the representation of Conservation Units focused on aquatic ecosystems in upland areas; (ii) providing greater incentives for ichthyological research, given the substantial ecological and economic value of fish to the region, alongside studies aimed at comprehending fisheries and socio-ecological dynamics; and (iii) incorporating scientific insights and fostering the active involvement of fishers in fisheries management processes.

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Attachments

Attachment 1. Fish species list present in the occurrence database used in the study, obtained from primary data and complemented with data from GBIF, FishNet, SpeciesLink and papers of Neotropical fish in the Upper Paraguay Basin.

Species list

Chondrichthyes

Myliobatiformes

Potamotrygonidae

Potamotrygon amandae Loboda & Carvalho, 2013

Potamotrygon brachyura (Günther, 1880)

Potamotrygon falkneri Castex & Maciel, 1963

Potamotrygon hystrix (Müller & Henle, 1834)

Potamotrygon motoro (Müller & Henle, 1841)

Potamotrygon pantanensis Loboda & Carvalho, 2013

Potamotrygon schuhmacheri Castex, 1964

Dipneusti

Ceratodontiformes

Lepidosirenidae

Lepidosiren paradoxa Fitzinger, 1837

Actinopterygii

Clupeiformes

Engraulidae

Lycengraulis grossidens (Spix & Agassiz, 1829)

Pristigasteridae

Pellona flavipinnis (Valenciennes, 1837)

Characiformes

Acestrorhynchidae

Acestrorhynchus pantaneiro Menezes, 1992

Anostomidae

Abramites hypselonotus (Günther, 1868)

Leporellus vittatus (Valenciennes, 1850)

Leporinus friderici (Bloch, 1794)

Leporinus lacustris Campos, 1945

Leporinus octomaculatus Britski & Garavello, 1993

Leporinus striatus Kner, 1858

Megaleporinus macrocephalus (Garavello & Britski, 1988)

Megaleporinus obtusidens (Valenciennes, 1837)

Schizodon borelli (Boulenger, 1900)

Schizodon isognathus Kner, 1858

Bryconidae

Brycon hilarii (Valenciennes, 1850)

Salminus brasiliensis (Cuvier, 1816)

Characidae

Aphyocharax anisitsi Eigenmann & Kennedy, 1903

Aphyocharax dentatus Eigenmann & Kennedy, 1903

Aphyocharax nattereri (Steindachner, 1882)

Aphyocharax rathbuni Eigenmann, 1907

Astyanax abramis (Jenys, 1842)

Astyanax alleni (Eigenmann & McAtee, 1907)

Astyanax dolinae Graça, Oliveira, Lima, Silva & Fernandes, 2017

Astyanax lacustris (Lütken, 1875)

Astyanax lineatus (Perugia, 1891)

Astyanax moorii (Boulenger, 1892)

Astyanax nobre Dagosta & Marinho 2022

Astyanax pirapuan Tagliacollo, Britske, Silva & Benine, 2011

Brachychalcinus retrospina Boulenger, 1892

Bryconamericus exodon Eigenmann, 1907

Charax leticiae Lucena, 1987

Creagrutus meridionalis Vari & Harold, 2001

Creagrutus paraguayensis Mahnert & Géry, 1988

Cynopotamus argenteus (Valenciennes, 1837)

Cynopotamus kincaidi (Schultz, 1950)

Deuterodon luetkeni (Boulenger, 1887)

Galeocharax humeralis (Valenciennes, 1834)

Gephyrocharax machadoi Ferreira, Faria, Ribeiro, Santana, Quagio-Grassioto & Menezes

Gymnocorymbus ternetzi (Boulenger, 1895)

Hemigrammus durbinae Ota, Lima & Pavanelli, 2015

Hemigrammus lunatus Durbin, 1918

Hemigrammus machadoi Ota, Lima & Pavanelli, 2014

Hemigrammus mahnerti Uj & Géry, 1989

Hemigrammus Neptunus Zarske & Géry, 2002

Hemigrammus tridens Eigenmann, 1907

Hemigrammus ulreyi (Boulenger, 1895)

Hyphessobrycon elachys Weitzman, 1985

Hyphessobrycon eques (Steindachner, 1882

Hyphessobrycon herbertaxelrodi Géry, 1961

Hyphessobrycon megalopterus (Eigenmann, 1915)

Hyphessobrycon rutiliflavidus Carvalho, Langeani, Miyazawa & Troy, 2008

Hyphessobrycon vilmae Géry, 1966

Jupiaba acanthogaster (Eigenmann, 1911)

Knodus chapadae (Fowler, 1906)

Knodus geryi Lima, Britski & Machado, 2004

Markiana nigripinnis (Perugia, 1891)

Moenkhausia australis Eigenmann, 1908

Moenkhausia bonita Benine, Castro & Sabino, 2004

Moenkhausia cosmops Lima, Britski & Machado, 2007

Moenkhausia dichroura (Kner, 1858)

Moenkhausia flava Britzke, Troy, Oliveira & Benine, 2018

Moenkhausia forestii Benine, Mariguela & Oliveira, 2009

Moenkhausia lopesi Britski & Silimon, 2001

Moenkhausia oligolepis (Günther, 1864)

Moenkhausia phaeonota Fink, 1979

Odontostilbe paraguayensis Eigenmann & Kennedy, 1903

Odontostilbe pequira (Steindachner, 1882)

Oligosarcus perdido Ribeiro, Cavallaro & Froehlich, 2007

Oligosarcus pintoi Amaral Campos, 1945

Phenacogaster jancupa Malabarba & Lucena, 1995

Phenacogaster tegatus (Eigenmann, 1911)

Piabarchus analis (Eigenmann, 1914)

Piabarchus torrenticula Mahnert & Géry, 1988

Poptella paraguayensis (Eigenmann, 1907)

Prionobrama paraguayensis (Eigenmann, 1914)

Psalidodon marionae (Eigenmann, 1911)

Psellogrammus kennedyi (Eigenmann, 1903)

Roeboides affinis (Günther, 1868)

Roeboides descalvadensis Fowler, 1932

Roeboides microlepis (Reinhardt, 1851)

Serrapinnus calliurus (Boulenger, 1900)

Serrapinnus kriegi (Schindler, 1937)

Serrapinnus microdon (Eigenmann, 1915)

Tetragonopterus argenteus Cuvier, 1816

Xenurobrycon macropus Myers & Miranda Ribeiro, 1945

Crenuchidae

Characidium chicoi Graça, Ota & Domingues, 2019

Characidium aff. *gomesi* Travassos, 1956

Characidium laterale (Boulenger, 1895)

Characidium nupelia Graça, Pavanelli, Buckup, 2008

Characidium aff. *zebra* Eigenmann, 1909

Curimatidae

Curimatella dorsalis (Eigenmann & Eigenmann, 1889)

Curimatopsis myersi Vari, 1982

Cyphocharax caboclo Melo, Tencatt & Oliveira, 2022

Cyphocharax gillii (Eigenmann & Kennedy, 1903)

Potamorhina squamoralevis (Braga & Azpelicueta, 1983)

Psectrogaster curviventris Eigenmann & Kennedy, 1903

Steindachnerina brevipinna (Eigenmann & Eigenmann, 1889)

Steindachnerina conspersa (Holmberg, 1891)

Steindachnerina nigrotaenia (Boulenger, 1902)

Cynodontidae

Rhaphiodon vulpinus Spix & Agassiz, 1829

Erythrinidae

Erythrinus erythrinus (Bloch & Schnider, 1801)

Hoplerythrinus unitaeniatus (Spix & Agassiz, 1829)

Hoplias cf. *malabaricus* (Bloch, 1794)

Hoplias mbigua Azpelicueta, Benítez, Aichino & Mendez, 2015

Hoplias missioneira Rosso, Mabragaña, González-Castro, Delpiani, Avigliano, Schenone & Días de Astarlo, 2016

Gasteropelecidae

Gasteropelecus sternicla (Linnaeus, 1758)

Thoracocharax stellatus (Kner, 1858)

Hemiodontidae

Hemiodus orthonops Eigenmann & Kennedy, 1903

Hemiodus semitaeniatus Kner, 1858

Iguanodectidae

Bryconops melanurus (Bloch, 1794)

Piabucus melanostoma Holmberg, 1891

Lebiasinidae

Pyrrhulina australis Eigenmann & Kennedy, 1903

Parodontidae

Apareiodon affinis (Steindachner, 1879)

Parodon nasus Kner, 1859

Prochilodontidae

Prochilodus lineatus (Valenciennes, 1836)

Serrasalmidae

Catoprion mento (Cuvier, 1819)

Metynnis cuiaba Pavanelli, Ota & Petry, 2009

Metynnis maculatus (Kner, 1858)

Metynnis mola Eigenmann & Kennedy, 1903

Myloplus levis (Eigenmann & McAtee, 1907)

Mylossoma duriventre (Cuvier, 1818)

Piaractus mesopotamicus (Holmberg, 1887)

Pygocentrus nattereri Kner, 1858

Serrasalmus maculatus Kner 1858

Serrasalmus marginatus Valenciennes, 1837

Triportheidae

Clupeacharax anchoveoides Pearson, 1924

Engraulisoma taeniatum Castro, 1981

Triportheus nematurus (Kner, 1858)

Triportheus pantanensis Malabarba, 2004

Gymnotiformes

Apteronotidae

Apteronotus albifrons Linnaeus, 1766

Apteronotus caudimaculosus de Santana, 2003

Apteronotus ellisi (Alonso de Arámburu, 1957)

Gymnotidae

Gymnotus carapo australis Craig, Crampton & Albert, 2017

Gymnotus inaequilabiatus (Valencienes, 1839)

Gymnotus pantanal Fernandes, Albert, Daniel-Silva, Lopes, Crampton & Almeida-Toledo, 2005

Gymnotus paraguensis Albert & Crampton, 2003

Hypopomidae

Brachyhypopomus bombilla Loureiro & Silva, 2006

Brachyhypopomus brevirostris (Steindachner, 1868)

Brachyhypopomus gauderio Giora & Malabarba, 2009

Brachyhypopomus walteri Sullivan, Zuanon & Cox Fernandes, 2013

Rhamphichthyidae

Gymnorhamphichthys britskii Carvalho, Ramos & Albert, 2011

Hypopygus lepturus Hoedeman, 1962

Rhamphichthys hahni (Meinken, 1937)

Sternopygidae

Eigenmannia correntes Campos da Paz & Queiroz, 2017

Eigenmannia desantanai Peixoto, Dutra & Wosiacki, 2015

Eigenmannia aff. *trilineata* López & Castello, 1966

Eigenmannia aff. *virescens* (Valenciennes, 1836)

Sternopygus macrurus (Bloch & Schneider, 1801)

Siluriformes

Aspredinidae

Amaralia oviraptor Friel & Carvalho, 2016

Bunocephalus doriae Boulenger, 1902

Ernstichthys taquari Dagosta & de Pinna, 2021

Pseudobunocephalus rugosus (Eigenmann & Kennedy, 1903)

Pterobunocephalus depressus (Haseman, 1911)

Xyliphius barbatus Alonso de Arámburu & Arámburu, 1962

Auchenipteridae

Ageneiosus inermis (Linnaeus, 1766)

Ageneiosus militaris Valenciennes, 1836

Auchenipterus nigripinnis (Boulenger, 1895)

Auchenipterus osteomistax (Miranda Ribeiro, 1918)

Duringlanis perugiae (Steindachner, 1882)

Entomocorus radiosus Reis & Borges, 2006

Epapterus dispilurus Cope, 1878

Tatia neivai (Ihering, 1930)

Trachelyopterus coriaceus Valenciennes, 1840

Trachelyopterus galeatus Cope, 1878

Trachelyopterus porosus (Eigenmann & Eigenmann, 1888)

Callichthyidae

Aspidoras taurus Lima & Britto, 2001

Callichthys callichthys (Linnaeus, 1758)

Corydoras aff. *aeneus* (Gill, 1858)

Corydoras areio Knaack, 2000

Corydoras aurofrenatus Eigenmann & Kennedy, 1903

Corydoras britskii (Nijssen & Isbrücker, 1903)

Corydoras hastatus Eigenmann & Eigenmann, 1888

Corydoras pantanalensis Knaack, 2001

Corydoras polystictus Regan, 1912

Corydoras splendens (Castelnau, 1855)

Hoplosternum littorale (Hancock, 1828)

Lepthoplosternum pectorale (Boulenger, 1895)

Megalechi picta (Müller & Troschell, 1849)

Megalechis thoracata (Valenciennes, 1840)

Cetopsidae

Cetopsis gobioides Kner, 1858

Doradidae

Anadoras weddellii (Castelnau, 1855)

Amblydoras nheco (Higuchi, Birindelli, Sousa & Britski, 2007)

Ossancora eigenmanni (Boulenger, 1895)

Ossancora punctata (Kner, 1853)

Oxydoras kneri Bleeker, 1862

Platydoras armatulus (Valenciennes, 1840)

Pterodoras granulosus (Valenciennes, 1821)

Rhinodoras dorbignyi (Kner, 1855)

Trachydoras paraguayensis (Eigenmann & Ward, 1907)

Heptapteridae

Imparfinis mirini Haseman, 1911

Pimelodella gracilis (Valenciennes, 1835)

Pimelodella griffini Eigenmann, 1917

Pimelodella megalura Miranda Ribeiro, 1918

Pimelodella mucosa Eigenmann & Ward, 1907

Pimelodella notomelas Eigenmann, 1917

Pimelodella serrata Eigenmann, 1917

Pimelodella taeniophora (Regan, 1903)

Pimelodella taenioptera Miranda Ribeiro, 1914

Phenacorhamdia hoehni (Miranda Ribeiro, 1914)

Rhamdia aff. *quelen* (Quoy & Gaimard, 1824)

Loricariidae

Ancistrus claro Knaack, 1999

Ancistrus cuiabae Knaack, 1999

Ancistrus formoso Sabino & Trajano, 1997

Ancistrus sp.

Brochiloricaria macrodon (Kner, 1853)

Curculionichthys coxipone Roxo, Silva, Ochoa & Oliveira, 2015

Curculionichthys paresi (Roxo, Zawadzki & Troy, 2014)

Farlowella isbruckeri Retzer & Page, 1997

Farlowella jauruensis Eigenmann & Vance, 1917

Farlowella paraguayensis Retzer & Page, 1997

Hemiodontichthys acipenserinus (Kner, 1853)

Hypoptopoma inexpectatum (Holmberg, 1893)

Hypostomus basilisko Tencatt, Zawadzki & Froehlich, 2014

Hypostomus boulengeri (Eigenmann & Kennedy, 1903)

Hypostomus careopinnatus Martins, Marinho, Langeani & Serra, 2012

Hypostomus cochliodon Kner, 1854

Hypostomus froehlichi Zawadzki, Nardi & Tencatt, 2021

Hypostomus khimaera Tencatt, Zawadzki & Froehlich, 2014

Hypostomus latifrons Weber, 1986

Hypostomus latirostris (Regan, 1904)

Hypostomus mutucae Knaack, 1999

Hypostomus peckoltoides Zawadzki, Weber & Pavanelli, 2010

Hypostomus perdido Zawadzki, Tencatt & Froehlich, 2014

Hypostomus regani (Ihering, 1905)

Hypostomus renestoi Zawadzki, da Silva & Troy, 2018

Hypostomus ternetzi (Boulenger, 1895)

Loricaria apeltogaster Boulenger, 1895

Loricaria coximensis Rodriguez, Cavallaro & Thomas, 2012

Loricariichthys labialis (Boulenger, 1895)

Loricariichthys platymetopon Isbrücker & Nijssen, 1979

Megalancistrus parananus (Peters, 1881)

Otocinclus bororo Schaefer 1997

Otocinclus vittatus Regan, 1904

Pseudohemiodon laticeps (Regan, 1904)

Pseudohemiodon platycephalus (Kner, 1853)

Pterygoplichthys ambrosettii (Holmberg, 1893)

Pyxiloricaria menezesi Isbrücker & Nijssen, 1984

Rhineleps strigosa Valenciennes, 1840

Rineloricaria aurata (Knaack, 2002)

Rineloricaria cacerensis (Miranda Ribeiro, 1912)

Rineloricaria lanceolata (Günther, 1868)

Rineloricaria parva (Boulenger, 1895)

Spatuloricaria evansii (Boulenger, 1892)

Sturisoma barbatum (Kner, 1853)

Pimelodidae

Hemisorubim plathyrhynchos (Valenciennes, 1840)

Hypophthalmus oreomaculatus Nani & Fuster, 1947

Iheringichthys labrosus (Lütken, 1874)

Iheringichthys megalops Eigenmann & Ward, 1907

Luciopimelodus pati (Valenciennes, 1835)

Megalonema platanum (Günther, 1880)

Pimelodus absconditus Azpelicueta, 1995

Pimelodus argenteus Perugia, 1891

Pimelodus misteriosus Azpelicueta, 1998

Pimelodus ornatus Kner, 1858

Pimelodus pantaneiro Souza-Filho & Shibatta, 2007

Pinirampus pinirampu (Spix & Agassiz, 1829)

Pseudoplatystoma corruscans (Spix & Agassiz, 1829)

Pseudoplatystoma reticulatum (Eigenmann & Eigenmann, 1889)

Sorubim lima (Bloch & Schnider, 1801)

Zungaro jahu (Ihering 1898)

Pseudopimelodidae

Batrochoglanis melanurus Shibatta & Pavanelli, 2005

Microglanis leniciae Shibatta, 2016

Pseudopimelodus mangurus (Valenciennes, 1835)

Rhyacoglanis paranensis Shibatta & Vari, 2017

Rhyacoglanis variolosus (Miranda Ribeiro, 1914)

Scoloplacidae

Scoloplax distolothrix Schaefer, Weitzman & Britski, 1989

Scoloplax empousa Schaefer, Weitzman & Britski, 1989

Trichomycteridae

Ituglanis eichhorniarum (Miranda Ribeiro, 1912)

Ituglanis herberti (Miranda Ribeiro, 1940)

Ochmacanthus batracostoma (Miranda Ribeiro, 1912)

Paracanthopoma saci Dagosta & de Pinna, 2021

Paravandellia oxyptera Miranda Ribeiro, 1912

Potamoglanis johnsoni (Fowler, 1932)

Tridentopsis cahuali Azpelicueta, 1990

Trichomycterus chapadensis Katz & Costa, 2021

Trichomycterus dali Rizzato, Costa, Trajano & Bichuette, 2011

Cichliformes

Cichlidae

Aequidens plagiozonatus Kullander, 1984

Apistogramma borellii (Regan, 1906)

Apistogramma commbrae (Regan, 1906)

Apistograma trifasciata (Eigenmann & Kennedy, 1903)

Astronotus crassipinnis (Heckel, 1840)

Bujurquina vittata (Heckel, 1840)

Chaetobranchopsis australis Eigenmann & Ward, 1907

Cichlasoma dimerus (Heckel, 1840)

Crenicichla semifasciata (Heckel, 1840)

Crenicichla vittata Heckel, 1840

Gymnogeophagus balzanii (Perugia, 1891)

Laetacara dorsigera (Heckel, 1840)

Mesonauta festivus (Heckel, 1840)

Satanoperca pappaterra (Heckel, 1840)

Saxatilia lepidota (Heckel, 1840)

Saxatilia ploegi Varella, Loeb, Lima & Kullander, 2018

Cyprinodontiformes

Poecilidae

Pamphorichthys hasemani (Hehn, 1916)

Rivulidae

Austrolebias ephemerus Volcan & Severo Neto, 2019

Melanorivulus bororo (Costa, 2008)

Melanorivulus cyanopterus (Costa, 2005)

Melanorivulus dapazi (Costa, 2005)

Melanorivulus nelsoni (Deprá, Silva & Graça, 2017)

Melanorivulus paresi (Costa, 2008)

Melanorivulus punctatus (Boulenger, 1895)

Moema heterostigma Costa, 2003

Neofundulus aureomaculatus Costa, 2015

Neofundulus paraguayensis (Eigenmann & Kennedy, 1903)

Neofundulus parvipinnis Costa, 1988

Neofundulus rubrofasciatus Costa, 2015

Plesiolebias glaucopterus (Costa & Lacerda, 1988)

Pterolebias longipinnis Garman, 1895

Pterolebias phasianus Costa, 1988

Stenolebias bellus (Costa, 1995)

Stenolebias damascenoi (Costa, 1991)

Trigonectes balzanii (Perugia, 1891)

Beloniformes

Belonidae

Potamorrhaphis eigenmanni Miranda Ribeiro, 1915

Pseudotylosurus angusticeps (Günther, 1866)

Acanthuriformes

Sciaenidae

Pachyurus bonariensis Steindachner, 1879

Plagioscion ternetzi Boulenger, 1895

Carangiformes

Achiridae

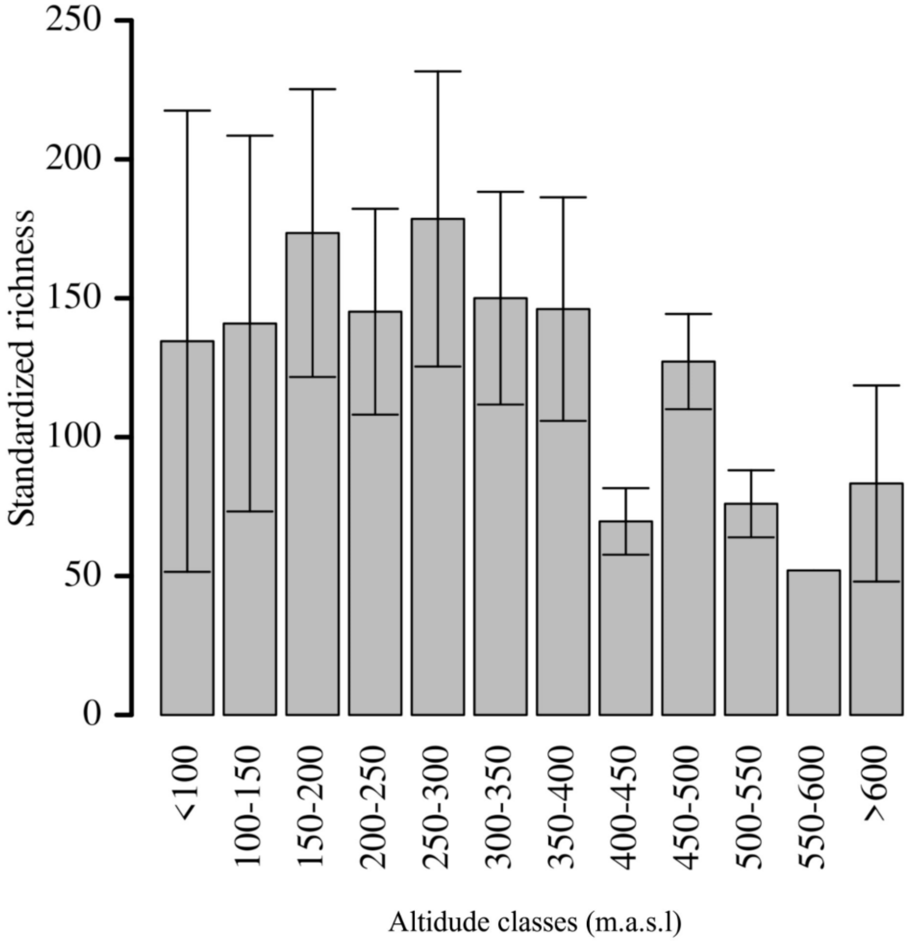
Catathyridium jenynsii (Günther, 1862)

Synbranchiformes

Synbranchidae

Synbranchus marmoratus Bloch, 1795

Synbranchus madeirae Rosen & Rumney, 1872



Attachment 2. Estimated richness with standardized sample size (± standard deviation) along altitude classes in the Upper Paraguay River Basin.