

Programa de Pós-Graduação em Ecologia e Conservação

Instituto de Biociências Universidade Federal de Mato Grosso do Sul

### What explains the structuring of fish assemblages in the upper

### Paraná river basin, Mato Grosso do Sul?

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Tese apresentada como requisito para a obtenção do título de **Doutor em Ecologia**, pelo Programa de Pós-Graduação em Ecologia e Conservação, Universidade Federal de Mato Grosso do Sul.

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#### **Resumo Geral**

Este estudo aborda a riqueza e a composição das espécies nas assembleias de peixes na bacia do alto rio Paraná. Correlacionei a riqueza e a distribuição das espécies com fatores regionais como posição das sub-bacias e a conectividades entres as ottobacias e fatores locais como as características físico/química da água e cobertura do solo como influência antrópica nas áreas coletadas. Para compreender melhor as interações entre as variáveis, suas influências na riqueza, e composição das assembleias, dividi esse estudo em dois capítulos. No primeiro capítulo, investiguei a contribuição local (LCBD) e contribuição específica (SCBD) para a beta diversidade. Avaliei 275 pontos de riachos de baixo fluxo (<5m<sup>3</sup>/s) distribuídos em quatro sub-bacias do alto rio Paraná foram avaliados. Descobri que a diversidade beta é mais influenciada pelas características limnológicas e pela posição dos locais de amostragem ao longo do gradiente longitudinal. Maiores valores de LCBD foram encontrados em trechos com menor riqueza de espécies, já os maiores valores de SCBD vieram de espécies com maior frequência de ocorrência ao longo da área estudada. Essas contribuições para a beta diversidade ressalta a importância das características hidrológicas na composição das assembleias de peixes. No segundo capítulo, somei registros primários de 23 anos de amostragens de assembleias de peixes na bacia do alto rio Paraná, em terras do MS, com os registros de coleções disponíveis em banco de dados. Com isso, busquei compreender como a riqueza e composição dessas assembleias em relação a espécies nativas e não nativas. Não encontrei diferença significativa entre a proporção de espécies nativas e não nativas nas assembleias de peixes entre as sub-bacias. Encontrei que dentre as variáveis regionais que melhor explicam a riqueza e composição das espécies nativas e não nativas são a altitude, declividade e pluviosidade. A declividade é uma variável que influi diretamente na riqueza e composição pois os principais rios das sub-bacias Amambai e Iguatemi apresentam maior tendência a apresentar maiores quedas d'águas e corredeiras, o que está ligado ao fato de que as composições das assembleias, nessas sub-bacias, serem bem definidas no sentido cabeceira-foz. Conclui que as variáveis regionais interagem com as variáveis locais para influenciar a riqueza e composição das espécies de peixes na bacia do alto rio Paraná, sejam elas nativas e não nativas. Isso significa que os rios e riachos das sub-bacias do alto rio Paraná são únicos e possuem vários habitats que contribuem para o aumento da diversidade, razão pela qual precisam ser vistos como alvo no desenvolvimento de políticas ambientais concisas para conservar as espécies de peixes que ocorrem em sua extensão.

#### **General Abstract**

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This study investigates the species richness and composition of fish assemblages in the upper Paraná River basin. I correlated species richness and distribution with regional factors, such as the position of sub-basins and the connectivity between ottobasins, and local factors, such as the physicochemical characteristics of water and land cover as an anthropogenic influence on the areas collected. To further explore the interplay among these factors and their impact on assemblage richness and composition, i divided my study into two chapters. In the first chapter, I investigated the local (LCBD) and specific (SCBD) contribution to beta diversity. I evaluated 275 sites in low-flow streams (<5m3/s) distributed in four sub-basins of the upper Paraná River. I found beta diversity to be more influenced by limnological characteristics and the position of sampling sites along the longitudinal gradient. Higher LCBD values were found in stretches with lower species richness, while the highest SCBD values came from species with a higher frequency of occurrence throughout the study area. These contributions to beta diversity highlight the importance of hydrological characteristics in the composition of fish assemblages. In the second chapter, I combined primary record covering 23 years of sampling fish assemblages in the upper Paraná River basin, in the satate of Mato Grosso do Sul, with record from collections available in databases. With this, I sought to understand how the richness and composition of assemblages in relation to native and non-native species. I found no significant difference between the proportion of native and non-native species in the fish assemblages among sub-basins. The regional variables that best explain the richness and composition of native and non-native species are altitude, slope and rainfall. Slope is a variable that directly influences richness and composition because the main rivers in the Amambai and Iguatemi sub-basins tend to have higher waterfalls and rapids. Thus, variation in the composition of fish assemblages can be best defined in the context of slope with sub-basins occurring from headwaters to river mouth. I conclude that regional variables interact with local variables to influence the richness and composition of fish species, both native and non-native, in the upper Paraná River basin. This means that rivers and streams of the upper Paraná River sub-basins are unique and have various habitats that contribute to increased diversity, which explains their importance as a target in the development of suitable environmental policies to conserve the fish species that occur in these waters.

#### **General Introduction**

A main objective of community ecology is to define which and how many species occur in a community and then explain the processes that generate and maintain these communities (Strange et al. 1993). In this sense, some regions are better studied than others, and the level of knowledge about communities differs both across space and between different biological groups. For this reason, advanced studies on ecological communities seek to clarify how environmental, biological and historical factors (Escalera-Vázquez & Zambrano 2010, Gomes et al. 2023) act at different scales, isolation or together, in structuring the richness and composition of species in communities (Vieira et al. 2018).

Variation in species composition among different habitats is a relevant topic for community ecology (Heino et al. 2015, Zorzal-Almeida et al. 2017). Community structure and variation are governed by biotic, abiotic and historical factors at different spatial scales, and these factors have been used to explain patterns of species composition in communities (Sharma et al. 2011, Brown 2014, Soares & Nakamura 2021). Therefore, the scale chosen to study a community, or species composition of a community, becomes fundamentally important in developing the questions to be addressed (Ruhi et al. 2017). In this respect, studies of Neotropical fish assemblages have largely contributed to the understanding of community ecology. Such studies are supported by the large quantity and availability of data that allow different scales to be evaluated and correlated and, hence, the diversity of a region to be understood at different levels (Caley & Schluter, Angermeier & Winston, 1998, Dagosta et al. 2024).

When examining an established aquatic community, we must take into account the processes that have guided its assembly and order its structure from smallest to largest level, individuals to populations to communities (Casatti et al. 2006, Sharma et al. 2011). These processes can be hierarchically scaled, acting as filters for the distribution and richness of species. On a broader scale, biogeographic factors related to continental formation and the establishment of habitats constitute the first filter guiding the richness and composition of aquatic communities (Castellanos-Galindo et al. 2015, Machado et al. 2018). The second filter, on a smaller scale, involves spatial factors (Ricklefs, 1987) that select species based on physical attributes, such as basin position (Roa-Fuentes et al. 2022), waterfalls, assessed portion (Sutela et al. 2020) or river connectivity (Thiele et al. 2018). These are the factors that influence longitudinal changes in the composition and richness of fish assemblages (Tejerina-Garro et al. 2005). Environmental factors are the third filter, including characteristics associated with the sampling site (e.g., pH, salinity, conductivity) (Lamourox et al. 1999, Palheta et al. 2021). Finally, interactions between species predict community structure (Dunson & Travis 1991, Gilliam et al. 1993), and this factor is best observed in controlled experiments (Giacomini et al. 2013).

The understanding of diversity is associated with the scale at which an area is evaluated, and this diversity is partitioned into measures of richness, such as alpha diversity, i.e., quantifying the number of species within a given site, and gamma diversity, i.e., representing a set of specimens from sites within a larger region. Beta diversity analyzes the composition of a community, measuring the dissimilarity of species along a gradient (Whittaker 1972, Magurran & Henderson 2003, Tuomisto, 2010). Based on this measure, turnover rates can be estimated. Turnover occurs when species are replaced by other species, while nestedness occurs when species are lost along a gradient (Baselga 2010). Legendre & De Cáceres (2013) evaluating beta diversity metrics, understood that the environment in which the community is located and the frequency of occurrence of species can contribute to variation in diversity. They proposed a method of estimating the contribution of species to beta diversity (SCBD) and the contribution of sites to beta diversity (LCBD). The relationship between these measures can indicate how species occurrence and environmental conditions contribute to community composition.

A total of 469 fish species have been recorded for the upper Paraná River basin, of which 341 are native and 128 are non-native, making it the most biodiverse basin after the Amazon basin in Brazil (Dagosta et al. 2024). This richness is linked to the variety of habitats provided by the geological formation of the basin over time (Junior et al. 2009, Apodaca et al. 2019). However, it is the Neotropical region with the highest density of dams, around 389 along 209 rivers (Makrakis et al. 2019), which directly impacts species diversity, either by altering migratory cycles for reproduction or environmental changes, such as deforestation, sewage and contaminant disposal (Speranza et al. 2020) and changes in soil cover (Mello et al. 2020). These anthropogenic activities affect the diversity and composition of fish assemblages at different scales (Su et al. 2015, Borges et al. 2020) and reveal the need to understand the parameters that interfere with these assemblages so that actions can be proposed to promote the conservation and protection of the basin's biodiversity.

Outlined above are key factors that interfere with species richness and composition in fish assemblages in the upper Paraná River basin. Accordingly, this thesis was structured in two chapters to address the patterns of species richness and composition at different scales. The first chapter analyzes beta diversity with an emphasis on the contribution of species (SCBD) and sites (LCBD) to fish assemblages in four sub-basins in the upper Paraná River basin. The influence of local and regional factors on beta diversity and contributions (SCBD and LCBD) is then tested. Primary data from 23 years of unrepeated collections over time were used for these analyses. The second chapter uses the same primary data plus secondary data from biological collections in order to quantify the maximum number of fish species for the upper Paraná River basin. Richness and species composition of the assemblages are then analyzed by partitioning the upper Paraná River basin into ottobasins defined from the database of the National Water Agency (ANA, 2017). This chapter reports the effect of 28 ottobasins, as well as the influence of regional factors, on the richness and composition of native and non-native species in fish assemblages.

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## Chapter 1. Small streams improve beta diversity in neotropical fish assemblages in the Upper Paraná River Basin

#### Resumo

A variação da composição das espécies ao longo de um gradiente ambiental (βdiversidade) pode melhorar a nossa compreensão dos padrões de biodiversidade e da composição das espécies em uma região estudada. A diversidade beta pode ser particionada pelas contribuições das espécies para a diversidade beta (SCBD) e pelas contribuições locais para a diversidade beta (LCBD), sendo essa última uma maneira de que identificar os locais que, mais ou menos, contribuem para a variação global da composição de espécies entre as regiões amostradas. Métricas recentemente desenvolvidas permitiram estimar a contribuição das espécies (SCBD) e dos locais (LCBD) para a diversidade β total. Aplicamos essas estimativas para avaliar a composição de assembleias de peixes em quatro sub-bacias da bacia hidrográfica do Alto Rio Paraná, que perfazem um conjunto de dados único de 275 pontos amostrados em riachos de baixo fluxo (<5m<sup>3</sup>/s). Nossos resultados mostram que influências limnológicas em diferentes escalas contribuem para o aumento da LCBD. No entanto, o uso do solo e a riqueza de espécies não estão diretamente relacionados com este aumento, por isso, os locais com menos espécies de peixes ao longo das sub-bacias contribuam para uma maior diversidade beta. Concluímos que a diversidade beta é mais influenciada pelas caraterísticas limnológicas e pela posição dos locais de amostragem ao longo do gradiente longitudinal. Maiores valores de LCBD são encontrados em trechos com menor riqueza de espécies, e isso significa que os pequenos riachos das sub-bacias do alto rio Paraná são únicos e possuem vários habitats que contribuem para o aumento da diversidade, razão pela qual essas regiões precisam ser aparadas por políticas públicas concisa para conservar suas características ambientais primordiais.

#### Abstract

Variation in species composition along an environmental gradient (*β*-diversity) can improve our understanding of biodiversity patterns and species composition in each study area. Beta diversity can be partitioned into species contributions to beta diversity (SCBD) and local contributions to beta diversity (LCBD), which identify the biota and locations that contribute disproportionately more or less to overall variation in species composition among samples. Recently developed metrics enabled the estimation of species contribution to total  $\beta$  diversity (SCBD) and local contribution to total  $\beta$  diversity (LCBD). Utilizing these metrics, a one-time survey of 275 sampling points within four sub-basins of the Upper Paraná River Hydrographic Basin (low-flow streams, <5 m3/s) was conducted to assess fish community composition. Our results show that limnological influences at different scales contribute to higher in LCBD. However, land use and species richness are not directly linked to this higher. Maybe that's why, the sites fewer fish species along the sub-basins contributes to higher in beta diversity. We conclude that beta diversity is more influenced by limnological characteristics and the position of sampling sites along the longitudinal gradient. Higher LCBD values are found, even in portions with lower species richness. This means that the small streams in the sub-basins of the upper Paraná River are unique and have various habitats that contribute to increasing diversity, which is why they need to be seen as a target in the development of concise environmental policies to conserve their pristine conditions.

#### 1. Introduction

Biodiversity encompasses the richness and variety of species found in a particular area. This variation stems from a complex interplay of environmental factors, including biogeography, spatial patterns across different scales, and biological interactions (Zbinden et al. 2017). Biodiversity highers from the poles to the equator and reach the highest values in tropical regions, varying among and within geographic regions, between terrestrial and aquatic ecosystems, and among different groups of organisms (Antonelli et al. 2018).

To better understand biodiversity, Whittaker (1960) divided diversity into Alpha, Gamma and Beta. Alpha diversity quantifies the species richness within a local community, while gamma diversity represents the total species richness in a regional scale. Beta diversity measures the dissimilarity in species composition among sites or along an environmental gradient or between habitats in a region, reflecting the spatial turnover or nesting of species (Whittaker 1972, Tuomisto 2010). Notably, the Neotropical region has one the most diversified assemblages, also evidenced for aquatic biota (Aguirre et al. 2021) since the Neotropical ecosystems harbor one-quarter of the world's freshwater fish diversity (Pelicice et al. 2017), encompassing over 5,600 species across Central and South America with estimations of additional undescribed species (Pelicice et al. 2017, Van Der Sleen & Albert 2017). It is worth highlighting that variation in fish assemblages is associated with geographic, local environmental and biotic interactions (Cilleros et al. 2017, Vieira et al. 2018).

The frequent evaluation of fish diversity patterns has generated diverse hypotheses about how spatial scales or environmental characteristics affect alpha diversity (Roa-Fuentes et al. 2022, Ngor et al. 2023, Ficklin et al. 2023). More specifically, Legendre & De Cáceres (2013) introduced a framework for estimating beta diversity from species abundance or presence-absence matrices. This method enables the quantification of both local contributions to beta diversity (LCBD) and species-specific contributions to beta diversity (SCBD). Accordingly, the relationship between LCBD/SCBD may indicate levels of ecological uniqueness and differences in environmental conditions in relation to species composition (Legendre & De Cáceres 2013).

Estimating LCBD and SCBD has evolved from calculating beta diversity based on either additive partitioning (Lande 1996) or multiplicative methods (Jost 2007). Additionally, measures like relative abundance (Legendre et al. 2005) and taxonomic, phylogenetic, and functional composition (Swenson et al. 2011) can be used to analyze different aspects of beta diversity. Numerous studies have demonstrated the influence of regional or local characteristics on the structural complexity of stream fish assemblages across several scales (Xia et al. 2022, Gavioli et al. 2022). Furthermore, habitat changes along gradients can affect various ecological attributes of populations (Torgersen & Close 2004) and communities (Snyder et al. 2006, Schneider & Winemiller 2008) at diverse spatial and temporal scales (Pusey et al. 1998). Understanding the interplay among these factors is crucial for elucidating regional diversity patterns in fish assemblages and understanding how environmental characteristics shape biodiversity in distinct aquatic environments (Vellend 2010, Baselga & Leprieur 2015), especially in streams systems.

Small Neotropical streams are unique in terms of fish community richness because they have varied hydrology, including recurrent droughts and floods, which diversify habitats and favor the abundance of aquatic organisms and terrestrial conferring greater species richness, especially endemics (Winemiller et al. 2008, Vieira & Tejerina-Garro 2014). However, geomorphology and geology the small Neotropical streams also contribute to unique characteristics that provide variation biodiversity along the longitudinal route (source/mouth gradient) (Wantzen et al., 2006). Anthropogenic interference is another factor that can add to changes in stream structure since land use affect with stream flow, solid transport, salinity and the amount of organic matter (Synder et al., 2003), noting, in consequence, a greater distribution and presence of fish species downstream than upstream in the continuous river (Vannote et al., 1980).

Diversity patterns of fish communities in neotropical streams can be explained by a combination of limnological factors, energy, productivity and temporal heterogeneity (Vieira et al. 2018). In the streams of the upper Paraná River basin, physico-chemical and hydrological characteristics as stream flow, altitude, conductivity, and the conservation of riparian vegetation influence with assemblage composition as they act as a filter for local assemblages (Abes & Agostinho, 2001; Borges et al., 2020; Nakamura et al., 2021). However, other environmental factors can also have a substantial impact on species composition and differentiation between local assemblages (Munyai et al. 2023). Therefore, choosing the most suitable method for estimating beta diversity remains crucial. The sampled area itself can act as a filter that affects biodiversity (Anderson et al., 2011; Chao et al., 2012) because anthropogenic impacts alter species composition, decreasing overall diversity or increasing the convergence of similar species (Su et al. 2015). Therefore, the proper choice for estimating beta diversity is crucial.

In the present work, we follow Langeani et al. (2007) and Súarez et al. (2011) who found patterns of richness to be influenced by environmental and spatial patterns and we hypothesise that local limnological, spatial and anthropogenic (e.g., land use) characteristics interact at different levels in streams to explain local contributions to beta diversity. Based on this hypothesis, we predicted that streams with higher fish species richness contribute more to LCBD. We also predicted that limnological characteristics (e.g., water velocity, width, depth and conductivity) contribute more to LCBD compared to regional factors (e.g., stream position within the watershed), but that this contribution may be altered by land use. Finally, we predicted a positive correlation between SCBD and occurrence frequency owing to the predominance of small fish species that have colonised new habitats.

#### 2. Methods

#### 2.1 Study area

The La Plata Basin, encompassing a vast area of 3.19 x 106 m<sup>2</sup> harbors approximately 1,000 validated fish species. Notably, the Upper Paraná River presents a pronounced richness of species, of which 341 native and others 128 non-native species (Dagosta et al. 2024). However, the Upper Paraná also faces substantial anthropogenic pressure in the form of 130 dams built along its course, representing one of the highest dam densities in the world (Amsler & Drago 2009). This dam construction threatens the region's biodiversity through the introduction of new species (Dagosta et al. 2024). Nevertheless, certain sub-basins within the Brazilian state of Mato Grosso do Sul, such as the Ivinhema, Amambai, Iguatemi and Maracaí Rivers, remain largely undammed (Froehlich et al. 2017), offering crucial refuge for fish populations and maintaining critical migratory pathways (Súarez 2008).

The selected sub-basins are located within a landscape predominantly characterized by agricultural activities, featuring small towns typically below 30.000 inhabitants. The Ivinhema River basin boasts the largest area at 39.765 km<sup>2</sup>, originating at an elevation of approximately 700 meters above sea level. Following in size are the Amambai (10.119 km<sup>2</sup>), Maracaí (3.721,3 km<sup>2</sup>), and Iguatemi (8.278 km<sup>2</sup>) basins. We grouped very small basins within larger basins near the Maracaí River. Notably, additional smaller micro-basins, primarily located between the Amambai and Iguatemi Rivers, contribute an additional 1.430 km<sup>2</sup> by directly flowing into the Paraná River. Collectively,

these watersheds drain into the Paraná River floodplain situated between the Porto Primavera and Itaipú dams (Figure 1).



Figure 1. Sampled sites along the studied rivers of the Upper Paraná River Basin in Brazil from 1999 to 2023.

#### 2.2 Samples

This study is based on data collected from multiple sampling campaigns conducted between 1999 and 2023. We chose low-flow streams ( $<5m^3/s$ ) aiming to obtain better sample efficiency, as well as less influence from urbanization and avoiding temporal replication. Each sampled stretch with nearly 100m long, was sampled by a combination of fishing methods, including rectangular sieves (0.8x1.2m) with a mesh size of  $\sim2mm$ , trawl nets (5x1.5m) with a mesh size of  $\sim2mm$ , five fish nets (1.7x10m) with various mesh sizes (15, 25, 30,40 and 50mm opposite knots with exposition time nearly to 14 hours) and electrofishing (backpack Electrofisher LR-24 Smith & Root) also in a 100m long stretch. Each stretch is sampled approximately during 2 hours.

Captured fish were anesthetized with Eugenol solution, followed by euthanasia according to established ethical protocols of the State University of Mato Grosso do Sul (UEMS). Fixation utilized 10% formaldehyde and preservation in 70% ethanol. Taxonomic identification relied primarily on Graça & Pavanelli (2007) and Ota et al. (2018), while incorporating updated taxonomic revisions. Specimens were deposited in recognized zoological collections, such as Limnology and Ichthyology, housed at the Aquaculture Research Center of the State University of Maringá (NUP/UEM), Zoology Museum of the University of São Paulo (MZUSP), Museum of the Federal University of Rio Grande do Sul (UFRGS), Zoology Museum of the State University of Londrina (MZUEL), and Mato Grosso do Sul State University Fish Collection (CPUEMS).

Local environmental variables, such as altitude and coordinates, were determined by using GPS with an altimeter. Limnological characteristics, such as current velocity, average depth, electrical conductivity, dissolved oxygen, pH, water temperature and turbidity, were collected using a Horiba U-52 multiparameter probe and FP110 flowmeter. Land use and cover information (primary productivity, forested area, flooded area, pasture, and agricultural area) was obtained for a 1 km radius around each sampling point using MapBiomas, Collection 8 (https://mapbiomas.org/download-dos-atbds) for the year each point was sampled. The estimated slope and stream order were taken from the HydroSheds database (https://www.hydrosheds.org/products/hydrorivers), and estimated average net primary productivity was obtained from available MODIS satellite data, considering the average for the years 2001 to 2022.

#### 2.3 Statistical analysis

#### 2.3.1 Fish species richness and contributions to beta diversity

All analyses were run in the R environment (R Core Team 2022). Considering differences in sampling methods among sites and temporal variation, we decided to use only the occurrence data of the species in each stretch of stream. We began the analysis by estimating species richness for each sub-basin using the bootstrap procedure through the "specpool" function of the "vegan" package (Oksanen et al. 2022) and species composition through occurrence data. Therefore, Total and partitioned beta diversity (turnover and nestedness) were calculated using the "beta.sample" function from the "betapart" (Baselga et al. 2017) package using the Sorensen dissimilarity index, but turnover and nesting rates were considered together because both contribute to beta diversity (Valente-Neto et al. 2020). Species contribution to beta diversity (SCBD) and local contribution to beta diversity (LCBD) were obtained using the "beta.div" function from the "adespatial" (Dray et al. 2018) package. To help evaluate predictions, we correlated the local contribution to beta diversity with species richness and for this we used the Spearman index (r) to explain the clarity between the LCBD and species richness.

#### 2.3.2 Contributions to LCBD and its relationship with FO

To estimate influence of environmental heterogeneity at subbasin scale on total beta diversity we generated four Principal Coordinates Analysis (PCoA) using 'betadisper' function from the "vegan" (Oksanen et al. 2022) package to (latitude and longitude) to represent spatial distance measure; using land uses representing landscape heterogeneity, limnological variables (with standardized variables) representing limnological heterogeneity and basin area. In all these analyses we used a mean centroid distance to measure of heterogeneity. We used the Pearson correlation coefficient (r) to explain how basin characteristics are correlated with beta diversity of small stream fish assemblages. Continuing, we measured limnological characteristics (current velocity, average depth, electrical conductivity, dissolved oxygen, pH, water temperature and turbidity), regional (sub-basins, altitude, slope) and land use (productivity, forest and wetland) variables to LCBD beta diversity, a conditional inference tree (ctree) (Hothorn et al. 2006) was modeled using the "ctree" function of the "partykit" package (Hothorn & Zeileis 2015). The importance of the variables retained in the final model was estimated using the "varimp" function.

Finally, we use a linear correlation (r) is used to verify if species contributions to beta diversity are correlated with species frequency of occurrence (FO) defined as the number of sites with a particular species occurrence/total number of analyzed sites.

#### 3. Results

#### 3.1 Fish species richness in assemblages

Across the four sub-basins, a total of 131 fish species were registered. The Ivinhema subbasin exhibited the highest species richness with 115 species, followed by Iguatemi (60 species), Amambai (45 species), and Maracaí (38 species). Bootstrapping estimates also suggest that the Ivinhema sub-basin has the richest assemblages (129 $\pm$ 4 species), followed by Iguatemi (69 $\pm$ 4 species), Amambai (51 $\pm$ 3 species), and Maracaí (45 $\pm$ 4 species) (Figure 2).

Inter-basin variability was observed in the composition of dominant species. While some species (e.g., *Astyanax lacustris*, *Psalidodon fasciatus*, *Piabarchus stramineus*, *Hypostomus ancistroides*) displayed widespread sub-basins distribution, others exhibited more localized occurrences. For instance, *Psalidodon* cf. *Paranae* was primarily found in the Amambai sub-basin, while *P. bockmanni* was restricted to the Iguatemi sub-basin. An undescribed Rivulidae species was discovered in the Iguatemi sub-basin, and *Phallotorynus pankalos*, previously known only from the Iguatemi sub-basin, was encountered in a headwater stream of the Amambai sub-basin.



Figure 2. Accumulated (bar) and estimated fish species richness (bootstrap) with confidence interval ( $\alpha$ =0.05) in the sub-basins sampled in the Upper Paraná from 1999 to 2023.

#### 3.2 Streams with higher fish species richness contribute more to LCBD

Total beta diversity is higher in the Iguatemi River (0.88), followed by the Maracaí River (0.87), Ivinhema River (0.85) and Amambai River (0.84), and this result is mainly influenced by turnover in species composition along the sub-basins (Figure 3) when compared to nestedness. Our results also showed that landscape and limnological diversity in sampled sub-basins are negatively associated with total beta diversity, even though some landscapes present significant correlation (Figure 4).



Figure 3. Total and partitioned (turnover= dark gray and nestedness= light gray) beta diversity for stream fish assemblages in the Upper Paraná River Basin.



Figure 4. Pearson correlation between total beta diversity and mean distance to centroid for spatial, limnological, landscape and sub-basin area for stream fish assemblages in the Upper Paraná River Basin. The red, green, blue and black colors correspond to the sub-basins Amambai, Iguatemi, Ivinhema and Maracaí, respectively.

The local contribution to beta diversity (LCBD) was negatively correlated with species richness (Spearman r=-0.68; p<0.001), suggesting that portions of stream that contribute most to beta diversity are those that also have fewer fish species suggesting that portions of stream that contribute most to beta diversity are those that also have fewer fish species following a longitudinal direction to headwaters. (Figure 5).



Figure 5. Scatterplot of local contribution to beta diversity (LCBD) in relation to species richness in stream fish assemblages in the Upper Paraná River Basin.

3.3 Watercourses in the lower part of the basin have higher LCBD due to the occurrence of species with lower dispersal capacity

LCBD was mainly explained by water velocity, followed by electrical conductivity of the water and sub-basins. Thus, portions of stream with a current velocity of less than 0.4 m/s-1, an electrical conductivity up to 18  $\mu$ S/cm-1 and narrowing width (up to 1.7 m) made the greatest contribution to beta diversity. On the other hand, streams with a velocity greater than 0.4 m/s-1 located in the Amambai and Ivinhema River sub-basins had the lowest contributions to beta diversity (Figure 6). Stream portions located in Iguatemi and Maracaí sub-basins are predominant when compared to the Ivinhema sub-basin among those statistically different from zero (Figure 7).



Figure 6. Conditional inference tree of LCBD in response to environmental descriptors for stream fish assemblages in the Upper Paraná River Basin from 1999 to 2023.



Figure 7. Scatterplot of the local contribution to beta diversity of stream fish assemblages along hydrological gradients in the sampled areas. Circle sizes are proportional to LCBD. Gray circles represent LCBD not significantly different from zero, and red circles represent statistical difference from zero in the Upper Paraná River Basin.

3.4 Species frequency of occurrence (FO) with SCBD

We also observed that species with higher contribution to beta diversity (SCBD) are those with larger occurrence frequency in the sub-basins; despite this, some species contributed more than expected by their occurrence (e.g., *Psalidodon bockmanni*, *Astyanax* sp., *P. Paranae*, *Phalloceros harpagos* and *P. bifasciatus*) (Figure 8).



Figure 8. Relationship between SCBD and frequency of occurrence of fish species in stream assemblages in the Upper Paraná River Basin.

#### 4. Discussion

Based on our analysis, we can infer that small streams species richness is negatively correlated with LCBD, and as predicted limnological factors such as velocity and conductivity contributed more to the increase in LCBD than regional factors (sub-basins, altitude and slope) and land use factors (primary production, portion of wetlands, forests and agriculture). Our results partially corroborated our hypothesis, since we expected a positive relationship between species richness and LCBD, and the significant interference of anthropogenic factor such as land use on LCBD. As we also predicted, species with a higher frequency of occurrence contribute more to the SCBD in the sub-basins of the upper Paraná River.

#### 4.1 Streams with higher fish species richness contribute more to LCBD

A more complete estimation of fish species richness in the floodplain portion of the Upper Paraná River Basin listed 469 fish species (Dagosta et al. 2024). We observed 131 (27.93%) of these species in our stream samples; however, since we did not include large rivers and repeated sites, this selectivity explains smaller species richness in sub-basins sampled. Among the studied sub-basins, only Ivinhema has available species list that includes 141 fish species (Vicentin et al. 2019), 115 of which are registered in this study. It is important to highlight this study presents the first published information about stream fish assemblages in the Maracaí sub-basin. We also provide additional details on the richness and composition of fish assemblages throughout the Amambai and Iguatemi subbasin. However, for the Iguatemi River sub-basin, previously published information is available only at a smaller scale than the one employed in this study (Súarez & Petrere Jr. 2006, Batista-Silva et al. 2018).

Since the most frequent species observed are those with higher occupation at the regional scale, this result represents the ability of these species to disperse and use resources along the Upper Paraná River Basin. Despite this, differences among sampled sub-basins suggest that these they present environmental characteristics that act as filters to species occurrence (Ortega et al. 2015, Pelaez & Pavanelli 2019).

Our study revealed that the Iguatemi and Maracaí sub-basins exhibited higher total beta diversity compared to the larger Ivinhema and Amambai sub-basins. Considering basin localization, the Iguatemi and Maracaí sub-basins are located near the upstream of Itaipú reservoir (lake), which, in 1982, caused the disappearance of an important biogeographical barrier (Sete Quedas Falls) that limited the Upper and Middle Paraná River Basin (Lira et al. 2017). Few studies are carried out in these tributaries of the Upper Paraná Basin, and our results showed that *P. bockmanni*, *P. bifasciatus* and an undescribed species of *Psalidodon* are widely distributed in these basin portions. *Psalidodon bifasciatus* is from the Iguaçu River Basin and have been recently registered in the Upper Paraná Basin (Neves et al. 2020). The low frequency of occurrence of *P. bockmanni* in the Amambai and Iguatemi sub-basins may be associated with recent occupation by *P. bifasciatus*. Longitudinal features in the Maracaí sub-basin, which is almost entirely located in the floodplain portion, may have facilitated colonization by *P. fasciatus* in the Iguatemi and Maracaí sub-basins.

We were expecting that streams in the sub-basins of the upper Paraná River that have greater fish species richness contributes more to LCBD but this was not supported by our result since there is a negative correlation between species richness and LCBD (Figure 5) which has also been observed in other studies (e.g. Heino & Grönroos 2017, Xia et al. 2022).

One explanation for this result could involve environmental characteristics, mainly limnological characteristics (Figure 6), that act as filters for species occupation in

smaller, fast-moving streams, particularly those with waterfalls, thus allowing for more unique assemblages composed of species able to transcend these barriers (Lamourox et al. 1999, Palheta et al. 2021) and maintain viable populations in these basin portions.

## 4.2 Watercourses in the lower part of the basin have higher LCBD due to the occurrence of species with lower dispersal capacity

The sampled sub-basins presented fewer waterfalls and smaller height differences; however, Iguatemi has many portions with rapids, both in the main channel and tributaries, which can also contribute to higher LCBD. Along the Iguatemi sub-basin, some species are restricted to headwater portions, while others are more frequent in lower portions (e.g. *P. fasciatus, A. ibitiensis* and *P. argentea*) which are associated with stretches of higher speed, such as rapids from the middle of the streams towards the headwaters. This differentiation in species occurrence, which is discussed in the recent literature, shows the effect of rapids and waterfalls on limiting fish species groups in specified basin portions (Súarez & Petrere Jr 2003, Súarez & Petrere Jr 2005, Súarez & Petrere Jr 2006, Lopes et al. 2016).

We also tested the influence of land use variables (primary productivity, flooded area, forest, and agricultural area) and regional characteristics (sub-basins, altitude, slope) on the LCBD in the sampled watercourses, but the influence was minimal, with only the percentage of flooded areas showing little relevance to the LCBD. Although of lesser importance, this relationship can be explained by the colonization of floodplain species in streams located nearby. Similar results were observed in the beta diversity of stream invertebrates in New Zealand and Serra da Bodoquena (Astorga et al. 2014, Valente-Neto et al. 2020). Although land use variables did not show significant values for LCBD, such activities as agriculture and pasture planting can use substrates, pesticides and fertilizers, thus increasing the volume of particulate matter which, when carried into streams, alters such characteristics as pH, conductivity, salinity and siltation (Silva et al. 2018, Mello et al. 2020). Nonetheless, variations in habitat characteristics can allow species with greater tolerance to establish themselves in sites of more heterogeneous populations, thus allowing the formation of assemblages with species of broad tolerance and environmental flexibility (Leão et al. 2020, Xia et al. 2022).

Other studies, such as those of Borges et al. (2020) and Valente-Neto et al. (2020), have suggested that streams located at basin borders present greater uniqueness, i.e., higher LCBD, possibly in response to headwater capture from other basins. In contrast, our study reported higher LCBD values along the whole longitudinal gradient in sampled areas, mainly in the Iguatemi and Maracaí sub-basins as well as higher levels of uniqueness. However, the highest levels of uniqueness were still observed in the Iguatemi and Maracaí sub-basins. The contrast could be explained by large-scale effects (basin effect) that acted to generate an ecoregion biota in larger rivers where the sampling was performed, whereas our study suggests that smaller streams contributed more to the LCBD (Figure 7).

#### 4.3 Species frequency of occurrence (FO) with SCBD

As we predicted, FO is positively correlated with SCBD because portions the studied fish assemblages have a predominance of small fish species, except for *H. ancistroides* (Figure 8). They also predominate based on a specific combination of habitat characteristics. For example, *P. bockmanni* predominates in Iguatemi streams, while *P. stramineus* and *P. fasciatus* occupy streams with higher water velocity. Based on our results *P. bifasciatus* is only present in small streams of the floodplains, thereby increasing its importance to species-specific beta diversity at the regional scale. Some studied species contributed

more than expected by their frequency of occurrence, probably in response to recent occupation or competitive interaction influencing predominance among sub-basins. However, both niche breadth and niche position play important roles toward explaining species distribution (Heino & Grönroos 2017, da Silva et al. 2018, Siegloch et al. 2018).

The importance of streams in floodplains can be viewed through the prism of disproportionately higher occurrences of *P. bockmanni*, *P. bifasciatus* and *Astyanax* sp., mainly registered in the Iguatemi River (*P. bockmanni*) or exclusively in the Maracai subbasin (*P. bifasciatus* and *Astyanax* sp.). On the other hand, *H. ancistroides*, *P. stramineus*, and *P. fasciatus* are also considered species with higher contribution to species-specific beta diversity (SCBD), and they have high frequency along the entire studied area as represented by the entire Upper Paraná River Basin (Pelaez & Pavanelli 2019). This pattern underscores the importance of hydrological characteristics that can generally act as a filter affecting the dispersal, habitat formation and reproductive dynamics of fish species (Poff & Allan 1995) and, given such factors as flow rate, current velocity and water temperature, influence the composition of whole Neotropical fish communities (Mendonça et al. 2005).

The linear correlation between SCBD and frequency of occurrence differs from that observed in other studies. For example, Heino & Grönross (2017) recorded quadratic distribution, suggesting that species frequency of occurrence (FO) near 50% (30 sampling points) presents higher SCBD. In our study, the maximum FO reaches almost 50%, thus explaining the linear behavior of this species metric.

#### 5. Conclusion

Our study showed that although limnological factors contribute most to defining the fish assemblages of the small streams in the sub-basins of the upper Paraná River, they interact with regional factors and thus act as a filter on the composition of these assemblages. Small streams also have species with limited distribution, although with a clear spatial pattern that raises the LCBD of these environments. Although anthropogenic factors, such as land use and occupation, have not been significant, they can still contribute to the modification of landscapes (Larentis et al., 2022) and thus interfere with limnological factors, such as pH and conductivity, as well as water narrowing and velocity, essential factors that contribute to the region's beta diversity (Borges et al., 2020). Despite this, the role that functional and phylogenetic characteristics play in beta diversity has yet to be elucidated. These results can help to draw up public policies aimed in rehabilitating the pristine characteristics and at protecting the biodiversity of the small streams.

#### Chapter 2. Regional characteristics determine the diversity and composition of native and non-native fish assemblages in the Upper Paraná River Basin

#### Resumo

O entendimento da composição e riqueza de espécies de uma assembleia de peixes é fundamental para avaliar ações ambientais que visam conservar e preservar a diversidade de espécies. Nesse contexto compreender como fatores regionais como a altitude, declividade, pluviosidade, centralidade (conexão entres as regiões), temperatura, área, ordens de rios e densidade de drenagem contribuem para riqueza e distribuição das espécies ao longo do gradiente longitudinal. Para entender como esses fatores podem predizer a riqueza e a composição das espécies nas assembleias de peixes na bacia do alto rio Paraná, fizemos a modelagem desses fatores em ralação a riqueza de espécies. Separamos em quatro sub-bacias e, seguidamente, em ottobacias para melhor compreender a mudança da composição e riqueza nos gradientes longitudinais. Também separamos a riqueza de espécies nativas de não nativas e investigamos como esses fatores predizem a composição das espécies nas sub-bacias. Obtivemos como resultados que a riqueza geral das espécies é influenciada pela altitude, declividade e pluviosidade (r2 = 0.26). Já a riqueza das espécies nativas está diretamente associada a declividade e centralidade ( $r_2 = 0.16$ ). A proporção de espécies nativas e não nativas não se alterou significativamente entre as sub-bacias avaliadas. Concluímos que os fatores regionais podem estar associados à fatores locais e antrópicos para influenciar a composição e riqueza de espécies na bacia do alto rio Paraná. E a declividade é um fator importante que prediz a riqueza de espécies nativas e não nativas na região por interferir em cachoeiras e corredeiras em rios e riachos que podem estar atuando como filtros ambientais e histórico para as espécies. Conhecer essas influências sobre as assembleias permite alavancar políticas e ações ambientais que promovam conservação eficaz das espécies de peixes na bacia do alto rio Paraná.

#### Abstract

Understanding the composition and species richness of a fish assemblage is an essential step in evaluating environmental actions aimed at conserving and preserving species diversity. Accordingly, such factors as altitude, slope, rainfall, centrality (connection between regions), temperature, area, river orders, and drainage density determine species richness and diversity along a logitudinal gradient. Herein I modeled these factors as specifically predictive of species richness and composition in fish assemblages in the Upper Paraná River basin. First, I divided the basin into four sub-basins and again into eight sub-basins, or ottobasins, to better understand the change in composition and richness along the longitudinal gradient. Next, I separated native and non-native species richness and investigated how regional factors can predict species composition in the subbasins. Our results indicate that species richness is influenced by altitude, slope, and rainfall ( $r^2 = 0.26$ ), while the richness of native species is directly associated with slope and centrality ( $r^2 = 0.16$ ). Slope emerged as a significant predictor of both native and nonnative species richness, potentially acting as an environmental and historical filter through its influence on waterfalls and rapids. However, the proportion of native and non-native species did not vary significantly among the assessed sub-basins. We conclude that regional factors, when combined with local and anthropogenic factors, likely influence species composition and richness in the Upper Paraná River basin and that such understanding can inform effective conservation management in the Upper Paraná River basin.

#### 1. Introduction

The Neotropical region is known for its high richness of freshwater fish species since approximately one quarter of all freshwater species in the world are distributed in this region (Albert et al. 2020, Aguirre et al. 2021). The geographical position of the Neotropical region defines the proper scales by which to understand the composition of fish species in the different habitats of this region (Loureiro et al. 2023). Notably, neotropical fish assemblages are influenced on global (e.g., climatic stability and higher net primary productivity), regional (e.g., watershed sizes and geomorphological diversity) and local (e.g., pH, conductivity and dissolved oxygen) scales. These scales can act individually or interact to determine the richness and composition of fish assemblages (Angermeier & Winston 1998, Uchida & Inoue 2010). Therefore, we cannot dissociate scale from an assessment of diversity. In alignment, recent studies (Faquim et al. 2022, Matins et al. 2023, Córdova Junior et al. 2024) have reported how the factors that determine species richness and composition interact to form fish assemblages at different scales.

The homogenization of environments in response to anthropic activities affects the aquatic habitat, and it has become a worldwide threat to freshwater fish assemblages (Vitule et al. 2012, Bezerra et al. 2019). The combined effect of habitat loss, water quality degradation and biotic interactions with exotic species can represent an even higher threat to the conservation of fish assemblages. Moreover, anthropogenic activity acts as an environmental filter by the alteration of land use and cover (Melo et al. 2020), allowing different contaminants to enter streams and rivers in a way that interferes with natural hydrological filters (Pelicice et al. 2021).

Of the large freshwater river basins that make up the Neotropical region, the upper Paraná River basin is second only to the Amazon basin in terms of size and richness of fish species (Dagosta et al. 2024). With its unique hydrological (e.g., rapids and waterfalls, flooded areas) and limnological (e.g., conductivity, salinity and pH) characteristics, it provides a variety of habitats that are home to a high diversity of fish species (Frota et al. 2019, Apodaca et al. 2019, Monaghan et al. 2020, Córdova Júnior et al. 2024). Such variety of habitats and connectivity between them may have facilitated the occupation and spread of non-native species after flooding of the Sete Quedas (Seven Waterfalls), which had been a natural geological barrier for the creation of the Itaipu reservoir in the 1980s (Júlio Junior et al. 2009, Garcia et al. 2018). This event allowed the massive introduction of several species of fish into the Upper Paraná River basin with impacts that have yet to be fully measured and understood (Deprá et al. 2021, Garcia et al. 2021).

However, if we analyze species richness and composition in relation to regional factors, such as altitude, temperature and primary productivity, as well as the effects of their interaction, we can elucidate the distribution of fish richness to, in turn, understand how both native and non-native species respond to these factors (Súarez et al. 2011, Lemke & Súarez, 2013, Larentis et al. 2022). This will allow us to develop more effective policies and environmental programs aimed at protecting and conserving specific regions within the upper Paraná River basin in order to ensure fish diversity in the region for posterity (Gogola et al. 2013, Borges et al. 2020). Current studies in the region are all focused on primary punctual data acquisition, while ignoring secondary data occurrence along other areas. These data have grown in recent studies based on large-scale ecological patterns (e.g., Dornelas et al. 2018, Tonella et al. 2023). However, secondary data are increasingly being used in ecological studies on a regional scale, with the aim of understanding how communities are structured on a broader scale (e.g., Dornelas et al. 2023).

The present study is driven by three hypotheses. First, overall species richness is directly related to two or more regional factors, such as altitude, mean annual temperature, net primary production, connectivity, slope, rainfall, area, river order and density. If species richness is proportional to area, then species richness increases as the area of ottobasins increases. However, stream order and density may also be correlated with species richness. This is supported by the River Continuum Concept (RCC) whereby a river system continuously integrates a series of physical gradients and associated biotic adjustments as the river flows from headwater to mouth. This phenomenon could account for the increase in net primary productivity and differences based on slope. Second, the composition of native and non-native species is predicted by the same regional factors and shows a similar pattern along the environmental gradient (Hughes et al. 2023). Here, it is assumed that 1) both native and introduced species are small, allowing for greater occupation of habitats (Frederico et al. 2019), and 2) the richness of both native and introduced species decreases inversely from mouth to headwaters. Third, based on the effect of altitudinal gradient on the composition of native species, it is hypothesized that altitude, slope, connectivity between ottobasins (Shao et al. 2019) and net primary production (Dodson et al. 2000) explain the distribution of species with restricted distribution upstream of the sub-basins in the upper Paraná River basin on a regional scale.

#### 2. Methods

#### 2.1. Study area

The Upper Paraná River is located in the eastern portion of the La Plata basin, along one the most economically developed portions of the Paraná River in Brazil. This river runs through Goiás, Minas Gerais, São Paulo, Mato Grosso do Sul and Paraná states and passes through Paraguay until it flows into the Atlantic Ocean. In the Brazilian portion, the Paraná River has the largest number of dams used for hydroelectric production. Despite this, in the state of Mato Grosso do Sul, its tributaries, including Ivinhema, Amambai, Iguatemi and Maracaí, are free of dams, presenting only three small-scale hydroelectric power plants ("Pequena Central Hidrelétrica" (PCH)), two in the Ivinhema River and one in the Amambai River.

In this study, we divided the portion of the upper Paraná River basin in the state of Mato Grosso do Sul into ottobasins. To do this, we consulted the Multiscale Ottocoded Hydrographic Base (BHO), level 7, of the National Water Agency (ANA 2017) and the HydroSHEDS (Hydrological data and maps based on SHuttle Elevation Derivatives at multiple Scales) database (https://www.hydrosheds. org/). I compared the two cartographic bases to adjust delimitations of the ottobasins and then compared the data collected to verify the representativeness of the sample for the basin (Figure 1).



Figure 1. Map of the study area and ottobasins belonging to the lvinhema, Amambai, Iguatemi and Maracaí sub-basins.

#### 2.2. Data collection

Fish collections carried out in various sampling campaigns during the month of May from 1999 to 2024 provided the primary data. To do this, I adopted different sampling methods according to different environments. For example, I used rectangular sieves (0.8x1.2m) with a mesh size of ~2mm, trawl nets (5x1.5m) with a mesh size of ~2mm, gillnets (1.7x10m) with various mesh sizes (15, 25, 30,40 50, 60 and 70 mm with opposite knots and exposure time of nearly 14 hours) and electrofishing (backpack Electrofisher LR-24, Smith & Root). I anesthetized captured fish with Eugenol solution, followed by euthanasia according to established ethical protocols of the State University of Mato Grosso do Sul (UEMS). Fixation utilized 10% formaldehyde and preservation in 70% ethanol. Taxonomic identification relied primarily on Ota et al. (2018), while incorporating updated taxonomic revisions. Specimens were deposited in recognized zoological collections of the Limnology, Ichthyology and Aquaculture Research Center at the State University of Maringá (NUPELIA/UEM), Zoology Museum of the University of São Paulo (MZUSP), Museum of the Federal University of Rio Grande do Sul (UFRGS), Zoology Museum of the State University of Londrina (MZUEL), and Mato Grosso do Sul State University Fish Collection (CPUEMS). I supplemented primary data with the occurrence records of fish species for the region in secondary data obtained from Tonella et al. (2023), SpeciesLink (http://splink.cria.org.br) and the Global Biodiversity Information Facility (GBIF) (http://gbif.org).

I generated regional variables, such as altitude, rainfall, slope, temperature, stream order, and stream density, by averaging pixels in rasters from the HydroSHEDS database (https://www.hydrosheds.org/products/hydrorivers) for each ottobasin. Since our study involved the Neotropical region, we considered mean temperature and mean rainfall. I measured altitude in meters and slope in degrees. I obtained net primary productivity from available MODIS satellite data, taking the average from 2001 to 2022. To determine centrality of the connection between ottobasins, I created an adjacency matrix based on the connection between ottobasins according to cartographic watercourses and then used the function "closeness" in the "igraph" package to create this variable.

#### 2.3. Data analysis

I estimated species richness for each sub-basin using the bootstrap procedure via the "specpool" function in the 'vegan' package (Oksanen et al., 2022), and I investigated the relationship between native and non-native species using chi-square. Based on the obtained species richness, I evaluated the contribution of environmental factors to the richness of native and non-native species in ottobasins within sub-basins of the upper Paraná River, using linear regression models. I tested each of the three hypotheses noted above as follows:

Hypothesis 1: I used linear models to test the influence of regional variables, including altitude, temperature, rainfall, slope, centrality, stream order, stream density, area and net primary production, on species richness in the ottobasins. To detect multicollinearity among variables, I used the Variance Inflation Factor (VIF) based on the "vif" function in the "car" package. As proposed by Draper & Smith (1998), VIF values greater than 10 may indicate the presence of multicollinearity between or among variables. I used Pearson coordinate correlation (PCC) to estimate redundancy among variables, and I removed variables with r > 0.7 (Hughes et al. 2023) before determining model estimates. To reduce the number of variables in the model, I used a chi-squared test to determine the statistical significance of differences between variables in the model.

Hypothesis 2: To investigate the interference of regional variables on the composition of native and non-native fish assemblages, I carried out a Principal

Coordinates Analysis (PCoA) using the "cmdscale" function with two axes and a Jaccard distance matrix ("vegdist" function). Subsequently, I estimated the effect of regional variables on the distribution of species using the "envfit" function of the "vegan" package. Using the occurrences of non-native species in the ottobasins, I carried out a descriptive analysis using the "multipatt" function of the "indicspecies" R package (Caceres et al. 2011) with 9999 permutations to visualize the characterization of sub-basins according to the occurrences of introduced species. This metric complements the discussion of results obtained in the other analyses.

Hypothesis 3: Based on the preferred nomenclature of species with restricted distribution, rather than "endemic species," I estimated the weighted endemism for each ottobasin. To avoid collinearity with species richness, I realized a linear regression between weighted endemism (response variables) and species richness (explanatory variables) and used the residual of this regression as a measure of richness of species with restricted distribution not otherwise explained by species richness. With these residuals, I ran a new linear regression model, considering the residuals from the previous regression as a function of the regional variables as the response variable, and, hence, the composition of assemblages in the sub-basins of the upper Paraná River. To better visualize the distribution of species richness and composition in the ottobasins, I created maps showing richness values, native species, non-native species, PCoA axis scores and residual values. These maps helped in assessing diversity along the longitudinal gradient of the ottobasins in the upper Paraná River basin.

#### 3. Results

#### 3.1 General richness x regional variables

I compiled a total of 21,293 species occurrences for the study area within the Upper Paraná River basin. After checking for inconsistencies with the currently known ichthyofauna, I found 214 species distributed in 10 orders: 94 species of Characiformes (43.9%); 79 species of Siluriformes (36.9%); 14 species of Gymnotiformes (6.6%); 13 species of Cichliformes (6.1%); 7 species of Cyprinodontiformes (3.3%); 3 species of Myliobatiformes (1.4%); and one species each for the orders Cypriniformes, Perciformes, Pleuronectiformes and Synbranchiformes. The richness of each sub-basin with bootstrapping estimates suggests that the Ivinhema sub-basin has the richest assemblages with 190 (206±11), followed by Iguatemi 157 (179±21), Amambai 115 (134±14) and Maracaí 98 (110+14). Of the species surveyed, 129 (60.3%) are native and 85 (39.7%) are non-native, even though the proportion of native vs. non-native is statistically equivalent among studied subbasins ( $\chi 2 = 3.73$ ; p= 0.285). These values are close to those of species summarized by Dagosta et al. (2024) who reported 381 (72.7%) native and 128 (27.3%) non-native species (Figure 2).



Figure 2. Accumulated richness in the sub-basins of the upper Paraná River and the correlation between native and non-native species ( $x^2 = 3.73$  and p = 0.29).

None of the variables tested in the model had a VIF value of 10 or more, but the variables watercourse order and density were autocorrelated (r > 0.7); therefore, the variable stream order was removed from the models (Figure 3). The best linear model suggests that altitude, slope, and rainfall are the best predictors of species richness (Model 3) (Table 1) and that they explain 26% of the variation of general richness (Figure 4). In the present study, this means that sub-basins located in regions with steeper slope, lower altitude and less cumulative rainfall presented higher species richness (Figure 4). Even though models 1, 2 and 3 are plausible (delta AICc  $\sim$  2), model 3 was chosen because it has fewer variables, which is consistent with the sample size used in the analysis.



Figure 3. Variance Inflation Factors (A) for the regional variables tested in the models. PCC results (B) among the regional variables to avoid dundancy.

Table 1. Results of model selection for species richness and weighted endemism (residuals) for fish assemblages in the Upper Paraná River Basin. Adjusted  $r^2$  (Adj.  $r^2$ ), F value (F), p value (p) and Akaike Information Criterion (AIC).

Models for Richness	Adj. r <sup>2</sup>	F	р	AIC
1: Richness ~ Altitude+Slope+Rainfall+NPP+Temperature	0.33	3.71	0.01	267.46
2 Richness ~ Altitude+Slope+Rainfall+Temperature	0.26	3.38	0.02	269.58
3: Richness ~ Altitude+Slope+Rainfall	0.26	4.20	0.01	268.71
4: 4: Richness ~ Altitude+Rainfall	0.06	2.01	0.15	274.36
Models for Residuals of Weighted Endemism				
1: Residual of weighted endemism ~	0.12	2.0	0.13	95.47
Altitude+Slope+Rainfall+Centrality				
2: Residual of weighted endemism ~ Slope+Rainfall+Centrality	0.15	2.67	0.06	93.64
3: Residual of weighted endemism ~ Slope+Centrality	0.16	3.58	0.04	92.67
4: Residual of weighted endemism ~~ Slope	0.05	2.71	0.11	94.94



Figure 4. Scatterplot of species richness (A) and residuals of weighted endemism (B) in response to selected regional variables of fish assemblages in the Upper Paraná River Basin. The units for variables are: altitude (m), slope (degrees), rainfall (mm) and centrality (%).

The lower portions of the Ivinhema and Iguatemi Rivers present higher native and non-native species richness, whereas the upper portions of the Ivinhema and Amambai Rivers present lower species richness (Figure 5).



Figure 5. Richness of native species (A) and richness of non-native (B) species distributed in the upper Paraná River ottobasins in Mato Grosso do Sul state.

#### 3. 2 Species composition x regional variations

Axis 1 (A) of the native species PCoA explains 24.56% of the variation observed, with *Trachelyopterus galeatus*, *Pyrrhulina australis* and *Leporinus lacustris* having most influence. Axis 2 (B) explains 11.87% of the variation observed, with *Serrasalmus maculatus*, *Hypostomus iheringii* and *Leporinus friderici* having most influence. Axis 1 (C) of the non-native PCoA explained 19.33% of the variation observed, with *Sorubim lima*, *Schizodon borellii* and *Loricariichthys platymetopon* having most influence. Axis 2 (D) explained 14.46% of the variation observed, with *Cyphocharax nagelii*, *Microglanis garavelloi* and *Hypostomus strigaticeps* having most influence (Figure 6).

The "envfit" result pointed to altitude (r2=0.34; p<0.001) as the main predictor of the composition of native species, whereas centrality (r2=0.30; p<0.001) was the main predictor of the composition of non-native species (Table 2). Our interpolation of "multipatt" allowed us to characterize sub-basins by species. Accordingly, I associated larger native species with their occurrence in the lower portions of the sub-basin Iguatemi (e.g., *Pinirampus pirinampu*), while I associated smaller fish species, such as *Schizodon altoparanae*, with their occurrence in the upper portions of the sub-basin Maracaí. On the other hand, I also found differentiation in the occurrence of non-native species between the upper portions of sub-basins, especially in the upper Amambai and Brilhante Rivers. Such specimens as *Hypostomus cochliodon* and *Pimelodus mysteriosus*, among other smaller species, occurred predominantly in the lower portions of these sub-basins.

	PCoA results for native species		PCoA results for non-native species	
	$r^2$	Pr(>r)	r <sup>2</sup>	Pr(>r)
Order	0.02	0.79	0.002	0.97
Centrality	0.19	0.06	0.30	0.01
Altitude	0.34	0.004	0.18	0.08
Slope	0.01	0.82	0.01	0.84
Rainfall	0.27	0.71	0.01	0.87
Area	0.10	0.24	0.14	0.14
NPP	0.06	0.43	0.07	0.40
Density	0.02	0.77	0.06	0.42

Table 2. Results (envfit) showing the influence of variables on the composition of native and non-native species for the upper Paraná River basin.



Figure 6. Scatterplot of first two axes of PCoAs with envfit for native (A) and nonnative (B) species correlating regional predictors with species composition in the upper Paraná River basin. Ivinhema = green, Amambai= black, Iguatemi= pink, Maracaí= blue, and the size of the circle indicates the number of species.

The composition of native and non-native fish species changes among ottobasins such that the greatest similarity is found in regions close to the floodplain, whereas the least similarity is found in areas more distant from the floodplain. More native species occur in headwater regions since introduced species need connectivity between ottobasins to disperse. These species occur near the Paraná River channel where they were introduced, mainly owing to construction of Itaipú reservoirs (Figure 7).



Figure 7. Results of the visual PCoAs for species composition, with A (axis 1) and B (axis 2) showing the distribution of native species and C (axis 1) and D (axis 2) showing the distribution of non-native species for the ottobasins of the upper Paraná River basin in the state of Mato Grosso do Sul.

#### 3.3 Spatial variation in richness of species with restrict distribution

For species with restricted distribution (weighted endemism), I observed a positive correlation between river slope and centrality such that the central portion of sub-basins with steeper slope presents a higher frequency of species with restricted distribution (Figure 4-B). Spatially, I observed that lower portions between the Ivinhema and Amambai sub-basins and lower portions of Iguatemi and some others in the Upper Vacaria and Amambai Rivers present a higher number of species with restricted distribution than expected by species richness (Figure 8). On the other hand, the richness of species with restricted distribution in many middle and lower portions of the studied area can be characterized as homogeneous, thus showing the influence of slope on the longitudinal gradient of fish assemblages.



Figure 8. Scatterplot of richness (residual) of fish species with restricted distribution in the Upper Paraná River basin.

#### 4. Discussion

#### 4.1 General richness x regional variables

Hypothesis 1 held that species richness is related to such regional factors as altitude, mean annual temperature, net primary production, connectivity, slope, rainfall, area, river order and density. This was partially corroborated since species richness was influenced by altitude, slope and rainfall, but was not significantly influenced by net primary production, as shown in other studies of fish assemblages in neotropical streams (Vieira et al. 2018, Brasil et al. 2019). Indeed, the proposed linear model showed that the regional factors noted above had a significant influence on richness, corroborating other studies using the same approach (e.g., De Moura et al. 2015, Guo et al. 2015, Ter Steege et al. 2023).

Altitude is often used to explain species richness because it leads to climatic and volume variation in rivers and streams. Rapids and waterfalls typically occur when altitude suddenly changes along a river. Rapids and waterfalls act as a species filter for the colonization and maintenance of headwater portions (Soo et al. 2021). Rainfall also has a significant influence on species richness and the composition of fish assemblages in the Neotropics (Cilleros et al. 2017). However, rainfall is not an isolated factor since the amount and seasonality of rainfall influence other variables, such as productivity, environmental heterogeneity and the dynamics of hydrological characteristics like river flow, volume and depth, or physicochemistry, which also influence the richness and composition of assemblages (Maltchik et al. 2010, Cajado et al. 2022, Vergès et al. 2022).

Slope is associated with species richness because variation in the transition gradient between higher and lower regions is characterized as an ecotone (Daru et al. 2020, Loyola-Bartra et al. 2022). Ecotones, or transitional areas between two or more ecological communities, ecosystems, or bioregions, are well known to have higher species richness and diversity in their assemblages (Carvajal-Quintero et al. 2015, Ter Steege et al. 2023). In the case of ottobasins, these differences may be associated with waterfalls or rapids that occur along rivers and streams and which finally differentiate the richness and composition of species in headwaters, middle reaches, and mouths (Torrente-Vilara et al. 2011). This characteristic favors ottobasins with more restricted species, which is evidenced by the significant correlation between slope and residual richness of weighted endemism (Shipley & McGuire, 2022). This is why rivers, such as the Amambai and the Ivinhema, may have higher richness in restricted species by the higher number of waterfalls and rapids (Súarez et al. 2011, Córdova Junior et al. 2024).

The correlation between species richness and altitude, slope or rainfall is evident since lower portions in larger rivers with higher net primary production can offer more resources and niche diversity, thus maintaining higher species richness (Costa et al. 2018, Cavalheiro & Fialho, 2020). This richness is linked to lowland regions with periodic floods, which can vary in intensity. This phenomenon keeps the lower part more interconnected, which implies that centrality is a variable correlated with overall richness.

In addition, the lower values of adjusted  $r^2$  of 0.26 indicate that the factors considered explain only a portion of the variability in richness, suggesting the presence of other factors not included in the model, but possibly related to specific local factors, such as local hydrological characteristics, including stream width, flow and connectivity, which can interact with regional factors, thus assuming the role of species filter (Carvajal-Quintero et al. 2015, Ganassin et al. 2021). Anthropogenic activities can also interact and influence fish species richness and composition in Neotropical streams when land use is directly correlated with changes in hydrological characteristics (Pelecice et al. 2021, Jacob et al. 2021, Larentis et al. 2022), thereby intensifying the effects of local filters on assemblages. Undersampling may result in smaller predictive power of the final model. Thus, despite the integration of primary and secondary data, some portions of sub-basins would have smaller species richness than that historically registered. The errors associated with the sampling methods and the potential lack of standardization (Jackson & Harvey, 1997) should be noted. However, in the present study, the variation and adaptation of collection methods according to the characteristics of streams allowed for greater sampling of the assemblages. Therefore, to account for possible sampling error in this analysis, I used occurrence data (presence/absence). Fisher et al. (1946) proposed that sampling size is the main predictor of species richness; therefore, equivalently, ottobasins offer better sampling opportunities and therefore better characterization of assemblages. Fisher et al. (1946) also proposed that sampling size is the main predictor of species richness; therefore, in an equivalent way, ottobasins provide better sampling opportunity and, hence, better assemblage characterization.

#### 4.2 Species composition x regional variations

Hypothesis 2 held that the same regional factors predict the richness of native and nonnative species factors and show a similar pattern along the environmental gradient. This hypothesis had no support because the main factor predicting native species richness is altitude, which is well evidenced in neotropical streams (Cilleros et al. 2017, Costa et al. 2018, Bertora et al. 2021). The main factor predicting the richness of non-native species is, however, centrality. The ottobasins located in the southeast tend to have a higher number of non-native species since they are flatter regions with recurrent flooding and proximity to the Paraná River. On a regional scale, flooding is the main link between ottobasins, but they need to be in a flat region to allow connectedness between them and the resultant dispersal of non-invasive species (Hughes et al. 2023, Trovillion et al. 2023). Moreover, the proximity of ottobasins to the Paraná River channel is the main dispersal vector for these introduced species, which are more similar in the eastern and southern regions. This result is consistent with recent introductory activities, such as the flooding of Sete Quedas (Seven Falls) (Agostinho et al. 2016), construction of the Piracema Channel (Monaghan et al. 2020) or fish farming and species marketing activities that involve aquaculture and live bait (Duarte et al. 2023).

For native species, altitude was a determinant for species composition in the upper Paraná River basin. The influence of altitude on the ecology of neotropical freshwater fish is well known (Poff & Allan 1995, Tondato & Súarez 2010, Lemke & Súarez 2013, Soo et al. 2021) and is inversely proportional to species richness. Similarly, centrality was also a determinant of native species composition, and both altitude and centrality can lead to an increase or decrease in fish diversity (Cavalheiro & Fialho 2020, Córdova Junior et al. 2024), whether native or non-native.

Non-native species have lower occurrence in the southwestern portion because of the greater proximity to springs and, consequently, an increase in altitude, slope (Poff & Allan 1995) and waterfalls, which isolate ottobasins, even while connected (Borges et al. 2020, Nakamura et al. 2021). In this study, I did not examine the isolated effect of connectivity and waterfalls as local filters for species, but it can be speculated that these factors can explain the low occurrence of non-native species farther west and north in the upper Paraná River basin. The connectivity of ottobasins allows non-native species to occupy new environments, which may limit their occurrence by the action of local environmental filters, such as water velocity, waterfalls, conductivity, width and depth of the streams (Súarez & Petrere Jr. 2006, Lopes et al. 2016, Palheta et al. 2021).

#### 4.3 Spatial variation in richness of species with restrict distribution

Species with restricted distribution and the highest richness are located at lower portions of the Ivinhema sub-basin between two conservation units, the State Park of Ivinhema River floodplain and the Natural Municipal Park of Naviraí City. This region has a combination of large rivers like the Ivinhema and Paraná, along with marginal lakes and different seasonally flooded habitats with higher species richness, but some with lower occupancy along the whole studied area.

The lower Iguatemi region has a high residual value of weighted endemism, which may be associated with the existence of several small, high-current stretches, possibly determining a specific pattern of organization for each stretch of the river (Súarez & Pretere Júnior 2006). Species composition varies longitudinally and is linked to regional variations, but the explanation for the greater richness of native and non-native species may be associated with local characteristics, such as turbidity, conductivity and velocity, of the streams in the final stretch of the Iguatemi River sub-basin (Córdova Junior et al. Melanorivulus amambaiesis and Melanorivulus ivinhemensis are species 2024). described as endemic to the Amambai and Ivinhema sub-basins (Volcan et al. 2018). However, species were also found in some portions of other Maracaí sub-basins, as well as Atlantirivulus enigmaticus described in the Ivinhema sub-basin (Volcan et al. 2024). These species are not endemic to these sub-basins; instead, they are widespread among the sub-basins as long as environmental characteristics support their occurrence. Therefore, the restriction of these species is subject to the influence of such variables as the connectivity of ottobasins, slope and limnological characteristics.

The richness of species with restricted distribution is influenced by connectivity since slope acts as a species filter, and centrality is higher in more connected portions of the basin. Hypothesis three holds that altitude, slope, and connectivity between ottobasins, together with net primary production, explain the distribution of native species and determine the restricted distribution of native species upstream of the sub-basins in the upper Paraná River basin on a regional scale. The results show that this was partially corroborated because connectivity and slope directly influence the distribution of species richness along the upper Paraná River basin. In general, the filter effect of altitude is well established in the ecological literature. However, slope, as a variable, is usually neglected as a consideration in freshwater fish assemblages. Rapids and waterfalls make it impossible for some species to spread out (Súarez & Petrere 2006, Lopes et al. 2016).

Similarly, although connectivity is an important regional aspect for the occupation of native species (Shao et al. 2019), it can also act as a local filter. It reflects the natural geological connection between ottobasins, and it is a highly pliable variable, owing to the siltation of streams (Leão et al. 2020, Mello et al. 2020), as well as destruction or capture of springs (Aquino & Colli 2017, Nakamura et al. 2021). For this reason, anthropogenic activities, which I did not assess in this work, should be measured at regional and local scales (Marmontel et al. 2018, Pelicice et al. 2021), directly and indirectly, as they can alter specific characteristics that directly affect the composition of native species richness. Deforestation alters net primary productivity, while increasing the transport of sediment, making streams shallower and narrower (Dagosta et al. 2024), and it interferes with turbidity, current velocity and connectivity of streams with main rivers (Angulo-Valencia et al. 2022). I did not evaluate this effect in the present study, but the protection of riparian woodland does have an effect on the maintenance of habitats, preserving the composition of assemblages.

#### 5. Conclusion

Altitude, slope and rainfall are the regional factors that explain the richness of fish species in the lower part of the upper Paraná River basin. Slope and stream connectivity explain part of the native species richness in the lower part of the basin. The composition of native fish assemblages is associated with altitude, which is a well-established relationship in fish assemblage ecology. The composition of non-native fish assemblages was influenced by connectivity of the streams. This is expected owing to the construction of the Sete Quedas reservoir and the Piracema Channel, which allowed species from the lower part of the basin to move up to higher regions. However, regional factors alone cannot sufficiently explain the distribution of species richness, and this indicates that local factors, such as stream width, water velocity and conductivity, also affect the distribution of species by acting as filters (Súarez & Petrere 2005, Silva et al. 2024, Córdova Junior et al. 2024) for the richness and composition of fish assemblages in the region.

#### 6. General Conclusion

The regional factors that best explain the species richness and composition of fish assemblages in the upper Paraná River basin are altitude, rainfall and slope. Slope is an important variable because it is correlated with waterfalls and rapids that act as filters for species richness and composition, especially in the Amambai and Iguatemi sub-basins. However, local variables, such as conductivity, current velocity and river/stream width, interact with regional factors to define species composition throughout the upper Paraná River basin. Although land use variables significantly influence the richness and composition of assemblages, anthropogenic activities can alter local characteristics (e.g., limnological and hydrological). Therefore, I concluded that local contributions to beta diversity, i.e., Local Contribution to Beta Diversity (LCBD), result in the formation of a basin with unique habitats and that regions with a lower number of species contribute positively to beta diversity. Similarly, species with a higher frequency of occurrence, i.e., Species Contribution to Beta Diversity (SCBD), also contribute to beta diversity. This evidence highlights the importance of the area of interest herein reported to the conservation of native species since the basin area encompasses entire rivers without dams, which allows the migration/reproduction of piracema species and species of commercial interest. Policies aimed at preserving riparian forests could lead to less erosion and damming of rivers and streams, further protecting habitats in the different sub-basins, making it a key region for the conservation of fish diversity in the upper Paraná River basin.

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