Under the surface: exploring the link between fish distribution and dissolved oxygen in macrophyte banks of Lake Catalão, Central Amazonia

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Abstract.

This study seeks to unravel the role of dissolved oxygen concentration on the distribution of ichthyofauna across 32 macrophyte banks in the Amazon River floodplains, a region that not only supports a rich diversity of fishes but is also subject to severe hypoxia. Dissolved oxygen concentrations across these macrophyte banks were sampled and correlated to the distribution and abundance of different fish families. The impact of low oxygen concentration on the sizes of individual fishes within these families was also evaluated. In addition, the study analysed how variations in dissolved oxygen influenced the nestedness and turnover components of beta diversity. Our findings indicated a relatively low range of dissolved oxygen concentration, between 0.0 mg/L and 2.7 mg/L, across the sampled locations. Certain fish families, such as Triportheidae, demonstrated a high prevalence in areas with lower dissolved oxygen concentrations, suggesting a morphological adaptation to hypoxic environments. A pattern of smaller fish sizes at lower dissolved oxygen levels was also observed, potentially indicating the use of macrophyte banks as resource and shelter hubs for juvenile fishes. A significant impact of dissolved oxygen variations on both the nestedness and turnover components of beta diversity was also identified, suggesting a substantial influence on ichthyofauna composition. These observations underline the critical importance of considering dissolved oxygen as a key determinant in species distribution in macrophyte banks studies, as well as its role in conserving the biodiversity of aquatic ecosystems.

Keywords: Floodplains, hypoxia, turnover, nestedness, community dynamics.

INTRODUCTION

The Amazon River basin and its floodplains are a unique and complex ecosystem that is maintained by a regular flood pulse, which reshapes channels and smaller lakes, yet indispensably, it also permeates beyond these apparent boundaries, influencing the hole ecosystem (Petry et al., 2003). The Amazon River basin and its floodplains are an intricate and unique ecosystem, regulated by the rhythm of a recurring flood pulse. This variation in the flood pulse can vary between 10 and 15 meters (Sánchez-Botero, 2001), providing a diverse range of habitats for aquatic biota (Val, 2019), including aquatic macrophyte banks that dominate the marginal areas of lakes and provide a complex and heterogeneous habitat that supports fish and aquatic invertebrate communities, and presenting high diversity in general (Sánchez-Botero et al., 2003; Ferreira et al., 2016), also directly interfering in the communities dynamics (Pinheiro et al., 2016).

These macrophytes banks play a critical role in the functioning of the Amazonian aquatic ecosystem. They are responsible for the variation of dissolved oxygen in rivers and lakes through photosynthesis and respiration processes (Almeida-Val et al., 1999), leading to severe episodes of hypoxia in Amazonian aquatic habitats (Val, 2019). As such, dissolved oxygen concentration limits the distribution of many fish species (Petry et al., 2003). These hypoxia situations lead fish species to a series of adjustments at different levels such as physiological, biochemical, behavioural, molecular and ecological responses (Almeida-Val et al., 2006).

Considering this information, the present study aims to evaluate the influence of dissolved oxygen concentration in macrophyte banks on the distribution of Lake Catalão ichthyofauna during the low water period, seeking to provide important information on the relationship between dissolved oxygen concentration and fish distribution in such habitat. We hope to provide a better understand of these mechanisms functioning and of the role that dissolved oxygen plays in shaping the distribution of fish species in macrophyte banks.

MATERIAL AND METHODS

Study area and data collection

This study was conducted in a floodplain area of Lake Catalão (03°16'S, 59°91'W), Manaus, Amazonas (Figure 1). The Lake Catalão is located in an area characterized by the presence of seasonally flooded floodplain forests during the period from December to June, presenting a regular flooding pattern with an amplitude of around 10 m. Starting in August, the water level begins to drop, a period that signals the start of macrophyte banks detaching and starting to drift. Influenced by the nearby major rivers, Solimões and Negro, these macrophyte banks move from the lake towards the river as the water starts to recede.

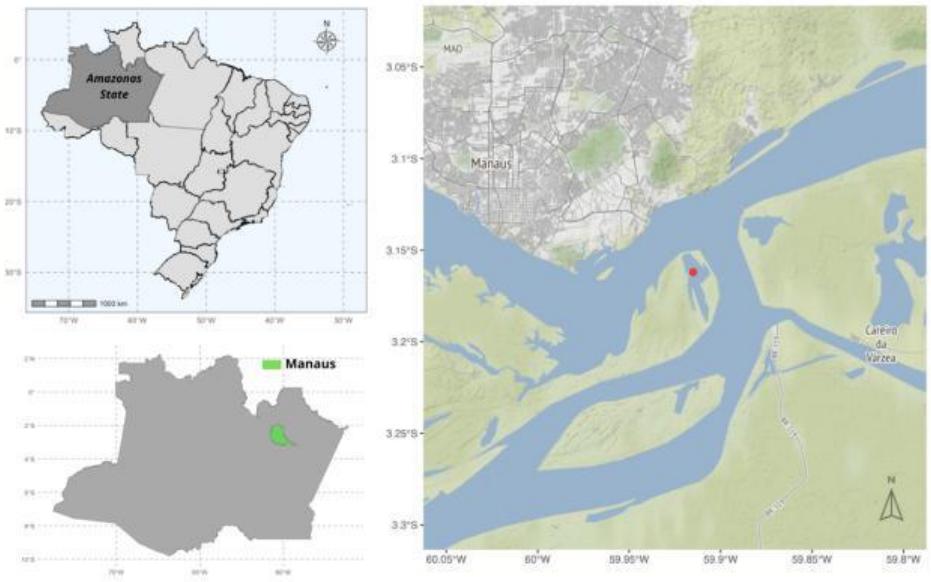


Figure 1. The Lake Catalão (red circle, 03°16'S, 59°91'W) in the Manaus county region, inside the Amazon State, Brazil.

Sampling was conducted during August 2010. Before collection of fish, dissolved oxygen concentration (mg/L) was measured with an oximeter at a depth of 1 m within the bank. To collect the fish associated with macrophyte banks, we used a seine net or throw net with 6 m x 3.5 m (6 mm mesh between knots). Macrophyte banks of similar size with predominance of *Paspalum repens* were chosen to minimize the effect of bank macrophyte species on the fish community. Eight banks were sampled twice a day (morning between 6:00 am and 8:00 am and afternoon between 4:00 pm and 6:00 pm) on four days (total 32 seine nets). The macrophyte banks were encircled and all vegetation was removed to bring the net to the boat and collect the fish. In the field, the fish were fixed in 10% formalin. All collected individuals were identified to the lowest possible taxonomic level possible, measured the standard length (cm) and weighted (g).

Statistical analysis

The relative frequency and abundance of fish orders were quantified, and the density and abundance of fish families were investigated in function of the dissolved oxygen variation. At the species level, the abundance of each species was also assessed under the dissolved oxygen variation. The Shannon diversity index was calculated and a Generalized Linear Model (GLM) utilizing a Gamma distribution was employed to ascertain the influence of variation in dissolved oxygen on the diversity index. To better understand if there is a strong action of species exchange along the dissolved oxygen variation, or if there is an increase of species added to a subset along the oxygen conditions, the compositional changes along the variation were evaluated by measuring the turnover and nestedness components relative contribution to total beta diversity (Legendre, 2014). The relative contributions of each component to beta diversity were assessed at the

community level using the Sørensen's similarity index. To perform this analysis, R packages *vegan* (Oksanen et al., 2013) and *betapart* (Baselga et al., 2012) were utilized. Subsequently, beta regression models were employed to examine the influence of the differences in dissolved oxygen between samples on the nestedness and turnover component contributions. To determine if fish size changed along the dissolved oxygen variation by family, simple linear regressions were performed.

RESULTS

Across the 32 sampled macrophyte banks, the dissolved oxygen concentration exhibited a variation ranging from 0.0 mg/L to 2.7 mg/L, with an average value of 1.1 mg/L and standard deviation of 0.78 mg/L. A total of 2,588 individuals belonging to six orders, 19 families and 67 species were collected and identified. Characiformes exhibited an abundance of 1597 individuals, while Cichliformes had 899, Gymnotiformes had 52, Synbranchiformes had five, and Tetraodontiformes had one individual. Therefore, this single Tetraodontiformes individual of the species *Colomesus asellus* (Müller & Troschel, 1849) was excluded from analysis at family and order level. The most abundant species were *Mesonauta festivus* (Heckel, 1840) (736 individuals) and *Hemigrammus melanochromis* Fowler, 1913 (365 individuals). The orders of Characiformes and Cichliformes were the most prevalent found across all oxygen concentrations (Figure 2), also showing a high abundance along the variation (Figure 3). Conversely, Gymnotiformes, Siluriformes, Synbranchiformes were infrequently distributed across nearly all dissolved oxygen concentrations in the macrophyte banks

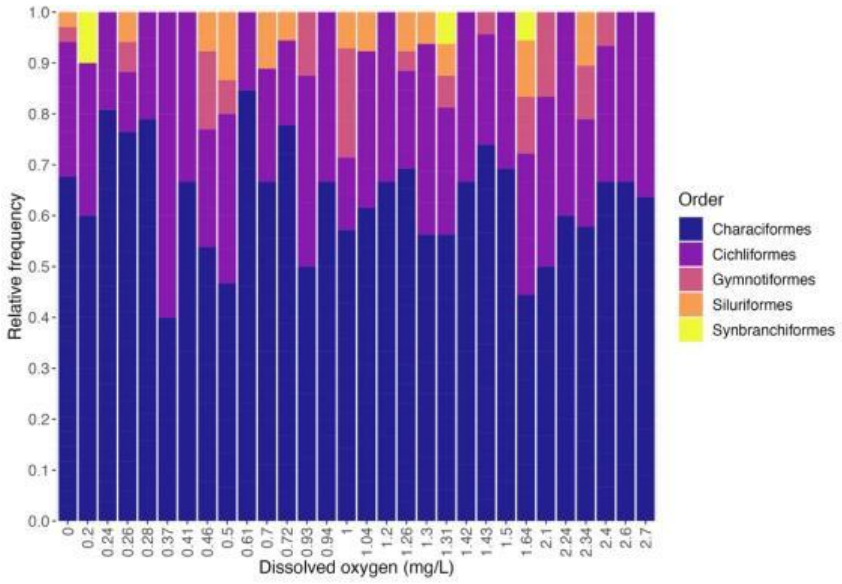


Figure 2. Relative frequency of the fish orders sampled in Lake Catalão (Manaus-AM, Brazil) macrophyte banks by the dissolved oxygen (mg/L) variation.

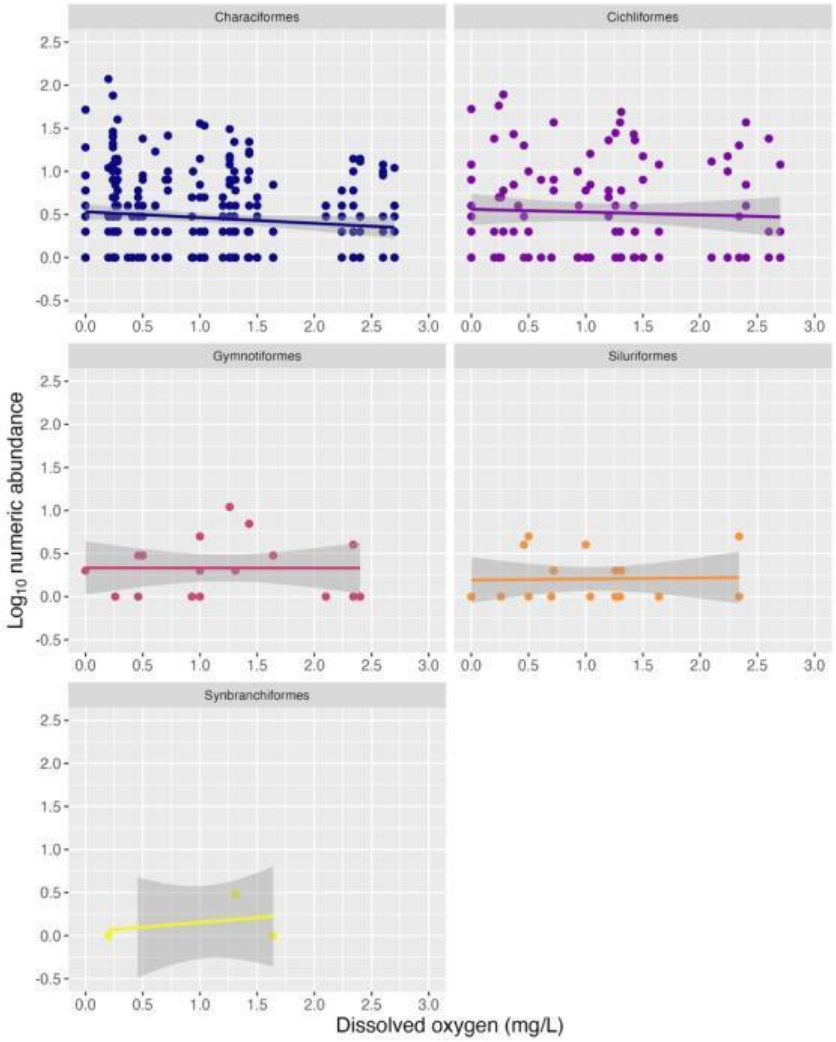


Figure 3. Numeric abundance each of the fish orders sampled in Lake Catalão (Manaus-AM, Brazil) macrophyte banks by dissolved oxygen (mg/L) variation. The line shows the adjusted trend of each order abundance along the variation, and the gray area around the line is representative of the confidence interval.

The total and median density of each family were compared along the dissolved oxygen variation, with Acestrorhynchidae, Triportheidae, and Rhamphichthyidae occurring only in extreme concentrations of dissolved oxygen, less than 1 mg/L (Figure 4A). Of these families, only Triportheidae had high values of abundance. Meanwhile, most families occurred with densities more evenly distributed along the dissolved oxygen variation (Figure 4B). The abundance along the dissolved oxygen variation was also visualized by species, with *Triportheus angulatus* (Spix & Agassiz, 1829), *Triportheus albus* Cope, 1872, *Trachelyopterus porosus* (Eigenmann & Eigenmann, 1888), *Mylossoma duriventre* (Cuvier, 1818), and *Serrapinnus* sp. prevailing in concentrations less than 1.5 mg/L (Figure 5).

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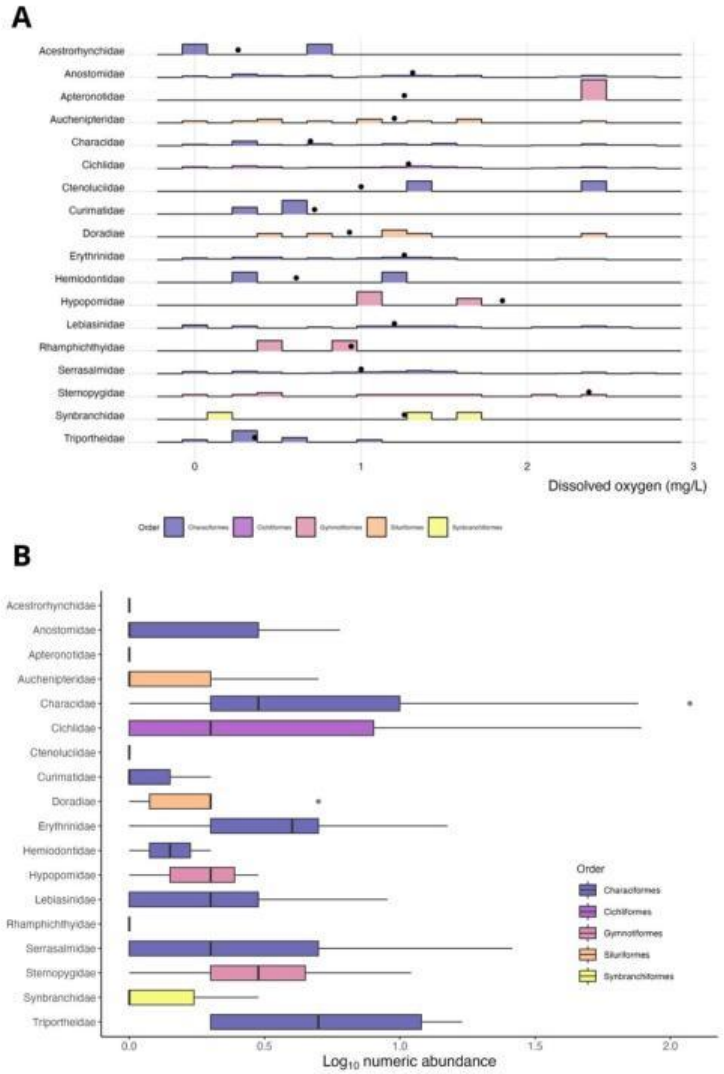


Figure 4. A) Density of the fish families sampled in Lake Catalão (Manaus-AM, Brazil) macrophyte banks and coloured by order explored by the dissolved oxygen (mg/L) variation. The black circle represents the median dissolved oxygen concentration of occurrence for each family. B) Abundance boxplot of the fish families sampled in Lake Catalão (Manaus-AM, Brazil) macrophyte banks and coloured by order explored by the dissolved oxygen (mg/L) variation.



Figure 5. Abundance of each fish sampled in Lake Catalão (Manaus-AM, Brazil) macrophyte banks and coloured by order explored by the dissolved oxygen (mg/L) variation.

The Shannon diversity index ranged from 0.97 to 2.57, and while there was no significant influence of dissolved oxygen on Shannon diversity

(GLM: t = 0.54, p = 0.58), a significant influence of dissolved oxygen difference on the nestedness component of beta diversity (β = 0.391, p < 0.01) and the turnover component of beta diversity (β = -0.177, p < 0.01) was observed. As the difference in dissolved oxygen between macrophyte banks increased, the nested component decreased (Figure 6A). Regarding the turnover component, banks with greater differences in dissolved oxygen between them showed a greater replacement of species (Figure 6B).

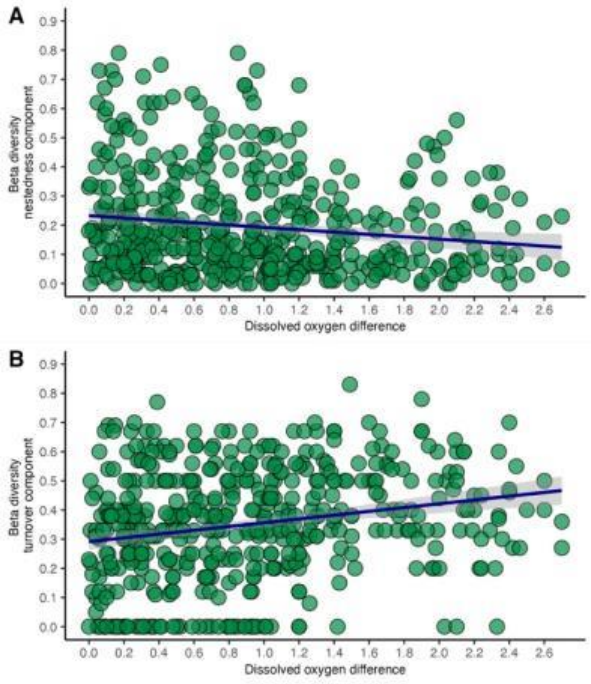


Figure 6. Beta diversity nestedness (A) and turnover (B) components by a dissolved oxygen (mg/L) variation difference of the fish sampled in Lake Catalão (Manaus-AM, Brazil) macrophyte banks. The blue line shows the model fit to the relationship between the variables and the gray area around the line represents the confidence interval.

The standard length of the measured fish ranged from 0.7 cm to 35.5 cm, with the average length and following standard deviation (SD) of Characiformes being 3.01 cm (SD = 2.34 cm), for Cichliformes 3.97 cm (SD = 1.81 cm), for Gymnotiformes 5.4 cm (SD = 5.05 cm), Siluriformes 6.57 cm (SD = 3.09 cm) and for Synbranchiformes 18.80 cm (SD = 3.74 cm). The standard length was compared by fish family along the dissolved oxygen variation, with some families significantly showing smaller individuals at lower oxygen concentrations and larger individuals at higher oxygen concentrations (Figure 7), although significant they presented a low R^2 value, such as Anostomidae ($t_{2,63}$ = 3.42, p < 0.01, R^2 = 0.14, β = 1.75), Apteronotidae ($t_{2,38}$ = 2.72, p < 0.01, R^2 = 0.14, β = 1.11), Triportheidae ($t_{2,61}$ = 3.422, p < 0.01, R^2 = 0.19, β = 2.57)

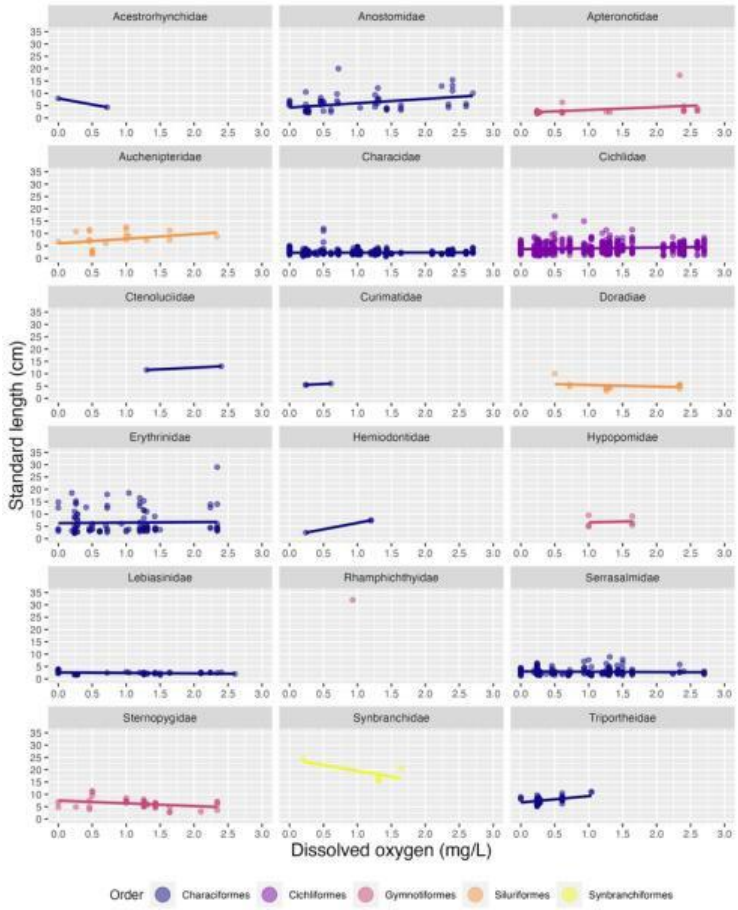


Figure 7. Standard length (cm) of 18 fish families sampled in Lake Catalão (Manaus-AM, Brazil) macrophyte banks along the dissolved oxygen (mg/L) variation. The line shows the adjusted trend of each order standard length.

DISCUSSION

The dissolved oxygen concentrations observed in this study were relatively low, with a range of 0.0 mg/L to 2.7 mg/L, presenting slightly lower values than that described for August between 2010 and 2014 by Röpke et al. (2015) in the same lake. This difference in dissolved oxygen concentration levels may be associated with the fact that our measurements were recorded only at a depth of 1 meter. Although the fish fauna of Lake Catalão is well described by Röpke et al. (2015) and Röpke et al. (2017), with more species than found, the focus on the ichthyofauna associated with macrophyte banks and their association with the dissolved oxygen variation, as well as the change in sizes along this variation, had not yet been given.

Furthermore, the findings on the relationship between dissolved oxygen concentration and the abundance of fish families is also noteworthy. The fact that certain families, such as Acestrorhynchidae, Triportheidae, and Rhamphichthyidae, occurred only in extreme lower concentrations of dissolved oxygen (less than 1 mg/L), which could imply that different tolerance levels to dissolved oxygen and an affect in their distribution. The Triportheidae, the most abundant of the

families in relation to low levels of dissolved oxygen, which studies have found a high abundance in Amazonian macrophyte banks (Soares et al., 2014; Oliveira et al., 2020), has as a morphological characteristic the development of the lower lips, with the genus *Triportheus* presenting the development of barbels in the anterior portion of the lower lip (Neto et al., 2020), a condition that is related to the expansion capacity of the these lips, supporting to efficiently capture the oxygen from the surface layer of the water column when exposed to low concentrations of oxygen (Val, 2019), being represented here by *T. angulatus*, and *T. albus*. Meanwhile, the Acestrorhynchidae and Rhamphichthyidae showed low abundance and variability, which makes it difficult to ensure a pattern for the individuals of these families.

There was also no significant influence of dissolved oxygen on Shannon diversity, which can be explained by the fact that fish species in the Amazon have high tolerance to low concentrations of dissolved oxygen, which is the result of a variety of morphological, physiological and behavioural adaptations to survive hypoxic conditions (Almeida-Val & Val, 1995; Val, 2019), allowing species richness and abundance to be similar along the dissolved oxygen variation, since a good part of the species can move between it. However, we observed a significant influence of dissolved oxygen difference on the nestedness component of beta diversity, meaning that banks with similar oxygen values tend to form smaller groups of species that are subsets of other sampled banks, and on the turnover component of beta diversity, meaning that there is a significant gradual change in the ichthyofaunal composition between extremes of the dissolved oxygen variation. This finding highlights the importance of considering both nestedness and turnover when assessing beta diversity in aquatic ecosystems, and how their function in a dissolved oxygen variation.

The standard length of the fish also varied according to dissolved oxygen concentration, with some families showing shorter individuals at lower oxygen concentrations and larger individuals at higher oxygen concentrations. Although, in the regression considering the standard length, R^2 values were considerably low, that is, the standard length variation was poorly explained by the dissolved oxygen variation, probably because of the lack of other variables that would help to provide a more complete explanation, but there was still a significant relationship, suggesting that dissolved oxygen may have an impact on the size of fish species, especially the ones from Anostomidae, Apteronotidae and Triphortheidae families, with Anostomidae juveniles being highly abundant in macrophyte banks in previous studies (Oliveira et al., 2020). That might be related to a compensation of negative effects of low oxygen dissolved in these banks by the availability of various food items (Santos et al., 2009) and refuge for smaller individuals (Killgore & Hoover, 2001), with these banks commonly acting as nursey areas for these small fishes (Zacardi et al., 2017), not uncommonly being record a great proportion of juveniles in distinct bank conditions from the Amazon floodplain lakes (Pinheiro et al., 2016). Corroborating with Anjos et al. (2008), who demonstrated in the Amazon River floodpain, that environments with low oxygen values act as a refuge against piscivores.

Overall, this study provides a comprehensive understanding of the ichthyofauna of *Paspalum repens* predominant macrophyte banks and how it is affected by dissolved oxygen concentration, especially with these habitats providing shelter and food resources for juveniles, while some families mainly occur in low concentrations due their adaptations. It highlights the importance of considering different approaches to measure composition changes in the community, such as beta diversity turnover and nestedness components, but also how distinct variations of dissolved oxygen and their different fauna should be considered in the management and conservation of aquatic ecosystems. However, it is important to point out that the ichthyofauna sampled here probably reflects the composition of the fish fauna of Lake Catalão, not just the macrophyte banks present there, and does not necessarily reflect the fish fauna of other macrophyte banks in Central Amazonia, as sampling was carried out in only one lake, considering banks with only *P. repens* as predominant, regardless of the bank size factor. In addition, a future comparison of the sampleable lake fauna outside the macrophyte banks and associated with them, at different times of the year, is necessary, since we were only able to sample in August 2010, reflecting just one period, and the lake suffers influence of two large rivers, which seasonally change this fish composition, as demonstrated by Röpke et al. (2015, 2017), and should be taken into account.

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