



ISOLATION AND LAGOON MORPHOMETRY DEFINE FISH DIVERSITY AND COMPOSITION IN NEARSHORE AREAS OF FLOODPLAIN LAGOONS OF THE SOUTHERN PANTANAL

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Abstract: Floodplain lagoons support high fish diversity, but the role of local *vs.* regional factors in structuring assemblages is little studied in the Brazilian Pantanal. Aiming to understand the importance of limnological, biological, and regional characteristics shaping fish assemblages in the Pantanal floodplain, we sampled 26 lagoons in the Rio Negro floodplain from September 2005 through November 2006. Our results suggest that widely distributed species are also more abundant locally. Fish species richness is defined by a combination of isolation level, area and mean depth of lagoons, while evenness is determined mainly by macrophyte richness, lagoon area, water conductivity and distance to the river. Distribution of the most abundant fish species in sampled lagoons was explained by macrophyte biomass, lagoon area, shoreline development index and macrophyte richness. Overall, a general pattern of species diversity and distribution was primarily defined by a regional characteristic, namely, isolation, interacting with lagoon morphometry, and secondarily by biotic characteristics.

Keywords: connectivity; dispersal capacity; regional factors; species composition; species distribution.

INTRODUCTION

The field of community ecology involves the search for consistent patterns of local *vs.* regional determinants of community organization across different environmental gradients (Leibold *et al.* 2004). For floodplain regions, variation in water level is a major determinant of biological species traits (Junk *et al.* 1989, Thomaz *et al.* 2007), species biological cycle and the dynamics of dispersal and habitat occupation, which, in turn, define spatial variation in diversity. During flood periods, some

studies have suggested that similarities in physical and biological features increase, causing the homogenization of aquatic communities (Thomaz *et al.* 2007). Thus, connectivity determines many habitat features and alters the accessibility of different aquatic habitat patches (Granado-Lorencio *et al.* 2005, Lasne *et al.* 2007). Different parts of a floodplain region within a gradient of connectivity can support species with different dispersal abilities and life history traits.

The Brazilian Pantanal is located at the center of South America, and with approximately 138,000

km², it is the largest floodplain area in the world (Silva & Abdon 1998). Flood pulse is the main determinant of ecological processes (Alho 2008), defining species diversity and life cycles for plants and animals. However, studies of aquatic communities in the Pantanal are still scarce and focus on temporospatial variation in fish communities in lagoons of the Rio Negro floodplain (Súarez *et al.* 2001, 2004), Cuiabá and Paraguay Rivers (Baginski *et al.* 2007, Baleroni & Silva 2009, Silva *et al.* 2010).

Given the greater area of the Pantanal, different subregions have different pedological, hydrological and biological characteristics. For example, the Nhecolândia Pantanal is a subregion with many floodplain lagoons classified according isolation level. Thus, lagoons frequently connected to rivers are called “baías”, while those connected only in times of exceptional flooding, or not at all, are called “salinas” and present higher pH and water conductivity in response to carbonate accumulation. Then, isolation associated with chemical characteristics acts as a filter to species occupation and survival in these lagoons (Mourão *et al.* 1988). Specifically, in “baías”, connectivity, depth and macrophyte cover can determine fish diversity and composition (Súarez *et al.* 2001, 2004).

We herein test the hypothesis that diversity and species composition in lagoon fish assemblages of the Pantanal are structured mainly in response to a combination of local and regional characteristics. If our hypothesis is true, a number of conclusions can be drawn. First, species with wide occupation will also be those with higher local abundance in sampled lagoons. According to our hypothesis, the sampled species will have different degrees of adaptation to this seasonally fluctuating environment and such adaptations can ultimately determine occupation and abundance in this environment. Second, species richness will be positively associated with lagoon area, depth and macrophyte abundance and richness. Our overall hypothesis assumes a species-area pattern that includes species-volume of the lagoon and habitat diversity and heterogeneity provided by macrophyte cover. Finally, we expect occurrence and abundance to be driven by a combination of local and regional biotic and abiotic characteristics. Consequently, isolated and small lagoons should have a different species composition from that of

frequently connected lagoons by virtue of different dispersion ability of fishes and different tolerance to environmental stressors.

MATERIAL AND METHODS

Study area

The headwaters of the Negro River are located in the Maracaju and Negro Hills, stretching approximately 530 km. This middle and lower wetland portion acts as a boundary of the Nhecolândia Pantanal, which is located between the Negro and Taquari Rivers. This region is characterized by many floodplain lagoons, nearly 17,600 (Oliveira *et al.* 2016). These lagoons vary in size, connectivity level and limnological characteristics and are divided into “baías” that are annually connected to the river and “salinas” that are disconnected lagoons with stressful limnological conditions by the higher pH and water conductivity. Most “salinas” have no fish species that respond to isolation and limnological characteristics (Mourão *et al.* 1988).

Rainy periods and corresponding higher water levels occur from October to March with drier periods that peak in August (Vicentin *et al.* 2013). This rise in water levels connects lagoons, otherwise isolated from one another, and leads fish to disperse from river to floodplain and between floodplain lagoons.

Sampling

We took ten subsamples from 26 lagoons in the Rio Negro floodplain, *i.e.*, Nhecolândia subregion of the Pantanal, but without resamples in the same lagoon, in September 2005, and four quarterly samples from February 2006 through November 2006 (Figure 1). The lagoon areas ranged from 2.53 to 24.14 ha, and the distance to the river ranged from 0.46 to 14.89 km. Seasonal variation in water level determines the length of the period of connection among the lagoons and with the river, such that longer periods of flooding will, in turn, increase connection time.

The fishes were caught using two types of traps. The throw trap (see Jordan *et al.* 1997) consisted of a square iron frame with the lateral portion covered by mosquito screening of approximately 1.5 mm mesh size. The fish sampling procedure required us to throw a trap over a selected site and quickly place it in the water, pressing it to the bottom. The

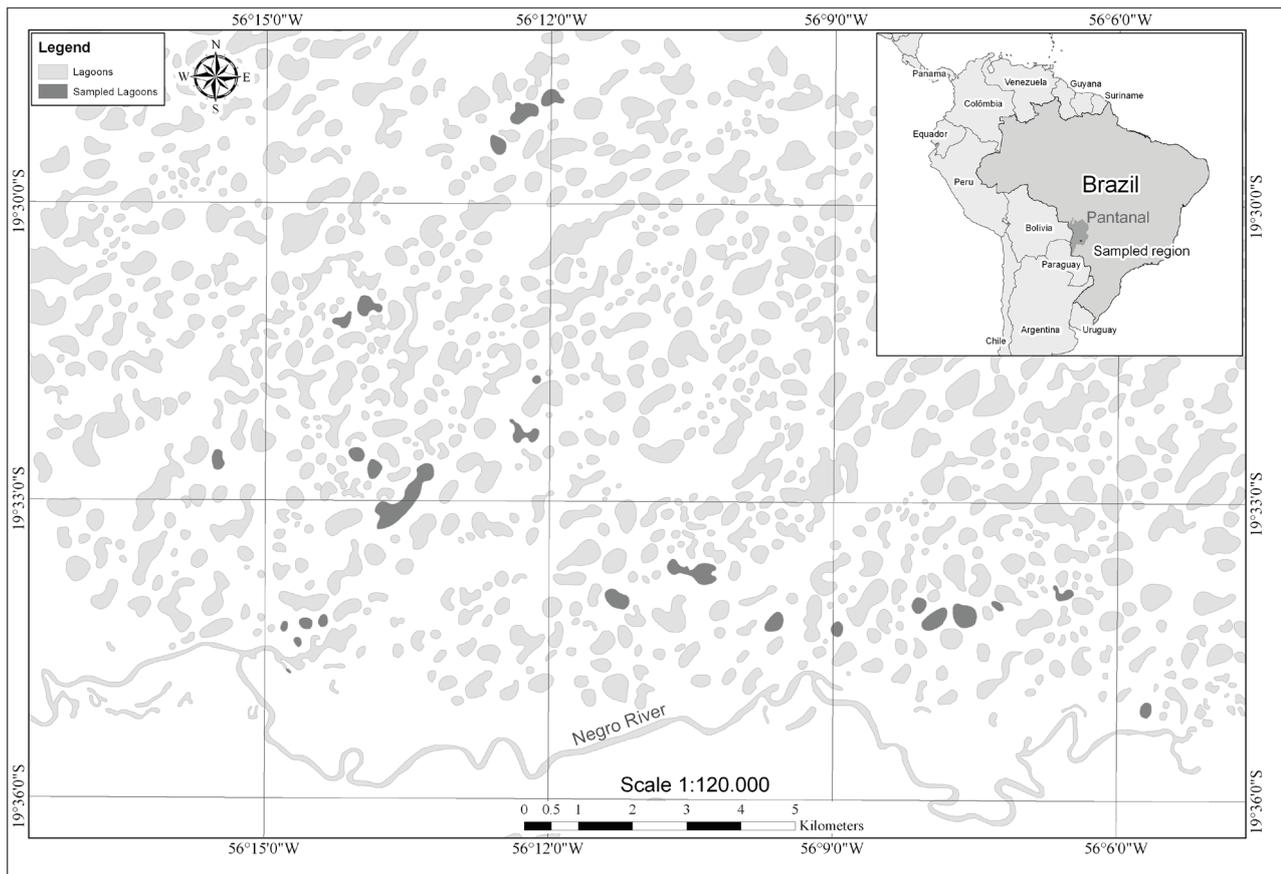


Figure 1. Rio Negro Floodplain in Southern Pantanal, Brazil, showing the 26 sampled lagoons.

second type, the emergent trap, also had a 1 m² iron frame with the bottom and sides of the trap covered with 2 mm mesh mosquito screening. This trap was maneuvered beneath the vegetation in a collapsed state with the side walls folded under the upper frame. Next, the upper frame was lifted quickly above the surface, trapping the fish in the box thus formed. This procedure allowed sampling in sites more than 1 m deep when it was not possible to use the throw trap. In each lagoon, a total of ten 1 m² samples were obtained, and the number of samples taken with each throw, or emergent, trap was determined by depth and macrophyte cover. At sites with small, sparse macrophytes under 1 m in depth, we used a throw trap. At sites with deeper water (over 1 m) and greater density of macrophytes, we used the emergent trap.

The fishes were censused inside the throw trap, using sieves of different sizes and 2 mm mesh size. The sieves were used until five consecutive throws caught no fish, indicating that all the fish in the trap had been sampled.

In the field, specimens were anesthetized with clove oil and posteriorly fixed in 10% formalin,

followed by preservation in 70% ethanol realized in the laboratory. Also, specimens were identified and counted in the laboratory. Identification followed Britski *et al.* (2007) and specialized references for each group. Voucher specimens were deposited in the fish collection of Laboratório de Ecologia, Centro de Estudos em Recursos Naturais (CERNA), in Universidade Estadual de Mato Grosso do Sul.

All aquatic macrophytes in the traps were identified according to Pott & Pott (2000) and weighed. Macrophyte species richness and biomass were included as biological descriptors of each sample. We also measured several limnological characteristics within the trap area, including pH, electrical conductivity, dissolved oxygen and water temperature, using a YSI Model 556 field multi-probe. Turbidity was measured using a portable turbidimeter (HACH) and depth using a graduated wooden stick.

For each lagoon, we obtained the geographical coordinates using GPS (Garmin Etrex). Using Pantanal mosaic software (Padovani *et al.* 2003), we measured the distance from the lagoon to the river, attempting to establish the route of the water

from the river to each lagoon during the flood period. The lagoon area and its perimeter were also obtained using the Pantanal mosaic, according to the following equation: $SDI = (LP/2) * (\text{square root}(\pi * LA))$, where SDI is the shoreline development index, LP is lagoon perimeter, and LA is lagoon area.

Data analysis

The bootstrap procedure was used to estimate total species richness for the littoral zone of the sampled lagoons, as well as the confidence interval ($\alpha = 0.05$), using presence/absence data for all samples. This procedure was selected for its robustness (Hellmann & Fowler 1999). This estimate was carried out using the “specpool” command in the “vegan” package (Oksanen *et al.* 2018).

To evaluate if more abundant species were also widely distributed (the occupancy-abundance relationship of Gaston *et al.* (2000)), we used a Pearson correlation of total species abundance (ln) and proportion of lagoon occupancy by each species.

To determine the effect of spatial connectivity on species distribution, we generated a principal coordinate analysis of neighbor matrices (PCNM), using distance among sampled lagoons. The first two axes of PCNM were used to represent the spatial connectivity among lagoons. We used the “pcnm” command of the “spdep” package in order to perform this analysis (Bivand *et al.* 2013, Bivand & Piras 2015).

Lagoon area, distance to the river, mean depth and SDI were all used as morphometric measures of each lagoon to generate a principal coordinate analysis (PCoA) estimated with Euclidean distance after standardization of variables. The first two axes of this PCoA represented the morphometric relationships among lagoons.

Macrophyte richness, macrophyte mean biomass, pH, electrical conductivity, oxygen concentration and water turbidity were all used as limnological characteristics in another PCoA, also using Euclidean distance after standardization of variables. The first two axes were used to summarize the limnological relationship among lagoons. To evaluate the role of space (PCNM axis), lagoon morphometry and limnology on species distribution using all species, or only the main species (with more than 1% of total abundance), we used a variance partitioning (Peres-Neto *et al.* 2006)

with the “varpart” command in the vegan package.

Stepwise linear regression was used to evaluate the role of lagoon characteristics in defining (total) species richness and (mean) evenness, as diversity descriptors of lagoons. We used “lm” and, later, “step” commands in the R package (R Core Team 2018). The relationships between response and explanatory variable were shown using the “visreg” package (Breheny & Burchett 2017).

A gradient in assemblage and the importance of environmental descriptors were verified using a Canonical Correspondence Analysis (CCA). Species with at least 1% of total species abundance were included in this analysis, and all environmental variables were included. This analysis was carried out using a total abundance in the entire lagoon (10 subsamples) in the R environment (R Core Team 2018). The significance of environmental variables was assessed by the “envfit” function in the “vegan” package (Oksanen *et al.* 2018) with 999 permutations.

RESULTS

Overall, we found 8470 individuals belonging to 54 fish species. *Serrapinnus kriegi* (Schindler 1937) presented 1962 individuals (23.2% of total caught) and *Serrapinnus calliurus* (Boulenger 1900) presented 1744 individuals (20.6% of total caught) as the most abundant species. The five most abundant species (*S. kriegi*, *S. calliurus*, *Moenkhausia dichroua*, *Pamphorichthys hasemani* and *Apistogramma borellii*) added up to 68.13% of total individuals. The more abundant species were also those more widely distributed in sampled lagoons (Pearson $r = 0.90$, $p < 0.001$), suggesting a congruence between occupancy and abundance in these fish assemblages (Figure 2).

Species richness varied from 3 to 26 fish species per lagoon with estimated total species richness (all lagoons), using the bootstrap procedure, of 60 species with a confidence interval from 53 to 68 species, suggesting that approximately 89.3% of estimated species richness had been sampled (Figure 3).

Results of linear regression suggest that lagoon species richness in the littoral zone of floodplain lagoons in the Rio Negro floodplain is mainly described by lagoon area, distance to the river and mean depth, explaining 48% of data variation

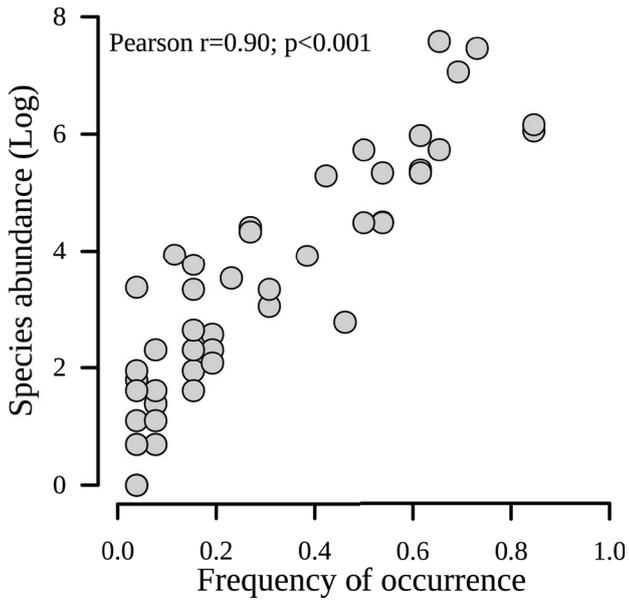


Figure 2. Correlation between species abundance and frequency of occurrence for fish assemblages in sampled lagoons in a floodplain area of the Negro River, Brazilian Pantanal.

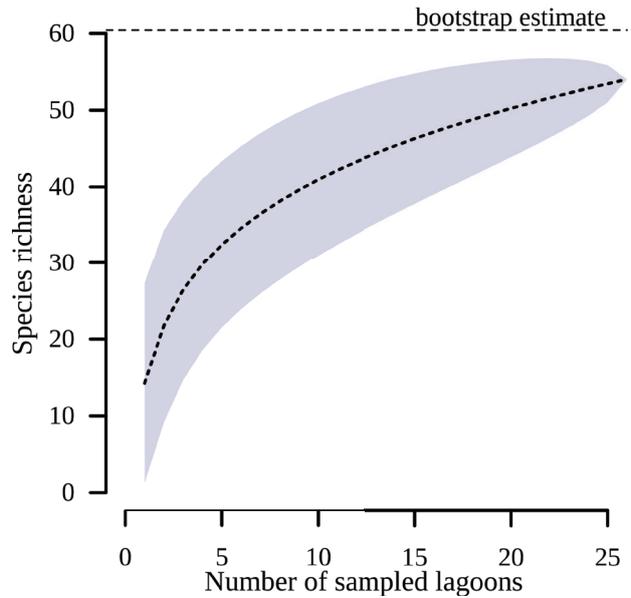


Figure 3. Species accumulation curve for fish assemblages in lagoons in a floodplain area of the Negro River, Brazilian Pantanal. Confidence interval is shown in grey.

(adjusted $r = 0.48$; $F = 5.61$; $p = 0.002$). The model indicated that larger lagoons were located closer to the river and had higher mean depth with greater species richness (Figure 4).

The mean evenness in the lagoons was mainly regulated by the positive influence of macrophyte richness and lagoon area, as well as water conductivity and distance to the river, leading to a decrease in mean evenness. Overall, these variables explain 52% of variation in species evenness (adjusted $r = 0.52$, $F = 6.39$; $p = 0.001$) (Figure 5).

Species distribution in abundance evaluated using variance partitioning is better explained by limnological characteristics (20%) and lagoon

morphometrics (6%) with less interaction between spatial and limnological characteristics (4%). For species occurrence, we also observed that limnological characteristics are the main determinants of assemblage characteristics (13%), followed by lagoon morphometry (4%) and the interaction between spatial position and limnological characteristics (3%). These conclusions are the same, whether for all species, or only main species, and also robust to the use of abundance or occurrence data (Figure 6).

Analyzing the distribution of the most abundant fish species in sampled lagoons by CCA, we explained 60.1% of the data set with lagoon area, macrophyte

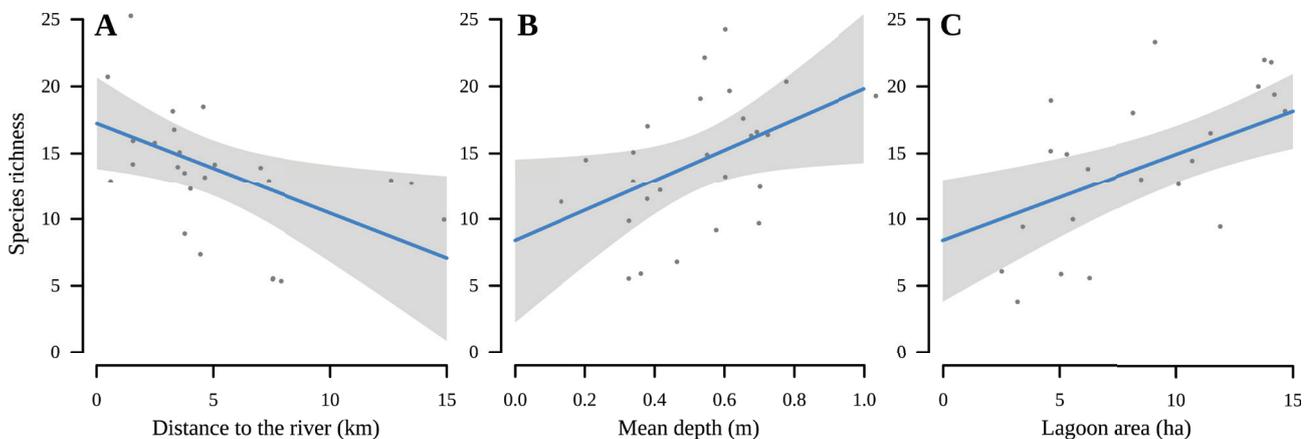


Figure 4. Effect of distance to the river (A), mean depth (B) and lagoon area (C) on lagoon species richness of fish assemblages in a floodplain area of the Negro River, Brazilian Pantanal.

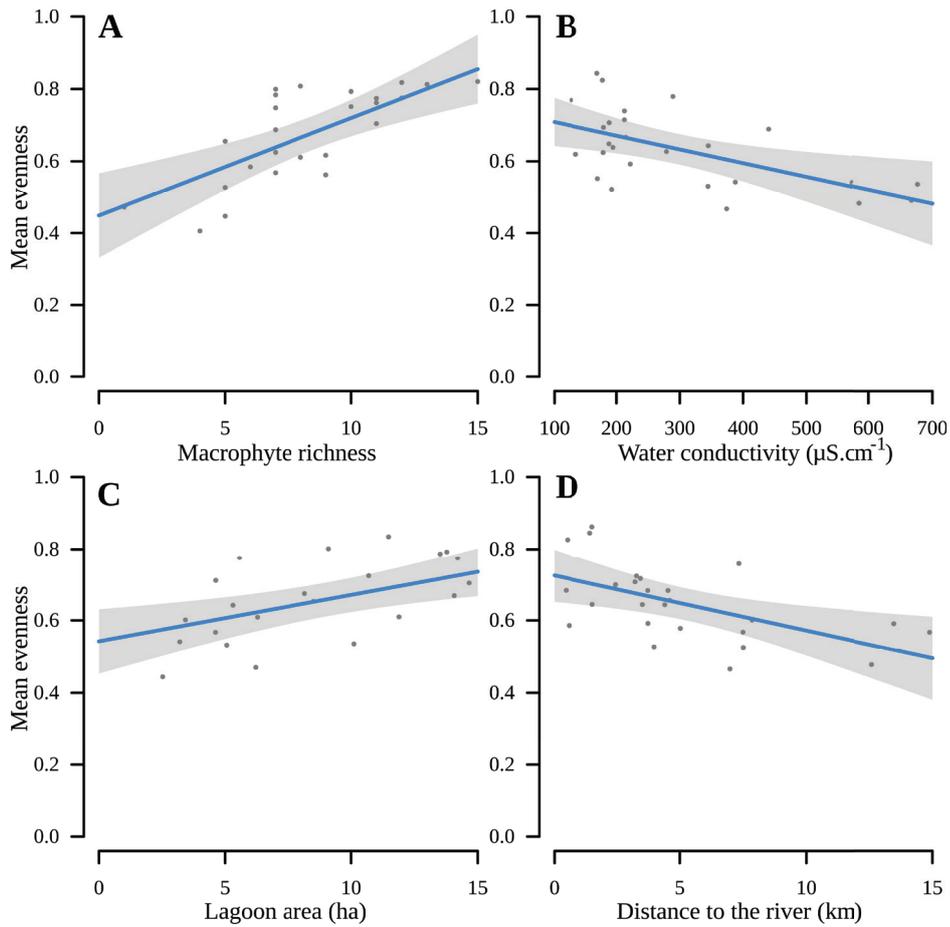


Figure 5. Effect of macrophyte richness (A), water conductivity (B), lagoon area (C) and distance to the river (D) on mean evenness of fish assemblages in a floodplain area of the Negro River, Brazilian Pantanal.

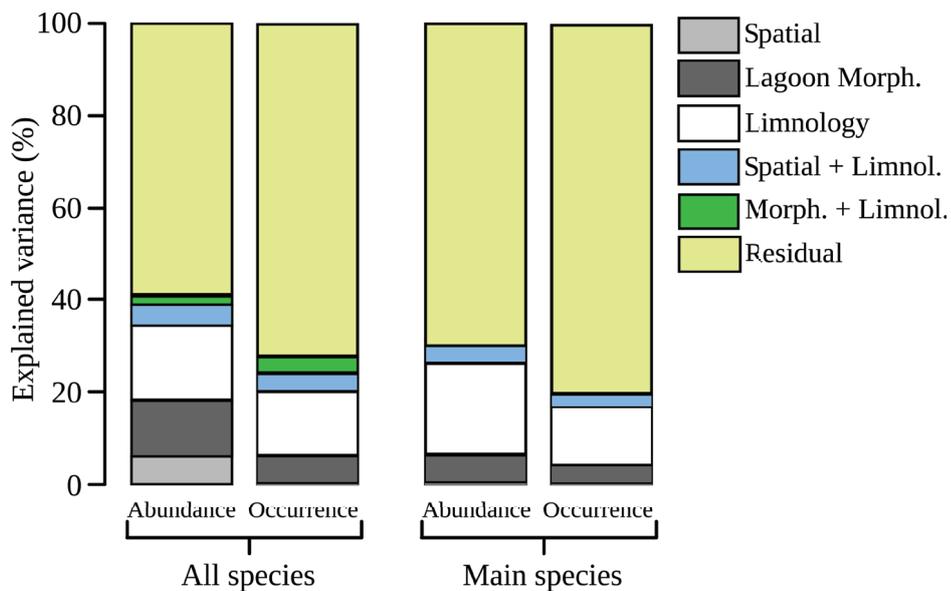


Figure 6. Variance partitioning of fish assemblages and spatial, morphometric and limnological characteristics of fish assemblages in a floodplain area of the Negro River, Brazilian Pantanal.

abundance, macrophyte richness and SDI, as the key explanatory variables (Table 1). The interaction of these variables explains the differences among assemblages dominated by *Aphyocharax rathbuni*, *Moekhausia dichrourea* and *Aphyocharax anisitsi* in lagoons with larger area, low macrophyte abundance and longer shoreline length and assemblages dominated by *Apistogramma borellii*, *A. trifasciata*

and *Melanorivulus punctatus*, mostly occurring in lagoons with higher macrophyte abundance. Lagoons with higher macrophyte richness were dominated by *Pyrrhulina australis*, *Pamphorichthys hasemani* and *Aequidens plagiozonatus* (Figure 7). On the other hand, *Serrapinnus calliurus* and *Hyphessobrycon eques*, among others, were widely distributed in sampled lagoons.

Table 1. Canonical Correspondence Analysis for main fish species abundance and environmental descriptors in lagoons of the Negro Floodplain, southern Pantanal, Brazil. ns = non significant; * = significant at $\alpha = 0.05$; ** = significant at $\alpha = 0.01$.

Environmental descriptors	Axis 1	Axis 2	r ²
Macrophyte richness	-0.85	-0.53	0.23*
Macrophyte biomass	-0.58	0.81	0.47**
pH	0.41	-0.91	0.17 ns
Conductivity	-0.37	-0.93	0.06 NS
Dissolved oxygen	0.77	-0.63	0.06 NS
Water Temperature	-0.63	-0.78	0.07 ns
Depth	0.75	0.67	0.12 ns
Lagoon area	0.98	-0.21	0.33 **
Shoreline length	0.94	-0.35	0.24 *
River distance	-0.08	-0.99	0.16 ns
Water turbidity	0.55	0.84	0.06 ns
Explained variation (%)	36.9%	23.2%	

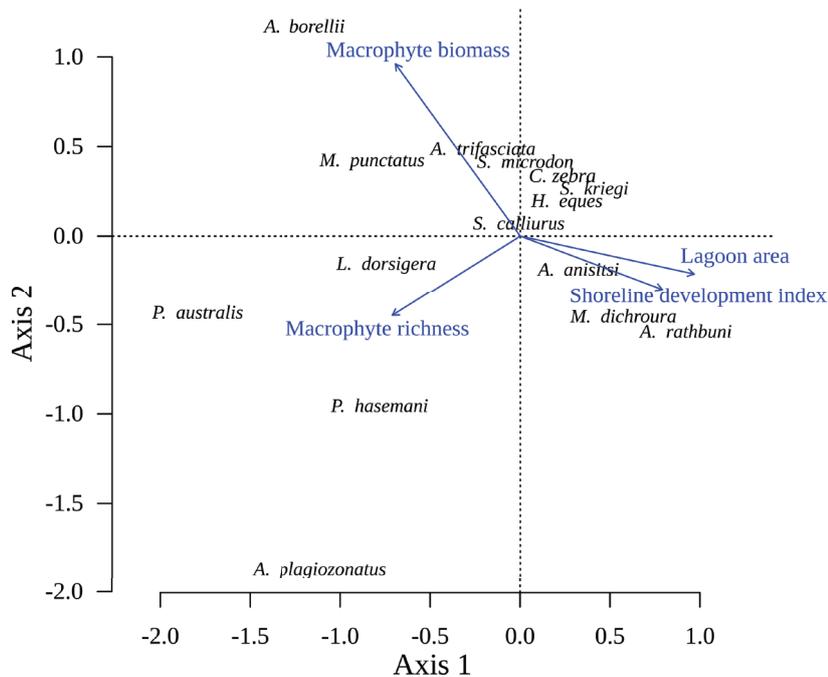


Figure 7. Canonical Correspondence Analysis showing the distribution of fish species assemblage along environmental gradients in a floodplain area of the Negro River, Brazilian Pantanal.

DISCUSSION

Our results show a consistently positive relationship between fish occupancy and abundance in the shallow lagoons of the Rio Negro, Brazilian Pantanal. Fish species richness is higher in the larger, deeper and less isolated lagoons, while evenness is higher in larger and less isolated lagoons with lower conductivity (*i.e.*, less productivity) and with higher macrophyte richness. Surprisingly, species distribution, which is affected by macrophyte biomass and richness, as well as lagoon morphometry, is not affected by spatial variables.

Total species richness

With regard to total fish species richness in floodplain lagoons, Suárez *et al.* (2001) found 51 fish species in 19 lagoons with a total species richness of 64, as estimated by the jackknife procedure. In our study, 26 lagoons were sampled in a part of the Negro River floodplain farther upriver than the study of Suárez *et al.* (2001), and despite the differences in sampling methods, a similar richness was observed (54 species) and estimated (60 species), albeit by using the bootstrap procedure. Species richness by lagoon was also similar to that found by Suárez *et al.* (2004) who registered species richness varying from 7 to 26 fish species, while our study found 3 to 26 fish species.

From a total of 45 lagoons sampled in the Negro River floodplain in these two studies, a total of 72 species were identified, suggesting that these lagoons have, in a regional context, a low beta diversity since few new species were added to the total species list with increased sample size. Consequently, it seems that patches of species in different regions of sampled lagoons did not exist. This corroborates the suggestion of Suárez *et al.* (2001) that only a few lagoons contain most of the fish diversity in this region.

A few studies have focused on the predominance of rare species in assemblages. Magurran & Henderson (2003) proposed that rare species are those not completing their life cycle in this environment, frequently migrating among habitats in search of conditions more conducive to their development. Although this hypothesis could explain species abundance in some assemblages, it is doubtful that it could be applied to floodplain

Pantanal lagoons. In different studies about fish assemblages in floodplain lentic habitats, Cheirodontinae usually predominates (Suarez *et al.* 2001, Suarez *et al.* 2013). This suggests that these fish species can present ecological traits allowing them to adapt to resource availability and unique environmental characteristics, such as fluctuations in river level or stressful limnological conditions. Nonetheless, the stochastic effect of flood pulse in connection with period among lagoons needs to be better evaluated.

The positive relationship between species abundance and lagoon occupancy observed in sampled lagoons is relatively well documented, *e.g.*, Gaston *et al.* (2000) and Granado-Lorencio *et al.* (2005), but it is still not well understood since many ecological traits can be related to occupancy and abundance of a species, *e.g.*, dispersion ability, size, and niche breadth. In a broad-scale analysis, species of lizards, birds and mammals did not have clear relationships between range size and population density (Novosolov *et al.* 2017). Therefore, in previous studies, authors suggested that positive relationships could be an artifact of incomplete sampling of range sizes. On the other hand, for stream diatoms and aquatic insects, niche position is considered the main predictor of variation in regional occupancy and local abundance (Rocha *et al.* 2018). In our study, the species with greatest occupancy in the sampled lagoons were small species widely distributed in the whole Pantanal floodplain, *e.g.*, *A. borellii*, *P. hasemani*, and *S. calliurus*, among others, and usually classified as generalist feeders. However, we did not have enough information about species traits to explain their abundance or occupancy in the Negro River floodplain.

Variation in species diversity

The role of isolation in floodplain lagoons and lakes is less studied in the Neotropics; however, Rodriguez & Lewis (1997), Tejerina-Garro *et al.* (1998) and Petry *et al.* (2003) all suggested that the degree of isolation was less important in the Orinoco, Araguaia (Amazon) and Upper Paraná floodplains, suggesting that the effect of migration during the dry season is less, or did not occur, compared to the effect of mortality in these lakes.

Importantly, in these two studies, the average distance to the river was shorter than that observed

in our study (Orinoco average = 0.8 km (max= 2.9km); Araguaia average = 2.9 km (max =5 km) and Upper Paraná with distance smaller than 500 m). In the present study, the mean distance to the river was found to be 5 km. Therefore, the greater importance of isolation observed in our study may have resulted from differences in the scale of isolation, similar to that observed in other studies where the most distant lagoon sampled was located 34 km from the river (Súarez *et al.* 2001, 2004).

In a complementary way, the isolated lakes of the upper Paraná floodplain supported higher fish biomass and density than those values in connected lagoons. Because a larger number of collected individuals is usually a better predictor of species richness, the higher species richness found in isolated lakes may result from the higher number of sampled individuals.

In the Pantanal floodplain, the different lagoon types (highly isolated and limnologically stressful = “salinas” *vs.* frequently connected = “baías”) present differences in species composition and diversity (Mourão *et al.* 1988) as a result of different species dispersal and survival capacity. Accordingly, fish usually do not occur in the “salinas”, and the more isolated “baías” contain only a few, highly tolerant species. More recently, Suárez *et al.* (2001, 2004) validated this idea, suggesting that isolation, macrophyte cover, and lagoon depth are the main determinants of species richness and evenness in the lower Rio Negro floodplain. However, “salinas” were not included in their study. In our study, this result was partially supported by the inclusion of lagoon area, which was not included among the important variables in the studies noted. Our study suggests that the interaction among lagoons with large areas, but shallow depth, decreases the importance of area to species richness.

Therefore, the results observed in the present study about fish species richness tend to support the role of isolation and lagoon volume as determinants of species diversity such that distant lagoons have less probability of colonization and more probability of extinction in response to limnologically stressful conditions in the dry season, as proposed by Suárez *et al.* (2001, 2004). However, the dominance of these assemblages is still influenced by habitat heterogeneity, isolation, and limnological stress.

Many ecological theories can be invoked to

explain this result, among them the increase of niche partitioning with greater structural complexity, which is associated with higher macrophyte species richness (Tonn & Magnusson, 1982). From another perspective, the distance from the river was also selected as a good predictor of mean evenness. The interaction of these environmental descriptors suggests that lagoons relatively far from the river contain only species with greater dispersal ability and resistance to higher conductivity. A few species with these characteristics tend to predominate in distant lagoons. These results may suggest, then, that the constraints of a more stressful environment with difficult dispersal can lead to a tradeoff in the characteristics necessary for fish to colonize and survive in these lagoons.

The relative importance of spatial and seasonal variations in structuring floodplain communities is frequently discussed with regard to different biological groups and regions. Several studies have suggested that flood pulse is the main determinant of aquatic communities (Junk *et al.* 1989, Junk 1997, Souza & Freitas 2008), defining not only the seasonality of species reproduction and recruitment (Johnson *et al.* 2007), but also the evolution of morphological, physiological, and ethological characteristics. However, other studies suggest that connectivity determines the variation of several community properties (Gilbert *et al.* 1998, Forbes & Chase 2002, Bini *et al.* 2003). In our study, we observed an interaction between local and regional characteristics to define the diversity of fish assemblages. More specifically, the degree of isolation is a regional factor that interacts with local characteristics to define how fish species occur in each lagoon, whereas mainly local biotic and abiotic characteristics, such as macrophyte diversity, can also define the dominance patterns in these lagoons.

Distribution of fish species

The distribution of fish species in these lagoons was significantly explained by shoreline development index, lagoon area, and macrophyte biomass and richness. Lagoons with larger macrophyte biomass and richness generally present a higher abundance of *P. australis*, *A. borellii*, *A. plagiozonatus* and *P. hasemani*, while lagoons with larger area and shoreline development index have assemblages with a predominance of *M. dichrourea* and *A.*

rathbuni. Shoreline development index is usually a descriptor of trophic characteristics of lakes. As such, more crenulated lagoons can offer more feeding resources (Rosenberger *et al.* 2008, Pan *et al.* 2014) by input of external nutrients to algae, invertebrates and fish species, consequently altering assemblage structure.

Taken together, our data support the association between fish and lagoon characteristics. Fish species associated with shallow sites, including Cichliformes (*L. dorsigera*) and Cyprinodontiformes (*P. hasemani*), can disperse to other lagoons, despite the shorter connection time among them, colonizing distant lagoons. Fish species that are strongly associated with medium to deep water depend on greater increases in water level to enable them to colonize distant lagoons.

In an integrated analysis of different biological groups in the Upper Paraná floodplain, Padial *et al.* (2014) observed that spatial dependency varies in importance according to dispersion ability of each group, and for sedentary fishes, it plays an important role in species distribution. Thus, in addition to scale of measurement of isolation, biological traits, mainly dispersion ability, should be evaluated as determinants of floodplain lagoon metacommunities.

In summary, our data showed that lagoons act as patchy habitats with respect to the spatial characteristics of distance to the river and lagoon morphology. These factors define local species diversity and composition according to the dispersal ability of the fish species across the floodplain, as predicted by the metacommunity concept (Wilson 1992). The interaction of regional and local characteristics affects fish species because functional traits can be selected for each combination of lagoon characteristics. Further studies in this region will allow the construction of spatially explicit models to predict the occupation of fish species and their functional traits in Pantanal lagoons.

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