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ОРИГИНАЛЬНЫЕ СТАТЬИ

ENVIRONMENTAL FILTERING AND LOW TRAIT REDUNDANCY CHARACTERISE FISH ASSEMBLAGES IN LAKE MAMO, ORINOCO RIVER FLOODPLAIN, VENEZUELA

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The study of assembly rules of fish communities in Neotropical floodplain lakes represents a major interest in community ecology due to their high species diversity and environmental variation, both spatial and temporal. In this study, assembly rules of freshwater fishes in Lake Mamo were explored. The main goals of this research were to analyse the seasonal variations in taxonomic and functional diversities of fishes in sandbanks and patches of aquatic macrophytes, in order to identify whether the fish assemblages are organised according to environmental filtering or limiting similarity, and to explore the relationships between taxonomic and functional diversity to determine if fish assemblages are either functionally redundant or complementary. In both mesohabitats, fishes were collected using seine nets during four hydrological seasons corresponding to low waters, rising waters, high waters and falling waters. Taxonomic and functional structure of fish assemblages in each habitat and across hydrological seasons was examined through multidimensional scaling (MDS), PERMANOVAs and principal co-ordinate analyses. Seasonal variations in taxonomic diversity were determined through Fligner tests of Shannon diversity indices, and for functional diversity, of functional richness (FRich), functional dispersion (FDisp), functional evenness (FEve) and functional divergence (FDiv). Null model analyses were used to determine if the functional indices diverged from randomness across hydrological seasons. Finally, relationships between functional indices and Shannon diversity were explored using linear, power, asymptotic and logistic models. There were significant differences in taxonomic and functional composition between mesohabitats and more markedly across hydrological seasons. All fish assemblages were significantly underdispersed at all instances, while functional evenness was higher than expected in both mesohabitats during low waters, signaling both a strong environmental filtering and niche packing. There were significant linear associations between the Shannon diversity and functional dispersion and between the Shannon diversity and functional evenness, suggesting that functional redundancy in these assemblages is low. In Lake Mamo, fish assemblages are filtered first by seasonality and then by habitat type. As more species are added to the assemblages, niches are more packed in the functional space, but the number of traits increases at a constant rate. This means that if a lake becomes impaired as a consequence of potential oil spills, the loss of fish species could represent also the loss of traits and functions in the ecosystem.

Key words: Critical Area with Treatment Priority Mesa de Guanipa, functional dispersion, functional evenness, niche packing, Orinoco Oil Belt, temporal trait turnover

Introduction

The study of assembly rules of fish communities has benefited greatly from the trait-based approach. Several functional diversity indices have been applied in freshwater ecosystems to identify the main mechanism that structure fish communities at different spatial and temporal scales (Mouillot et al., 2006; Montaña & Winemiller, 2010; Carvalho & Tejerina-Garro, 2015). This framework has been useful to identify if communities are assembled by environmental filters (Weiher & Keddy, 2004) or by limiting similarity (MacArthur & Levins, 1967). In Neotropical freshwaters, the study of fish functional diversity has brought contrasting results on the importance of environmental versus biotic drivers (Casatti et al., 2015; Rodrigues Bordignon et al., 2015).

Seasonality represents an important source of variation in the organisation of freshwater fish communities, particularly in the tropics. Seasonal variation in taxonomic and functional diversity takes place frequently, suggesting changes in the importance of biotic and abiotic drivers as a result of changes in environmental conditions, the availability of trophic resources and space (Vispo et al., 2003; Galacatos et al., 2004; Echevarría et al., 2017; Fitzgerald et al., 2017). Nevertheless, sometimes in highly diverse fish communities, seasonal turnover in species composition is not accompanied by changes in trait composition

(Echevarría & González, 2018), hinting that these communities might be functionally redundant.

The relationship between taxonomic and trait diversity is a subject that has been recently explored, offering an insight about ecosystem functioning. This determines if communities are redundant, i.e. all species share similar traits, or complementary: species have different traits and might carry out different functions (Guillemot et al., 2011). For instance, in deforested streams of the Amazon, functional redundancy of fish decreases as a result of colonisation by generalist, tolerant species (Camilo et al., 2018). It has been suggested that tropical fish communities are highly functionally redundant, implying that they might be more resilient to environmental disturbances than temperate ones (Toussaint et al., 2016). But this view has been debated arguing that functionality cannot be determined only by analysing morphological traits (Vitule et al., 2017).

At the patch level, fishes in floodplains show a high habitat selectivity, resulting in patches with very different species compositions, particularly during low waters (Arrington & Winemiller, 2006). Likewise, the strength of environmental filters varies according to the age of a patch (Arrington et al., 2005). In these floodplains, the taxonomic and functional structure of fish communities is determined by seasonality and substrate type (Echevarría & González, 2017b). However, functionally similar species can show spatial segregation for short periods (Echevarría & Rodríguez, 2017), while many pairs of species are randomly associated, implying that fish communities are determined not only by environmental filters, but also by biotic and stochastic factors.

The present study was conducted in Lake Mamo, the largest lake in the mid-Orinoco River floodplain, located within the Critical Area with Treatment Priority Mesa de Guanipa (UNEP-WCMC, 2022). The main goals of this study were 1) to test assembly rules through the exploration of the seasonal variations in taxonomic and functional diversity of fishes in sandbanks and patches of aquatic macrophytes, in order to identify whether the fish assemblages are organised according to environmental filtering or limiting similarity, and 2) to explore the relationships between these two facets of diversity in order to determine if fish assemblages are either functionally redundant or complementary. These mesohabitats were chosen because they are different in their structural complexity. Patches of macrophytes can be an important refuge and feeding areas for many species of miniature fish such as those of the genus *Hemigrammus*, *Moenkhausia*, *Anchovia*, and *Tricomycterus* (Valbo-Jørgensen et al., 2000). Besides, patches of macrophytes can be an important refuge and feeding areas for many species of miniature fish such as those of the genera *Anchovia* and *Tricomycterus* (Valbo-Jørgensen et al., 2000), whereas sandbanks are frequently occupied by small characins (Arrington & Winemiller, 2003). Therefore, inter-habitat differences in taxonomic and functional structure were expected.

Material and Methods

Study area

The study was conducted in Lake Mamo (08.45° N–63.15° W, and 08.40° N–63.06° W), Orinoco River floodplain in the Anzoátegui State, Venezuela (Fig. 1). Lake Mamo is located within the Critical Area with Treatment Priority (ACPT) Mesa de Guanipa, which encompasses a territory of 20 000 km^2 (UNEP-WCMC, 2022). Lake Mamo is also within the Orinoco Oil Belt, the largest oil reserve of Venezuela, an important oil reserve being recently explored (Blanco & Flores, 2013). Lake Mamo has an extension of approximately 55 km^2 and a maximum depth of 12 m. Heavy rains take place between May and August with a maximum over 250 mm, while the driest months are January to April, and the average annual temperature is 21.1°C with little variation across the year (Colonnello, 1990). The perimeter around Lake Mamo is surrounded by alluvial sedimentary depositions of the River Orinoco and its northern tributaries (Colonnello, 1990). It receives the waters from the River Merey and River Camoruco, and is connected to the River Orinoco through the Stream Mamo. This area is characterised by high fish diversity, with a richness of 114 species encompassing the orders Characiformes, Siluriformes, Gymnotiformes, Cichliformes, Myliobatiformes, Clupeiformes, and Cyprinodontiformes as the most diverse (Lasso, 1988).

Samplings

Fishes were collected through seining (5 m × 1.5 m, 1-mm mesh) in two mesohabitats: sandbanks and patches of macrophytes during four seasons of a hydrological cycle: low waters (February), raising waters (May), high waters (August), and falling waters (November) in 2008 and 2009. Macrophytes patches were constituted by several species of aquatic plants, but were dominated by *Eichornia* spp. and *Paspalum* spp. (Rial, 2009), and are characterised by a high structural complexity associated to the lattice of roots (Valbo-Jørgensen et al., 2000), floating nearby the border of the lake. Sandbanks were formed by deposits of fine, white sands on the littorals (Fig. 1). During each season, 20 trawls were made, including 10 in sandbanks and 10 in macrophytes patches. Samples were distributed in four sites along the Lake Mamo border during six days. Locations of sampling sites varied across seasons due to fluctuations in water level. All specimens were identified to the species level, when possible, and deposited in the collection of ichthyological reference of Estación de Investigaciones Hidrobiológicas de Guayana (CRI-EDHIG) belonging to the Fundación La Salle de Ciencias Naturales, Campus Guayana (Catalogue number: 3794-7716). Fishing and specimen preservation procedures were performed in compliance with the research guidelines of Fundación La Salle de Ciencias Naturales.

Fish traits

Five traits were chosen to perform the functional diversity analyses: standard length, average weight, trophic level, feeding category and body shape. Standard length and weight were measured for at least five specimens in the field and averaged by species. Trophic levels represent the approximate position of the fish occupy in a food web and was obtained from Froese & Pauly (2019). The feeding category represents the main trophic resource, on which the species diet is based. The fish species were classified in nine feeding categories: herbivores, zooplanktivores, piscivores, carnivores, omnivores, mucus feeders, lepidophages, and invertivores, based on previous studies in this area (González & Vispo, 2004; González et al., 2012). For the body shape, 25 categories were established based on the combination of general body shape (elongated, fusiform, oval, discoid, depressed, flattened, humped, cylindrical, ribbon shaped, streamlined, ventrally curved, pencil shaped, snake shaped) with head shape (pointed headed, elongated head, round headed). Trait information for all species is shown in the Electronic Supplement.

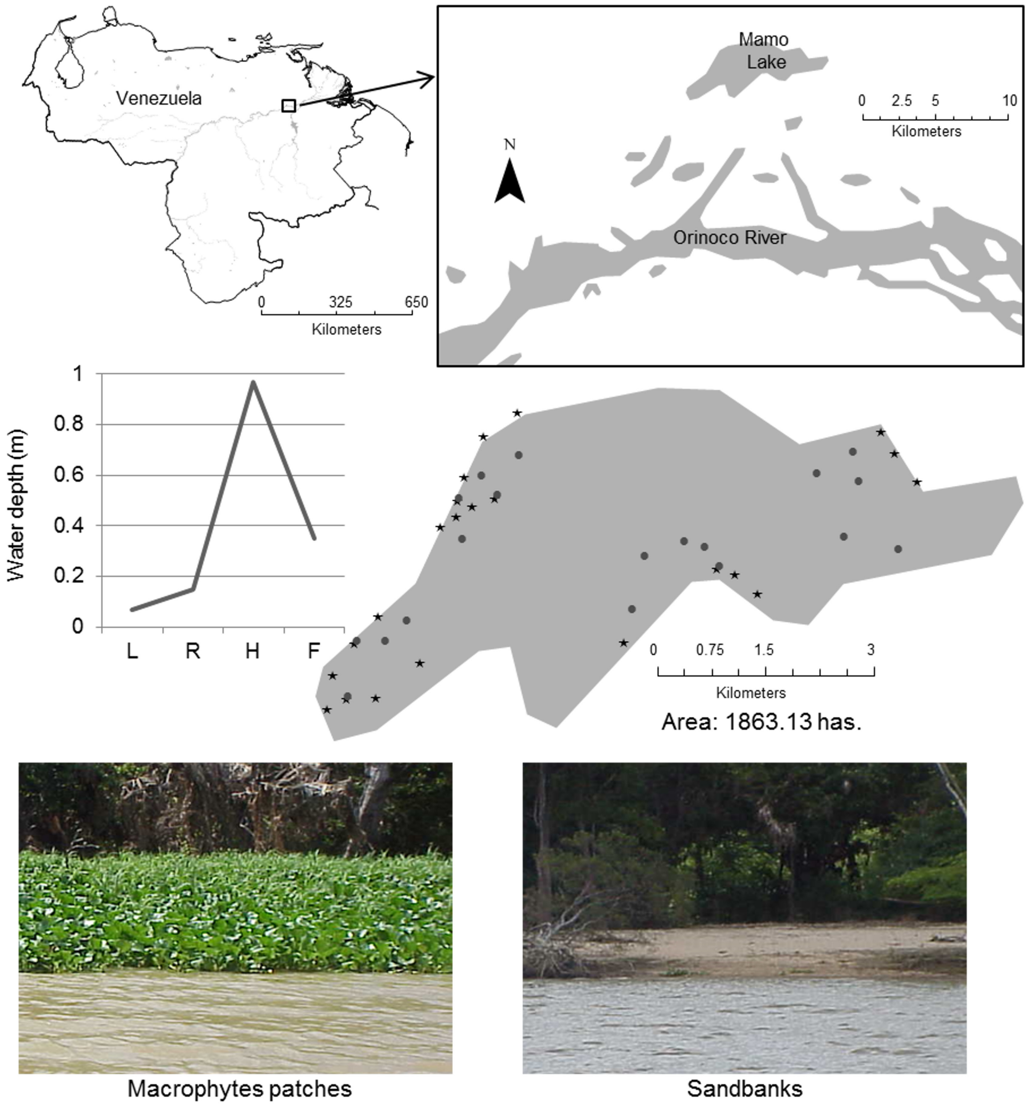

Fig. 1. Characteristics of the study area, the Lake Mamo, Venezuela, and mesohabitats sampled. Black stars indicate sandbanks and gray dots show macrophytes patches. Water depth variation across hydrological seasons: L – low waters, R – rising waters, H – high waters, F – falling waters.

Data analysis

Taxonomic diversity of mesohabitats was compared with Hill numbers of order q = 0 and q = 1, which are equivalent to species richness and the Shannon entropy respectively (Chao & Jost, 2012; Chao et al., 2014) using the R package iNEXT (Hsieh et al., 2016). Additionally, habitat and seasonal comparisons of the Shannon H' index of species diversity were performed through Fligner tests. The comparison of fish species composition between mesohabitats and across hydrological seasons was performed with non-metric multidimensional scaling (NMDS) and PERMANOVAs (Anderson, 2001) based on Bray-Curtis distances. Significance was obtained through 999 permutations of residuals under a reduced model (Clarke & Gorley, 2006). Trait composition was compared using a matrix of Gower distances among samples based on the community-level weighted means of the fish traits in each sample, previously obtained with the function «functcomp» of the package «FD» (Laliberté et al., 2014) in R (R Development Core Team, 2012). With this matrix, principal co-ordinate analysis and a PERMANOVA analysis were performed.

Four indices assessed the functional structure of fish assemblages: functional richness (F_{Ric}), which represents the volume of the functional niche, functional divergence (F_{Div}), which indicates how the abundances are distributed across the functional space, functional evenness (F_{Eve}), which measures how regularly the species are distributed in the functional space (Villéger et al., 2008) and functional dispersion (F_{Disp}), represented by the average distance to the centroid (Laliberté et al., 2014). All indices were computed from Gower distances among species by their traits obtained from the principal co-ordinate analysis, and matrices of species abundances per sample, using the package «picante» (Kembel et al., 2015) and FD (Laliberté et al., 2014) in R (R Development Core Team, 2012). In order to assess whether the functional indices deviated from randomness, they were contrasted against 999 simulated matrices under the independent swap null model (Gotelli, 2000). Standard effect sizes were calculated for the indices as: SES (mean observed – mean simulated) / SD simulated. Simulations were carried out with the function «RandomizeMatrix()» of the package «picante» (Kembel et al., 2015) in R (R Development Core Team, 2012). Additionally, seasonal and habitat comparisons of functional indices were carried out through Fligner tests. Finally, the relationships between the functional diversity indices and the Shannon H' index were assessed according to Guillemot et al. (2011), by linear, power, asymptotic and logistic models. Linear associations between functional and taxonomic diversity imply that each species plays a unique functional role in the ecosystem, asymptotic associations imply that after a number of species is reached no new functions are added to the community, power associations assume that the functions increase rapidly as new species are added to the community and logistic associations imply that there is influence of the environment in the addition of new functions.

Results

Taxonomic and functional structure

The total species richness in sandbanks was 41 and in macrophytes patches 44. The taxonomic diversity was higher in macrophytes patches. Hill number q = 0 indicated that the species richness was slightly higher in macrophytes (Fig. 2A), but Hill number q = 1 showed that fish diversity was higher, with around 15 species more, than within sandbanks (Fig. 2B). The fish composition differed between mesohabitats (pseudo-F = 1.68, P = 0.024) and seasons (pseudo-F = 8.5, P = 0.001), and the interaction of both factors had a significant effect (pseudo-F = 1.56, P = 0.004). Season explained the most variation (square root = 44.67, mesohabitat square root = 9.51, mesohabitat × season square root = 17.31). Differences among mesohabitats were more pronounced during low waters, while differences among seasons were larger between low and high waters (Fig. 2C). There were differences in trait composition between mesohabitats (pseudo-F = 4.23, P = 0.006) and seasons (pseudo-F = 4.55, P = 0.001), while the interaction between these factors was marginally significant (pseudo-F = 1.81, P = 0.086). Again, season explained the most variation (square root = 11.43) in comparison to mesohabitat (square root = 7.71) or the interaction between factors (square root = 7.71). Body shape was negatively correlated to trophic level and trophic category (Fig. 2D). Length and weight were positively correlated, and were associated to macrophytes patches during low waters. Trophic category and trophic level influenced the structure of fish assemblages during rising and falling waters, independently of the mesohabitat.

Seasonal variations in taxonomic and functional diversity

Fligner tests did not find seasonal differences in Shannon diversity within habitats (Fig. 3). Only in sandbanks, significant differences in functional evenness among seasons were observed. In macrophytes, there were marginally significant differences in functional richness. Functional richness was considerably lower in macrophytes in comparison to sandbanks (Fig. 3), which was corroborated by a Fligner test between mesohabitats that indicated significant differences (F test = 20.36, P < 0.001).

Functional richness and divergence did not differ from randomness in any of the mesohabitats (Table 1). Functional evenness was higher than randomly expected in both mesohabitats during low waters, and lower than randomly expected during high waters in sandbanks (Table 1). Functional dispersion was lower than randomly at all instances, indicating that fish assemblages in both mesohabitats were always underdispersed.

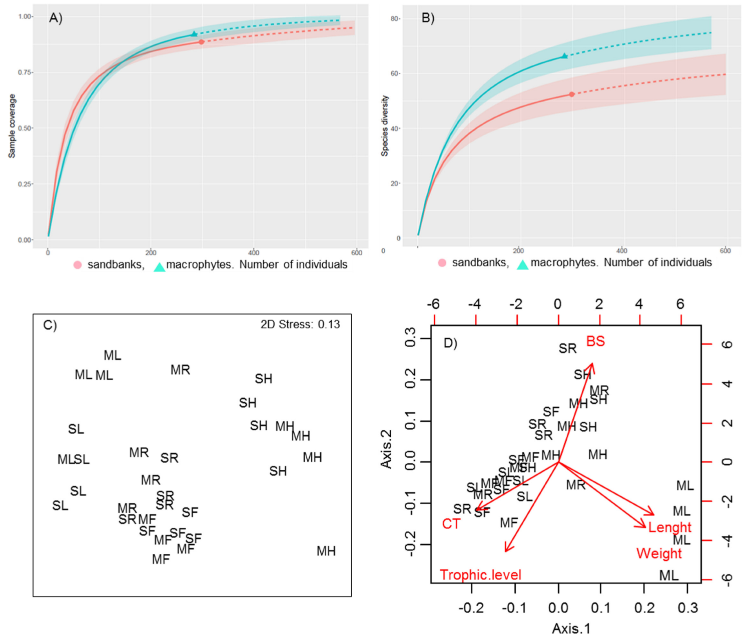

Fig. 2. Rarefaction curves, NMDS and principal coordinates analyses plots of the fish assemblages in Lake Mamo, Venezuela. Designations: A) Rarefaction curve with Hill number q = 0. B) Rarefaction curve with Hill number q = 2. C) NMDS plot of samples by species composition. D) Principal coordinates plot depicting the associations of samples and traits.

Table 1. Results of the null model analyses of the functional diversity indices for macrophytes patches and sandbanks in Lake Mamo, Venezuela

Sandbanks					Macrophytes				
FRic									
Season	Obs	Sim	P	SES	Season	Obs	Sim	P	SES
L	2.8×10^{-23}	5.31×10^{-21}	0.58	-0.06	L	1.53×10^{-12}	1.50×10^{-13}	0.55	-0.34
R	1.22×10^{-18}	4.99×10^{-19}	0.66	-0.18	R	3.65×10^{-16}	1.07×10^{-15}	0.49	-0.20
H	5.23×10^{-21}	2.37×10^{-18}	0.45	-0.27	H	2.34×10^{-22}	1.48×10^{-16}	0.73	-0.12
F	1.98×10^{-21}	1.04×10^{-17}	0.29	-0.35	F	4.55×10^{-15}	5.60×10^{-13}	0.46	-0.43
FEve									
Season	Obs	Sim	P	SES	Season	Obs	Sim	P	SES
L	0.59	0.58	**0.00**	-2.82	L	0.67	0.61	**0.00**	-2.92
R	0.43	0.31	0.98	2.39	R	0.47	0.49	0.99	2.92
H	0.64	0.65	**0.00**	-4.91	H	0.62	0.65	0.57	0.22
F	0.28	0.30	0.99	3.76	F	0.40	0.45	0.98	1.98
FDiv									
Season	Obs	Sim	P	SES	Season	Obs	Sim	P	SES
L	0.92	0.76	0.72	0.86	L	0.89	0.77	1.00	1.77
R	0.97	0.73	0.92	1.38	R	0.79	0.78	0.11	-1.20
H	0.72	0.74	1.00	3.14	H	0.61	0.78	0.76	0.83
F	0.89	1.12	0.84	1.12	F	0.88	0.76	0.84	0.84
FDis									
Season	Obs	Sim	P	SES	Season	Obs	Sim	P	SES
L	0.06	5.62	**0.001**	-0.77	L	0.19	20.16	**0.001**	-1.41
R	0.14	12.55	**0.001**	-0.84	R	0.16	20.11	**0.001**	-1.32
H	0.08	14.32	**0.001**	-1.60	H	0.05	20.21	**0.001**	-1.43
F	0.06	12.06	**0.001**	-0.85	F	0.06	18.48	**0.001**	-1.03

Note: Obs – observed values, Sim – average of simulated values, P – probability, SES – standardised size effect. Hydrological seasons: L – low waters, R – rising waters, H – high waters, F – falling waters. Indices: FRic – functional richness, FDisp – functional dispersion, FDiv – functional divergence, FEve – functional evenness.

Relationships between taxonomic and functional diversities

The best models to explain the association of Shannon diversity with functional dispersion and evenness were linear and power models (Table 2). A further analysis of power models indicated that the slope was more pronounced for functional evenness, as indicated by the coefficients (Table 2).

However, in both cases, b coefficient was near 1.0, signalling a linear association. Considering this, linear regressions were conducted for each mesohabitat separately, and significant associations were maintained for both mesohabitats (Fig. 4).

Discussion

In Lake Mamo, macrophytes patches harboured more taxonomically diverse communities than sandbanks, which are less structurally complex. Nonetheless, the functional space was higher in sandbanks across hydrological seasons. Traits showed a higher variation in this mesohabitat, a result that was not expected, considering that in Neotropical aquatic systems, functional richness is usually higher in more complex mesohabitats (Echevarría & González, 2018). In macrophytes patches, body length and weight were determinant in the assembly of fishes, particularly during low waters, suggesting a strong environmental filtering associated to the movement capacity of species within the maze of aquatic plants roots (Quirino et al., 2021). Observed differences in taxonomic and functional composition of fishes between mesohabitats, especially marked during low waters, further suggest the fish assemblages are determined by environmental filters.

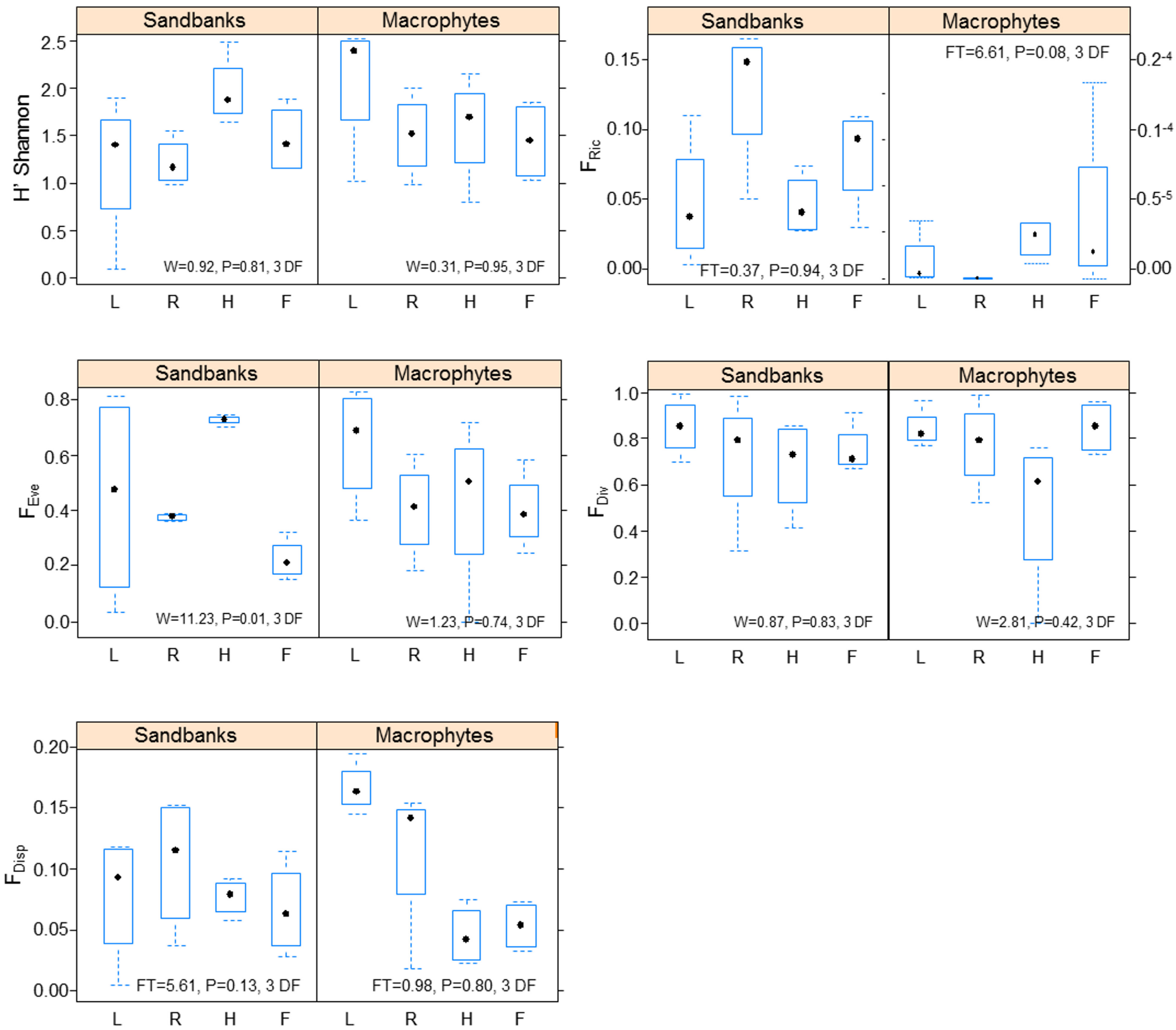

Fig. 3. Boxplots showing seasonal variations of taxonomic and functional indices of fish assemblages in Lake Mamo, Venezuela, with Fligner tests results. Hydrological seasons: L – low waters, R – rising waters, H – high waters, F – falling waters. Indices: FRic – functional richness, FDisp – functional dispersion, FDiv – functional divergence, FEve – functional evenness.

Table 2. Model selection parameters of the relationships between taxonomic and functional diversity indices of fish assemblages in Lake Mamo, Venezuela, and detailed results of the linear and power models

Associations	Model	R-squared	AIC	BIC	Associations	Model	R-squared	AIC	BIC
FDis~ Tdiv	Linear	0.32	-107.63	-103.23	FEve~ Tdiv	Linear	0.50	-20.11	-15.72
	Power	0.34	-107.64	-103.24		Power	0.52	-20.15	-15.76
	Asymptotic	0.32	-105.60	-99.74		Asymptotic	0.51	-18.04	-12.18
	Logistic	0.31	-105.16	-99.30		Logistic	0.49	-17.72	-11.85
	Exponential	0.32	-107.00	-102.61		Exponential	0.47	-19.07	-14.67
Linear model	Estimate	St. Error	T-value	P-value					
FDis~ Tdiv	0.06	0	3.97	4.00×10^{-4}					
FEve~ Tdiv	0.31	0.1	5.66	4.00×10^{-6}					
Power Model	Parameters	Estimate	T-value	P-value					
FDis~ Tdiv	a	0.1	5.18	1.37×10^{-5}					
	b	1	3.24	2.90×10^{-3}					
FEve~ Tdiv	a	0.3	6.58	2.74×10^{-7}					
	b	1.1	4.67	5.78×10^{-4}					

Note: AIC – Akaike's criterion, BIC – Bayesian information Criterion, FDis – functional dispersion, FEve – functional evenness, Tdiv – taxonomic diversity.

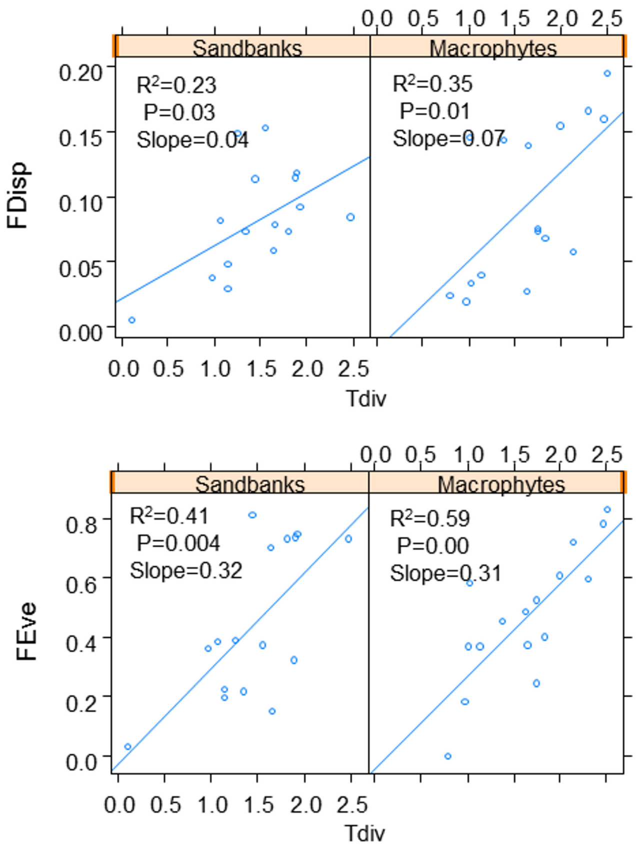

Fig. 4. Results of linear regressions of taxonomic diversity (Tdiv), measured as Shannon H' index, with functional dispersion (FDisp) and functional evenness (FEve) for each mesohabitat in Lake Mamo, Venezuela.

In other Neotropical floodplains, seasonal environmental changes are accompanied by variations in taxonomic and functional fish diversities (Echevarría et al., 2017; Fitzgerald et al., 2017). This was not the case in Lake Mamo. Nevertheless, there were significant species and trait turnovers across hydrological seasons. The species richness in Lake Mamo is very high in comparison to other floodplain lakes of the River Orinoco, with 193 species previously identified (Echevarria & González, 2017a). This high fish richness is apparently maintained through species adaptations to very specific environmental conditions that generate the spatial and temporal turnovers, without a decrease in taxonomic or functional diversities.

Stochastic patterns resulting from dispersion are frequent in newly formed habitat patches, (Arrington et al., 2005). In contrast, during low waters species show a higher patch selectivity (Arrington & Winemiller, 2006), leading to an increased importance of environmental and biotic factors. In Lake Mamo, stochastic patterns were not predominant in any hydrological season, since fish assemblages were functionally underdispersed at all instances, underlying once more a strong environmental filtering (Keddy, 1992; Weiher & Keddy, 2004). During low waters, high fish diversity resulted in a denser occupation of the functional space without an increase in its volume, following a niche packing model (MacArthur, 1970; Rappoldt & Hogeweg, 1980).

Relationships of taxonomic diversity with functional dispersion and evenness were linear, showing highly diverse assemblages are formed by increasingly specialised species. Therefore, fish assemblages in sandbanks and macrophytes patches were characterised by low trait redundancy, contrarily to what have been found in other tropical fish communities (Toussaint et al., 2016; Tuya et al., 2018), where linear relationships between taxonomic and functional diversities have been correlated to environmental disturbance in the form of substrate and riparian vegetation alteration (Casatti et al., 2015; Camilo et al., 2018). However, the majority of species occupying sandbanks and macrophytes patches are not targeted in the artisanal fisheries, suggesting these patterns might result from seasonality, evidencing that despite the strong environmental filtering and niche packing, as more species are added, the number of traits, and possibly the number of functions, increases at a constant rate. Thus, this study provides evidence against the suggestion by Toussaint et al. (2016) that fish communities in the tropics are predominantly redundant and therefore conservation efforts should be focused on temperate zones. As a matter of fact, such an approach might lead to the loss of ecosystem functions and traits resulting from the loss of taxonomic diversity in the most diverse region of the world.

In Lake Mamo, fish assembly rules could have important implications for their conservation, considering Lake Mamo is located within the Orinoco Oil Belt. Its exploitation might lead to oil spills that could cause the loss of fish species, and potentially of important ecosystem functions. In Venezuela, oil exploration have caused the impairment of several aquatic systems as a consequence of water pollution, changes in productivity, loss of aquatic vegetation and the alteration of the structure of river beds, all of which have been associated to the loss of freshwater biodiversity (Machado-Allison, 2017). This situation is worsened by the fact that the Critical Area with Treatment Priority (ACPT) Mesa de Guanipa still lacks a management plan (UNEP-WCMC, 2022). Considering its high fish richness and its importance for the artisanal fisheries of the eastern lowlands of Venezuela, the urgency of a plan that encompasses conservation measures for Lake Mamo and its fishes becomes evident.

Conclusions

Fish assemblages in Lake Mamo show very interesting assembly rules that are determined by hierarchical environmental filters represented first by seasonality and in a second order of magnitude by mesohabitat type. These highly diverse assemblages show both marked species and trait turnovers across hydrological seasons that suggest fish species are adapted to very specific environmental conditions, although these turnovers do not cause major variations in taxonomic or functional diversities. These fish assemblages are significantly underdispersed in both mesohabitats, and species niches are packed in the constrained functional spaces, especially during low waters. On the other hand, the characteristics of the lattice resulting from the masses of roots within macrophytes patches implicate that only small sized species can occupy this mesohabitat, considerably restricting the size of its functional space in comparison to sandbanks, which show a broader traits variation and larger functional spaces, even though macrophytes patches harbour a higher number of species than the latter. Strikingly, despite the marked environmental filtering and niche packing, in both mesohabitats the relationship between taxonomic and functional diversity does not follow an asymptotic curve, showing traits are not saturated and consequently that these fish assemblages exhibit low trait redundancy. These patterns highlight that in tropical lakes, there can be an important degree of functional specialisation at high species richness and restricted functional spaces, and therefore, the loss of species could result in the loss of traits. This is of particular importance in Lake Mamo, since fish diversity and ecosystem functions in this floodplain lake could be threatened in the near future if the exploration of oil advances in the area, bearing in mind the history of oil spills in Venezuela, particularly in the eastern lowlands of the country. Considering its remarkable fish diversity, more research and conservation efforts are needed in Lake Mamo.

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Supporting Information

The species composition of fishes and their functional traits from Lake Mamo (Electronic Supplement. Species collected in Lake Mamo and their functional traits) may be found in the **Supporting Information**.

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ЭКОЛОГИЧЕСКАЯ ФИЛЬТРАЦИЯ И НИЗКАЯ ИЗБЫТОЧНОСТЬ ПРИЗНАКОВ ХАРАКТЕРИЗУЮТ СООБЩЕСТВА РЫБ В ОЗЕРЕ МАМО, ПОЙМА РЕКИ ОРИНОКО, ВЕНЕСУЭЛА

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Изучение закономерностей формирования сообществ рыб в неотропических пойменных озерах представляет большой интерес для экологии сообществ в связи с их высоким видовым разнообразием и изменчивостью окружающей среды, как пространственной, так и временной. В этом исследовании были изучены закономерности формирования сообществ пресноводных рыб в пойменном озере Мамо. С целью определить, являются ли сообщества рыб функционально дублирующими или дополняющими друг друга были поставлены следующие основные задачи: 1) проанализировать сезонные вариации таксономического и функционального разнообразия рыб на песчаных отмелях и участках, занятых водными макрофитами; 2) определить, организованы ли сообщества рыб в соответствии с фильтрацией окружающей среды или ограничивающим сходством; 3) изучить соотношения между таксономическим и функциональным разнообразием. В обоих типах местообитаний рыб отлавливали неводами в течение четырех гидрологических сезонов, соответствующих низкой воде, подъему воды, паводку и спаду воды. Таксономическая и функциональная структура сообществ рыб в местообитаниях и во время гидрологических сезонов изучалась с помощью многомерного шкалирования, PERMANOVA и методом главных компонент. Сезонные изменения таксономического разнообразия определялись с помощью теста Флигнера индексов разнообразия Шеннона, а для функционального разнообразия – индексов функционального богатства (FRich), функциональной дисперсии (FDisp), функциональной равномерности (FEve) и функциональной дивергенции (FDiv). Анализ нулевой модели использовался для определения того, отклоняются ли функциональные индексы от случайности в течение гидрологических сезонов. Были исследованы взаимоотношения между функциональными индексами и разнообразием Шеннона с использованием линейной, степенной, асимптотической и логистической моделей. Были обнаружены статистически значимые различия в таксономическом и функциональном составе между типами местообитаний и еще более заметные между гидрологическими сезонами. Во всех случаях для всех сообщества рыб была отмечена статистически значимая недостаточная рассредоточенность. В то же время функциональная выровненность была выше, чем ожидалось, в обоих типах местообитаний во время низкой воды, что свидетельствует как о сильной фильтрации окружающей среды, так и о заполнении ниш. Были выявлены статистически значимые линейные связи между значением индекса разнообразия Шеннона и функциональной дисперсией, а также между индексом Шеннона и функциональной равномерностью. Это позволяет предположить, что функциональная избыточность в этих сообществах невелика. В пойменном озере Мамо сообщества рыб фильтруются сначала по сезонности, а затем по типу среды обитания. По мере того, как к сообществам добавляется больше видов, ниши в функциональном пространстве все больше заполняются, но количество признаков увеличивается с постоянной скоростью. Это означает, что если экосистема озера подвергнется нарушению в результате потенциальных разливов нефти, потеря видов рыб может также означать потерю свойств и функций в экосистеме.

Ключевые слова: критическая зона с приоритетом воздействия «Меса-де-Гуанипа», функциональная дисперсия, функциональная равномерность, заполнение ниши, нефтяной пояс Ориноко, оборот временных признаков