

Original article

Fish beta diversity responses to environmental heterogeneity and flood pulses are different according to reproductive guild

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In floodplain communities, beta diversity is influenced by different factors; however, environmental heterogeneity and floods are believed to be particularly influential. The influence of environmental heterogeneity and floods on beta diversity may vary among guilds that present different ecological traits. This study evaluated the correlation between the environmental heterogeneity and flood periods and the beta diversity of trophic and reproductive guilds of fish assemblages. Sampling was conducted quarterly between 2000 and 2012 in the upper Paraná River floodplain. The environmental heterogeneity and period (*i.e.*, dry or flood) were associated with the beta diversity of each guild based on the results of generalized least squares linear models. Only guilds with parental care were influenced by the interaction between environmental heterogeneity and period. The beta diversity of the other guilds presented no relationship between environmental heterogeneity and period. It is likely that species with parental care presented less dispersal capacity, which increased the dissimilarity among assemblages. The higher dispersion rates of the other guilds may be responsible for the lack of relationship between the beta diversity and the environmental heterogeneity and period. In sum, these results suggest that reproductive guilds influence how environmental heterogeneity and floods affect beta diversity variation.

Keywords: Dissimilarity, Fish assemblages, Flood pulse, Reproductive guilds, Trophic guilds.

A diversidade beta é influenciada por diferentes fatores em comunidades de planícies de inundação; contudo, acredita-se que a heterogeneidade ambiental e inundações sejam particularmente influentes. A influência da heterogeneidade ambiental e inundações na diversidade beta podem variar entre guildas que apresentam diferentes características ecológicas. Este estudo avaliou a correlação entre heterogeneidade ambiental, os períodos de inundação e a diversidade beta de guildas tróficas e reprodutivas de peixes. A amostragem foi realizada trimestralmente entre 2000 e 2012 na planície de inundação do Alto rio Paraná. Heterogeneidade ambiental e o período (*i.e.*, seca ou cheia) foram associados à diversidade beta de cada guilda por modelos lineares de quadrados mínimos generalizados. Somente guildas com cuidados parentais foram influenciadas pela interação entre heterogeneidade ambiental e período. A diversidade beta das outras guildas não apresentou relação com heterogeneidade ambiental e período. É provável que espécies com cuidados parentais apresentem menor capacidade de dispersão, o que aumenta a diferença entre as assembleias. As maiores taxas de dispersão de outras guildas podem ser responsáveis pela ausência de relação entre a diversidade beta e heterogeneidade ambiental e o período. Em suma, os resultados sugerem que as guildas reprodutivas influenciam a forma como a heterogeneidade ambiental e as inundações afetam a variação da diversidade beta.

Palavras-chave: Assembleias de peixes, Dissimilaridade, Guildas reprodutivas, Guildas tróficas, Pulso de inundação.

Introduction

The search for correlates of variation in community composition (beta diversity; Anderson *et al.*, 2011) is a central theme in community ecology (Chase, 2010; Heino *et al.*, 2015b; Zorzal-Almeida *et al.*, 2017). The interactions between environmental factors at regional geographic scales (Heino, 2001; Leprieur *et al.*, 2009; Al-Shami *et al.*, 2013; Heino *et al.*, 2015b;), productivity (Chase, 2010; Bini *et al.*, 2014) and environmental heterogeneity present sub-

stantial influences on beta diversity (Bini *et al.*, 2014; Heino *et al.*, 2015b; Zorzal-Almeida *et al.*, 2017). Specifically, environmental heterogeneity is expected to have a positive relationship with beta diversity. The similarities in species composition and environmental conditions and resources tend to decrease as the geographical distance between communities increases (Leprieur *et al.*, 2009; Anderson *et al.*, 2011; Nekola, McGill, 2014; Heino *et al.*, 2015b;). This effect can occur regardless of individual dispersal rates (*i.e.*, environmental control *sensu* Heino *et al.*, 2015b). Alternati-

vely, with increasing spatial scales, the dispersal capacity of species among communities will decrease; in contrast, the environmental heterogeneity increases (*i.e.*, environmental control-dispersion; Heino *et al.*, 2015b).

Temporal dynamics also influence beta diversity. In floodplains, the flood pulse is the main seasonal event that influences the abiotic and biotic structure (Junk *et al.*, 1989). The increase in the river level connects isolated lakes in the floodplain to the main rivers and homogenizes the environmental variability (*i.e.*, reduces environmental heterogeneity), while the receding of waters in the dry period increases the differences in the abiotic variables (*i.e.*, increases environmental variability) from different lakes (Thomaz *et al.*, 2007; Bozelli *et al.*, 2015). Flood pulses can also homogenize the species composition, as the increase in river level connects isolated lakes and the main river channel, enabling the dispersal of species (Thomaz *et al.*, 2007). Thus, floods can mix faunas and reduce beta diversity during flood periods; however, beta diversity can increase during periods of drought because isolation increases due to the absence of channels that connect ponds to the main rivers (Thomaz *et al.*, 2007; Bozelli *et al.*, 2015; Penha *et al.*, 2017).

Organisms from different taxonomic groups may respond differently to the effects of environmental heterogeneity (Soininen *et al.*, 2007; Padial *et al.*, 2014; Heino, 2001; Heino *et al.*, 2015b) and seasonal events (Padial *et al.*, 2014), which is why ecological studies consider the diversity of functional traits or the phylogeny of species; these studies can facilitate a better understanding of community dynamics (Swenson *et al.*, 2011). A useful tool for this approach is the classification of species into guilds (*e.g.*, trophic or reproductive guilds). A guild can be considered as a group of species that exploit a common resource or exhibit similar behaviors (*e.g.*, reproductive traits; Kikkawa, Anderson, 1986). This approach can provide a detailed view of the processes that influence beta diversity (Padial *et al.*, 2014; Brownscombe *et al.*, 2017).

Neotropical floodplains are models for evaluating the effects of environmental heterogeneity and seasonality on the beta diversity of fish assemblages. These environments are subjected to seasonal droughts and floods (Junk *et al.*, 1989; 2014; Thomaz *et al.*, 2007), with the latter homogenizing the abiotic conditions and increasing the connectivity of isolated environments with the main river channels (Thomaz *et al.*, 2007). Neotropical ichthyofauna has enormous species richness (Lévêque *et al.*, 2008), and species have different ecological roles. In terms of reproductive aspects, these species can be grouped as migratory or sedentary species, and the latter may or may not exhibit parental care. It is expected that migratory species have greater dispersal potential (Padial *et al.*, 2014), which is closely related to flood connectivity (Oliveira *et al.*, 2015).

In terms of trophic aspects, fish exhibit great plasticity, but groups of detritivorous, herbivorous, insectivorous, omnivorous and piscivorous species can be recognized within a community (Abelha *et al.*, 2001). This variety of trophic sta-

tuses may influence the responses of fish to variations in local or regional environmental factors (Heino *et al.*, 2015b). The variations in environmental conditions produced by flood pulses influence the availability of food for different guilds throughout the year. It is expected that this variation in the availability of resources affects the composition of the trophic guilds because it favors the wide distribution and presence of some species and negatively affects others, producing variations in the beta diversity linked to the different guilds. However, there are no previous studies that predict the behavior of insectivorous, herbivorous, detritivorous and omnivorous guilds; therefore, by considering ecological dynamics, distinct trends in beta diversity variation among guilds can be expected.

This study evaluates the effect of environmental heterogeneity and floods on the beta diversity of fishes in the upper Paraná River floodplain. The hypotheses evaluated were that there is a positive correlation between beta diversity and environmental heterogeneity, that beta diversity is smaller in flood periods than in dry periods and that these relations change from one guild to another. One can expect that these relations change with guilds because the exploration of food resources and the dispersal activities associated with each guild may influence their responses to environmental heterogeneity and seasonal events, which can scale to compositional differences (Soininen *et al.*, 2007; Padial *et al.*, 2014). For instance, during the dry period, piscivorous species will benefit from the increase in the availability of the species that serve as food because prey species are restricted to a smaller area than that during the flood period (Luz-Agostinho *et al.*, 2008). On the other hand, variations in omnivore beta diversity are not expected because omnivores have greater food plasticity and can find food resources at all times throughout the hydrological cycle (Hahn *et al.*, 2004). Similarly, in terms of reproductive guilds, migratory species travel longer distances than do species with some parental care traits (Suzuki *et al.*, 2004); thus, the former may be more likely than the latter to present different species composition (*i.e.*, higher beta diversity).

Material and Methods

Study area. Sampling was conducted in the floodplain of the upper Paraná River, in the stretch bounded between the upstream Porto Primavera Dam and the downstream Itaipu Reservoir, which is the only stretch of the Paraná River in the Brazilian territory that is free of impoundments. In this section, the river has an anastomosed channel that is characterized by a low slope (0.09 m/km), a wide floodplain and a high sedimentation rate, which generates bars and islands (Souza-Filho, Stevaux, 1997). The main channels of the drainage network in the lowlands are the Paraná, Ivinhema and Baía rivers, which are interconnected by secondary channels. The lagoons have permanent or intermittent connections with these channels, depending on the water levels of the main rivers (Vazzoler *et al.*, 1997) (Fig. 1).

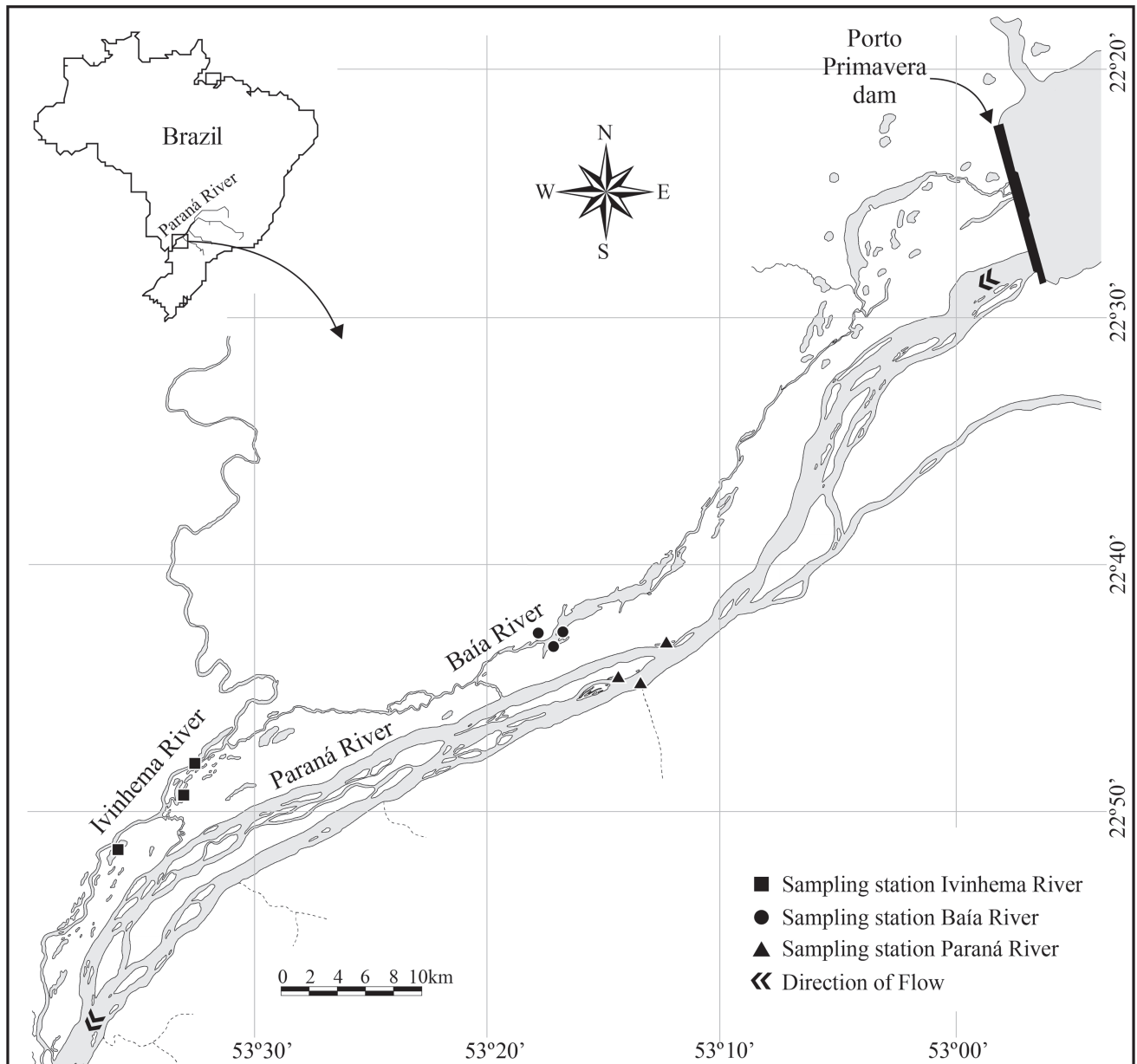


Fig. 1. Map of the Upper Paraná River floodplain. The triangles represent the sampling stations of the Paraná River sub-basin, the circles represent the sampling stations of the Baía River sub-basin, and the squares represent the sampling stations of the Ivinhema River sub-basin.

Sampling. Fish sampling was performed quarterly between 2000 and 2012 (*i.e.*, a total of 50 sampling campaigns were conducted) at nine collection stations; specifically, two lakes and the main channel of the river in each sub-basin were considered. In the sub-basin of the Paraná River, both Pousada das Garças and Ressaco do Pau Velho lakes, which have permanent connectivity to the Paraná River, were sampled; in the Baía sub-basin, Guaraná Lake, which has a permanent connection, and Closed Lake, which is isolated during the dry season, were sampled; finally, in the sub-basin of the Ivinhema River, Patos Lake, which has a permanent connection, and Ventura Lake, which has a seasonal connection, were sampled (Fig. 1).

Gillnets of different mesh sizes were used (30, 40, 50, 60, 70, 80, 100, 120, 140, and 160 mm between opposed knots); nets were deployed for 24 h, and fish were removed in the morning, afternoon and evening. The specimens were identified according to Ota *et al.* (2018), and voucher specimens were deposited in the Coleção Ictiológica of the Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura (NUPELIA) of the Universidade Estadual de Maringá (UEM). Abundance data were indexed by catch per unit effort (CPUE) (individuals/24 h/1000 m²).

Species were classified into six trophic guilds based on previous studies conducted in the region (Hahn *et al.*,

1997; 2004) and complementary information from the literature (Tab. S1 - Available only as online supplementary file accessed with the online version of the article at <http://www.scielo.br/ni>); these guilds included species that were detritivorous (DET), herbivorous (HER), insectivorous (INS), invertivorous (INV), omnivorous (ONI) and piscivorous (PIS). The four reproductive guilds followed the classification scheme proposed by Suzuki *et al.* (2004), *i.e.*, long-distance migratory and external fertilization (LMEF), non-migratory with external fertilization and parental care (NEFC), non-migratory with external fertilization without parental care (NEFW) and non-migratory with internal fertilization (NIF) species. We then generated 10 matrices using the per species CPUE data from each guild.

To measure EH, 15 physicochemical variables were measured: water temperature ($^{\circ}\text{C}$), transparency (Secchi depth; cm), pH, conductivity (μS), dissolved oxygen (mg/L), alkalinity (mEq/L), inorganic suspended material (mg/L), suspended organic material (mg/L), chlorophyll-*a* (mg/L), total nitrogen concentration (mg/L), ammonia concentration (NH_4 ; mg/L), total phosphorus concentration (mg/L), phosphate concentration (PO_4 ; mg/L) and zooplankton abundance (individuals/ml) (Tab. S2 - Available only as online supplementary file accessed with the online version of the article at <http://www.scielo.br/ni>). For each sampling campaign, the average value of each variable was calculated. Additionally, the river-level data (m) were measured at the Estação Fluviométrica of Porto São José, which is operated by the Agência Nacional de Águas (Fig. 2).

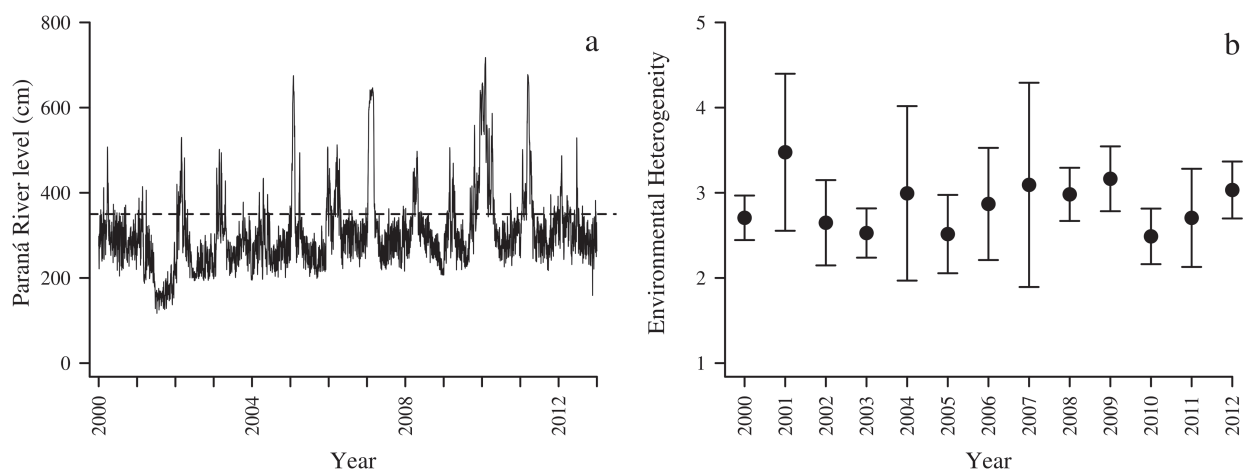


Fig. 2. Hydrometric-level (a) and environmental heterogeneity (b) variation between 2000 and 2012 in the Paraná River. The horizontal black dashed line indicates the flood level of the floodplain. Source: ANA - Estação Fluviométrica of Porto São José, PR.

Data analysis. Environmental heterogeneity was measured based on the mean dispersion among the samples in a multivariate space (Anderson *et al.*, 2006; Al-Shami *et al.*, 2013). The rationale for this approach was that sampling periods with a greater average distance to the centroid of the physicochemical variables presented greater environmental heterogeneity (Anderson *et al.*, 2006; Al-Shami *et al.*, 2013). First, the matrix of physicochemical variables was centralized by subtracting each observation of each variable from its mean and then dividing that value by its standard deviation. The centralized matrix was transformed into a Euclidean distance matrix and used to order the samples (sample sites per collection period per year) using principal coordinate analysis (PCoA). Then, the mean distance between each sample and the centroid of the group was calculated (Anderson *et al.*, 2006; dry or flood season by year).

Beta diversity was measured using the same procedure as that used for environmental heterogeneity. The CPUE matrix of each guild was first transformed by $\log_{10}(x + 1)$ and then transformed into a Bray-Curtis dissimilarity matrix. The logarithmic transformation was applied on the raw CPUE matrix to downweigh rare and abundant species in

the ordination results. The Bray-Curtis dissimilarity matrix was used to order the samples using PCoA, and then the mean distance to the centroid of the groups (*i.e.*, the sampling period) was calculated. This average distance to the centroid was the measure of beta diversity for each sampling period. Sampling periods with higher mean distances relative to the centroid of species composition showed greater beta diversity (Anderson *et al.*, 2006). Beta diversity was calculated for a species composition matrix using each trophic or reproductive guild (Fig. 3).

The influence of the period (a categorical variable with two levels: dry and flood) and the mean distance to the environmental centroid (a continuous variable represented by environmental heterogeneity) on the beta diversity (*i.e.*, the response variable) was evaluated using generalized least squares (GLS) linear models. When estimating the parameters of the linear model, GLS allows for the insertion of correlation structures in the residuals of the model, which results in more precise parameter estimates (Zuur *et al.*, 2009). This approach was used to overcome the potential lack of independence among sampling units because sampling campaigns that were closer in time may present similar values of

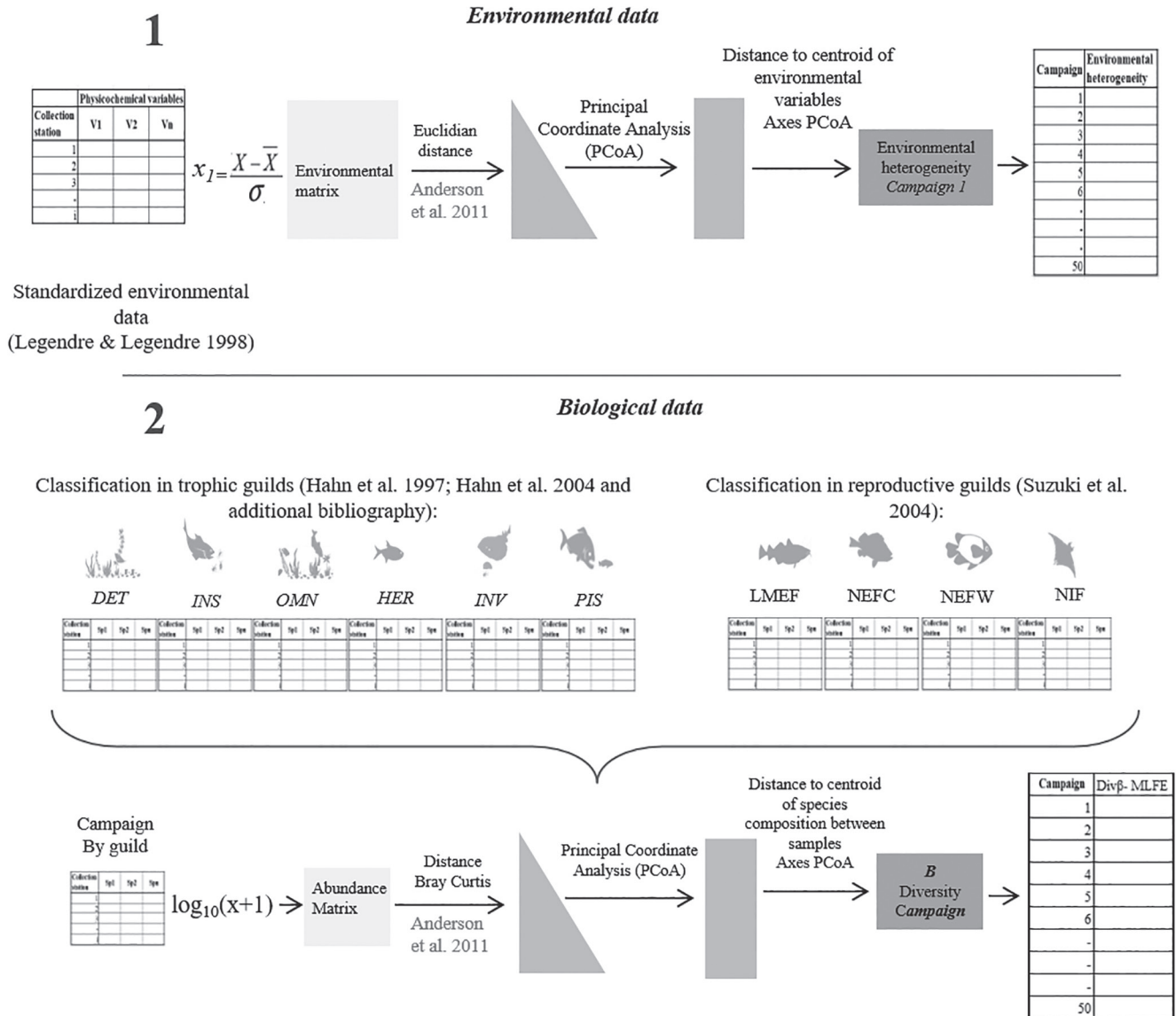


Fig. 3. Data analysis procedure for environmental heterogeneity and beta diversity for the different matrices of the trophic and reproductive guilds.

beta diversity or environmental heterogeneity (e.g., Zuur *et al.*, 2009; Ceschin *et al.*, 2018). Different structures of correlation (*i.e.*, no structure, first-order autoregressive, exponential, Gaussian, linear, rational quadratic, spherical, correlation matrix without structure; Pinheiro, Bates, 2000) were evaluated using the Akaike information criterion (AIC), and inferences were made using the model with the smallest AIC value. If more than one model shared the lowest AIC value, either of the two models was arbitrarily interpreted since the parameter estimates, standard errors and significance tests were the same. The GLS models were constructed separately for each guild. The residuals of the GLS models were homogeneous, and there was no multicollinearity since the hydrological period and the environmental heterogeneity were not correlated (polyserial correlation (Drasgow, 1986; Fox, 2016): $\rho = -0.26$, $P = 0.56$).

A significance level of 5% was adopted. All analyses were performed using the software R (R Core Team, 2015); additionally, the 'vegan' package (Oksanen *et al.*, 2015) was used to compute the distance to the centroid with the 'permdisp' function, and the 'nlme' package (Pinheiro *et al.*, 2015) was used for the GLS parameter estimates.

Results

The mean beta diversity measured for the reproductive guilds varied from 0.94 (non-migratory with internal fertilization) to 2.37 (non-migratory with external fertilization without parental care) (Fig. 4). For trophic guilds, herbivorous species presented the lowest mean values of beta diversity, while piscivorous and omnivorous species presented the highest values of beta diversity (Fig. 4).

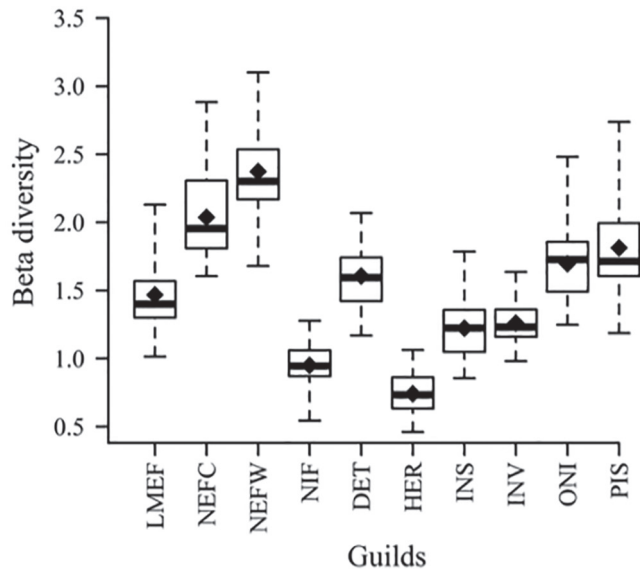


Fig. 4. Beta diversity variation among the guilds. The boxes represent the interquartile ranges, the horizontal lines indicate the medians, the bars indicate the minimum and maximum values, and the closed diamonds represent the mean beta diversity of each guild. LMEF: long-distance migratory and external fertilization; NEFC: non-migratory with external fertilization and parental care; NEFW: non-migratory with external fertilization without parental care; NIF: non-migratory with internal fertilization; DET: detritivorous; HER: herbivorous; INS: insectivorous; INV: invertivorous; ONI: omnivorous; and PIS: piscivorous.

The models indicated that the incorporation of autocorrelation structures improved the parameter estimates, except for the non-migratory with internal fertilization guild

(Tab. S3 - Available only as online supplementary file accessed with the online version of the article at <http://www.scie-lo.br/ni>). The first-order autocorrelation process described the correlation structure of the models for the species with long-distance migratory and external fertilization, non-migratory with external fertilization and parental care, non-migratory with external fertilization without parental care, and those that were detritivorous and piscivorous. The rational quadratic autocorrelation described the correlation structure of the model for the herbivorous, insectivorous, invertivorous and omnivorous trophic guilds.

In the non-migratory with external fertilization and parental care and the non-migratory with internal fertilization guilds (both guilds with parental care), the effect of environmental heterogeneity was moderated by the period (non-migratory with external fertilization and parental care: interaction between environmental heterogeneity and period, $t = 2.04$, $P = 0.05$; non-migratory with internal fertilization: interaction between environmental heterogeneity and period, $t = 2.19$, $P = 0.03$; Tab. 1; Fig. 5). For the non-migratory with external fertilization and parental care guild, during the dry period, the beta diversity tended to be higher as the environmental heterogeneity increased; in contrast, the beta diversity of this guild did not change in relation to the environmental heterogeneity during the flood period (Fig. 5a). The beta diversity of the non-migratory with internal fertilization guild followed a trend similar to that of the non-migratory with external fertilization and parental care guild during the dry period; however, during the flood period, there was a decreasing trend in beta diversity as environmental heterogeneity increased (Fig. 5b). The beta diversity of the other guilds did not vary in relation to periods or environmental heterogeneity (Tab. 1).

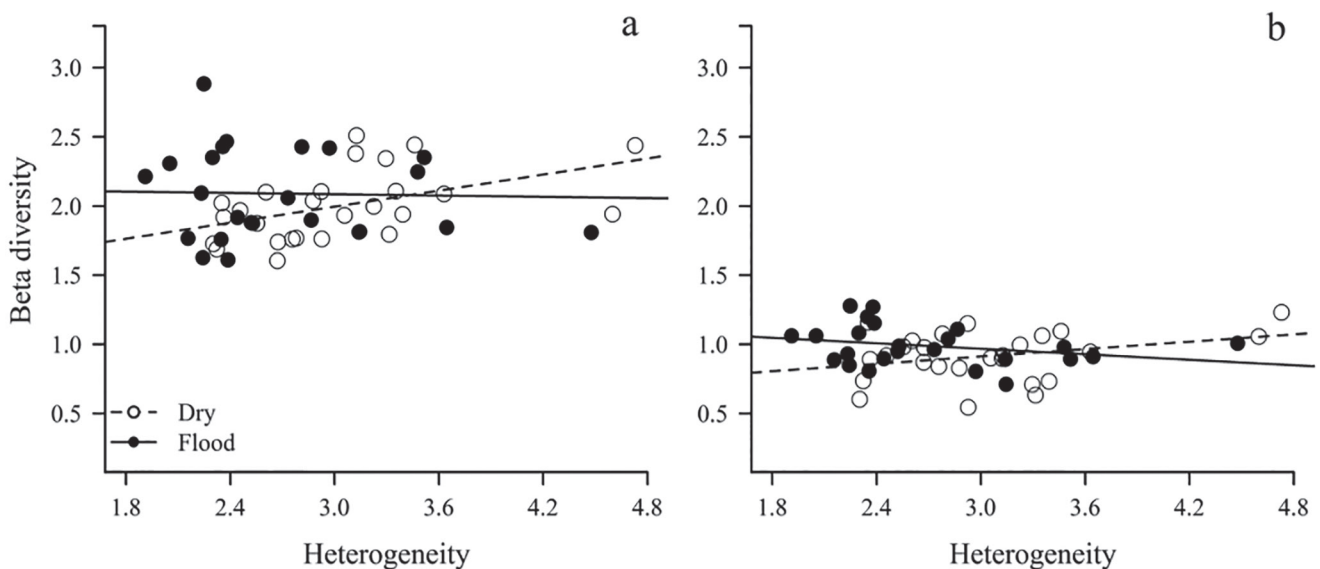


Fig. 5. Relationship between beta diversity (mean distance to centroid), environmental heterogeneity and period of the hydrological cycle. a. Beta diversity of non-migratory fish species with external fertilization and parental care (NEFC); b. beta diversity of non-migratory fish species with internal fertilization (NIF).

Tab. 1. Parameter estimates of generalized least squares linear models relating the beta diversity of each guild to the period and the environmental heterogeneity (EH). SE: standard error of the estimate. LMEF: long-distance migratory and external fertilization; NEFC: non-migratory with external fertilization and parental care; NEFW: non-migratory with external fertilization without parental care; NIF: non-migratory with internal fertilization; DET: detritivorous; HER: herbivorous; INS: insectivorous; INV: invertivorous; ONI: omnivorous; and PIS: piscivorous. EH*Per: interaction term between EH and period. The degrees of freedom for each parameter were 1, and the residual degrees of freedom of each model were 46. *The estimated parameters for the rational quadratic and 1st order autocorrelation were range and phi, respectively.

Guild	Parameter	Estimate	SE	<i>t</i>	<i>P</i>
MLFE	Intercept	1.66	0.18	9.26	< 0.01
	Period	-0.11	0.24	-0.47	0.64
	EH	-0.10	0.06	-1.73	0.09
	EH*Per	0.09	0.08	1.13	0.26
	1 st order autocorrelation	0.64			
NFEC	Intercept	2.14	0.21	10.10	< 0.01
	Period	-0.72	0.31	-2.37	0.02
	EH	-0.02	0.07	-0.24	0.81
	EH*Per	0.20	0.10	2.04	0.05
	1 st order autocorrelation	0.52			
NFES	Intercept	2.52	0.21	11.79	< 0.01
	Period	-0.52	0.30	-1.74	0.09
	EH	-0.05	0.07	-0.67	0.51
	EH*Per	0.16	0.10	1.66	0.10
	1 st order autocorrelation	0.61			
NFI	Intercept	1.11	0.15	7.62	< 0.01
	Period	-0.54	0.21	-2.53	0.01
	EH	-0.05	0.05	-0.88	0.38
	EH*Per	0.15	0.07	2.19	0.03
DET	Intercept	1.31	0.18	7.3	< 0.01
	Period	-0.04	0.26	-0.13	0.89
	EH	0.09	0.06	1.58	0.12
	EH*Per	0.03	0.08	0.32	0.75
	1 st order autocorrelation	0.48			
HER	Intercept	0.69	0.13	5.47	< 0.01
	Period	-0.16	0.18	-0.89	0.37
	EH	0.01	0.04	0.11	0.91
	EH*Per	0.08	0.06	1.35	0.18
	Rational quadratic autocorrelation	0.55			
INS	Intercept	1.24	0.17	7.36	< 0.01
	Period	-0.14	0.25	-0.55	0.59
	EH	-0.03	0.06	-0.44	0.66
	EH*Per	0.08	0.08	0.99	0.33
	Rational quadratic autocorrelation	0.73			
INV	Intercept	1.20	0.12	10.14	< 0.01
	Period	0.11	0.17	0.64	0.52
	EH	0.02	0.04	0.44	0.66

Guild	Parameter	Estimate	SE	<i>t</i>	<i>P</i>
ONI	EH*Per	-0.03	0.06	-0.48	0.63
	Rational quadratic autocorrelation	0.61			
	Intercept	1.85	0.23	8.21	< 0.01
	Period	-0.65	0.33	-1.94	0.06
	EH	-0.03	0.08	-0.45	0.65
PIS	EH*Per	0.18	0.11	1.64	0.11
	Rational quadratic autocorrelation	0.59			
	Intercept	1.97	0.23	8.55	< 0.01
	Period	-0.60	0.33	-1.81	0.08
	EH	-0.04	0.07	-0.47	0.64
	EH*Per	0.16	0.11	1.55	0.13
	1 st order autocorrelation	0.53			

Discussion

Several authors have reported positive relationships between beta diversity and environmental heterogeneity for many groups of organisms with different dispersion abilities (Soininen *et al.*, 2007; Bini *et al.*, 2014; Heino *et al.*, 2015b); this result is expected because heterogeneous conditions increase niche opportunities for a greater number of different species than do homogeneous conditions (Bini *et al.*, 2014). Thus, the increase in environmental heterogeneity reduces the similarity in assemblage composition and, consequently, increases beta diversity. The observed results suggest that this relationship may be particularly important for sedentary guilds because they cannot disperse to sites with better environmental conditions; thus, these guilds experience competition processes that can generate local extinctions that increase beta diversity. For instance, if two sites share the same species composition, the local extinction of a species from one site will increase the difference in composition (*i.e.*, an increase in beta diversity) between both sites (Olden, Poff, 2003; Petsch, 2016).

The hypothesis proposed in this study was partially supported since only the beta diversity of two guilds varied as a function of environmental heterogeneity or differed between periods of the hydrological cycle. None of the trophic guilds had beta diversity values that responded to the influence of environmental heterogeneity and periods of the hydrological cycle; these results suggest that (i) the beta diversity of trophic guilds is poorly predicted by these variables, and (ii) fish feeding is plastic enough to adapt to environmental changes without changing the composition of the fish assemblages that were analyzed in the Upper Paraná River floodplain. The effect of environmental heterogeneity on beta diversity was mediated by floods and dry periods in only two reproductive guilds, both of which had parental care (*i.e.*, non-migratory with external fertilization and parental care and non-migratory with internal fertilization). In these guilds, during the dry period, a positive relationship was observed between environmental heterogeneity and beta diversity. This result can be explained by the fact that species with parental care may have a lower dispersion ca-

capacity. This lower dispersion capacity causes a shorter duration of movements (Giam, Olden, 2018) because species that demonstrate parental care invest time and energy in caring for offspring instead of other activities, such as somatic growth, feeding and gonadal development (McBride *et al.*, 2015; Brownscombe *et al.*, 2017). When environmental conditions are not optimal, species of guilds with parental care may have more difficulty in dispersing to more suitable environments, and this lack of dispersion between environments increases the dissimilarity in the composition of the assemblages of these guilds (Heino, Grönroos, 2013).

The beta diversity of guilds that do not show parental care did not show variation in relation to environmental heterogeneity or dry and flood periods. A possible explanation for this lack of relationship is the active dispersal of these fish (Suzuki *et al.*, 2004). Fish dispersal is limited to the existence of channels connecting waterbodies (Suzuki *et al.*, 2004; Padiál *et al.*, 2014; Penha *et al.*, 2017). Thus, even an ephemeral connection between lakes and the main river in the dry period may allow fish dispersal and their presence in different sites, which may hinder a potential effect caused by the hydrological period. This hypothesis may even apply to guilds that do not migrate long distances. It is also worth mentioning that intermittent flow pulses that occur on the floodplain as a result of the operation of upstream dams to meet daily or weekly peaks in energy demand may have a potential influence (Souza-Filho *et al.*, 2004). These oscillations can provide sufficient connections that homogenize assemblages even in periods of drought. In addition, beta diversity may possibly be influenced by variables that were not considered in this work, such as primary productivity (Bini *et al.*, 2014) and interspecific interactions (Van Allen *et al.*, 2017).

Recently, several authors have questioned the relationship between beta diversity and environmental heterogeneity. Chase (2010) observed a weak or even absent relationship between environmental heterogeneity and beta diversity in experimental ponds, indicating that other factors, such as productivity, can control variation in beta diversity. Apparently, in environments with higher temperatures and nutrient richness, stochastic processes can determine the variation in beta diversity (Chase, 2010). In addition, Al-Shami *et al.* (2013) reported that environmental heterogeneity was not necessarily associated with beta diversity; rather, environmental heterogeneity may be collinear with other environmental variables that influence beta diversity. Heino *et al.* (2015a) reasoned that several factors influenced the environmental heterogeneity and beta diversity relationship, including the size of the study area, regional history, landscape characteristics and differential dispersal abilities of organisms. These studies show that even as our understanding about beta diversity patterns improves, we are still far from having a concise interpretation, especially in tropical floodplain ecosystems.

In conclusion, the compositions of the non-migratory with external fertilization and parental care and the non-migratory with internal fertilization guilds were more sensitive to environmental heterogeneity, which was caused by the pulse of

droughts and floods. On the other hand, the lack of interaction between the beta diversity and the environmental heterogeneity generated by the hydrological cycle in the other guilds may indicate that, in fish assemblages with high dispersion rates, the variation in beta diversity has no clear pattern, and it may be necessary to reconsider the processes that are currently used to interpret the relationship between beta-diversity, environmental heterogeneity and flood pulses. Specifically, the predicted positive relationship between beta-diversity and environmental heterogeneity or isolation (dry periods in our case) may not hold for guilds with high dispersal potential of these guilds (Logue *et al.*, 2011; Heino *et al.*, 2015a). The results of this study further suggest that reproductive guilds influence the assessment of correlates effects on beta diversity variation, such as environmental heterogeneity and flood events. Assessing the variation of beta-diversity separately by guilds other than dispersal in a deconstruction framework (*sensu* Marquet *et al.*, 2004) may provide information that dispersal alone cannot provide and to help to disentangle dispersal and environmental filtering effects on beta diversity. For instance, non-migratory guilds may be more prone to dispersal limitation. However, only the beta-diversity of guilds with some type of parental care responded to environmental heterogeneity and floods, suggesting that these guilds were more likely to be influenced by environmental filtering than non-migrants without parental care.

Acknowledgments

We thank the Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura (Nupélia) and the Programa de Pesquisas Ecológicas de Longa Duração (PELD/CNPq) that provided the infrastructure and database access required for this research. We are grateful to the constructive comments of anonymous reviewers that improved the manuscript. AG and JCGO thank the CNPq for scholarships, and AAA received CNPq research grants.

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Submitted March 03, 2018

Accepted November 13, 2018 by Franco Teixeira de Mello