Hydrobiologia (2018) 805:377–389
DOI 10.1007/s10750-017-3325-x

PRIMARY RESEARCH PAPER

Correlates of fish and aquatic macrophyte beta diversity in the Upper Paraná River floodplain

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Received: 20 July 2016 / Revised: 21 July 2017 / Accepted: 31 July 2017 / Published online: 8 August 2017

Abstract We investigated correlates of long-term temporal variation in the beta diversity of macrophytes, sedentary fish, and migratory fish communities in the Upper Paraná River floodplain. Two metrics of among-site variation in community composition were calculated in up to 45 sampling periods over 12 years for each biological group. We then tested the following beta diversity correlates: richness and proportion of non-native species, ecosystem productivity proxies, environmental heterogeneity, and hydrological regime proxies. Despite the uncertainty regarding the best model, we found that environmental heterogeneity was the most consistent predictor of beta diversity variation. Non-native species (richness or proportional abundance), productivity, and hydrology were not consistently correlated with beta diversity. However, models results suggest that the likely intensification of threats caused by oligotrophication, non-native species spread, and damming may trigger the effects of these predictors. Thus, we suggest that continuation of the long-term ecological study in the Upper Paraná River floodplain is key to our better understanding of the role of these processes in beta diversity variation.

Keywords Biotic homogenization · Hydrological regime · Non-native species · Environmental heterogeneity · Productivity · Temporal autocorrelation

Handling editor: Koen Martens

Electronic supplementary material The online version of this article (doi:10.1007/s10750-017-3325-x) contains supplementary material, which is available to authorized users.

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Introduction

Temporal changes in the compositional dissimilarity across space, beta diversity, can reveal the likely causes of biotic homogenization, one of the main threats to biodiversity in the Anthropocene (Olden & Poff, 2003). In this sense, research on correlates of beta diversity, the focus of our study, has increased over the last 10 years (Melo et al., 2011). Beta diversity can be quantified using different coefficients of (dis)similarity (Koleff et al., 2003). However, when beta diversity is quantified by these coefficients, two different components are "confounded" (Harrison et al., 1992; Baselga et al., 2007): turnover and nestedness. For this reason, Baselga et al. (2007) and Baselga (2010) derived indexes that disentangle these two components of beta diversity (see also Baselga & Orme, 2012). Following a slightly different approach, Anderson et al. (2011) described two conceptual types of beta diversity: directional turnover in community structure and variation in community structure. In the first type (i.e., directional turnover), beta diversity is given by the "change in community structure from one sampling unit to another along a spatial, temporal or environmental gradient" (Anderson et al., 2011). In a typical application of this type of beta diversity, an ecologist tests the relationship between compositional and environmental dissimilarities using matrix correlation methods. In the second type (i.e., variation), beta diversity is quantified considering community data (species × sites) gathered at different regions, time periods, or experimental treatments. For instance, variation in community structure can be quantified when community data are gathered at different areas (e.g., ecoregions). Thus, this type of beta diversity can be quantified for each area (Anderson et al., 2006, 2011; see Heino et al., 2013; Astorga et al., 2014; Bini et al., 2014 as examples of empirical studies using this approach).

Typically, correlates of beta diversity are used to infer the role of different mechanisms in explaining beta diversity variation. A positive relationship between beta diversity and spatial extent, for example, would suggest the importance of dispersal limitation (all else being equal). Similarly, beta diversity may increase with increasing environmental heterogeneity as different species compositions are sorted across local communities (Melo et al., 2009; Brown & Swan, 2010; Astorga et al., 2014). Productivity is another common predictor of beta diversity (e.g., Chase & Leibold, 2002; Bai et al., 2007; Gardezi & Gonzalez, 2008; Langenheder et al., 2012; Astorga et al., 2014). A positive relationship between beta diversity and productivity may arise because the strength of environmental filtering decreases with productivity (Chase, 2010). Thus, different sets of species from a species pool can thrive under high productivity conditions, resulting in high beta diversity. However, a decrease in beta diversity may occur in response to cultural eutrophication (i.e., in environments with high productivity due to the anthropogenic enrichment of nutrients; Zorzal-Almeida et al., 2017). In this case, one can envisage a scenario of dominance by a few high nutrient-tolerant species associated with the local extinction of nutrient-sensitive species. The spread of non-native species may decrease (biotic homogenization) or increase (biotic differentiation) beta diversity (Mckinney & Lockwood, 1999; Olden & Poff, 2003). For instance, Erös (2007) found evidence of an association between non-natives and the homogenization of fish communities in Hungary. Rahel (2000) found a similar pattern of decreased beta diversity across the United States (see also Rahel, 2002; Qian & Ricleffs, 2006 for a study with North American flora). On the other hand, Marchetti et al. (2006) found an increase in the beta diversity of freshwater fishes of California across time due to urbanization, introductions of non-native fishes, and the local extinction of natives.

In addition to the abovementioned correlates of beta diversity, water level is thought to be of paramount importance in floodplains (Thomaz et al., 2007). During floods, a decline in beta diversity may be predicted due to the increased similarity in environmental conditions (as water masses are environmentally more similar) and due to the increased hydrological connectivity between aquatic habitats (e.g., different lakes), facilitating the exchange of species between them (both via passive and active dispersal; Bozelli et al., 2015). In contrast, during periods of low water levels, different aquatic habitats within a floodplain may undergo idiosyncratic environmental variations. For example, in a given shallow lake, a turbidity pulse may occur due to bioturbation and the action of winds, whereas this pulse may not occur in another vegetated lake. Additionally, during periods of low water levels, the aquatic environments of a floodplain are less hydrologically connected. Thus, most likely due to both high environmental heterogeneity and low hydrological connectivity, an increase in beta diversity can be predicted.

In this study, we used a dataset from the Long-term Ecological Research Program in the Upper Paraná River floodplain (Brazil; Paraná and Mato Grosso do Sul states; see reports at http://www.peld.uem.br/), which was gathered over 12 years. For each sampling campaign, we estimated fish and aquatic macrophyte beta diversity using two metrics (turnover and variation in community structure; following Baselga, 2010 and Anderson et al., 2011, respectively). Our main goal was to model the relationship between metacommunity beta diversity (see Fig. S1) and the following explanatory variables: environmental heterogeneity (i.e., differences in environmental conditions between sampling sites within each sampling period), productivity (as proxied by total phosphorous and nitrogen concentrations), non-native species richness, and water level. We tested these relationships separately for sedentary fish, long-distance migratory fish, and macrophytes. These groups may differ in their responses to the explanatory variables because they have, for instance, different dispersal modes (active for fish with sedentary or migratory behavior and passive for macrophytes). De Bie et al. (2012), for instance, found that the community variation of active dispersals (fish and amphibians) showed strong spatial patterns and, in comparison to passive dispersal (e.g., bacteria, phytoplankton, and zooplankton), these groups were poorly predicted by environmental variables. Previous studies, as described above, have found mixed results regarding the relationship between beta diversity and explanatory variables, making it difficult to draw specific predictions. However, based on niche theory, previous experimental evidence, and results of studies with sampling designs similar to ours, we tentatively predicted positive relationships between beta diversity and both productivity (e.g., Chase, 2010) and environmental heterogeneity (e.g., Astorga et al., 2014). Similarly, we anticipate a negative relationship between beta diversity and water level (e.g., Bozelli et al., 2015). We also expected that beta diversity would be negatively correlated with non-native fish and macrophyte species richness and fish abundance. The study of the temporal variation in beta diversity (Langenheder et al., 2012; Angeler, 2013; Soares et al., 2015; Wojciechowski et al., 2017), as that described herein, has an advantage over some of the past attempts (see references above) because the sampling sites (local communities; Fig. S1) are the same in all sampling campaigns, and therefore, it is not necessary to control for the spatial extent. This is an important advantage because it rules out the confounding effect of spatial extent on environmental heterogeneity, which is thought to be a key predictor of beta diversity.

Materials and methods

Study area

Surveys were conducted at the Upper Paraná River floodplain (Brazil; 53°00′W–53°40′W; 22°30′S–23°00′S; Fig. S2), which encompasses two formal protected areas: the State Park of the Ivinhema River Floodplain and the Environmental Protection Area of the Isles and Floodplains of the Paraná River. The Upper Paraná River floodplain has a hydrological regime characterized by a dry season (June–September) and a wet season (October–February) with flood pulses (Agostinho et al., 2004). However, the frequency, amplitude, and duration of floods have been altered by the hydroelectric reservoirs upstream (Souza Filho, 2009). Nevertheless, peaks of floods and droughts were recorded from 2000 to 2012 (Fig. 1). In this area, a Long-Term Ecological Research Program has been in place since 2000, in which samplings were carried out in lakes and channels belonging to three hydrological and geomorphological subsystems: (i) the Paraná River Subsystem, (ii) the Baía River Subsystem, and (iii) the Ivinhema River Subsystem (Padial et al., 2012). The sampling sites were distributed over these three subsystems (Fig. S2), aiming to represent different environmental gradients in the floodplain (Padial et al., 2012). For example, the Paraná River subsystem is, comparatively, characterized by high water transparency and flow, low nutrient concentrations, low values of pH, and frequent flood pulses of low intensity; the Baía River subsystem has relatively low flow, a high nitrate concentration, low values of pH, and a high dissolved carbon concentration; and the Ivinhema River subsystem has relatively intermediate flow, high turbidity, and a high phosphorus concentration (Roberto et al., 2009). According to Souza Filho (2009), floods of the Paraná and Ivinhema Rivers affect the entire floodplain, during which water exchanges occur through the lakes, permanent channels, and over terrestrial landscapes and intermittent channels (see a detailed description of the flooding regime in the Upper Paraná River floodplain in Agostinho et al., 2004).

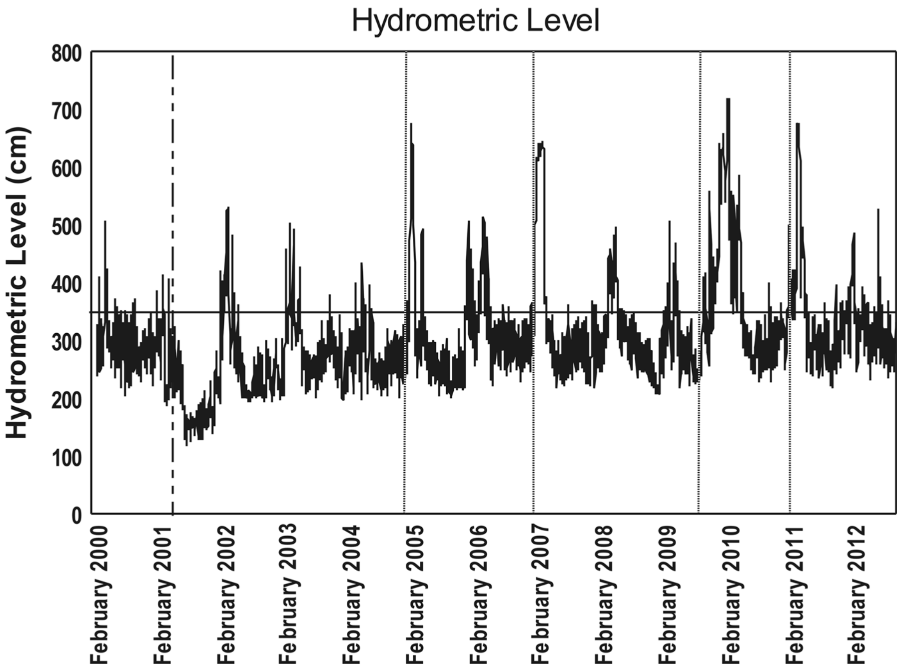

Fig. 1 Hydrometric levels (daily measures) in the Upper Paraná River floodplain over the 12 years of this study (modified from Dittrich et al., 2016). The *horizontal solid line* indicates the threshold for flooding events (3.5 m)

Data

Macrophytes, fish, and limnological variables were sampled quarterly from 2000 to 2012. Samplings were carried out in February/March, May/June, August/September, and November/December. The number of sampling campaigns (i.e., months) was 38 for macrophytes and 45 for fish. For macrophytes, samplings were carried out in connected and isolated lakes ($n = 6$ sites; Fig. S2). Connected lakes are those with a permanent connection with the river. Isolated lakes are those that are only rarely connected to the river (i.e., during extreme floods). We gathered data on the presence and absence of aquatic macrophytes by surveying the shorelines of the lakes from a boat, using a grapnel to record submerged vegetation. Fishes were caught both in channels and lakes ($n = 9$ sites; Fig. S2). We used gillnets with different mesh sizes to capture fish in lakes and channels. A detailed description of the sampling procedures can be found elsewhere (Padial et al., 2012, 2014). Because a previous study suggested that migration affects the relationship between community structure and environmental gradients (Padial et al., 2014), we analyzed the data of sedentary and migratory fish separately. The following limnological variables were obtained at all sampling sites and campaigns: water temperature (°C), dissolved oxygen (mg l^{-1}), pH, conductivity (µS cm^{-1}), Secchi disk depth (m), turbidity (NTU), inorganic suspended matter (mg l^{-1}), organic suspended matter (mg l^{-1}), chlorophyll-a (µg l^{-1}), total nitrogen (µg l^{-1}), and total phosphorus (µg l^{-1}).

Response variables and beta diversity components

For each month, beta diversity was estimated using two metrics (always using presence/absence data). First, we used the approach developed by Anderson et al. (2006). Accordingly, we applied a Principal Coordinate Analysis (PCoA; Gower, 1966) to the Sørensen dissimilarity matrix between samples. Then, the average distance from local communities to the centroid of the metacommunity was considered a measure of beta diversity in each period (d_{CEN}: Sørensen distance to group centroid; see Anderson et al., 2006 and Fig. S3). The second index, Simpson dissimilarity (β_{SIM}), was estimated using the approach proposed by Baselga (2010, 2013), which is a multiple-site dissimilarity index not affected by species richness variation. In this approach, beta diversity, as given by the Sørensen dissimilarity ($\beta_{\text{SØR}}$), can be additively partitioned into two components: "dissimilarity due to species replacement" (β_{SIM}) and "dissimilarity due to species nestedness"

(β_{NES}) (Baselga & Orme, 2012). Thus, to estimate β_{SIM}, we calculated $\beta_{SIM} = \beta_{SØR} - \beta_{NES}$. A higher value of β_{SIM}, compared to β_{NES}, would then indicate that beta diversity is mainly due to species replacement (or spatial turnover) during each sampling campaign.

Explanatory variables

We used the following sets of explanatory variables in this study (for acronyms and summary statistics, see Table 1):

Productivity—We included the mean values of total nitrogen and total phosphorus (across sites) as surrogates of productivity, since these variables are commonly related to the productivity of different aquatic ecosystems (Vitousek et al., 1997; Langenheder et al., 2012). *Environmental heterogeneity*—For each sampling period, environmental heterogeneity was estimated in two ways: (1) using the approach proposed by Anderson et al. (2006), with a PCoA applied to a standardized Euclidean matrix derived from the limnological variables (EH); and (2) by calculating the coefficient of variation of these variables across sampling sites per period (CV). *Hydrology*—Hydrometric levels data were measured at the Paraná River (Porto Rico Municipality, Paraná State, Brazil). We used different strategies to generate variables accounting for the effect of floods and droughts on beta diversity. We emphasize, however, that these variables have a common interpretation: a high hydrometric level is related to high connectivity that may decrease beta diversity by increasing dispersal. First, hydrometric levels were estimated considering different time lags, since community composition may respond to past hydrometric level variation (Thomaz et al., 2007; Soares et al., 2015). Based on the same approach, Soares et al. (2015) proposed five measures of hydrometric level: HL10, HL20, HL30, HL40, and HL50, where the numbers (after H) represent the number of days before samplings that were used to calculate the average hydrometric levels. We also propose two other approaches to represent flood events (i.e., when the water level exceeds 350 cm; see Thomaz et al., 2004 and Fig. 1). First, we used the following variables: number of days since the last flood (NDF), duration of the last flood (DF), and the ratio DF/NDF (*R*). This ratio aimed to represent a balance between how recent the flood was (represented by NDF) and its intensity (represented by DF). Higher values of *R* represent periods with high flood effects (recent

Table 1 Summary statistics of the explanatory variables used in this study

Explanatory variables	Acronyms	Units	Minimum	Maximum	Mean	SD
Environmental heterogeneity	EH		1.70	4.09	2.43	0.46
Average coefficient of variation (environmental variables)	CV	%	47.02	215.79	97.82	35.05
Total phosphorus	Total *P*	$\mu g\ l^{-1}$	15.90	98.70	47.37	15.92
Total nitrogen	Total *N*	$\mu g\ l^{-1}$	243.68	1357.40	699.94	314.66
Non-native species richness	NN	Number of species	20.00	50.00	36.33	7.39
Non-native species proportion	NNP	%	0.00	31.40	11.77	7.98
Number of days since the last flood	NDF	Days	1.00	220.00	60.84	61.04
Duration of the last flood	DF	Days	1.00	34.00	5.33	7.50
DF/NDF	R		0.01	28.00	1.91	5.76
Hydrometric level (average—10 days before sampling)	HL10	cm	153.05	467.20	303.89	60.07
Hydrometric level (average—20 days before sampling)	HL20	cm	152.85	443.00	305.28	58.41
Hydrometric level (average—30 days before sampling)	HL30	cm	155.35	469.00	303.32	55.87
Hydrometric level (average—40 days before sampling)	HL40	cm	155.21	524.00	303.84	59.78
Hydrometric level (average—50 days before sampling)	HL50	cm	155.22	539.00	305.75	62.36

The results for the binary variables [short-recent floods (SRF), long-recent floods (LRF), and long-old floods (LOF)] are not shown and/or intense floods), while lower values represent periods with low flood effects (old and/or bland floods). Second, we used binary proxies for the hydrological regime (considering 350 cm as a threshold) that indicated the presence/absence of (i) short-recent floods (SRF: floods that occurred during the last thirty days before sampling and lasted less than eight days); (ii) long-recent floods (LRF: floods that occurred during the last thirty days and lasted eight days or more); and (iii) long-old floods (LOF: floods that lasted eight days or more and occurred in the last year, but not in the last 30 days). Using alternative binary variables, it is possible that a certain sampling period has no flood event according to any classification above, and it is possible that another period has more than one flood event. The definitions of recent/old and short/long floods were arbitrary, as well as the time span used to calculate hydrometric levels (see also Soares et al., 2015). *Invasion*—We also tested for relationships between beta diversity and non-native species richness (NN) and relative abundance of non-native species (NNP—only for fish metacommunities given the lack of abundance data for macrophytes). *Trends in beta diversity*—We also used a variable called "time" to represent the temporal patterns of biotic differentiation or homogenization. This variable was a vector containing the chronological order of the sampling periods (from 1 to 38 for macrophytes and from 1 to 45 for fish).

Data analysis

To analyze the relationships between beta diversity (d_{CEN} or β_{SIM}, in separate models) and the aforementioned explanatory variables, we used generalized least square (GLS) models assuming a compound symmetry error structure (see Pinheiro & Bates, 2000). Different models (44 for d_{CEN} and β_{SIM}; see Table S1) for each biological group were compared using the Akaike information criterion and Akaike weights. Inferences were based on the model-averaging approach, considering models within a 95% confidence set (Burnham & Anderson, 2002). Analyses were performed in the R environment (R Core Team, 2015), using the 'vegan' (Oksanen et al., 2013), 'nlme' (Pinheiro et al., 2015), and "MuMIn" (Bartón, 2016) packages.

Results

Beta diversity varied widely over time for all biological groups (Fig. 2). In general, beta diversity values for fish were higher than those for macrophytes (time series averages: $d_{\mathrm{CEN}} = 0.48$, 0.44, and 0.35 and $\beta_{\mathrm{SIM}} = 0.60$, 0.66, and 0.58 for migratory fish, sedentary fish, and aquatic macrophytes, respectively). The comparison between the results of $ß_{\mathrm{SIM}}$ (above) and β_{NES} (0.17, 0.08, and 0.10, respectively) indicates that the total beta diversity in the Upper Paraná River floodplain is mainly attributable to spatial turnover. The correlations between our metrics of beta diversity (d_{CEN} and β_{SIM}) were all significant, but these correlations were not strong enough (e.g., ≥ 0.95) to justify the use of only one metric (Pearson's correlations between d_{CEN} and $\beta_{\mathrm{SIM}} = 0.56$, 0.76, and 0.84 for migratory fish, sedentary fish, and aquatic macrophytes, respectively; P values <0.001).

Our results indicated a high uncertainty regarding the best model to predict beta diversity (Akaike weights ranging from zero to 0.31; for all results, see Table S2). Model-averaging results indicated that migratory fish beta diversity, as measured by d_{CEN}, declined over time and with the increase in total P. NPP and EH (or CV) were positively correlated with this metric. We did not find strong correlates of migratory fish beta diversity as measured by β_{SIM}. Sedentary fish beta diversity (d_{CEN}) was positively correlated with NPP, CV, and hydrometric levels (HL10 and HL20). Similar results were obtained for β_{SIM}; however, only NNP and EH appeared to be important predictors. Aquatic macrophytes beta diversity (d_{CEN}) was positively correlated with our measures of environmental heterogeneity (CV and EH) and negatively correlated with DF. Using β_{SIM}, the aquatic macrophyte beta diversity was negatively correlated with DF and R (Table 2).

Discussion

Macrophyte and fish beta diversity in the Upper Paraná River floodplain was, on average, dominated by the turnover component of beta diversity (species replacement), as indicated by the highest values of the Simpson-based multiple-site index ($\beta_{\mathrm{SIM}} > \beta_{\mathrm{NES}}$, following Baselga, 2010). The high spatial heterogeneity of environmental factors in floodplain systems may

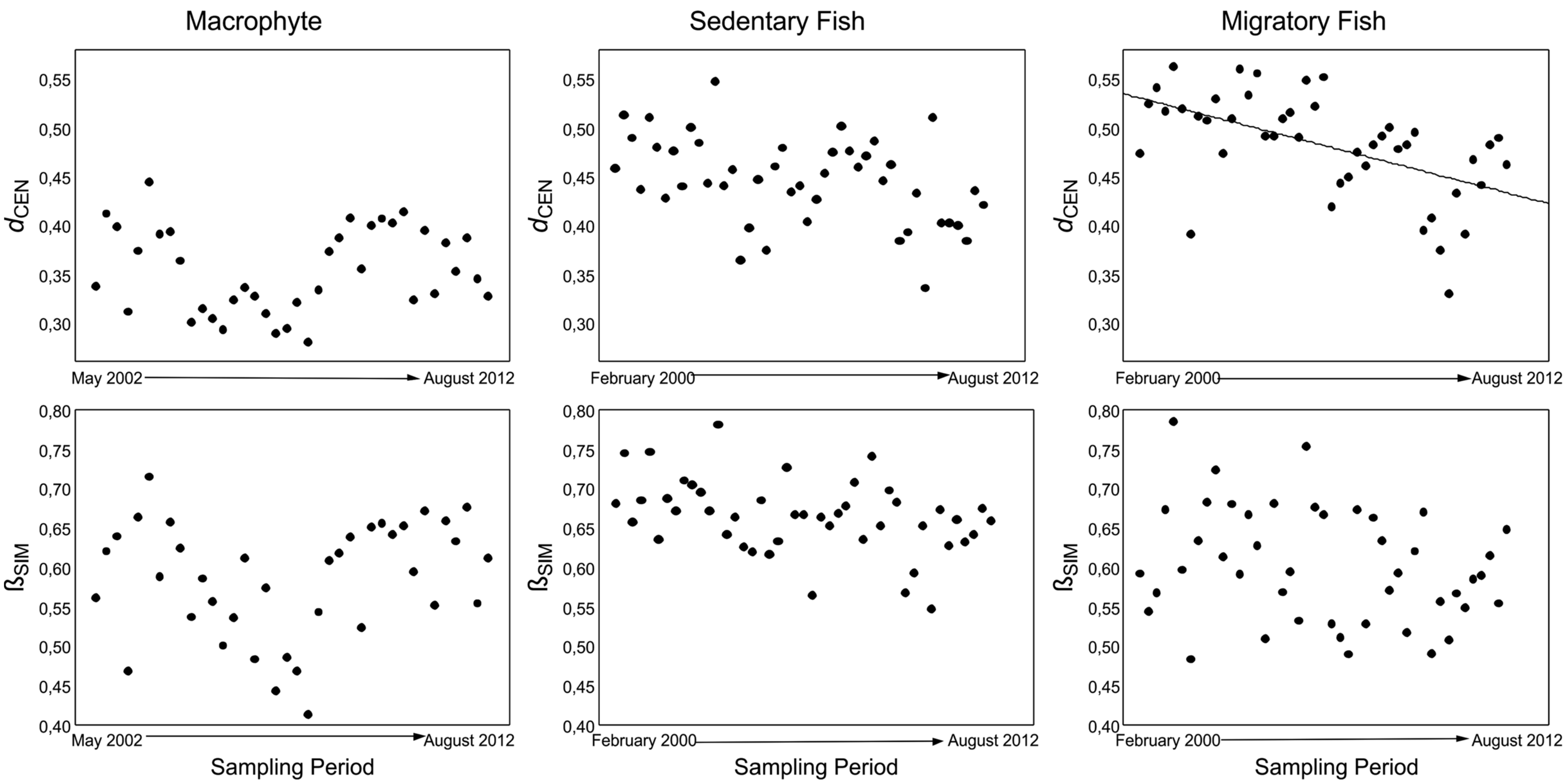

Fig. 2 Temporal patterns of Sørensen distance to group centroid (d_{CEN}) and Simpson dissimilarity (β_{SIM}) for all metacommunities

Table 2 Model-averaging results predicting beta diversity variation in the Upper Paraná River floodplain

Groups	Metric	Correlates	Estimate	SE	Adj SE	Z	P
Migratory Fish	d_{CEN}	(Intercept)	0.4732	0.0475	0.0488	9.69	0.0000
		Time	−0.0025	0.0008	0.0008	3.12	0.0018
		NN	−0.0003	0.0013	0.0013	0.24	0.8124
		NNP	0.2737	0.0732	0.0756	3.62	0.0003
		EH	0.0436	0.0155	0.0160	2.73	0.0063
		Total P	−0.0010	0.0005	0.0005	2.03	0.0423
		LRF	0.0099	0.0145	0.0150	0.66	0.5094
		LOF	0.0049	0.0179	0.0185	0.26	0.7927
		SRF	0.0038	0.0129	0.0134	0.28	0.7784
		CV	0.0456	0.0197	0.0204	2.24	0.0253
	β_{SIM}	(Intercept)	0.5688	0.0839	0.0865	6.57	0.0000
		Time	−0.0020	0.0015	0.0016	1.30	0.1950
		NN	0.0028	0.0025	0.0025	1.09	0.2740
		NNP	0.1187	0.1419	0.1465	0.81	0.4180
		CV	−0.0142	0.0371	0.0383	0.37	0.7110
		Total P	−0.0001	0.0009	0.0009	0.08	0.9330
		LOF	−0.0498	0.0331	0.0342	1.46	0.1450
		EH	0.0050	0.0308	0.0318	0.16	0.8740
		SRF	−0.0200	0.0253	0.0262	0.77	0.4440
		LRF	0.0008	0.0282	0.0291	0.03	0.9790
		Total N	0.0000	0.0001	0.0001	0.42	0.6730
Sedentary Fish	d_{CEN}	(Intercept)	0.4509	0.0476	0.0489	9.23	0.0000
		Time	−0.0004	0.0008	0.0008	0.51	0.6122
		NN	−0.0024	0.0012	0.0013	1.89	0.0589
		NNP	0.1364	0.0527	0.0542	2.52	0.0118
		CV	0.0444	0.0187	0.0193	2.31	0.0210
		Total P	−0.0004	0.0004	0.0004	0.85	0.3930
		LOF	0.0206	0.0165	0.0171	1.21	0.2275
		LRF	0.0193	0.0147	0.0152	1.27	0.2030
		SRF	0.0066	0.0128	0.0132	0.50	0.6168
		EH	0.0282	0.0154	0.0158	1.78	0.0745
		HL10	0.0003	0.0001	0.0001	2.85	0.0043
		R	0.0018	0.0010	0.0011	1.68	0.0935
		Total N	0.0000	0.0000	0.0000	1.09	0.2780
		HL20	0.0002	0.0001	0.0001	2.19	0.0287
	β_{SIM}	(Intercept)	0.6047	0.0540	0.0555	10.89	0.0000
		Time	−0.0010	0.0009	0.0009	1.09	0.2741
		NN	−0.0011	0.0014	0.0014	0.76	0.4454
		NNP	0.1178	0.0555	0.0572	2.06	0.0395
		EH	0.0429	0.0170	0.0176	2.44	0.0147
		Total P	−0.0003	0.0005	0.0005	0.53	0.5975
		LOF	0.0133	0.0194	0.0200	0.66	0.5067
		SRF	0.0132	0.0138	0.0142	0.93	0.3551
		LRF	0.0068	0.0167	0.0172	0.40	0.6914

Table 2 continued

Groups	Metric	Correlates	Estimate	SE	Adj SE	*Z*	*P*
		CV	0.0418	0.0219	0.0226	1.85	0.0647
		Total *N*	0.0000	0.0000	0.0000	0.01	0.9919
		R	0.0001	0.0011	0.0012	0.05	0.9644
		DF	0.0005	0.0009	0.0009	0.56	0.5776
Macrophytes	d_{CEN}	(Intercept)	0.3097	0.0408	0.0420	7.38	0.0000
		Time	−0.0001	0.0006	0.0007	0.10	0.9239
		NN	0.0023	0.0159	0.0165	0.14	0.8890
		CV	0.0740	0.0252	0.0262	2.83	0.0047
		Total *P*	−0.0004	0.0003	0.0003	1.40	0.1631
		LOF	−0.0177	0.0232	0.0241	0.73	0.4634
		LRF	−0.0144	0.0186	0.0192	0.75	0.4522
		SRF	−0.0067	0.0168	0.0174	0.39	0.7001
		EH	0.0466	0.0173	0.0180	2.59	0.0096
		DF	−0.0012	0.0005	0.0006	2.21	0.0274
		R	−0.0009	0.0006	0.0006	1.43	0.1518
		Total *N*	0.0000	0.0000	0.0000	1.04	0.2982
	β_{SIM}	(Intercept)	0.5827	0.0747	0.0770	7.57	0.0000
		Time	0.0006	0.0011	0.0012	0.53	0.5972
		NN	−0.0101	0.0306	0.0316	0.32	0.7482
		CV	0.0671	0.0441	0.0458	1.46	0.1431
		Total *P*	−0.0009	0.0005	0.0006	1.65	0.0997
		LOF	−0.0642	0.0405	0.0421	1.53	0.1271
		EH	0.0476	0.0299	0.0311	1.53	0.1260
		LRF	−0.0392	0.0317	0.0329	1.19	0.2330
		SRF	−0.0064	0.0299	0.0311	0.21	0.8367
		DF	−0.0023	0.0010	0.0010	2.21	0.0274
		R	−0.0022	0.0011	0.0011	1.96	0.0500
		Total *N*	0.0000	0.0000	0.0000	1.10	0.2695

NN non-native species richness, *NNP* non-native species proportion (only for fish beta diversity), *CV* average coefficient of variation of environmental variables, *EH* environmental heterogeneity, *Total P* total phosphorus, *Total N* total nitrogen, *HL10/HL20/HL30/HL40/HL50* time-lagged hydrometric level, *NDF* number of days since the last flood, *DF* duration of the last flood, *R* DF/NDF, *SRF* floods that occurred on the last thirty days before sampling and lasted less than eight days, *LOF* floods that lasted eight days or more and occurred in the last year, but not in the last 30 days, d_{CEN} distance to group centroid, β_{SIM} Simpson dissimilarity

account for this general result (Junk et al., 1989; Neiff, 1990; Tockner et al., 1999, 2000). In our study area, we believe that the environmental heterogeneity among the three subsystems (i.e., the Paraná, Baía and Ivinhema Rivers) is of paramount importance to maintain these levels of beta diversity (as suggested by previous studies, e.g., Padial et al., 2012 and references therein). This inference is substantiated by the high average coefficients of variation (measuring the environmental heterogeneity among sampling sites for each sampling campaign), which ranged from 47 to 216% over time (see Table 1).

The main correlates of migratory fish beta diversity (as given by d_{CEN}) in the Upper Paraná River floodplain were the proportional abundance of non-native species (positively), environmental heterogeneity (positively), and productivity (negatively). We also detected a decline in this response variable over time. The proportional abundance of non-native species, environmental heterogeneity, and hydrographic level were the main correlates of sedentary fish beta diversity. Finally, the temporal dynamics of aquatic macrophyte beta diversity was mainly correlated with environmental heterogeneity, flood duration, and intensity. These results suggest that environmental heterogeneity (as proxied by EH or CV) was, in general, an important predictor of the beta diversity of the three biological groups analyzed. It is also noteworthy that the relationship between beta diversity and environmental heterogeneity was positive and thus in the direction expected by theory. These results are, therefore, in line with a growing body of evidence showing a positive relationship between beta diversity and environmental heterogeneity among local communities (Ellingsen & Gray, 2002; Anderson et al., 2006; McKnight et al., 2007; Melo et al., 2009; Astorga et al., 2014; Zorzal-Almeida et al., 2017). In our study, the effect of variation in spatial extent as a confounding factor (due to the relationship between spatial extent and environment heterogeneity) was ruled out, as the same sets of local communities were surveyed over time. In general, the positive relationship between beta diversity and environmental heterogeneity adds evidence to the role species sorting processes in controlling the variation in species composition (see also Wojciechowski et al., 2017).

We did not find a positive relationship between productivity and beta diversity. This result is not in agreement with previous studies suggesting such a relationship (e.g., Bai et al., 2007; Gardezi & Gonzalez, 2008; Chase, 2010; Langenheder et al., 2012). Instead, our results are more in line with those of Chalcraft et al. (2004) and Soares et al. (2015), who also did not find a positive relationship between beta diversity and productivity. A failure to detect a significant and positive relationship between beta diversity and productivity could be explained by the low variability in this explanatory variable. However, this was not the case in our study, as the variations in total phosphorus and total nitrogen concentrations (our proxies for productivity) were substantial (Table 1). In addition to positive (see references above) and non-significant relationships (this study), negative relationships have also been found between beta diversity and productivity (Astorga et al., 2014; Zorzal-Almeida et al., 2017). In general, these results suggest that this relationship depends on a number of factors [e.g., type of study (experimental x observational), group of organisms, and the nature of the trophic gradient (i.e., natural or human induced)].

The role of hydrology in biological communities and ecological processes in floodplains has been long discussed (Junk et al., 1989; Neiff, 1990). Additionally, understanding the role of hydrological regime has become central in the face of extensive river regulation and habitat degradation (Tockner et al., 2000; Ward & Tockner, 2001; Agostinho et al. 2005). Previous studies in the Upper Paraná River have indicated that beta diversity was high during low water levels and low during high water levels (e.g., Velho et al., 2004; Borges & Train, 2009; Fernandes et al., 2009; Lansac-Tôha et al., 2009; Rosin et al., 2009; Thomaz et al., 2009). We found that aquatic macrophyte beta diversity was negatively correlated with the intensity of floods. In general, these results support the flood homogenization hypothesis (FHH; Thomaz et al., 2007). However, we did not detect a significant relationship between hydrological variables and migratory fish beta diversity, and the relationships between these variables and sedentary fish beta diversity were positive (i.e., contrary to the expected). Thus, our long-term study suggests that a relationship between beta diversity and hydrology, as predicted by the FHH, is not so general (Soares et al., 2015). Additionally, we cannot rule out the fact that the hydrological regime in the Upper Paraná River floodplain is severely impacted by upstream reservoirs (Souza Filho, 2009), and therefore, it may be that the FHH for the fish community could be supported in the absence of such an impact.

We found that fish beta diversity increased with the proportional abundance of non-native species (Olden & Poff, 2003). In general, this result agrees with those obtained by Toussaint et al. (2016). First, the authors suggest that "the majority of exotics contribute to a differentiation effect." Second, they found that in Neotropical regions, 18 out of the 20 non-native species analyzed increased the compositional dissimilarity between freshwater systems after introduction (consistent with a scenario of biotic differentiation). We also detected a negative temporal trend in migratory fish beta diversity. Although we cannot test them, the impacts of damming on migratory fish communities are, in our opinion, the most likely explanation for this trend (Gubiani et al., 2007; Agostinho et al., 2008; Fernandes et al., 2009; Dugan et al., 2010; Petsch, 2016).

Interpreting the relationships between predictors and metacommunity beta diversity is central to inform conservation (Socolar et al., 2016). We found that environmental heterogeneity was the most consistent predictor of beta diversity, despite the uncertainty regarding the best model (as indicated by the low Akaike weights). We did not find strong support for the roles of productivity, non-native species, and hydrology. However, the Upper Paraná River floodplain is under continuous threats, and the relevancy of the predictors used here may increase in the future. Indeed, given the cumulative impacts caused by oligotrophication, non-native species spread and damming, and due to the possibility of their lagged effects, we believe that the continuation of the long-term ecological study is key to a better understanding of the processes that drive beta diversity variation in the Upper Paraná River floodplain.

Acknowledgements We acknowledge the NUPELIA staff for providing all the data, particularly Angelo Antonio Agostinho, Sidinei M. Thomaz, and Maria do C. Roberto. We also acknowledge CNPq for supporting the long-term ecological program in the Upper Paraná River floodplain. A.A. Agostinho and an anonymous reviewer provided valuable suggestions on early drafts of the manuscript. A.A.P. and L.M.B. receive continuous grants and research scholarships from CNPq, and F.C. receives a student scholarship from CAPES. This work was also developed in the context of the National Institutes for Science and Technology (INCT) in Ecology, Evolution and Biodiversity Conservation, supported by MCTIC/CNPq (proc. 465610/2014-5) and FAPEG.

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