1   Zooplankton community beta diversity in an Amazonian floodplain lake

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16   partitioning

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Abstract

Understanding the mechanisms that generate organism distribution patterns from the beta diversity perspective can assist in environmental monitoring strategies. In this study, we emphasized the limnic zooplankton due to the ability of these organisms to respond quickly to environmental variations. Therefore, we evaluated the following questions: (i) Do different regions of the same lake have the same importance in contributing to beta diversity? (ii) Do beta diversity and its components vary over the hydrological cycle? (iii) What is the importance of local and spatial predictors in beta diversity and its components? (iv) Do beta diversity and its components show a consistent pattern throughout the hydrological cycle? We found that the contribution of different sites to diversity was more associated with regions with low abundance and richness of organisms values, such as the littoral and *igarapés*, which shows the relevance of these areas for biological monitoring and for the delimitation of priority areas for the zooplankton diversity conservation. Despite the peculiarities of each hydrological period and regarding beta diversity components, we verified a species substitution and differences in abundance pattern in the lake. We also found low concordance patterns between the periods and low environmental and spatial variables prediction on beta diversity patterns.

Introduction

Species can present different distribution patterns in response to natural factors such as competition, predation, dispersive processes limitations, and/or local and regional environmental variables influences (Guisan & Thuiller, 2005). These factors may be intensified by human activities, which makes even more relevant to understand the mechanisms that generate such structuring patterns in biological communities. Thus, the understanding of these mechanisms can assist in the formulation of efficient environmental monitoring strategies and, even, in the delimitation of priority areas for conservation in several ecosystems (Socolar *et al.*, 2016). The comparative diversity across multiple sites, known as beta diversity (Whittaker, 1960), has undergone advances over the years both for understanding patterns of presence-absence of organisms and for density values per site (Baselga, 2010; Podani & Schmera, 2011; Podani, Ricotta & Schmera, 2013).

Both for organism occurrence and abundance, Podani family of beta diversity (Podani & Schmera, 2011; Podani *et al.*, 2013) can be partitioned into the following main components: (i) *species similarities*: commonly measured by the Jaccard index for presence-absence data and Ruzicka, for abundance data. High values of this partition mean that the pairs of sites put in comparison share many species or species with similar abundances; (ii) *difference in relative richness/abundance*: is the difference in species richness, or species abundance, between pairs of

53   sites. Therefore, high values of that partition show that the number of species or specimens between

54   compared sites is discrepant; (iii) *species replacement/abundance:* it can be maximized when there is

55   a high replacement of species, or species with equivalent abundances, along an environmental

56   gradient or between pairs of sites. Therefore, high replacement values for the abundance data mean

57   that, although the sites in comparison have similar abundances, the species composition is different.

58   Also, although the approach with abundance data may represent more subtle differences concerning

59   environmental variations, the values between the assessments for abundance and presence-absence

60   data can be quite different, even if evaluated with the same data set (Podani *et al.*, 2013).

61   The evaluation of the factors that influence beta diversity and its components can be even

62   more complex in floodplain lakes since they are predominantly dominated by the flood pulse that

63   controls the dynamics of entry and output of sediments, water and organisms that naturally contribute

64   for changes in biological diversity in the ecosystem (Junk *et al.*, 2012). These plains are continuously

65   or periodically flooded by direct precipitation or by the overflow of the main river and, depending on

66   the level of connectivity with the river, there may be a loss of connection between habitats during

67   periods of low water (Thomaz, Bini & Bozelli, 2007). However, as the cycle of extensive floodplains

68   is usually slow and monomodal, the biological dynamics of organisms can adapt in order to maximize

69   their performance according to hydrological cycles (Junk *et al.*, 2011).

70   In Amazonian rivers, the flow tends to be more intense and requires a high resilience capacity

71   of the organisms. Therefore, smaller aquatic organisms tend to be present with greater richness and

72   density in the lakes of these plains, where they can find shelter against predation and food (Junk,

73   Bayley & Sparks, 1989). Furthermore, according to the hydrological period, these organisms may

74   present beta diversity patterns that change over time (Bozelli *et al.*, 2015).

75   Assessing beta diversity and its components over space, but also highlighting whether the

76   pattern generated is consistent throughout the hydrological cycle is important in different aspects. For

77   example, due to the scarcity of financial resources and time allocated in environmental monitoring

78   programs and scientific research, if different hydrological periods show a concordant pattern of

79   diversity, there is a real possibility of adjustment in the sampling effort, reducing the number of

80   sampling campaigns, which would save financial resources and time. In the same way, it is possible

81   to use other alternatives as is the case of using lower taxonomic resolutions and or presence-absence

82   data instead of abundance data (Carneiro *et al.*, 2013; Vieira *et al.*, 2017; de Morais *et al.*, 2018).

83   In this study, we emphasized the limnic zooplankton due to the ability of these organisms to

84   respond quickly to environmental variations. Therefore, we evaluated the following questions: (i) Do

85   different regions of the same lake have the same importance in contributing to beta diversity? (ii) Do

86   beta diversity and its components vary over the hydrological cycle? (iii) What is the importance of

87   local (environmental characterization) and spatial (dispersive processes) predictors in beta diversity

88   and its components? (iv) Do beta diversity and its components show a consistent pattern throughout

89   the hydrological cycle? Taking into account that the ecological dynamics of floodplains is temporally

90   complex, we expected that the sites contribution to beta diversity would be different between

91   hydrological periods. Besides, due to the spatial extent of the study area, we expected that species

92   replacement patterns would be predominant, considering values of presence-absence of organisms,

93   and patterns of differences in abundance, considering values of species abundance per site. Also, due

94   to the complex interactions that dominate the occurrence of organisms, we expected that there would

95   be a variation between environmental and spatial predictors in biological diversity patterns and,

96   finally, as each period comprises a different hydrological dynamics, we did not expect to find many

97   concordant values, being important to evalute in all hydrological periods to understand the

98   distribution patterns of the zooplankton community.

99

100   **Material and methods**

101   Study area

102

103   The study area comprises an Amazonian floodplain lake called *Lago Grande do Curuai*,

104   located in the State of Pará, Brazil. The majority of the water supply comes from the Amazon River

105   (77%), while the others are subdivided between rainfall, runoff, and outcropping of groundwater

106   (Bonnet *et al.*, 2008). The hydrological dynamics generate a monomodal cycle in this lake,

107   comprising the periods of flooding (from January to the end of February), high water (from April to

108   the end of June), flushing (from August to October) and low water (mid-October to November) (de

109   Moraes Novo *et al.*, 2006).

110   The environmental characteristics of Lago Grande do Curuai are quite variable throughout the

111   year, mainly concerning chlorophyll-*a* and dissolved oxygen. During the flooding period,

112   chlorophyll-*a* levels are low enough for human consumption. However, the values in the flushing

113   period rise to such an extent that water is not recommended for any type of activity (Affonso, Barbosa

114   & Novo, 2011).

115   Sampling were carried out in 17 sample units (Figure 1) in four campaigns: March / 2013

116   (flooding period), September / 2013 (flushing period), May / 2014 (high water period) and November

117   / 2014 (low water period).
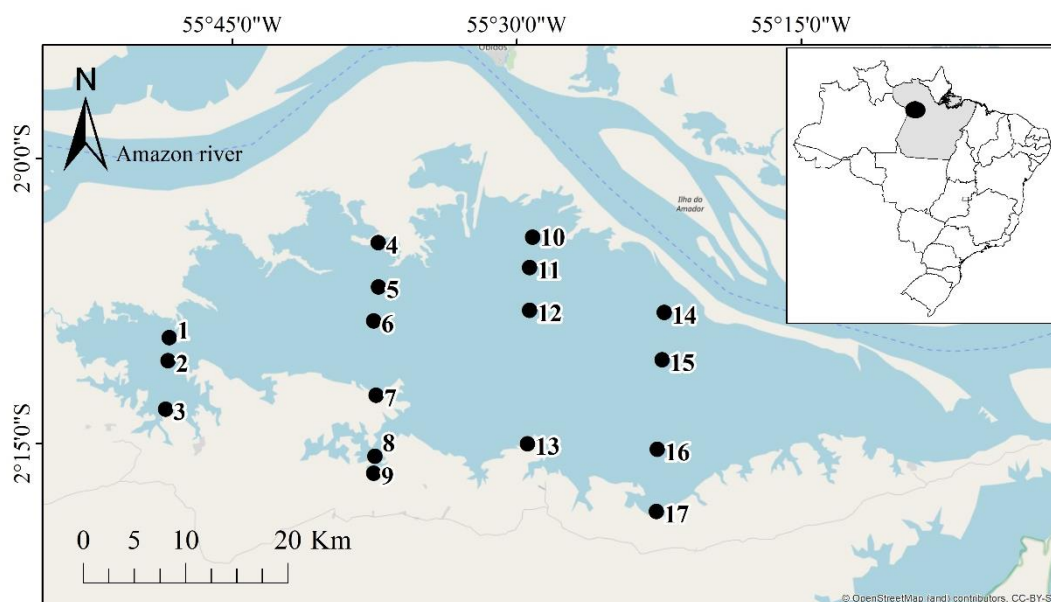
Fig. 1 Map of the study area and sampling units in Lago Grande do Curuai. Blue area: aquatic environments; beige area: terrestrial environments

Environmental variables

In each sampling unit, we used a multi-parameter YSY probe, model EXO2 to measure the variables dissolved oxygen (mg/L), blue-green algae (µg/L), fluorescent organic dissolved matter (raw), pH, water temperature (ºC), conductivity (µS/cm), total dissolved solids (mg/L), and turbidity (NTU). According to the protocol (APHA, 2005), water samples were obtained and frozen for further quantification in the laboratory of: alkalinity (mg/L), total chlorophyll (µg/L), total phosphorus (µg/L), total nitrogen (µg/L), total dissolved nitrogen (mg/L), ammonia (mg/L), nitrate (mg/L), and silica (mg/L).

Zooplankton

In each sampling unit, we sampled the zooplankton community on the subsurface (*ca* 50 cm). Therefore, we filtered 300 liters of water in a net with a 68 µm opening mesh. Samples were stored in polyethylene bottles, preserved with formaldehyde (5%), and buffered with sodium tetraborate. In the laboratory, the samples were concentrated in 75 mL. To quantify the densities of zooplanktonic organisms per sample unit, a 7.5 mL subsampling was performed with a *Hensen-Stempel* pipette. We read the subsampled organisms in a Sedgewick Rafter chamber for identification and counting using an optical microscope. Additionally, we carried out qualitative sampling to verify and record the existence of new *taxa* that were not identified during quantitative sampling (Bottrell *et al.*, 1976).

142   Data analysis

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144   We performed a Local Contribution to Beta Diversity (LCBD) (Borcard, Gillet & Legendre,

145   2018) to obtain the degree of exclusivity of the sites in the species composition in each hydrological

146   period using the function *beta.div*, package *adespatial* (Dray *et al.*, 2018). To evaluate and partition

147   Podani family beta diversity by sample period, we used the function *beta.div.comp* of *adespatial*

148   package (Dray *et al.*, 2018). In both cases, we used the *Jaccard* index for presence and absence values

149   and *Ruzicka* for organism density data.

150   To verify if there were significant differences in the values resulting from the beta diversity

151   partitioning by period, we performed a Permutational Multivariate Analysis of Variance Using

152   Distance Matrices (PERMANOVA). We obtained these matrices using the *beta.div.comp* function for

153   both create a matrix encompassing all periods and generate matrices by pairs of periods. For

154   PERMANOVA, we use the *adonis2* function of the *vegan* package (Oksanen *et al.*, 2016) and the

155   matrices resulted from the partition were inserted in response to hydrological periods. Additionally,

156   we constructed triangular plots (simplex) to check the distributions of the pairs of sites concerning

157   the partitive components of beta diversity for both *Ruzicka* distance matrices and *Jaccard* in each

158   hydrological periods.

159   To assess the influence of environmental and spatial variables in the beta diversity partitions

160   of zooplankton community by hydrological period, we performed Distance-Based Redundancy

161   Analysis (dbRDA's) (Legendre & Andersson, 1999) with different matrices resulted from the beta

162   diversity partitioning (as response variables) and different environmental and spatial variables (as

163   predictor variables). To determine which variables would be inserted in the dbRDA, we performed

164   the analysis of variation inflation factor (VIF) (Borcard *et al.*, 2018), removing the environmental

165   variables that showed high collinearity in each sample period (VIF values greater than 20). To

166   determine the spatial predictors (geographic coordinates), we first converted the coordinates to

167   Cartesian distances using the *geoXY* function of the *SoDA* package (Chambers, 2013). Then, we

168   ordered the variables in a Distance-Based Moran's Eigenvector Maps (dbMEM) (Dray, Legendre &

169   Peres-Neto, 2006; Legendre & Legendre, 2012) using the dbmem function of the adespatial package

170   (Dray *et al.*, 2018).

171   To evaluate the temporal concordance in the distribution patterns of the different zooplankton

172   community beta diversity partitions between hydrological periods, we performed *Procrustes* tests

173   (Gower, 1975). For that, we ordered the matrices resulting from the beta diversity partitioning in

174   different Non-metric multidimensional scaling (NMDS), then we extracted the values from the

175   ordering scores and inserted them into the *protest* function, from *vegan* package (Oksanen *et al.*,

176   2013). To check the significance, 9999 permutations were performed.

177   For all the mentioned analyzes, we used the statistical software R (R Core Team, 2016).

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179 **Results**

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181   Regarding the contribution of sites to beta diversity (LCBD) using presence-absence data of

182 the zooplankton community, only the hydrological periods of flooding and low water presented sites

183 with significant contributions, with site 9 being important for the beta diversity in both periods (Figure

184 2). All significant sites (8, 9, and 13) are located in the southern region of the lake. When we evaluated

185 the LCBD using abundance data (Figure 3), the four periods presented significant sample units. In

186 the flooding and flushing periods, the significant sampling units were located in the north region of

187 the lake (sites 14 and 10, respectively); in the high waters, they were located in the south, and in the

188 low water period they were located in the west region of the lake.
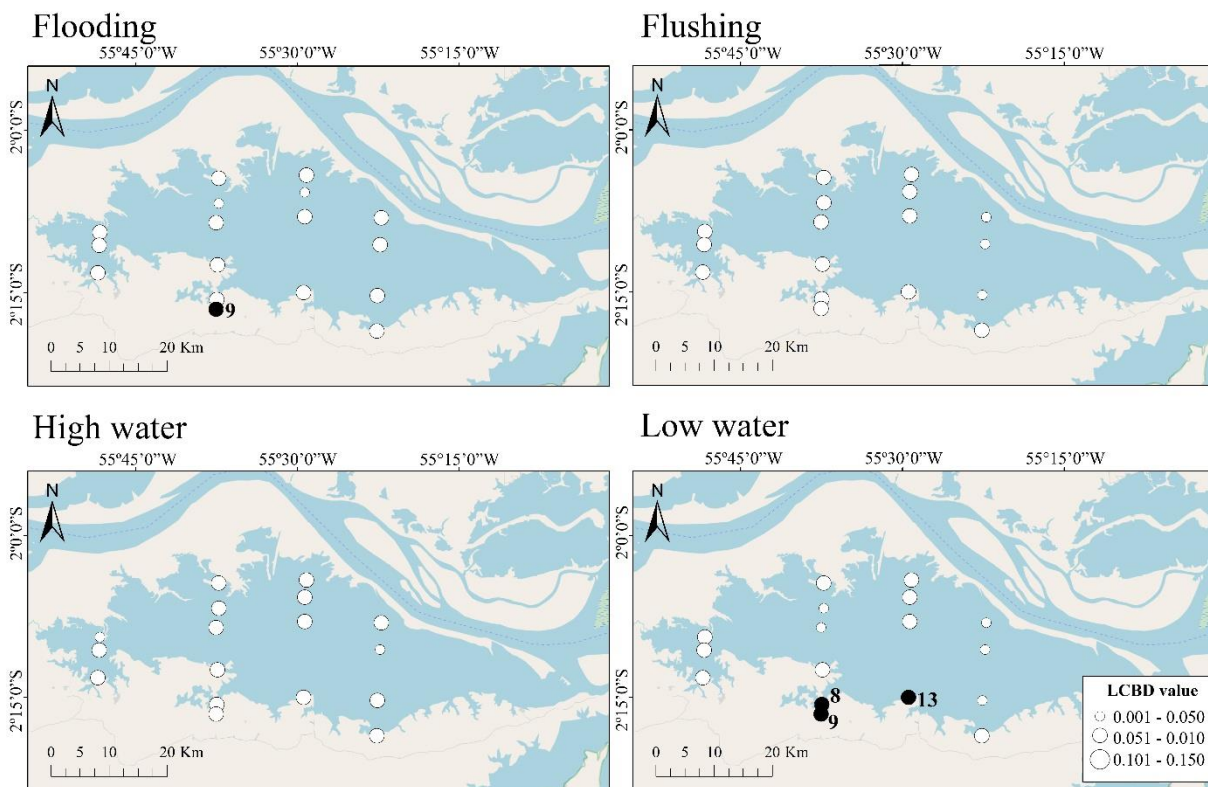
189

190 **Fig. 2** Map of the local contribution to beta diversity (LCBD) for zooplankton presence/absence data

191 with *Jaccard* matrix of the sample units by hydrological period. Filled circles represent sites with

192 significant contributions

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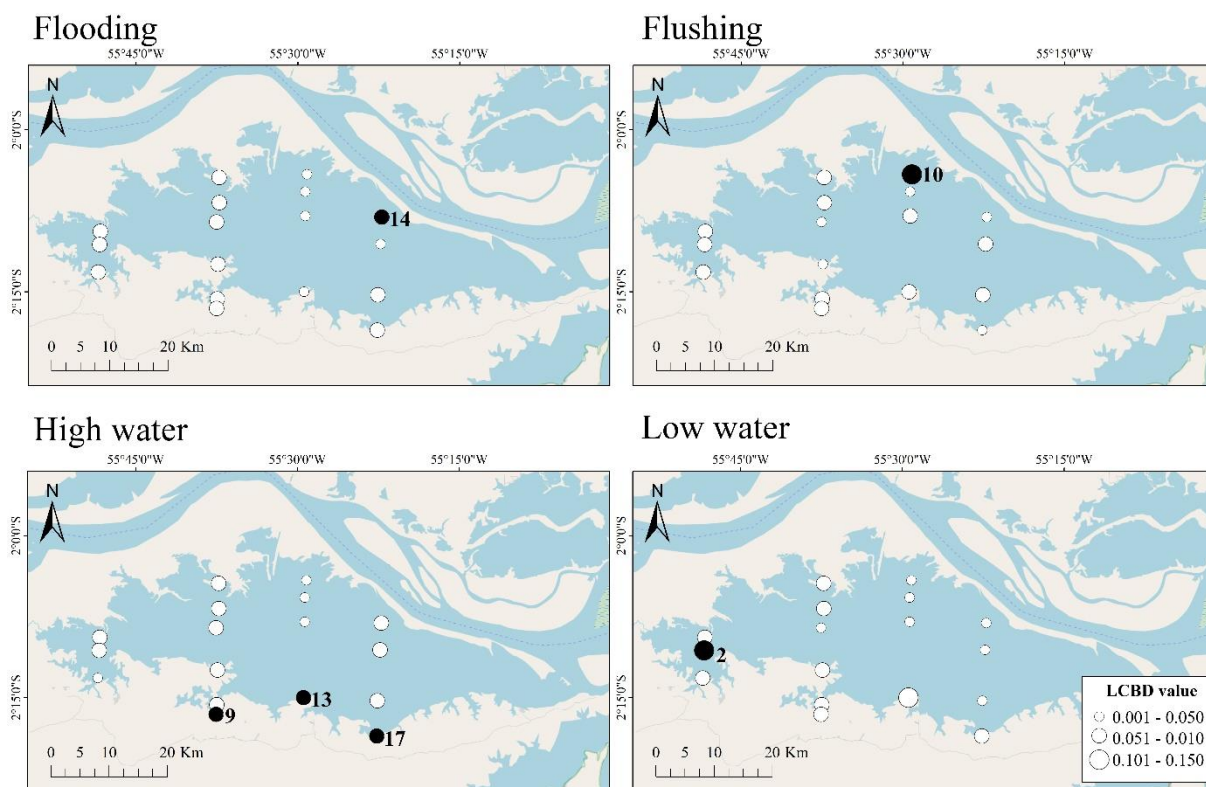
Fig. 3 Map of the local contribution to beta diversity (LCBD) for zooplankton abundance data with Ruzicka matrix of the sample units by hydrological period. Filled circles represent sites with significant contributions

Evaluating the beta diversity partitions using presence and absence species data (Table 1), we verified a replacement dominant pattern (values comprised 73% to 81% of the beta diversity between hydrological periods), while we verified an abundance difference dominance pattern when using abundance data (values comprised 58% to 74% of the beta diversity between hydrological periods).

Table 1. Beta diversity partitioning for all hydrological periods with presence and absence and abundance values. BD = total beta diversity; Rep = replacement; RD = richness difference; AD = abundance difference; Rep/BD = ratio of replacement to total beta diversity; RD/BD = ratio of richness difference to total beta diversity; AD/BD = ratio of abundance difference to total beta diversity

	Period	BD	Rep	RD	Rep/BD	RD/BD
Presence-Absence	Flooding	0.34	0.25	0.09	0.73	0.27
(*Jaccard*)	Flushing	0.28	0.23	0.05	0.81	0.19
	High water	0.35	0.27	0.09	0.75	0.25

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	Period	BD	Rep	AD	Rep/BD	AD/BD
	Low water	0.28	0.22	0.06	0.78	0.22
Abundance (*Ruzicka*)	**Period**	**BD**	**Rep**	**AD**	**Rep/BD**	**AD/BD**
	Flooding	0.43	0.14	0.29	0.32	0.68
	Flushing	0.38	0.15	0.23	0.40	0.60
	High water	0.41	0.11	0.31	0.26	0.74
	Low water	0.36	0.15	0.21	0.42	0.58

When we compared the beta diversity partitions obtained by the hydrological periods (Table 2) using presence/absence data, the richness difference component was similar among all hydrological periods, while the beta diversity and replacement component were different among them all. When considering abundance data, beta diversity was different across all hydrological periods, while the abundance difference component was different only in flooding and flushing periods, flushing and high water, and high waters and low waters. There were no differences in the abundance replacement component.

Table 2. Permutational multivariate analysis of variance using distance matrices (PERMANOVA) between the matrices resulting from the partition of the beta diversity for the different hydrological periods. Significant values are in bold

	Period	Beta diversity (Jaccard)			Richness difference			Replacement		
		R^2	F	p	R^2	F	p	R^2	F	p
Presence-absence	Global	**0.31**	**9.78**	**0.001**	-0.04	-0.79	1.000	**0.38**	**12.84**	**0.001**
	Flooding x Flushing	**0.21**	**8.58**	**0.001**	-	-	-	**0.27**	**11.90**	**0.001**
	Flooding x High water	**0.18**	**7.15**	**0.001**	-	-	-	**0.22**	**9.27**	**0.001**
	Flooding x Low water	**0.25**	**10.66**	**0.001**	-	-	-	**0.32**	**15.26**	**0.001**
	Flushing x High water	**0.24**	**9.87**	**0.001**	-	-	-	**0.27**	**12.01**	**0.001**
	Flushing x Low water	**0.25**	**10.43**	**0.001**	-	-	-	**0.30**	**13.66**	**0.001**
	High water x Low water	**0.28**	**12.49**	**0.001**	-	-	-	**0.33**	**15.50**	**0.001**

	Period	Beta diversity (Ruzicka)			Abundance difference			Replacement		
		R^2	F	p	R^2	F	p	R^2	F	p
Abundance	Global	**0.20**	**5.32**	**0.001**	**0.27**	**7.92**	**0.001**	0.10	2.48	0.077
	Flooding x Flushing	**0.12**	**4.52**	**0.001**	**0.12**	**4.27**	**0.012**	-	-	-
	Flooding x High water	**0.10**	**3.63**	**0.001**	0.14	5.35	0.004	-	-	-
	Flooding x Low water	**0.13**	**4.66**	**0.001**	0.09	3.19	0.035	-	-	-

|									
Flushing x High water	**0.17**	**6.70**	**0.001**	**0.33**	**16.04**	**0.001**	-	-	-
Flushing x Low water	**0.13**	**4.81**	**0.001**	-0.01	-0.27	0.997	-	-	-
High water x Low water	**0.20**	**7.88**	**0.001**	**0.34**	**16.66**	**0.001**	-	-	-

223

224   In proportion, when we partitioned the beta diversity using presence-absence data, the pairs
225 of sample units were more associated with greater similarities and replacement values considering all
226 periods (Figure 4). On the other hand, when we evaluated the partition using abundance data, the
227 pairs of sample units were more associated with abundance difference component and, secondly, with
228 higher replacement levels (Figure 5).
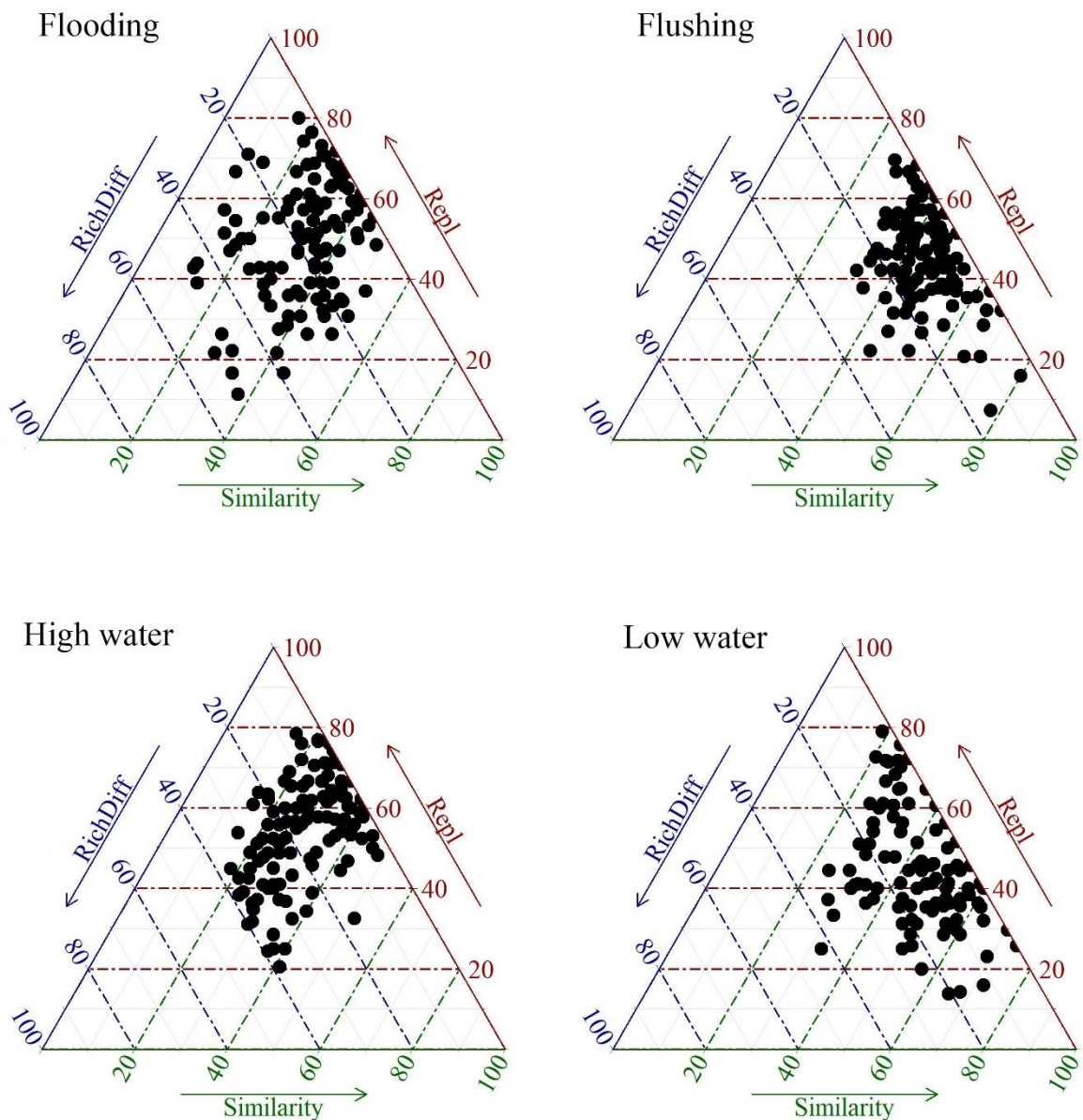
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230 **Fig. 4** Triangular graph (simplex) of the proportion of elements of the beta diversity partition per pair
231 of sample units for values of presence-absence of organisms. RichDiff = richness difference and
232 Repl= species replacement.
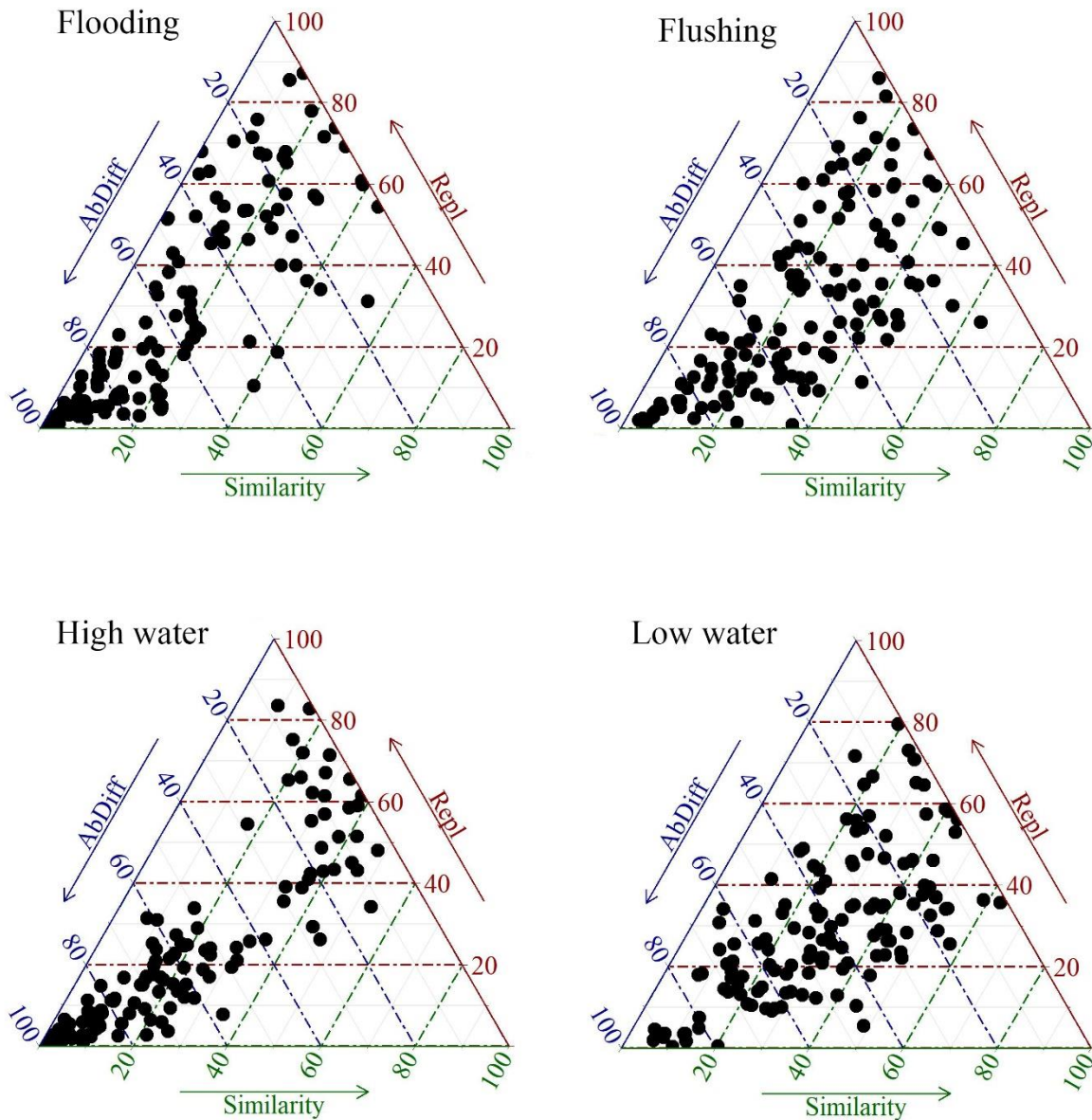
Fig. 5 Triangular graph (simplex) of the proportion of elements in the beta diversity partition per pair of sample units for organism abundance values. AbDiff = abundance difference and Repl = species abundance replacement.

Because presented high collinearity or multicollinearity values, we removed the following environmental variables of each hydrological period: total chlorophyll, pH, conductivity and total dissolved solids (flooding); dissolved oxygen, pH, conductivity and total dissolved nitrogen (flushing); temperature, conductivity and total dissolved solids (high water) and dissolved oxygen, blue-green algae, pH, conductivity and total dissolved nitrogen (low water).

The environmental and spatial variables showed little influence on the distribution patterns of beta diversity and its components, regardless the hydrological period (Table 3). Considering the

246 presence-absence species data, the environmental variables explained the beta diversity patterns in

247 flushing and low waters periods and the richness difference component in in the low water period.

248 Regarding the abundance data, the environmental variables explained the beta diversity and the

249 abundance difference component in the high water period (Table 3).

250   Concerning the presence-absence values, spatial variables explained the beta diversity

251 patterns in flooding, flushing, and low water periods, and replacement component in flushing and low

252 water periods. However, concerning the abundance data, spatial variables did not explain beta

253 diversity nor its components in any of the hydrological periods analyzed (Table 3).

254

Table 3. Distance-based redundancy analysis (dbRDA) of the influence of environmental and spatial predictors on the matrices resulting from the
256   beta diversity partition. Rep = replacement; RD = richness difference; AD = abundance difference. Significant values are in bold

Data	Season	Environmental variables									Spatial variables								
		Beta diversity (Jaccard)			Rep			RD			Beta diversity (Jaccard)			Rep			RD		
		R^2_{adj}	F	p	R^2_{adj}	F	p	R^2_{adj}	F	p	R^2_{adj}	F	p	R^2_{adj}	F	p	R^2_{adj}	F	p
Presence-Absence	Flooding	0.07	1.09	0.290	0.01	1.01	0.453	0.09	1.13	0.425	**0.05**	**1.275**	**0.034**	0.01	1.06	0.251	0.03	1.19	0.300
	Flushing	**0.31**	**1.61**	**0.008**	0.09	1.13	0.125	0.37	1.79	0.124	**0.14**	**1.848**	**0.001**	**0.06**	**1.33**	**0.003**	0.02	1.12	0.356
	High water	0.08	1.11	0.238	0.00	0.97	0.665	0.32	1.57	0.200	0.02	1.114	0.216	0.00	0.93	0.841	0.14	1.87	0.084
	Low water	**0.31**	**1.66**	**0.005**	0.07	1.11	0.181	**0.45**	**2.19**	**0.019**	**0.15**	**1.926**	**0.002**	**0.05**	**1.26**	**0.020**	0.13	1.83	0.072
		Beta diversity (Ruzicka)			Rep			AD			Beta diversity (Ruzicka)			Rep			AD		
		R^2_{adj}	F	p	R^2_{adj}	F	p	R^2_{adj}	F	p	R^2_{adj}	F	p	R^2_{adj}	F	p	R^2_{adj}	F	p
Abundance	Flooding	0.02	1.02	0.494	0.02	1.02	0.375	-0.04	0.95	0.574	0.03	1.156	0.257	0.01	1.04	0.316	-0.01	0.95	0.462
	Flushing	0.06	1.09	0.407	-0.01	0.98	0.615	0.07	1.10	0.430	0.08	1.474	0.080	0.01	1.06	0.252	0.02	1.12	0.325
	High water	**0.54**	**2.42**	**0.007**	-0.10	0.89	0.974	**0.63**	**3.06**	**0.008**	0.07	1.372	0.159	-0.01	0.93	0.831	0.09	1.51	0.138
	Low water	0.25	1.49	0.089	-0.03	0.96	0.746	0.23	1.44	0.163	0.03	1.168	0.256	0.02	1.09	0.090	-0.02	0.88	0.577

258   Regarding the concordance analyzes, zooplankton beta diversity and its components

259   showed low values between hydrological periods (Table 4). Taking into account the presence

260   and absence species data, there was concordance of beta diversity only in the comparisons

261   between low water and flushing periods, and low water and high water periods (Table 4).

262   Concerning the beta diversity components, there was concordance only in the comparisons

263   between high water and low water (richness difference component) and between flooding and

264   flushing (richness replacement component) and flooding and low water (richness replacement

265   component). On the other hand, the abundance data did not show concordant patterns between

266   the hydrological periods.

267

268   **Table 4.** Procrustes test evaluating the concordance of beta diversity and its components values

269   between hydrological periods. Significant values are in bold

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	Season	Beta diversity (Jaccard)		Richness difference		Replacement	
		r	*p*	*r*	*p*	*r*	*p*
	Flooding x Flushing	0.39	0.153	0.38	0.173	**0.62**	**0.003**
Presence-absence	Flooding x High water	0.42	0.096	0.17	0.832	0.41	0.124
	Flooding x Low water	0.45	0.088	0.26	0.468	**0.49**	**0.031**
	Flushing x High water	0.42	0.110	0.13	0.917	0.46	0.058
	Flushing x Low water	**0.47**	**0.045**	0.27	0.404	0.36	0.242
	High water x Low water	**0.69**	**0.001**	**0.66**	**0.001**	0.41	0.125

	Season	Beta diversity (Ruzicka)		Abundance difference		Replacement	
		r	*p*	*r*	*p*	*r*	*p*
	Flooding x Flushing	0.26	0.522	0.06	0.909	0.27	0.574
Abundance	Flooding x High water	0.35	0.205	0.25	0.277	0.27	0.543
	Flooding x Low water	0.35	0.241	0.22	0.398	0.19	0.823
	Flushing x High water	0.35	0.208	0.34	0.196	0.19	0.847
	Flushing x Low water	0.44	0.075	0.18	0.602	0.36	0.253
	High water x Low water	0.23	0.555	0.09	0.974	0.17	0.890

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272   **Discussion**

273   Local contributions to beta diversity

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275   When evaluating the beta diversity local contributions patterns using the presence-
276   absence data, we found that the main contribution sites were located in the south during flooding
277   and low water periods. This lake region has a higher proportion of areas with pastoral use
278   (Peres, Gurgel & Laques, 2018) and also the highest proportion of *igarapés* area. On the other
279   hand, the northern region connects more predominantly with the Amazon River (Bonnet *et al.*,
280   2008). Given that the variation in species composition and abundance influence the LCBD
281   contributions, the land use may have influenced the difference in species composition between
282   sites, what, consequently, influenced the increase the beta diversity contribution.

283   The significant LCBD site located in the southern region presented the lowest richness
284   of individuals per sampling unit during the flooding period, while in the flushing period, it
285   showed a different occurrence of species comparing to the other sites. High LCBD values may
286   not be directly associated with high richness or abundance values, since areas with low richness
287   and occurrences of differentiated species may also present higher contribution values, which
288   may denote these areas as priorities for species conservation (Legendre & De Cáceres, 2013).

289   In the flooding and flushing periods, some sites in the northern region were
290   differentiated concerning organism abundance. There was low abundance of zooplanktonic
291   organisms at the significant site during the flooding period. Moreover, in flushing, the sampling
292   unit ten, which most contributed to the beta diversity, stood out for the occurrence of different
293   species compared to others sampling units in the same period (e.g., *Lecane elsa*, *Lecane luna*
294   and *Nebela collaris*). In the low water period, the sampling unit also showed distinct species
295   (e.g., *Difflugia elegans*). This distinction in the diversity patterns of the sampling units by
296   hydrological period showed that the flood pulse promoted different dynamics in the floodplain
297   lake. In the low water period, the sampling units were isolated from the main river, which means
298   that the considerable environmental heterogeneity may have been influenced differences in
299   species with different characteristics in each sampling period (Thomaz *et al.*, 2007). In this
300   case, as the sampling unit two, which has a higher LCBD value, is on the opposite side of the
301   most important contribution area of the river's water flow, located to the east, the isolation of
302   the site may have justified such differentiation.

303   Whereas zooplanktonic organisms respond effectively to environmental variations
304   (Vieira *et al.*, 2011; Wang *et al.*, 2016) and even greater impacts such as hydrological changes
305   in cases of dams (Souza *et al.*, 2019), we consider that the sampling units highlighted
306   accordingly to the criteria of uniqueness by the LCBD analysis, being always associated with

307 the marginal regions of the lake. These regions have higher interactions with *igarapés* and are

308 in contact with the aquatic-terrestrial transition zones. Therefore, despite the hydrological

309 importance of the flood pulse over the lake and the control over ecological dynamics, it is also

310 important to take into account the importance that these *igarapés* and vegetation areas have for

311 the existence of unique sites in relation to biodiversity for the Lago Grande do Curuai.

312

313 Beta diversity partition

314   Related to the presence-absence data, there was a predominance of replacement

315 concerning total beta diversity. It means that, despite a greater constancy in species richness per

316 sampling unit, the species composition between pairs of units was different. Species are

317 expected to show a substitution pattern over large environmental gradients, depending on other

318 factors such as ecological tolerance of species (Legendre, 2014). Some studies report the

319 sensitivity of organisms in the zooplankton community to environmental variations (Vieira *et*

320 *al.*, 2011), in some cases responding through changes in the trophic structure of the community

321 (Ejsmont-Karabin *et al.*, 2018) and changes in reproductive rates and species composition in

322 the presence of other organisms (e.g., fish) (Feniova *et al.*, 2019).

323   The high water period showed the highest beta diversity values and species replacement

324 rate. It differed from our expectations, since we expected a greater environmental homogeneity

325 and consequent biological homogeneity, reflecting a higher biological similarity between the

326 sites due to the flood pulse in the high water period and due to the greater interconnectivity

327 between habitats (Thomaz *et al.*, 2007; Bozelli *et al.*, 2015). Despite this, the increase in beta

328 diversity values may have been attributable to a greater interaction area with the floodplain that

329 began during the flooding period (Junk *et al.*, 1989) and continued to settle during the high

330 water period. This same pattern may have justified the lower beta diversity and replacement

331 values in low water and flushing periods where, despite the isolation of habitats promoted by

332 the reduction in the water volume, consequently minimized the interaction with the floodplain

333 region and the main river.

334   On the other hand, although the beta diversity patterns using abundance data were the

335 same for the presence-absence data with the highest values in the high water and flooding

336 periods, the abundance difference component predominated over the replacement component.

337 These values denote that, despite a greater tendency to replace species along the environmental

338 gradient, these species had wide variations in abundance values. It highlighted the importance

339 of understanding the zooplankton community abundance variations that, despite the ability to

340 respond to environmental variations (e.g., variation in trophic status and phosphorus

341   concentration in water), is often overlooked in some ecological studies (García-Chicote,

342   Armengol & Rojo, 2018).

343

344   Environmental and spatial predictors

345   Despite the distinctions observed in the patterns of similarity and substitution of species

346   between hydrological periods, we observed that the environmental variables showed little

347   prediction about the diversity patterns of the zooplankton community for presence and absence

348   data. These variables explained only the patterns of similarity in the flushing and low water

349   periods and the richness difference in the low water period.

350   On the other hand, there was a higher pattern of prediction of spatial variables over

351   patterns of similarity in the composition of species, not explaining only in the high water period.

352   These values denote that spatial variation may have a greater control over the organisms

353   composition dynamics than environmental variation. Despite this, this control was only related

354   to presence-absence values. The patterns of organism abundance and presence-absence refer to

355   different factors. For example, for presence and absence data, beta diversity corresponding to

356   the inverse of similarity in the composition is prioritized (Podani & Schmera, 2011), while for

357   abundance data, besides the composition, variations in the number of individuals of each

358   species are also considered. Therefore, when abundance is taken into account, sites with high

359   species dissimilarity values are those that present a high distinction in species composition and

360   the corresponding organisms abundance (Podani *et al.*, 2013).

361   Therefore, the explanation obtained in the low water period using the presence-absence

362   data may be related to the heterogeneity of ecological niches (Legendre, 2014). The low water

363   period may have promoted the existence of different niches, some with more species and others

364   with fewer species, due to the isolation. The substitution of species explained spatially may also

365   be based on the isolation that makes the species of an environment unable to reach other places

366   (Thomaz *et al.*, 2007). For this reason, spatial isolation can drive the pattern of differentiation

367   of species within the habitat and this same pattern may explain the spatial prediction in the

368   period of flushing.

369   For the beta diversity components using abundance data, there was a low standard of

370   explanation for both environmental and spatial variables, which showed that there was a greater

371   complexity of factors (e.g., competition and predation) that may have been the most responsible

372   for these variations and that were not evaluated in this study. This low pattern of response shows

373   that the zooplankton community is not responding only to environmental variations at that time,

374   but to changes that occurred in other periods before the sampling carried out. Besides, as the

375   abundance and presence-absence data responded differently to different factors, we emphasize

376   that both approaches can be complementary when used for biological monitoring purposes.

377

378   Temporal concordance between beta diversity components

379

380   Despite the occurrence of significant values when evaluating the temporal concordance

381   between the beta diversity patterns using presence-absence values, no pair of periods showed

382   concordance between all the diversity patterns over the hydrological cycle. There was also no

383   concordance between the periods using the abundance values. These results are in agreement

384   with our expectations since even in other environments, there is a low standard of predictability

385   and synchrony of zooplankton with other variables that allow us to predict a constant and

386   predictable pattern for this community (Vieira *et al.*, 2019).

387   These results also show that the environmental and biological dynamics of the

388   floodplains are complex to be predictable and, depending on the hydrological period, which

389   changes the entrance of river sediments and the inflow or outflow of water in the floodplain,

390   and the evaluated group, the structuring of the communities can be different (Amoros &

391   Bornette, 2002). There are proposals that the dynamics are so distinct and susceptible to

392   hydrological variations that the high water period acts as a resumption of the successional

393   regime of the structure and composition of the zooplankton community (Baranyi *et al.*, 2002;

394   Bozelli *et al.*, 2015). Therefore, despite the economic advantages of sampling in less

395   hydrological periods, we found that, in order to understand the beta diversity patterns of the

396   zooplankton community, sampling are necessary to occur in all the hydrological periods of high

397   and low waters, as well as in the flood and ebb intermediate periods.

398   **Conclusions**

399   Hydrological variations govern the zooplankton community dynamics, thus the

400   contribution of different locations depending on the hydrological period evaluated. With some

401   exceptions, the sites that most contributed to the beta diversity presented less organism richness

402   or abundance and also showed proximity to the coastal regions of the lake, especially those

403   associated with *Igarapés* when using the organisms presence-absence data. This result denotes

404   the relevance of these areas for biological monitoring and for the delimitation of priority areas

405   for the conservation of zooplankton diversity.

406   Beta diversity was greatest in flooding and high water periods. Despite the differences

407   in the partition values by hydrological period, the species replacement was dominant in all

408   hydrological periods using the organisms presence-absence data, while the abundance

409   difference was dominant using the quantitative values of organisms per sample unit. Therefore,

410   the studies must evaluate both abundance and presence-absence data as a complementary way,

411   considering that they can portray different processes in the face of environmental and spatial

412   variations. Due to the complexity of factors that govern the distribution of zooplankton

413   organisms in floodplains, there was a little prediction of environmental and spatial variables on

414   the beta diversity distribution patterns for the community. Also, there was a low concordance

415   between the patterns for the different hydrological periods, which highlights the need to study

416   the hydrological periods of high and low waters, as well as the transient periods of flooding and

417   flushing to obtain an adequate assessment of the dynamics distribution patterns of the

418   zooplankton community from the perspective of beta diversity.

419

427

Data availability statement

429

430   Data are available on request from the corresponding author.

431

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