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Concordance among zooplankton groups in a near-pristine floodplain system

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ABSTRACT

The search for biological surrogate groups has been an active and contentious area of research. A surrogate group is defined as one that allows researchers to detect a known spatial and temporal environmental gradient and to represent the responses of other biological groups to those gradients. Using spatiotemporal zooplankton data from a near-pristine floodplain (the Araguaia River floodplain in Central Brazil), we first assessed the capacity of four zooplankton assemblages (Cladocera, Copepoda, Rotifera and Protozoa) to depict the effects of flooding. Second, we evaluated whether, during each hydrological period, ordination patterns derived from an assemblage matched those patterns shown by a second assemblage and by the environmental dataset. All four assemblages satisfactorily detected the environmental differences caused by the flood event. Most pairs of assemblages were significantly concordant. Additionally, the ordination patterns generated by these assemblages matched those generated by the environmental data. These results suggest that the patterns of concordance were mediated by similar responses to environmental gradients. However, the strengths of concordance between the assemblages, albeit significant, were low. Our results suggest the potential for use of the surrogacy approach in monitoring hydrological changes. However, due to the low strengths of concordance, the biodiversity pattern revealed by a specific assemblage is unlikely to be a good predictor of another. We also highlighted that conducting a formal meta-analysis on strengths of concordance between assemblages would be a promising avenue for further research.

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1. Introduction

Aquatic biomonitoring programs often rely on the use of different biological assemblages and environmental variables. The choice of a biological assemblage for a particular biomonitoring program should be influenced by the kind of environmental problem involved and, according to Resh (2008), "ultimately depends on the characteristics of the area to be studied and the program objectives". Although we generally agree with this statement, in different situations, idiosyncratic reasons, such as the availability of a taxonomic specialist in a given region, may also explain why a particular assemblage has been monitored. Moreover, due to the lack of taxonomic knowledge and financial hindrances, in most cases, only a few biological groups are used as surrogates of biodiversity patterns in space and time (Paavola et al., 2003).

However, the use of a single group in many biomonitoring programs, generally defined in terms of taxonomic relatedness, presupposes that this group covaries with other biological assemblages in space and time. This presumption is testable, albeit rarely. It is verified when different groups are concordant or, specifically, when they exhibit similar patterns in species richness or community structure across a set of sites or through time (Allen et al., 1999; Jackson and Harvey, 1993). Beyond evaluating the reliability of surrogate groups for biomonitoring (Gioria et al., 2010; Kilgour and Barton, 1999), analyses of concordance between assemblages provide important insights on community organization (Paszkowski and Tonn, 2000). One mechanism responsible for concordance is a shared response to environmental gradients

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(Paavola et al., 2006). The strength of concordance is expected to be stronger for weakly dispersing groups than for highly dispersing ones (Grenouillet et al., 2008). Recent studies have also shown that biological interactions may influence community concordance (Padial et al., 2012), primarily when biological groups under analysis respond differently to environmental variables (Grenouillet et al., 2008).

Different frameworks can be used to study patterns of concordance (Gioria et al., 2011) and surrogacy capacity (i.e., "the capacity of a single group of taxa to represent other components of biodiversity"; see Hermoso et al., 2012). For instance, seasonal flood pulses have been shown to strongly shape the structure of floodplain-dwelling communities, and due to overwhelming environmental differences, periods of low and high water are recurrently characterized by different species compositions (Junk et al., 1989; Thomaz et al., 2007). Therefore, a potential surrogate group should, at least, be able to represent this major change in hydrological, sedimentological and physical–chemical factors. In addition to its capacity to detect seasonal patterns, a potential surrogate group should also allow us to recover the spatial patterns depicted by different biological groups.

The construction of dams is an important source of impacts to freshwater biodiversity. Dams can disrupt river connectivity, weaken the flood pulse in floodplain systems and cause biodiversity loss. For example, the Tocantins River, one of the longest rivers in the Brazilian territory and belonging to the Tocantins-Araguaia Basin, is already impacted by several dams (Barrow, 1987; Ribeiro et al., 1995). On the other hand, the Araguaia River, where this study was undertaken, still does not present any dam along its entire course, thereby generating an increasingly rare opportunity to study the functioning of relatively natural ecosystems, focusing on changes in biological composition caused by the flood pulse.

We gathered temporal and spatial data in the near pristine floodplain system of the Araguaia River in Central Brazil to address two questions: (1) are different zooplankton assemblages (cladocerans, copepods, rotifers and protozoans) able to detect the environmental differences caused by a flood event, and (2) are these assemblages concordant independently of the hydrological period? We expected all assemblages to respond similarly to the effect of flooding (i.e., differences between hydrological periods would be well represented in ordination plots by all groups). This response would result from the strong effects of floods on assemblage structure, environmental factors and processes in floodplain systems (Junk et al., 1989; Neiff, 1990; Ward et al., 1999). Therefore, all assemblages should be able to reflect these differences between hydrological periods. Beyond the differences resulting from water level variation, a reliable surrogate group should also be able to represent the spatial patterns of different aquatic assemblages and do so during both low and high water level periods.

2. Materials and methods

2.1. Study area

The Araguaia River drains the central highlands of Brazil, with a basin of 377,000 km^2. The regional climate is humid tropical (Koppen Aw), with two distinct hydrologic seasons characterized by wet summers and dry winters. The mean annual discharge of the Araguaia River is ca. 6400 m^3/s (Aquino et al., 2005), with peak discharges occurring from November to April (Latrubesse and Stevaux, 2002). The Araguaia River floodplain encompasses a variety of aquatic habitats (e.g., blocked valleys, channels, oxbow lakes and meander lakes) characterized primarily by the Cerrado Biome (Brazilian Savanna) (Latrubesse and Stevaux, 2002).

A salient feature of the Araguaia River floodplain is the absence of dams along the entire river. This characteristic is key to one of the primary goals of this study, i.e., to assess the ability of different aquatic assemblages to detect a seasonal pattern. Patterns of hydrological variation are therefore nearly unaltered.

2.2. Sampling

This study was carried out in January 2006, during a period of high water level (with a mean water flow of ca. 2542 m^3/s), and July 2006, during a period of low water level (with a mean water flow of ca. 567 m^3/s). For each period, we sampled 22 lakes of the Araguaia River floodplain (Fig. 1 – lake 1 S15°00′56.16″/W51°21′47.1″ and lake 22 S12°50′52.1″/W50°34′14.0″). The Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA) and Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) issued the permits for sampling and access to each location. All lakes were permanently connected to the main river channel.

Zooplankton samples were gathered at subsurface (ca. 50 cm) by pumping 2000 L of water (1000 L were taken from the middle and from near the shores of each lake) through a plankton net of 68 μm mesh size and were fixed in a solution of 4% formaldehyde buffered with calcium carbonate. Densities of cladocerans, copepods, rotifers and protozoans (ind/L) were estimated by counting subsamples (2.5 ml) taken with a Hensen-Stempel pipette. At least 200 individuals of each group were counted per sample using a Sedgwick-Rafter cell (Bottrell et al., 1976). Organisms were identified to the lowest possible taxonomic level (usually species).

In the field, near the middle of each lake, we measured water depth (m). Also near the middle of each lake and at subsurface (ca. 50 cm), we measured the following variables: water temperature (°C), pH, turbidity (NTU), and conductivity (μS/cm). Water samples were analyzed for total phosphorus (μg/L), total nitrogen (μg/L) and chlorophyll-*a* (μg/L) (Golterman et al., 1978; Mackereth et al., 1978).

2.3. Data analysis

A log $(y+1)$ transformation was applied to abundance data before statistical analysis to minimize the effect of extreme values. For the whole dataset and for each assemblage (Cladocera, Copepoda, Rotifera and Protozoa), compositional dissimilarities between lakes were calculated using the Bray–Curtis coefficient. We then subjected each Bray–Curtis distance matrix to a principal coordinate analysis (PCoA; Legendre and Legengre, 2012) to ordinate the samples. We also used each Bray–Curtis distance matrix in a permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001) to test for differences in assemblage structure between hydrological periods. An indicator species analysis (Dufrene and Legendre, 1997) was used to characterize the species composition of each period.

To quantify and test the strengths of concordance between pairs of assemblages for each period, we used the PCoA scores from each assemblage in a Procrustes Analysis (Jackson, 1995; Peres-Neto and Jackson, 2001). The residual sum-of-squares statistics (m^2), derived from a Procrustes Analysis, was transformed in r_P by calculating $r_p = \sqrt{1 - m^2}$. The higher the r_P, the higher the similarity between the ordination patterns generated by the assemblages under comparison.

With the exception of pH, the environmental variables were log-transformed. The standardized Euclidean distances between sampling sites were then subjected to a principal coordinate analysis (PCoA). To test for relationships between biological and environmental datasets, we also used Procrustes analysis on PCoA scores (summarizing the environmental and the biological datasets; see above). Next, the standardized Euclidean distances

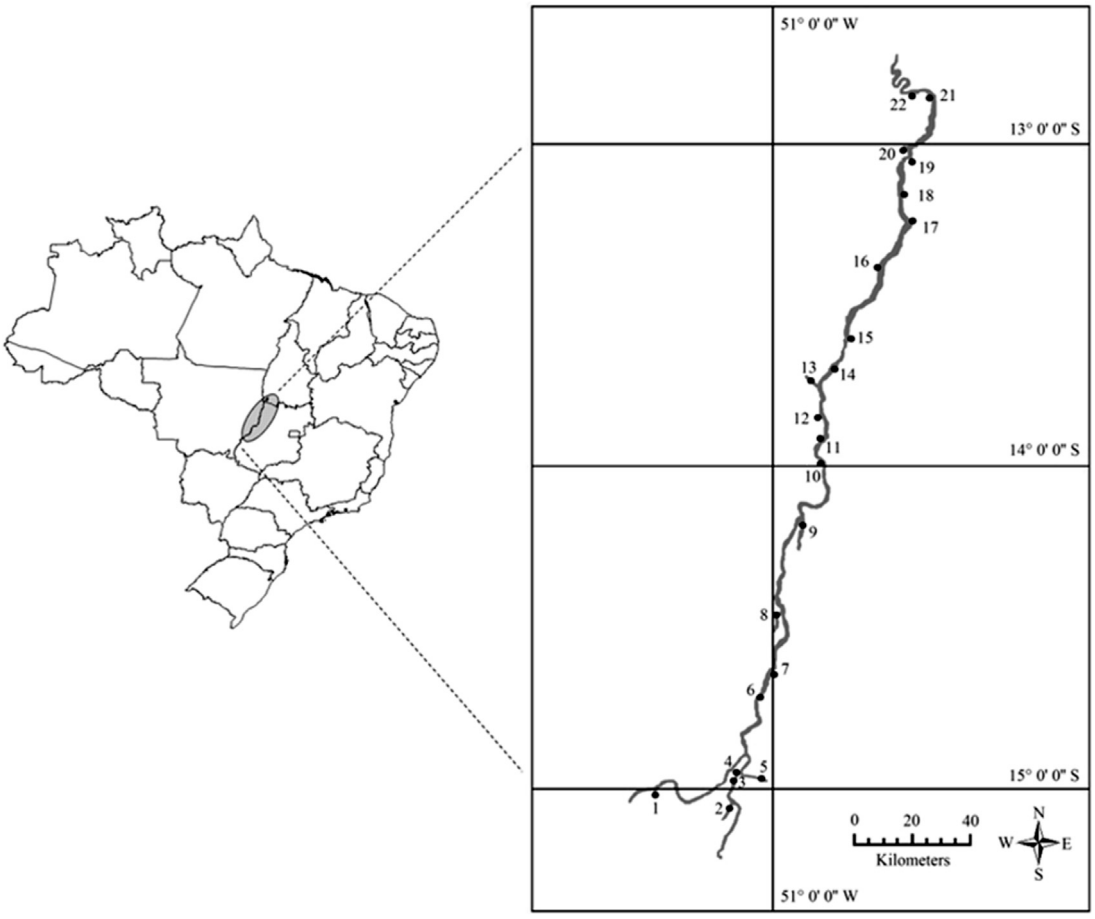

Fig. 1. Study area in the Araguaia River floodplain showing the sampling sites.

Table 1
Means and standard deviations of the limnological variables during two hydrological periods in the Araguaia River floodplain (n per period = 22 lakes).

Variables		High water (January/2006)		Low water (July/2006)	
		Mean	S.D.	Mean	S.D.
Water temperature	°C	30.7	3.1	27.2	1.6
pH		6.2	0.2	6.6	0.3
Conductivity	μS/cm	33.9	11.6	34.0	11.8
Turbidity	NTU	46.4	29.9	22.8	7.8
Secchi depth	m	51.8	35.5	54.0	16.7
Depth	m	6.6	1.2	3.0	1.4
Total P	μg/L	49.9	14.1	37.3	17.1
Total N	μg/L	651.3	93.2	508.5	221.5
Chlorophyll-*a*	μg/L	4.0	2.5	9.1	8.0

between the lakes were used in a PERMANOVA to test for differences in environmental conditions between hydrological periods.

All tests were conducted using 10,000 permutations, and all analyses were carried out using the packages "vegan" (Oksanen et al., 2013) and "labdsv" (Roberts, 2012) on R (R Core Team, 2013).

3. Results

We recorded a total of 184 taxa (36, 14, 91 and 43 for cladocerans, copepods, rotifers and testate amoebae, respectively). Using either the entire biological dataset (i.e., all four assemblages in the same matrix) or the environmental dataset, we observed a clear difference between hydrological periods (Fig. 2 and Tables 1 and 2). The Pearson's correlation between PCoA scores and variables indicated that the values of turbidity ($r = -0.79$), water depth ($r = -0.71$), water temperature ($r = -0.57$) and total N ($r = -0.55$) were higher during the high water period than the low water period. During the low water period, we registered low values for these variables and high pH values ($r = 0.58$).

Table 2
PERMANOVA results testing for differences between hydrological periods (high and low water levels).

Datasets	F	R^2	P
Environmental	13.04	0.237	<0.001
Total zooplankton	12.34	0.227	<0.001
Cladocera	11.06	0.208	<0.001
Copepoda	12.45	0.229	<0.001
Rotifera	11.59	0.216	<0.001
Protozoa	8.93	0.175	<0.001

Indicator species analysis revealed 37 indicators significantly responding to water level variation, 17 of which were

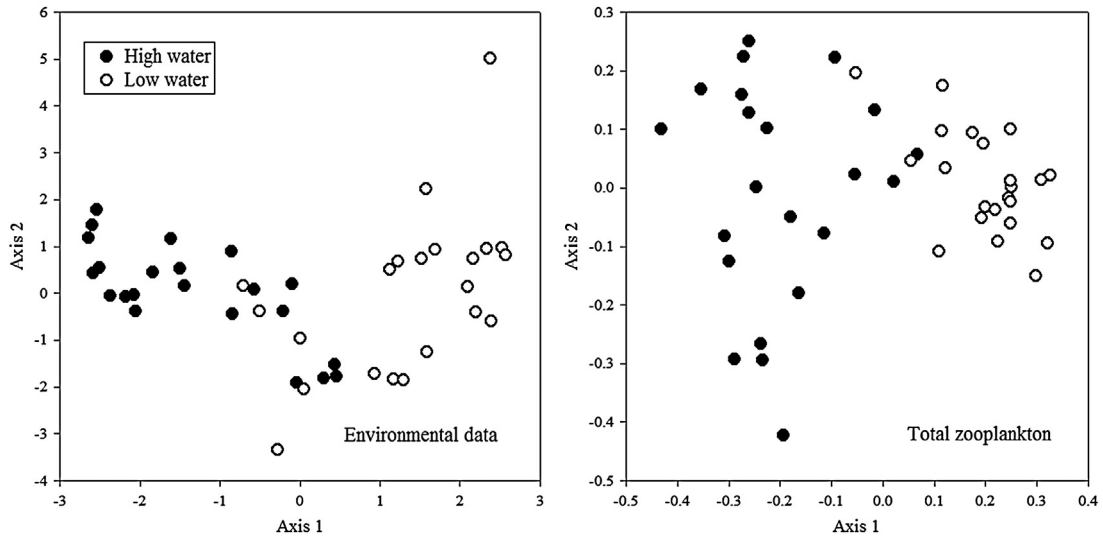

Fig. 2. Ordination of sites and periods according to the environmental and total zooplankton datasets. The first two axes of each analysis explained 54.8% and 38.5% of the variance, respectively.

Table 3
Results of indicator species analysis on the data obtained in the Araguaia River floodplain. The second column shows whether the indicator value of a species (*IV*) was highest during the high water period or during the low water period.

Groups	Period	Species	*IV*	*P*
Cladocera	High water	*Euryalona brasiliensis*	0.50	0.001
		Ilyocryptus spinifer	0.36	0.006
	Low water	*Moina minuta*	0.95	0.001
		Bosmina hagmanni	0.91	0.001
		Ceriodaphnia cornuta	0.76	0.036
Copepoda	Low water	Copepodite (Cyclopidae)	0.95	0.001
		Nauplii (Cyclopidae)	0.89	0.001
		Copepodite (Diaptomidae)	0.88	0.002
		Thermocyclops decipiens	0.67	0.041
		Notodiaptomus amazonicus	0.65	0.020
Rotifera	High water	*Lecane curvicornis*	0.82	0.001
		Plationus patulus var. *macracanthus*	0.77	0.001
		Lecane bulla	0.77	0.001
		Lecane leontina	0.73	0.001
		Testudinella patina	0.69	0.001
		Dipleuchlanis propatula	0.45	0.002
		Lecane elsa	0.41	0.001
		Lecane lunaris	0.36	0.007
		Lecane quadridentata	0.23	0.048
		Notommata pachyura	0.23	0.046
	Low water	*Filinia longiseta*	0.80	0.004
		Brachionus mirus	0.68	0.007
		Polyarthra vulgaris	0.67	0.022
		Brachionus caudatus f. *austrogenitus*	0.64	0.001
		Trichocerca cylindrica	0.60	0.005
		Trichocerca pusilla	0.57	0.004
		Brachionus caudatus var. *caudatus*	0.57	0.015
		Brachionus falcatus	0.44	0.034
		Anuraeopsis fissa	0.41	0.004
		Hexarthra mira	0.40	0.014
		Brachionus caudatus f. *insuetus*	0.32	0.011
		Hexarthra fennica	0.31	0.029
Protozoa	High water	*Arcella conica*	0.63	0.001
		Arcella megastoma	0.45	0.032
		Arcella costata	0.32	0.034
		Cucurbitella dentata	0.31	0.024
		Arcella dentata	0.23	0.047
	Low water	*Difflugia gramen*	0.78	0.045
		Difflugia cf. *kabylica*	0.64	0.001
		Cucurbitella mespiliformis	0.49	0.004

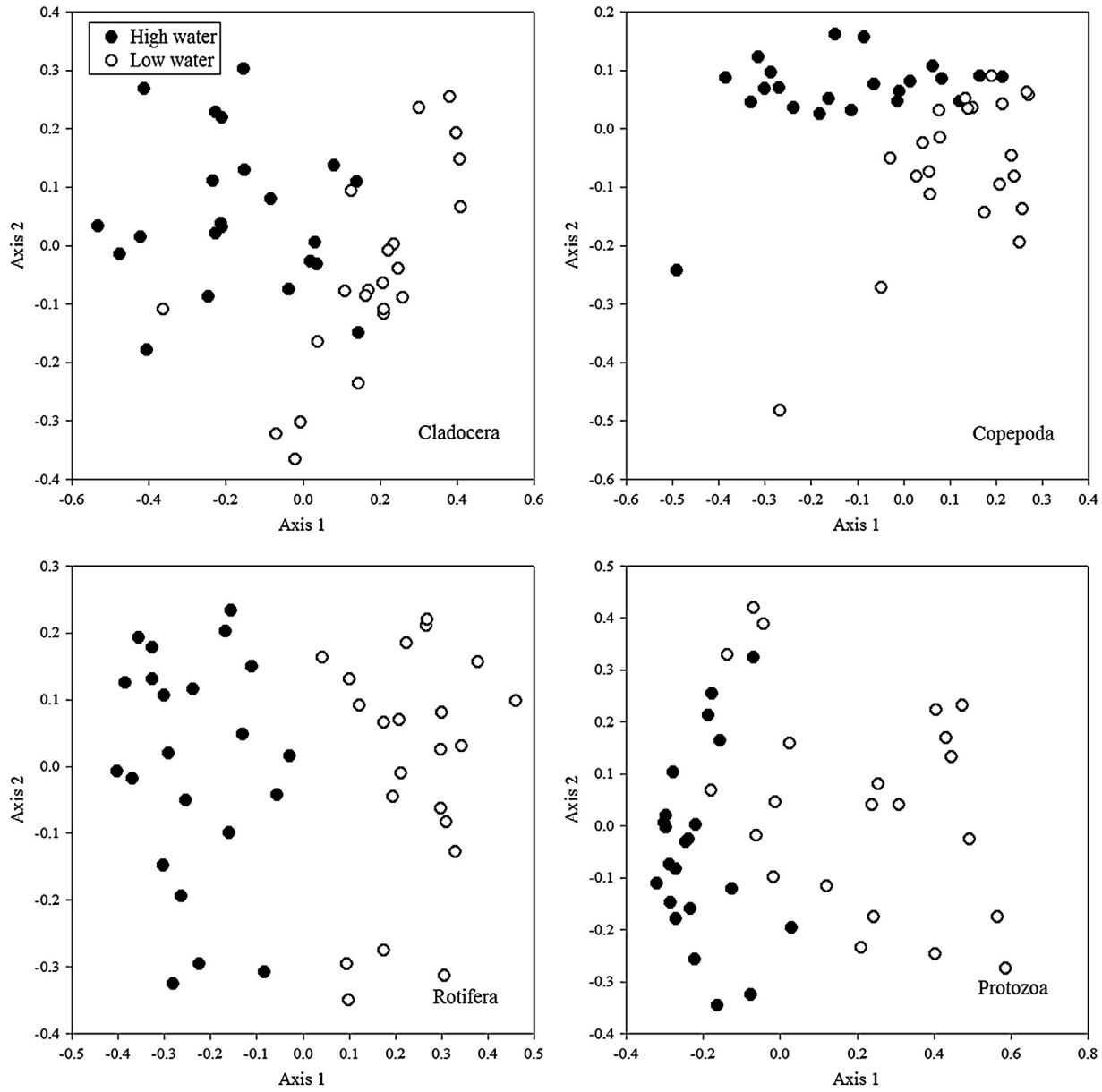

Fig. 3. Ordination of sampling sites and periods according to Cladocera, Copepoda, Rotifera and Protozoa datasets. The first two axes of each analysis explained 48.7%, 55.1%, 34.2% and 35.9% of the variance, respectively.

associated with the high water period and 20 of which were associated with the low water period (Table 3). Rotifers (e.g., *Lecane curvicornis*, *Plationus patulus*, *Lecane bulla* and *Lecane leontina*) were the primary indicators of the high water period (i.e., with indicator indexes higher than 0.70). *Moina minuta*, *Bosmina hagmanni*, *Filinia longiseta*, *Difflugia gramen* and *Ceriodaphnia cornuta* were the primary indicators of the low water period.

All assemblages were similarly able to separate the low and high water level periods (Fig. 3 and Table 2). The Procrustes analysis revealed significant concordance between all pairs of assemblages during the high water period, with the highest r_P value being registered for the comparison between rotifers and testate amoebae (Table 4). Therefore, the spatial distributions of lakes in each ordination scatterplot were more similar than expected by chance. For all assemblages, we found a significant concordance between the environmental and biological ordinations (Table 4) during the high water period. On the other hand, during the low water period we found that (i) the concordance values between cladocerans and testate amoebae and between copepods and testate were not significant; (ii) the highest concordance was found between cladocerans and copepods; and (iii) the concordance between environmental and biological ordinations was not significant for copepods and testate amoebae (Table 4).

4. Discussion

4.1. Are the zooplankton assemblages (rotifers, testate amoebae, cladocerans and copepods) able to detect the impact of flooding?

Using data gathered in the nearly pristine Araguaia River floodplain, we found that four assemblages, obtained from planktonic samples, were able to represent the hydro-sedimentological and physicochemical changes caused by seasonal flooding. Graphically, these abilities can be observed in the ordination plots showing that the lakes had different assemblage structures depending on the period. For an evaluation in terms of effect size, the magnitudes of the *F*-values (from PERMANOVA) also indicated that the four assemblages were similarly able to detect the flooding effect.

Table 4
Results of Procrustes analyses evaluating the relationships between pairs of assemblages and between these assemblages and the environmental dataset. The acronyms used in this table were Clad, Cope, Roti, Prot and Env for the ordinations generated by Cladocera, Copepoda, Rotifera, Protozoa and environmental datasets, respectively. H: high water level; L: low water level. *P*-values are given between brackets.

	Clad		Cope		Roti		Prot	
	H	L	H	L	H	L	H	L
Cope	**0.56** (0.001)	**0.54** (0.003)						
Roti	**0.55** (0.002)	**0.45** (0.02)	**0.48** (0.009)	**0.5** (0.008)				
Prot	**0.52** (0.008)	0.35 (0.123)	**0.44** (0.02)	0.3 (0.29)	**0.66** (<0.001)	**0.41** (0.051)		
Env	**0.57** (<0.001)	**0.49** (0.006)	**0.45** (0.022)	0.32 (0.234)	**0.48** (0.006)	**0.45** (0.007)	**0.52** (0.001)	0.26 (0.484)

Significant *r* values (< 0.05) are in bold.

The same conclusion applies to the comparison between the entire biological dataset and the four assemblages. Indeed, since the publication of the paper by Junk et al. (1989), a growing number of studies are showing that floods are major processes structuring river-floodplain ecosystems (Gorski et al., 2013; Roach et al., 2014; Thomaz et al., 2007).

Our results suggest that turbidity was a key variable in differentiating the hydrological periods. Although floods in other floodplain systems tend to have a diluting effect (Carvalho et al., 2001), we recorded an increase in abiogenic turbidity in the Araguaia River floodplain. It is worth noting that Tejerina-Garro et al. (1998) have also shown evidence that water transparency and depth were the main variables accounting for variation in fish communities. This may be even more important if we consider that the Araguaia River floodplain has been undergoing a rapid process of sedimentation during recent decades, most likely due to deforestation of the Brazilian Savannas (Latrubesse et al., 2009). However, we do not favor the hypothesis of a single underlying factor accounting for temporal variability in the Araguaia River floodplain. It is more likely that multiple processes, including variation in water flow, turbidity, connectivity and primary productivity, influence the conspicuous differences in zooplankton community structure between hydrological periods.

Despite the complexity of the processes affecting zooplankton community structure in floodplain systems, we found evidence supporting the use of surrogate groups, at least in biomonitoring programs aiming to evaluate the impact of hydrological changes. Specifically, we have shown that the four taxonomic groups analyzed were able to show the differences between hydrological periods depicted by the whole community. However, support for the use of surrogates groups for biomonitoring purposes in the Araguaia River floodplain should be contextualized. First, the knowledge of biodiversity in this region is plagued by the so-called Linnean shortfall (i.e., most species are still not formally described; Whittaker et al., 2005). Second, because of inadequate financial and human resources, the use of surrogates is probably the best that can be done in the short term. We recognize that, in a practical situation, the specific surrogate to be monitored would be contingent on the availability of experts in government environmental agencies and universities engaged in biomonitoring programs and long-term ecological studies. However, our results suggest that a Rotifera-based monitoring program would be the best choice. Indeed, in addition to being the most species-rich assemblage, it best depicted the difference between hydrological periods in the ordination plots. A large number of significant indicator species (22 out of 37) was also found among rotifers. Further studies with longer time frames are necessary to select particular indicator species of the complex changes caused by hydrological variation in floodplain systems. It is worth highlighting, however, the species with the largest indicator values (e.g., ≥0.80). *Lecane curvicornis* was a strong indicator of the high water period, whereas *Moina minuta*, *Bosmina hagmanni* and *Filinia longiseta* were the primary indicators of the low water period.

4.2. Patterns of assemblage concordance

In most cases, we found significant patterns of community concordance. We cannot pinpoint unequivocally the primary mechanism accounting for these patterns. However, the consistent relationships among the ordination scores generated by biological and environmental datasets suggest that the similarity in responses to environmental gradients was likely an important mechanism driving community concordance in our study. Similar responses to environmental gradients, as suggested by our results (see also Allen et al., 1999; Bilton et al., 2006; Gioria et al., 2010; Kilgour and Barton, 1999; Paavola et al., 2006; Paszkowski and Tonn, 2000; Rooney and Bayley, 2012), and biotic interactions (see Jackson and Harvey, 1993; Larsen et al., 2012; Padial et al., 2012) seem to be important mechanisms accounting for community concordance. In addition to these studies that indicate the relative importance of the mechanisms underlying community concordance, there are also a number of studies that failed to detect significant relationships between communities (e.g., Bowman et al., 2008; Doi et al., 2013; Infante et al., 2009; Paavola et al., 2003). A systematic review or a formal meta-analysis of this issue would therefore be a promising avenue for further research with important theoretical and applied implications.

4.3. How reliable is the surrogacy approach?

Despite results indicating that all groups were able to show the difference between hydrological periods, a reliable surrogate group should also exhibit strong and time-invariant patterns of concordance with other biological groups (Padial et al., 2012). An interpretation of our concordance analyses based solely on statistical significance would suggest a high potential for the use of surrogate groups. Indeed, the comparisons between pairs of assemblages formed by cladocerans, copepods and rotifers were statistically significant in both periods. However, we detected levels of concordance that were always lower than 0.7. If we concur with Heino (2010) that, beyond statistical significance, a high level of concordance should be detected for the reliable use of surrogates in biodiversity assessments, our results would suggest that this approach is flawed. Temporal stability in the strengths of concordance, a result that was not found in some of the comparisons we made, can be considered another requisite for the reliable use of surrogates. Our results are therefore consistent with previous studies suggesting a lack of support for the surrogacy approach in freshwater ecosystems (Bini et al., 2007; Doi et al., 2013; Dolph et al., 2011; Heino, 2010; Heino et al., 2003, 2005; Larsen et al.,

2012; Padial et al., 2012; Paavola et al., 2003; Rooney and Bayley, 2012). However, the weight of evidence for this view appears to be offset by the view promoting the use of surrogates as justifiable shortcuts in biomonitoring programs (e.g., Bilton et al., 2006; Bini et al., 2008; Gioria et al., 2010; Johnson et al., 2007; Johnson and Hering, 2009, 2010; Soininen et al., 2009). In addition, because different methods have been used to measure community concordance (Gioria et al., 2011), meaningful comparisons are difficult. Further, there is strong evidence that the strengths of community concordance are scale dependent (Bowman et al., 2008; Grenouillet et al., 2008; Paavola et al., 2006). Therefore, as with the issue of the relative importance of the main mechanism driving community concordance, we believe that a formal meta-analysis would greatly improve our capacity to judge the reliability of the surrogacy approach (e.g., see Velghe and Gregory-Eaves, 2013 for a meta-analysis evaluating concordance in species richness patterns). We are willing to cooperate with other aquatic ecologists in such an effort.

Different aquatic assemblages were able to recover the temporal pattern depicted by the whole biological dataset. This result shows the overwhelming importance of floods in shaping the structure of zooplankton assemblages and it also suggests that any of the assemblages may be a useful indicator of hydrosedimentological changes. However, the low level of concordance between pairs of assemblages within each hydrological period casted doubts on the reliability of these assemblages as surrogates of each other. We believe that systematic reviews of the factors accounting for variation in the strength of community concordance, and of the mechanisms underlying this pattern, would be fruitful avenues for further research.

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