



Temporal changes in zooplankton species diversity in response to environmental changes in an alluvial valley

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ABSTRACT

Monitoring the components of diversity may provide important information about diversity dynamics and processes that modify ecosystems. We investigated the temporal diversity of the zooplankton groups (testate amoebae, rotifers and microcrustaceans) over ten years (2000–2009) at local and regional scales in the alluvial valley of the Upper Paraná River in order to test: temporal changes in alpha, beta and gamma diversities of zooplankton groups, association of diversity dynamics with environmental factors, and synchronisation in temporal diversity between different subsystems. The gamma and alpha diversities of testate amoebae increased over time, while that of rotifers decreased. In contrast, microcrustacean diversity did not show a linear temporal trend. Beta diversity of microcrustaceans and rotifers increased over time. The models of temporal diversity variation explained between 10% and 46% of the total variability. Inorganic solids suspended and chlorophyll *a* were the environmental predictors selected in the models of best fit. Alpha diversity showed spatial synchronisation, suggesting that the regional dynamics contributed to the temporal variation of diversity. Zooplankton diversities followed a temporal dynamics in response to local and regional factors (water level, inorganic solids suspended and chlorophyll *a*), but the groups showed different responses. Thus, we corroborated the hypothesis of diversity synchrony of each zooplankton group between the sub-systems, but the responses to the environmental variations were found to be dependent on the group studied.

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Introduction

The term biodiversity indicates the variety of life at several scales, from genes to habitat, of a given site or region (Gaston 2000). The taxonomic diversity is the biodiversity aspect most frequently used to address this issue and is measured in three components: gamma (diversity within a large area), alpha (diversity of a site) and beta diversities (spatial replacement of species between sites of an area) (Koleff et al. 2003; Whittaker 1972). The monitoring of these diversity components contributes important information about the patterns of diversity and processes that modify the ecosystems (Ricklefs 2004; Magurran et al. 2010; Cingolani et al. 2010), especially currently due to the intense anthropogenic pressures experienced by natural ecosystems. In aquatic environments, changes in the natural flow regime, overexploitation of natural resources, water pollution, habitat degradation and species invasion are effects of human activities that have made these natural environments among the most threatened, and damaging their

biodiversity (Tockner et al. 2002; Agostinho et al. 2004; Dudgeon et al. 2006).

Recently, long-term ecological studies have provided a database sufficient to obtain a more accurate knowledge of diversity patterns, bringing diversity monitoring into a new stage of understanding of the phenomena that promote changes in these patterns, whether they result from global climate change (Hannah et al. 2002), land use (Foley et al. 2005), and/or physical and chemical changes in the water (Frost et al. 1998; Dudgeon et al. 2006). Environmental monitoring should (i) mitigate biodiversity loss, (ii) assess ecological responses to natural and human disturbances, and (iii) detect changes in the structure and function of ecosystems (Lindenmayer and Likens 2010; Magurran et al. 2010; Cingolani et al. 2010). While environmental monitoring does not allow direct inferences about cause–effect relationships, it may facilitate understanding of complex dynamic patterns (Franklin 1987), and generate hypotheses about ecological relationships.

Among aquatic communities, zooplankton can be used as a model to understand some aspects of temporal diversity dynamics because it is constituted by groups of phylogenetically different organisms (Protozoa, Rotifera and Crustacea) that share the same natural limitation: they do not have mobility to enable them to

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overcome water currents (Hutchinson 1967). Recent studies have assessed the global biodiversity of these organisms in freshwater and pointed out that these groups are negatively affected by human activities, which may lead to a decrease of diversity or even local extinction of some species (Smith et al. 2007; Segers 2008; Boxshall and Defaye 2008; Forró et al. 2008). However, the effect of human activities may not be similar between groups because their ecology and life histories are different (Allan 1976). For instance, rotifer and crustacean diversities can show divergent responses to environmental changes, favouring one of them to the disadvantage of the other (Simões et al. in press), or, stimulating exploratory competition between them (Lampert and Sommer 1997).

By studying how different zooplankton groups respond to temporal variations in environmental conditions, insights into how natural and anthropogenic variations influence diversity patterns may be obtained. The literature has shown that the diversity of the zooplankton is influenced by local and regional factors (Dodson 1992; Shurin 2000; Hobaek et al. 2002). In a temporal perspective, the physical and chemical water characteristics (Frost et al. 1998; Lansac-Tôha et al. 2009; Wagner and Adrian 2011), and interspecific interactions (Brooks and Dodson 1965; Carpenter et al. 2001), modify the diversity of zooplankton. Moreover, studying the diversity components (alpha, beta and gamma), allows the elucidation of finer information on the communities' responses to environmental changes. In this way, even if environmental modifications are sufficient to affect the alpha diversity of a locality and/or beta diversity in a given region, the gamma diversity can remain unchanged because other sites maintain the regional species pool. A location whose alpha diversity has been affected can be re-established if regional factors favour the input of species from other places (Shurin 2000; Cottenie and De Meester 2003), and contribute to synchronise temporal diversity dynamics. Synchrony of diversity may arise when regional mechanisms disperse species (such as predicted by the homogenisation effect in floodplains, Thomaz et al. 2007).

The present study aimed at identifying the temporal trends of diversity components (gamma, beta and alpha) of zooplanktonic groups, their relationships with environmental predictors (physical and chemical characteristics of the water, chlorophyll *a*, and variation in water level). Three hypotheses (hereinafter called H) were tested, H1: Temporal changes occur in the alpha, beta and gamma diversities of different zooplankton groups (protozoa, rotifers and crustaceans) driven by changes in human pressures in the alluvial valley of the Upper Paraná River, H2: Zooplankton groups differ in their temporal diversity dynamics because they respond differently to environmental changes, and H3: Regional environmental fluctuations drive synchronic changes in the diversity of each zooplankton group.

Material and methods

The hydrographic basin of the Paraná River is the second largest in South America, in terms of length and drainage area. At its upper stretch, where the alluvial valley of the Upper Paraná River floodplain is situated (latitude 22°30' and 22°00' south; longitude 53°00' and 53°30' west) (Fig. 1), the water landscape is formed by rivers, secondary channels, backwaters, and temporary and isolated lakes (Agostinho et al. 2004). Its conservation is indispensable for the biodiversity of Brazil, since this region shelters an important fraction of the original biota of the basin. Three protected areas are present in this region, indicating their relevance for biodiversity conservation; however, their ecological integrity is threatened by a chain of upstream reservoirs (Agostinho et al. 2004). The importance of the ecological integrity of this region extends past the borders of the Brazilian territory continuing into Argentina and Paraguay.

This study was carried out during a long-term ecological research (Brazilian Council of Research and Development – CNPq – site 6). Over ten years (2000–2009), samples were obtained every three months (except in 2003, when only two samplings were conducted) from localities associated with the three larger tributaries of the region (Paraná, Ivinheima and Baía rivers), which form three distinct sub-systems (Fig. 1). In each sub-system, we selected four sampling sites to maximise the environmental heterogeneity. The Paraná sub-system is directly associated with water levels of the Paraná River, which are strongly related to the operation of a reservoir located 30 km upstream. The Baía River, which follows a course parallel to the Paraná River, is also influenced by the operation of that upstream reservoir. The Ivinheima sub-system is located in a dam-free region in the Ivinheima River State Park. Therefore, this last sub-system is less affected by the upstream dams.

Zooplankton communities were sampled in the pelagic region of each environment in the morning (to minimise the effects of migration) using a motorised pump and a plankton net (68 µm). Samples were always obtained using a boat moving at constant speed and depth ranging between 1 m and 1.5 m. The 68 µm mesh is not effective for capturing all species of rotifer (Chick et al. 2010) and testate amoebae, but was standardised for all samples, leading to a systematic error which can underestimate the diversity of rotifers and testate amoebae. The samples were preserved in a formaldehyde solution (4%) buffered with calcium carbonate. The species were identified using specialised literature (see Lansac-Tôha et al. 2009). In each sample, 600 L of water was filtered to standardise the sampling effort. The identification effort stopped until the species accumulation curve reached stabilisation.

The zooplankton diversity was examined for each taxonomic group, considering three components of taxonomic diversity: gamma, alpha and beta diversities. The gamma diversity was defined as species richness in the region (i.e. number of species accumulated in all samples collected in a given time), the alpha diversity was defined as species richness of a sub-system (i.e. number of species accumulated in each sub-systems collected in a given time), and the beta diversity was defined as the change in species composition across water bodies within the same sampling period (Whittaker 1972).

Numerous dissimilarity measures have been applied to estimate beta diversity (Koleff et al. 2003). Most studies calculate the pairwise dissimilarity for all combinations of pairs of sites; however, a regional evaluation involves a greater number of sites. Thus, for each sampled time we used a multiple dissimilarity index as a measure of beta diversity (Baselga 2010), in order to encompass the average rate of species replacement between sites:

$$\beta_{SOR} = \frac{\left[\sum_{i < j} \min(b_{ij}, b_{ji}) \right] + \left[\sum_{i < j} \max(b_{ij}, b_{ji}) \right]}{2 \left[\sum_i S_i - S_t \right] + \left[\sum_{i < j} \min(b_{ij}, b_{ji}) \right] + \left[\sum_{i < j} \max(b_{ij}, b_{ji}) \right]}$$

where S_i is the number of species in site i , S_t is the total number of species in all sites considered together, and b_{ij} and b_{ji} are the number of species exclusive to sites i and j , respectively, when compared pairwise. β_{SOR} ranges from zero to one, with values near zero indicating the highest similarity and values near one indicating lowest similarity.

In order to test H1 (which diversity components presented temporal trends) and H2 (whether the diversity of each group had the same pattern of temporal response), time series of diversity (gamma, beta and alpha) were analysed, with the aim of identifying the temporal trend of increase or decline in diversity in

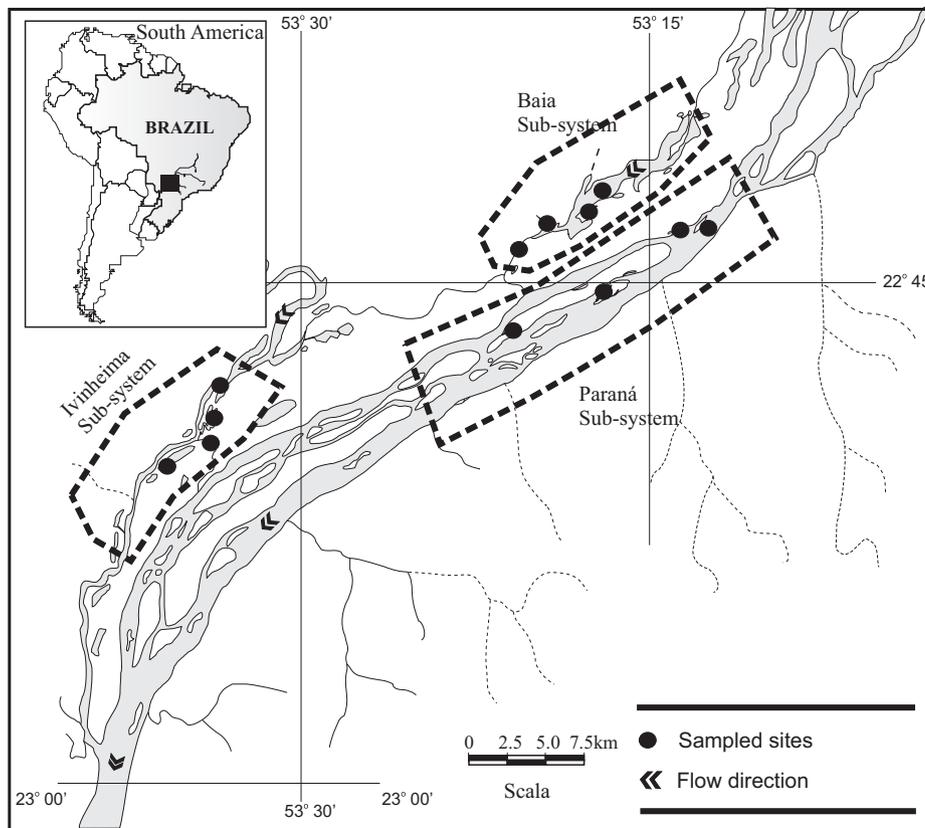


Fig. 1. Location of the sampling stations in the alluvial valley of the Upper Paraná River.

addition to their relationships with environmental factors. This procedure was performed in two steps: first, the temporal trend of increase or decline in diversity was tested; second, models were fitted to represent the temporal diversity variation as a function of environmental factors. Initially, trends were tested using mixed models by comparing two models with different fixed effects using the maximum likelihood ratio (Crawley 2007; Shumway and Stoffer 2011): one model with the trend ($y = \alpha + \tau T$, where: y is the diversity, α is the intercept, τ is the slope that shows the relationship between diversity and time, and T is a discrete sequence ranging 1–40); and another model without trend (only, $y = \alpha$). If the models are significantly different, this indicates the temporal trend ‘ τ ’ has a monotonic relationship with diversity ‘ y ’ (Crawley 2007; Shumway and Stoffer 2011).

To verify which environmental predictors correspond to temporal variations of the series diversity (alpha-local and gamma-regional), we used a model selection procedure based on Akaike’s information criterion (Burnham and Anderson 2002). This approach works by comparing different candidate models, weighing evidence for multiple hypotheses (Johnson and Omland 2004). However, to be more constrained on the procedure of selection model, the parameters of each model were tested if significantly different from zero to the significance level of 5%. These two steps described come from different philosophical approaches (multimodel inference and classical hypothesis test). Despite philosophical controversy, we used of this method to produce more reliable relationships and prioritise the parsimony principle.

The series were fitted assuming an additive model with linear and quadratic relationships and interaction among variables, according to the equation $y_t = \alpha + \sum \beta_i x_i + \sum \beta_j x_i \times x_j + \beta_k \text{Chl}^2$, where: y_t is the diversity (alpha or gamma); α is the intercept; $\beta_i x_i$ is the intensity of the relationship between the predictor x_i

(environmental variables) and the response variable y ; $\beta_j x_i \times x_j$ is the interaction between predictors; Chl is the chlorophyll a concentration; and t is the time. The environmental predictors used were: pH, inorganic suspended solids (mg L^{-1}), chlorophyll a ($\mu\text{g L}^{-1}$), nitrate ($\mu\text{g NL}^{-1}$), soluble reactive phosphorus ($\mu\text{g P L}^{-1}$) and water level. Details of the methods employed for obtaining limnological variables can be found in a specific limnological study of this floodplain (Roberto et al. 2009). Nitrate, soluble reactive phosphorus (SRP) and pH can affect indirectly the zooplankton diversity and were selected as they are sensitive to environmental modification, showing signs of cultural eutrophication (Wetzel 2001). Inorganic suspended solids can be harmful for Cladocera because they congest their filtration apparatus (Bozelli 1998), but can be positive to Rotifera as they favour the range of food resources, such as bacteria and ciliate protozoa (Starkweather 1980). The water level and chlorophyll a are variables mechanistic that affect the zooplankton diversity (Paidere et al. 2007; Simões et al. in press): the first increases zooplankton diversity as the connectivity allows the exchange and dispersion of species; the second supports the hypothesis that food availability increases community diversity. We also tested if these mechanisms interact to affect the zooplankton diversity, inserting interaction between variables in the models. Ultimately, we inserted a quadratic term to Chl, in order to test if intermediary quantities of resources favour the diversity (Dodson et al. 2000). To avoid multicollinearity in the models, we used only the variables with VIF (Variance Inflation Factors) below 5. The assumptions of each model were observed by a visual inspection of residuals. The diversities were log-transformed to minimise data variability and achieve the normality and homoscedasticity of the residuals. Herein only the model best adjusted to each data series will be presented.

A simple temporal association between environmental predictors and time was run using the Spearman correlation in order

Table 1

Summary of limnological characteristics in the alluvial valley of the Upper Paraná River during the period of 2000–2009. Spearman correlation between limnological characteristics and time (2000–2009).

	pH	Inorganic suspended solids (mg L ⁻¹)	Chlorophyll <i>a</i> (µg L ⁻¹)	Total nitrogen (µg L ⁻¹)	N-Nitrate (µg N L ⁻¹)	Total phosphorus (µg L ⁻¹)	Soluble reactive phosphorus (µg P L ⁻¹)
Mean	6.6	1.5	8.6	677.6	64.6	52.8	10
Minimum	4.8	0.1	0	73.3	0.1	3.3	0.1
Maximum	8.8	8.8	109.2	4473	993.1	313.6	92.9
Lower quartile	6.2	0.7	1.9	316.1	6.2	22.8	3.8
Upper quartile	6.9	1.8	10.1	854.8	112.9	67.3	13
Standard deviation	0.6	1.4	12.8	544.2	77.9	44.2	10.5
Spearman correlation							
Ivinheima sub-system	0.079	-0.059	-0.324*	0.630*	-0.006	0.014	0.320*
Baia sub-system	-0.121	-0.400*	-0.390*	0.554*	-0.229	-0.014	0.341*
Paraná sub-system	0.228	-0.445*	-0.384*	0.439*	0.064	0.088	0.522*

* Significant correlation after Bonferroni adjustment.

to identify a monotonic trend of increase or decrease of the environmental predictors. We control the problem of multiple comparisons by using the Bonferroni correction.

H3 (whether there is synchrony of diversity between the sub-systems) was tested by correlating the temporal series (alpha × alpha) between the sub-systems using a Pearson product–moment correlation coefficient. A significant positive association indicates that the variability of diversity components between the sub-systems follows similar temporal variation.

The analyses were performed with the software R version 2.14.0 (R Development Core Team 2011).

Results

A summary of limnological characteristics is shown in Table 1. The pH values ranged from acid to alkaline. As the locales are shallow lakes (maximum depth of 3.9 m), the wind facilitates the re-suspension of sediment leaving the environment with a high

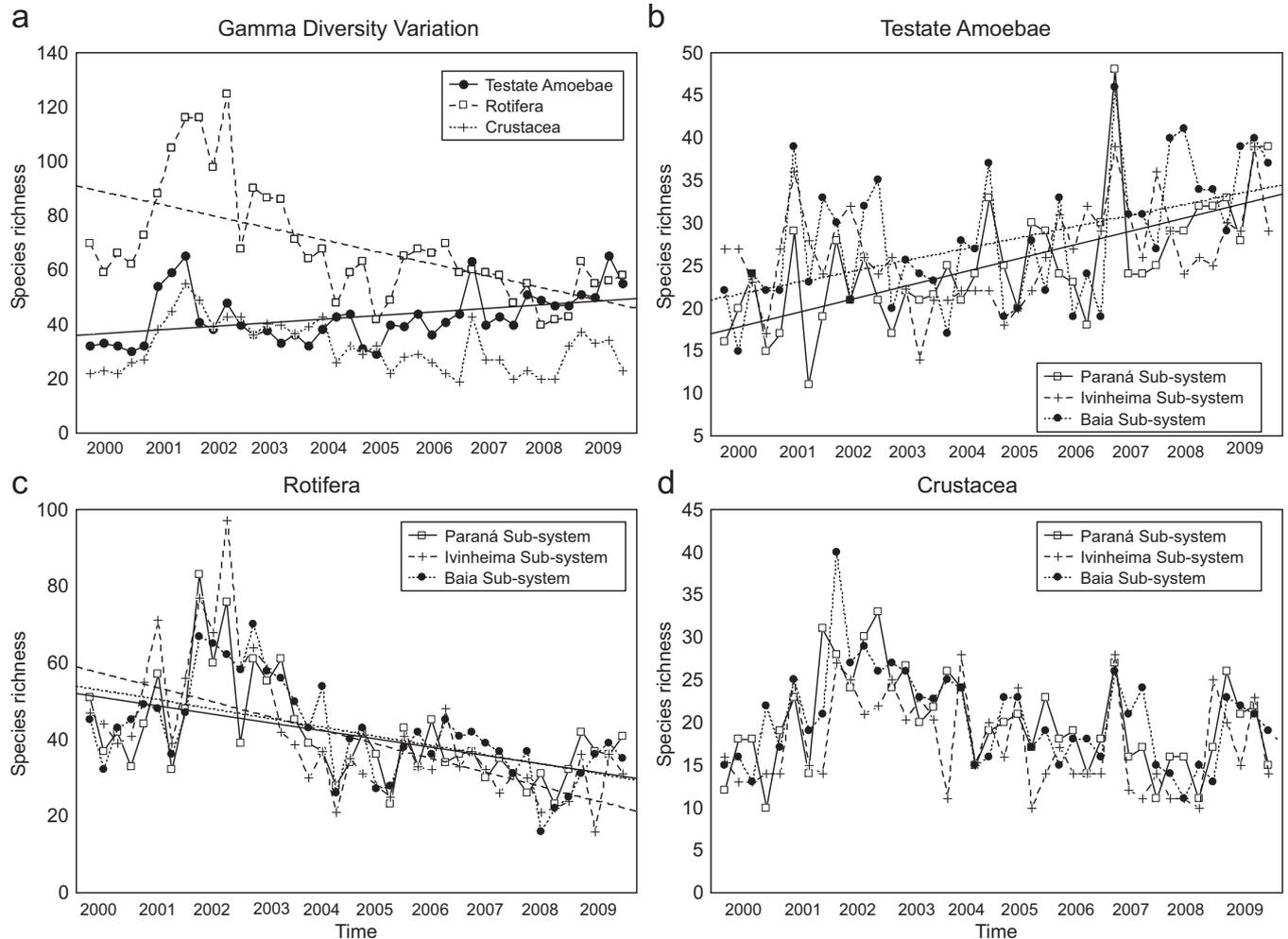


Fig. 2. Temporal series of zooplankton diversities in the alluvial valley of the Upper Paraná River during 2000–2009. Gamma diversity (a); Testate Amoebae alpha diversity (b); Rotifera alpha diversity (c); Microcrustaceans alpha diversity (d).

Table 2
The most parsimonious models fitted to temporal variation of diversity in taxonomic series of the zooplankton groups from the alluvial valley of the Upper Paraná River floodplain during 2000–2009 period. ISS – Inorganic suspended solids (mg L^{-1}); Chl – chlorophyll *a* ($\mu\text{g L}^{-1}$); NO_3 – N-nitrate ($\mu\text{g N L}^{-1}$); SPR – soluble reactive phosphorus ($\mu\text{g P L}^{-1}$); le – water level (m).

		R^2_{adj}
Gamma diversity – total floodplain		
Testate amoebae	$5.47 - 0.45_{\text{ISS}} - 0.07_{\text{Chl}} + 0.01_{\text{NO}_3} + 0.04_{\text{SPR}} + 0.05_{\text{ISS} \times \text{Chl}}$	0.46
Rotifera	$6.10 + 0.18_{\text{ISS}} + 0.27_{\text{ISS} \times \text{pH}} - 2.44_{\text{pH} \times \text{Chl}} - 0.14_{\text{ISS} \times \text{NO}_3} + 0.21_{\text{Chl} \times \text{NO}_3}$	0.37
Crustacea	$4.95 + 0.19_{\text{ISS} \times \text{Chl}}$	0.10
Testate amoebae – diversity alpha (sub-systems)		
Paraná	$4.61 + 0.22_{\text{le}}$	0.26
Ivinheima	$4.64 + 0.10_{\text{SPR}} - 0.15_{\text{NO}_3 \times \text{Chl}} - 0.23_{\text{Chl} \times \text{le}}$	0.21
Baia	$4.38 - 0.68_{\text{Chl}} + 0.11_{\text{SPR}} + 0.01_{\text{Chl}^2} - 0.09_{\text{ISS} \times \text{le}}$	0.42
Rotifera – diversity alpha (sub-systems)		
Paraná	$5.75 + 0.11_{\text{ISS}} + 0.74_{\text{Chl}} + 0.24_{\text{le}} - 0.01_{\text{Chl}^2} + 0.18_{\text{Chl} \times \text{le}}$	0.34
Ivinheima	$^a 5.22 + 0.15_{\text{Chl}} + 0.15_{\text{Chl} \times \text{ISS}}$	0.19
Baia	None β was selected	
Crustacea – diversity alpha (sub-systems)		
Paraná	$4.25 - 0.14_{\text{Chl}} - 0.15_{\text{SPR}} + 0.06_{\text{le} \times \text{NO}_3} - 0.27_{\text{SPR} \times \text{le}}$	0.22
Ivinheima	$4.09 - 0.19_{\text{ISS}} + 0.18_{\text{Chl} \times \text{le}} - 0.33_{\text{ISS} \times \text{le}} + 0.31_{\text{le} \times \text{NO}_3}$	0.18
Baia	$4.76 + 0.60_{\text{Chl}} - 0.12_{\text{SPR}} - 0.01_{\text{Chl}^2} - 0.23_{\text{Chl} \times \text{le}} + 0.11_{\text{le} \times \text{NO}_3}$	0.33

^a Residuals without normality.

amount of inorganic suspended material. The concentration of nutrients showed high variation (Table 1), and during some periods, the phytoplankton biomass reached $109 \mu\text{g L}^{-1}$ (chlorophyll *a*).

Some limnological variables changed over time. SRP and total nitrogen correlated positively with time, while Chlorophyll *a* decreased in the all sub-system (Table 1, Fig. S1). Inorganic suspended solids decreased in the Baia and Paraná sub-system.

The zooplankton community was represented by 501 taxa and rotifers were the most speciose group, with 270 taxa, followed by microcrustaceans (125 taxa) and testate amoebae (106 taxa) (a species list can found at: <http://www.peld.uem.br/Relat2008/pdf/Capitulo05.pdf>).

The gamma diversity of testate amoebae ranged from 29 to 65 taxa (Fig. 2a) and had an increasing trend over time ($\tau = 0.36$; $p < 0.05$), unlike rotifers, whose diversity decreased over time ($\tau = -1.08$; $p < 0.01$) (Fig. 2a) and ranged from 40 to 125 taxa. The microcrustaceans diversity presented a temporal variation between 19 and 55 taxa, but no linear temporal trend was not observed.

The most parsimonious models of gamma diversities of Testate Amoebae and Rotifera showed, respectively, 46% and 37% (R^2_{adj}) of temporal variability of the data (Table 2). Inorganic solids suspended (ISS) and chlorophyll *a* (Chl) stood out because they were present in models selected for all groups. ISS diminished over 10 years (Table 1), and was negatively associated with testate amoebae, was positively associated with Rotifera and interacted with Chlorophyll *a* to influence the Crustacea. The Rotifera's model showed many interactions between environmental predictors, showing the complexity of factors affecting its diversity.

The testate amoebae presented an increasing trend in alpha diversity in the Paraná and Baia sub-systems ($\tau = 0.40$ and $\tau = 0.33$, respectively) (Fig. 2b), where they presented associations with water level (Table 2). SRP concentration presented a positive association with diversity in the Ivinheima and Paraná sub-system (Table 2).

Rotifer alpha diversity decreased in the three sub-systems (Fig. 2c) ($\tau = -0.603$, -0.936 and -0.656 for Paraná, Ivinheima, and Baia, respectively). In the models of temporal variation, the chlorophyll *a* and ISS were positively associated with rotifer diversity. In the Paraná sub-system, the water level increased the rotifer diversity.

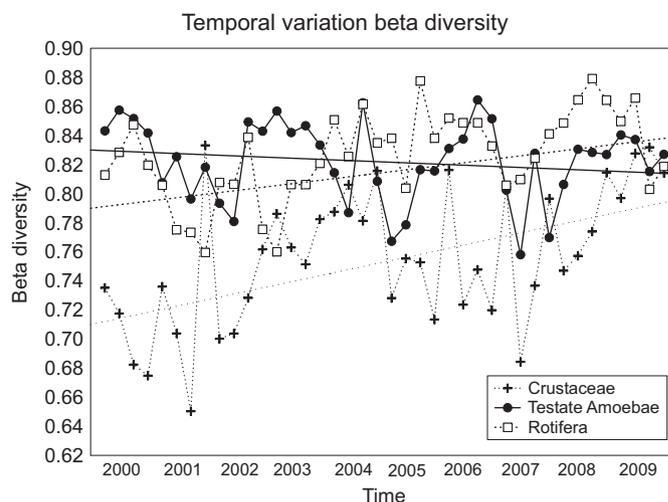


Fig. 3. Temporal series of the zooplankton beta diversities in the alluvial valley of the Upper Paraná River during 2000–2009.

The microcrustaceans did not present significant trends in alpha diversity (Fig. 2d). Among the environmental variables, the interaction water level \times nitrate was present in every model adjusted, and SRP concentration in the Baia and Paraná sub-system (Table 2) presented a negative association with diversity in these sub-systems.

The beta diversity of zooplankton assemblages varied between 0.76 and 0.86 (testate amoebae), 0.76 and 0.88 (rotifers), and 0.65 and 0.83 (microcrustaceans). With regard to regional scale, microcrustaceans and rotifers presented a significant temporal trend of increase in beta diversity ($\tau = 0.0012$ and $\tau = 0.0021$, respectively) (Fig. 3).

Alpha diversity was positively correlated between all the sub-systems analysed (Table 3), indicating that diversity of the groups showed similar temporal variation between the sub-systems, with all taxonomic groups presenting spatial synchrony of diversity.

Discussion

Regional and local diversities (gamma and alpha diversities, respectively) of the zooplankton community has changed continuously, but with different trends. These trends are related to seasonal, local and regional features; mainly, whether such features

Table 3

Pearson product–moment correlation of the alpha diversity between sub-systems from the Upper Paraná River floodplain during the period of 2000–2009.

	Paraná × Ivinheima		Paraná × Baía		Baía × Ivinheima	
	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>
Testate amoebae	0.426	0.008	0.656	0.001	0.421	0.008
Rotifera	0.835	0.001	0.779	0.001	0.809	0.001
Microcrustaceans	0.546	0.001	0.675	0.001	0.589	0.001

are associated with recent changes in the characteristics of the alluvial valley of the Upper Paraná River, such as hydrodynamic, physical, chemical and biological changes (Lansac-Tôha et al. 2009; Souza Filho 2009; Fernandes et al. 2009; Roberto et al. 2009; Rodrigues et al. 2009). One feature that operates at the regional scale and is related to these trends is variability in the water level due to the increase in the number of upstream reservoirs in the basin (Agostinho et al. 2008). The higher frequency of floods in recent years favoured the diversity of testate amoebae because the environments became more hydrodynamic, and thus these organisms (mainly associated with macrophytes and sediment) are easily displaced to the plankton (Alves et al. 2010); moreover, the shorter generation time allows them to respond better to hydrometric variability (Obertegger et al. 2007). On the other hand, the diversity of rotifers, which require greater hydrodynamic stability (De Emiliani 1997; Casanova et al. 2009), may have been diminished by the greater variability in water level. Other studies have pointed out that the reduction in the frequency, intensity and amplitude of the floods determined the decrease in species richness of these invertebrates (Bonecker et al. 2009).

The model selection supported evidence of relationships between zooplankton diversities and environmental predictors, chiefly water level, inorganic solids suspended and chlorophyll *a* (which changed over time), confirming our expectations concerning selection of variables a priori to include in the model. Considering the approach of this study (mensurative field study), the fitted models to regional diversity presented good approximations to Testate amoebae and Rotifera (46% and 37%, respectively), but the selected variables depended on the group, such as we expected. Usually some limnological characteristics (chlorophyll *a* and ISS) have a joint temporal dynamics in response to the seasonal cycle of the flood (Rocha et al. 2009; Simões et al. in press), and this cycle is a determinant of the temporal variation in the diversity of zooplankton species (Saunders III and Lewis Jr, 1989; José De Paggi and Paggi 2007; Paidere et al. 2007). However, ISS and chlorophyll *a* decayed over time (Table 1) and SRP and total nitrogen increased, indicating that these trends were detrimental to the rotifer diversity, but favoured testate amoebae diversity (the model selection has supported this hypothesis). Although the input of nutrients into the aquatic environment leads to an increase in the primary productivity of the plankton (Carpenter et al. 2001; Cottingham et al. 2004), it also causes a decrease in the heterogeneity of resources for the zooplankton, due to the predominance of a few phytoplankton species (Watson et al. 1997). In the alluvial valley of the upper Paraná River, the nutrient concentration (mainly forms of nitrogen) increases the density of phytoplankton organisms, but decreased the richness of phytoplankton species in the Paraná River (Rodrigues et al. 2009), indicating a decrease in resource heterogeneity for zooplankton. Temporal changes in rotifer diversity have been ascribed to changes in the planktonic trophic chains (Virro et al. 2009; Wagner and Adrian 2011), mainly, when decreases in phytoplankton abundance and size occur (Obertegger and Manca 2011). The reduction in rotifer diversity may be a response to these changes. Such characteristics have allowed the use of Rotifera as bioindicators (Duggan et al. 2001; Segers 2008).

We cannot infer causal mechanisms between the variation of these limnological characteristics and zooplankton diversity; however, the trend analysis and selection model procedure supported H1 (temporal changes of diversity are driven by changes environmental) and H2 (zooplankton groups differ in their temporal diversity dynamics because they respond differently to environmental changes). Moreover, the selection of nitrate and SRP in the models shows that continuous environmental changes, which affect such variables, may in the long run intensify the observed diversity trends in this alluvial valley.

The beta diversity of rotifers and microcrustaceans increased over time. As we have already observed, the main river and its closer locales have undergone a continuous reduction in water quality (considering the suspended load and flood attributes) (Souza Filho 2009), and temporal increase in the nutrient concentration. These observations indicate an increase in the variability of limnological conditions among the water bodies, and consequently, have made the communities more spatially heterogeneous over time, in response to different environmental locale conditions. The floodplain lakes have a key role in minimising the effect of environmental changes on the alluvial valley diversity and the functioning of the river-floodplain system (Junk et al. 1989), because, even if environmental modifications are sufficient to affect the alpha diversity of some localities, the gamma diversity can remain unchanged because other sites maintain the regional species pool.

Regional diversity (gamma diversity) showed higher values in 2001 and 2002, coinciding with La Niña period. The effect of this climatic event on the study region was a hydrological change that produced an unusual drought and decreased the amplitude of the floods, consequently, decreasing the connectivity between the water bodies. Under these circumstances, local processes (interactions between species and abiotic factors) produce divergent ecological dynamics (Ward et al. 1999; Thomaz et al. 2007) and may have initiated an increase in regional diversity.

Although local features have influenced the community species diversity, the regional dynamics contributed to maintaining the synchrony of components of diversity (alpha) between the sub-systems (Table 3), indicating that the communities in each sub-system may respond to similar environmental signals (Cottenie and De Meester 2005). According to Thomaz et al. (2007), the seasonal dynamics in water level operate as a regional factor because they increase the aquatic similarity in the floodplains during floods. This might be the case because the dispersal process is favoured due to interchange of organisms inside the hydrological network (Michels et al. 2001), which, along with the flood pulse, maintains the synchronism of diversity among the sampling sites, sustaining regional diversity.

Despite the synchrony and similar temporal trends of alpha diversity for each group in the three sub-systems, the beta diversity of rotifers and microcrustaceans has increased. This result is worrying because the increase in beta diversity can represent an increase of the influence of local processes on the communities, at the expense of regional processes, thus reducing the importance of the ecological effect of the floods (as a regional factor facilitating the dispersal) on the diversity (see Dudgeon et al. 2006 for a summary of the importance of the flood effects).

In this study, the monitoring of zooplankton diversities contributed to demonstrating the temporal trends in alpha, beta and gamma diversities, and that their temporal variations respond to changes in human pressures in the alluvial valley of the Upper Paraná River. Rotifer diversity was more affected than other groups, indicating that this group may constitute a useful indicator for monitoring programmes. Finally, we corroborated the hypothesis of diversity synchrony of each zooplankton group between the sub-systems, but the responses to the environmental variations were found to be dependent on the group studied.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.limno.2012.07.007>.

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