Zooplankton temporal beta diversity along the longitudinal axis of a tropical reservoir

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Abstract
Different processes, including ecological drift, environmental changes, and biotic homogenization, can explain variation in temporal beta diversity. Here, we aimed to analyze the temporal beta diversity of zooplankton communities along the longitudinal axis of a reservoir using two analytical approaches. As for the first approach, we predicted that that beta diversity would be positively correlated with limnological variability. We used multiple samples-based metrics to estimate beta diversity among 62 sampling months at six sampling sites; after, we correlated these metrics with within-site temporal variability in limnological factors. As for the second approach, we predicted that between-months variation in community composition would be positively correlated with time lags and between-months environmental distances. Considering the multiple samples approach, we did not detect a significant relationship between temporal beta diversity and variability in limnological factors. Between-months beta diversity was unrelated to between-months differences in limnological and hydrological factors. Only temporal lags were significantly correlated with between-months beta diversity. Beta diversity and species richness were substantially highest at the lotic zone of the reservoir. Our results indicate that temporal beta diversity tends to be highly unpredictable and that most of the taxa contributing to the regional diversity of the reservoir disperse via its lotic region.

Keywords Plankton dynamics · Turnover · Nestedness · Environmental variation

Introduction

Temporal beta diversity is defined as changes in species composition and community structure (which includes variation in patterns of rarity and dominance, in addition

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to changes in species identities) over time (Anderson et al. 2011, Dornelas et al. 2014; McGill et al. 2015; Shimadzu et al. 2015). These changes can be accounted for by different mechanisms. For example, temporal changes in species composition in a local community can be accounted for by temporal changes in influential environmental factors (Hatosy et al. 2013), such as hydrological and physical–chemical factors (Hillebrand et al. 2010; Bozelli et al. 2015). Similarly, within the context of the theory of multiple stable states (Scheffer 1990), a shift from one equilibrium state (e.g., clear water state) to another (turbid water state) would account for a high change in species composition. A reduction in beta diversity through time is consistent with the increase in abundance of dominant species due to a process of biotic homogenization (where few winners replace many losers, paraphrasing McKinney and Lockwood 1999; see also Olden and Poff 2003). Finally, temporal beta diversity, even for very short time lags and negligible differences in environmental factors, can be high due to ecological drift (random changes in species compositions and relative abundances over time; Vellend et al. 2014).

Depending on the goals and the data at hand, different approaches can be used to quantify temporal beta diversity (Korhonen et al. 2010; Anderson et al. 2011; McGill et al. 2015). Considering a community data table, with species in the columns and the time points in the rows, one can use, for example, multiple sample methods (Baselga et al. 2007; Baselga 2010) to calculate temporal beta diversity. To analyze the correlates of temporal beta diversity with this approach, one needs to have data for different local communities. A second approach consists in calculating a matrix of species composition dissimilarities between t time points (Collins et al. 2000). High values in this matrix, for any two time points, indicate high changes in species compositions (i.e., high temporal beta diversity). In a slightly different way, one can also analyze changes in community composition between the first sampling time (which is taken as a baseline) and successive times (e.g., Dornelas et al. 2014). Finally, one can also use a raw-data approach (e.g. partial Redundancy Analysis) to partition temporal variation in community composition among groups of explanatory variables (Legendre et al. 2005).

Most previous studies evaluating beta diversity patterns were based on spatial data (i.e., multiple sampling sites or local communities; see Brown et al. (2010) and Santos et al. (2016) for typical examples). However, there is an increase in the number of studies focusing on temporal beta diversity (Jones and Gilbert 2018). In an experimental study, for example, Brown (2007) found a negative relationship between macroinvertebrate community (temporal) variability and substrate heterogeneity. Tisseuil et al. (2012), using projected distribution of 18 fish species, reported a decrease in temporal beta diversity from upstream to downstream reaches within the Garonne River Basin (France). As a last example, Smol et al. (2005) analyzed 55 paleolimnological records from Arctic lakes and showed high temporal beta diversity in algae and invertebrate communities over the last 150 years. Given the remoteness of these lakes, these authors inferred that climate warming was the most likely process accounting for this result.

In general, the list of potential correlates of beta diversity is similar, independently of the way (spatial or temporal) in which beta diversity is calculated (Lopes et al. 2017). Environmental variability may be considered as a key correlate of temporal beta diversity: local communities subjected to high environmental variability are expected to exhibit high variation in community structure as temporal changes in environmental conditions may favor different species compositions. Thus, this prediction is equivalent to that made in studies focusing on spatial beta diversity (e.g., Heino et al. 2013; Astorga et al. 2014; Bini et al. 2014).

In this study, we gathered data on zooplankton composition and abundance for a period of 5 years (62 consecutive months) at 6 sites distributed along the longitudinal axis of a reservoir (State of Rio de Janeiro, Brazil). Considering the structure of this dataset, we posed the following questions: (1) which reservoir region (i.e., along the longitudinal axis of a reservoir, from fluvial to lacustrine regions) exhibits higher temporal beta diversity? (2) Is between-months beta diversity related to temporal, hydrological and limnological distances between sampling months? Due to their smaller size, environmental variation (considering limnological and hydrological factors) is likely to be higher in fluvial regions than in lacustrine regions of reservoirs. Thus, for our first question, we predict that the highest beta diversity should occur in the fluvial region of the reservoir as different environmental conditions may select for different species compositions over time. For the second question, we expect that between-months beta diversity would be positively correlated with environmental distances since a time lag of 1 month (or longer) would be sufficient for communities composed of small organisms to respond to environmental changes (De Bie et al. 2012; Padial et al. 2014). In general, the confirmation of both predictions, after accounting for time lags, would suggest the importance of species sorting processes (Leibold et al. 2004) in driving zooplankton community changes. On the other hand, a significant relationship with time lags (temporal distances) only, after accounting for environmental distances, would suggest the role of ecological drift. Also, this result may indicate that influential and temporally autocorrelated environmental variables were missing from the matrix of explanatory predictors.

Methods

Study area

Ribeirão das Lajes Reservoir, where this study was carried out, was built in 1905 to produce energy and supply water to some cities in the State of Rio de Janeiro. Nutrient and chlorophyll-*a* concentrations indicate that this reservoir can be classified as oligo-mesotrophic (Table S1). This reservoir has an average surface area of approximately 40 km^2 and average and maximum depth of 15 and 40 m, respectively. Water volume is about 450×10^6 m^3 and the water retention time is about 300 days. In general, water level variation, which reaches 8 m, follows rainfall patterns, with the lowest and highest values at the beginning (November) and at the end of the rainy season (April), respectively. The lacustrine region is thermally stratified during most of the year, except in the winter months (June, July and August), when partial or complete mixing may occur (Branco et al. 2009).

Data

We carried out 62 monthly sampling campaigns between November 2004 and December 2009. Subsurface samples for limnological and zooplankton analyzes were collected at 6 sites along the longitudinal axis of the reservoir, with average water depths ranging from 5 m (at site 1) to 35 m (site 6; Figure S1 and Table S1). We measured the following limnological variables at each sampling site and month: water temperature, dissolved oxygen concentration, conductivity, water transparency (Secchi depth), nutrient (nitrate, ammonium, orthophosphate, total phosphorus) and chlorophyll-*a* concentrations. A detailed description of the environmental data, sampling and zooplankton counting methods can be found elsewhere (Lopes et al., 2017). In this study, differently from Lopes et al. (2017), we have also included data on copepods.

Species richness and temporal beta diversity

Species richness accumulation curves (through time) were calculated for each site using the methods described by Gotelli and Colwell (2001). We calculated five temporal beta diversity measures for each sampling site (see Baselga et al. 2007; Baselga 2013 and references therein). Based on species presence and absence data, the version of the Simpson coefficient (βSIM) for multiple samples (months in our case), which only accounts for turnover or species replacement (see Table 2 in Baselga 2010), and nestedness (βNES) were the first and second measures estimated (see, respectively, Eqs. 6 and 7 in Baselga 2010). Other nestedness measure based on the overlap and decreasing fill (NODF) was also calculated (Almeida-Neto et al. 2008) for comparative purposes considering the discussions related to the suitability of NODF and βNES in measuring nestedness (Ulrich and Almeida-Neto 2012). Higher values of βSIM in a particular site (e.g. fluvial zone of the reservoir), as compared to another site (e.g. lacustrine zone of the reservoir), indicate higher temporal variability in species composition in the former than in the latter. Third, abundance data were transformed into logarithms after adding a constant (log $y + 1$). Then, a principal coordinates analysis (PCoA), based on the Bray–Curtis dissimilarity matrix, was used to calculate the distances between sampling months and the centroids of groups (sampling sites; Fig. S2). The average of these distances (dBC) was then estimated (Anderson 2006; Anderson et al. 2006). The greater the dispersion of sampling months around the centroid, the greater the temporal variation in community structure. High values of NODF (or βNES) indicate a decline in species richness over time since the chronological order of the matrix (i.e., months in the lines) was used in the calculations.

Fifth, we calculated the beta diversity measure proposed by Raup and Crick (1979) and modified by Chase et al. (2011) (βRC). The modification proposed by Chase et al. (2011) consisted in re-scaling the original Raup and Crick measure to vary from − 1.0 to 1.0, so that: "A value of 0 represents no difference in the observed (dis)similarity from the null expectation; a value of 1 indicates observed dissimilarity higher than the expected in any of the simulations (communities completely more different from each other than expected by chance), and vice versa for a value of −1 (communities completely less different [more similar] than expected by chance)". According to Chase et al. (2011), the "null model is needed to discern whether the difference in dissimilarity deviates from random expectation given the changes in α-diversity" (i.e. species richness). We calculated βRC between each pair of sampling months and averaged the values for each sampling site. When mean βRC approaches zero, stochastic processes of community assembly can be inferred. On the other hand, considering the temporal dimension of our study, when average βRC approaches − 1.0, a scenario of environmental filtering gains empirical support. In this case, low temporal variability of influential environmental factors causes highly similar communities over time. Finally, βRC approaches 1.0 when there is a high temporal variability of influential environmental factors, favoring dissimilar species compositions over time (Chase et al. 2011).

Measurements of environmental variation over time for each sampling site

We used multivariate dispersion analysis, based on distances, to estimate the temporal variation of limnological variables in each site (Anderson 2006; Anderson et al. 2006). For this analysis, we log-transformed the limnological variables (except for pH) and applied the standardized Euclidean metric to calculate the distances.

Modeling beta diversity over time

For each of the six sampling sites and using the (log-transformed) abundance data, a dissimilarity matrix between the months (with 62 rows × 62 columns) was calculated using the Bray–Curtis coefficient (Legendre and Legendre 2012). Matrices of environmental distances between pairs of months, based on limnological and hydrological (average rainfall, water level, input flow and output flow) data, were also calculated using the standardized Euclidean distance. Pairwise beta diversity (Bray–Curtis distances) matrices were then modeled as a function of environmental, hydrological and temporal (time lag, see Collins et al. 2000) distance matrices (Lichstein 2007). Significance tests of the standardized partial regression coefficients associated with each of these explanatory matrices were based on 1000

permutations. The intercepts of the models (one for each site) were used as measures of the stochastic components of community structure (Vellend et al. 2014), following the method proposed by Brownstein et al. (2012). A schematic representation of our analytical protocol can be found in Fig. S3.

Finally, using a raw-data approach (Legendre et al. 2005), we partitioned the total variation of the zooplankton community, for each site, between the environmental matrix and a matrix describing the temporal relationships among the samples (i.e. months). For variation partitioning, we employed a distance-based Redundancy Analysis (db-RDA; Legendre and Anderson 1999) using the Bray–Curtis dissimilarity matrices (one for each site). To represent different patterns of temporal autocorrelation, our explanatory matrix representing time was given by the following procedures: first, we create a matrix with two columns representing months (1–12) and years (from 2004 to 2009); second, we used a distance-based eigenvector map (db-MEM) to create our temporal variables (i.e. eigenvectors; see Siqueira et al. 2008 for a similar approach); third, we selected the eigenvectors using the function forward.sel of the package pack for (Dray et al. 2009). The forward-selected temporal eigenvectors were used in variation partitioning. We used the methods described in Peres-Neto et al. (2006) for variation partitioning, which include the estimation of the following adjusted fractions: the variation in zooplankton community composition accounted for by the environmental variables [a], by temporally autocorrelated environmental variables [b], by the temporal autocorrelation (temporal variables) [c] and the residual variation [d]. We applied 1000 permutations to test for the significance of fractions [a] and [c]. Analyzes were performed in R (R Core Team 2013) using the packages listed in Table 1.

Results

We recorded 170 species during the entire study. Species richness was highest at the fluvial region of the reservoir (site 1 = 117, site 2 = 107), whereas sites localized in the main body of the reservoir had lower species richness (from site 3 to 6 = 79, 78, 76 and 70, respectively; Fig. 1). The different measures of temporal beta diversity were highly correlated to each other (Pearson's $r_{(\beta SIM x dBC)} = 0.98$; $r_{(\beta SIM x \beta RC)} = 0.92$; $r_{(\beta dBC x \beta RC)} = 0.97$; $n = 6$, $P < 0.05$ in all cases). The results based on the Simpson coefficient for multiple samples indicated that zooplankton community dynamics were mainly caused by temporal variation in species composition, with a negligible contribution from nestedness (Fig. 2; see also results for NODF). Temporal beta diversity was higher at the fluvial region of the reservoir (site 1) than at the sites closer to the dam. The fluvial region of the reservoir also showed the highest environmental variability over time (Fig. 3). However, temporal beta diversity was not significantly correlated with the environmental variability (Table 2).

Time lag was the sole significant explanatory matrix for (pairwise) matrices of beta diversity along the longitudinal
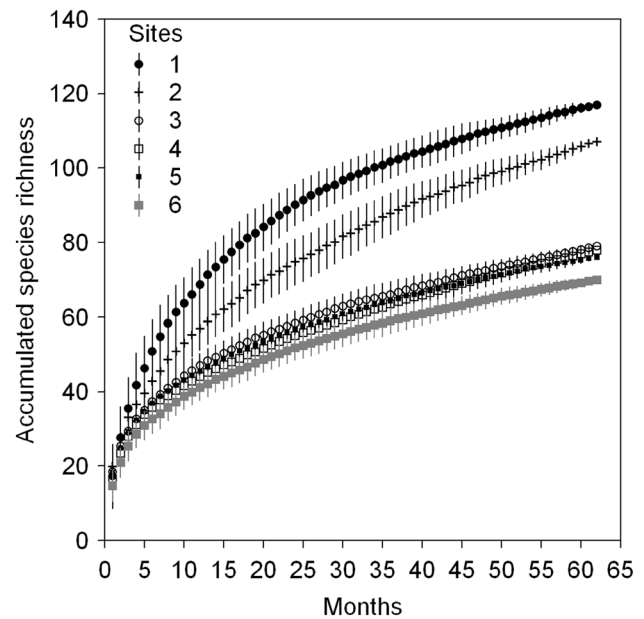

Fig. 1 Accumulated species richness for each sampling sites (1–6) on zooplankton community in Ribeirão das Lajes Reservoir

Table 1 Packages used in this study and their respective references. All analyses were performed using R (R Core Team 2013). The equations for the different metrics can be found in the articles cited under the column "References"

Method	Data	R function [package]	References
Species accumulation curves	presence-absence	specaccum [vegan]	Oksanen et al. (2017)
βSIM and βNES	presence-absence	beta.multi [betapart]	Baselga and Orme (2012)
NODF	presence-absence	NODF [RInSp]	Zaccarelli et al. (2013)
βRC	presence-absence		Chase et al. (2011)
Bray–Curtis distance	abundance	vegdist [vegan]	Oksanen et al. (2017)
Average distance to centroid	abundance	betadisper [vegan]	Oksanen et al. (2017)
Variance partitioning		varpart [vegan]	Oksanen et al. (2017)
Multiple regression with distances		MRM [ecodist]	Goslee and Urban (2007)
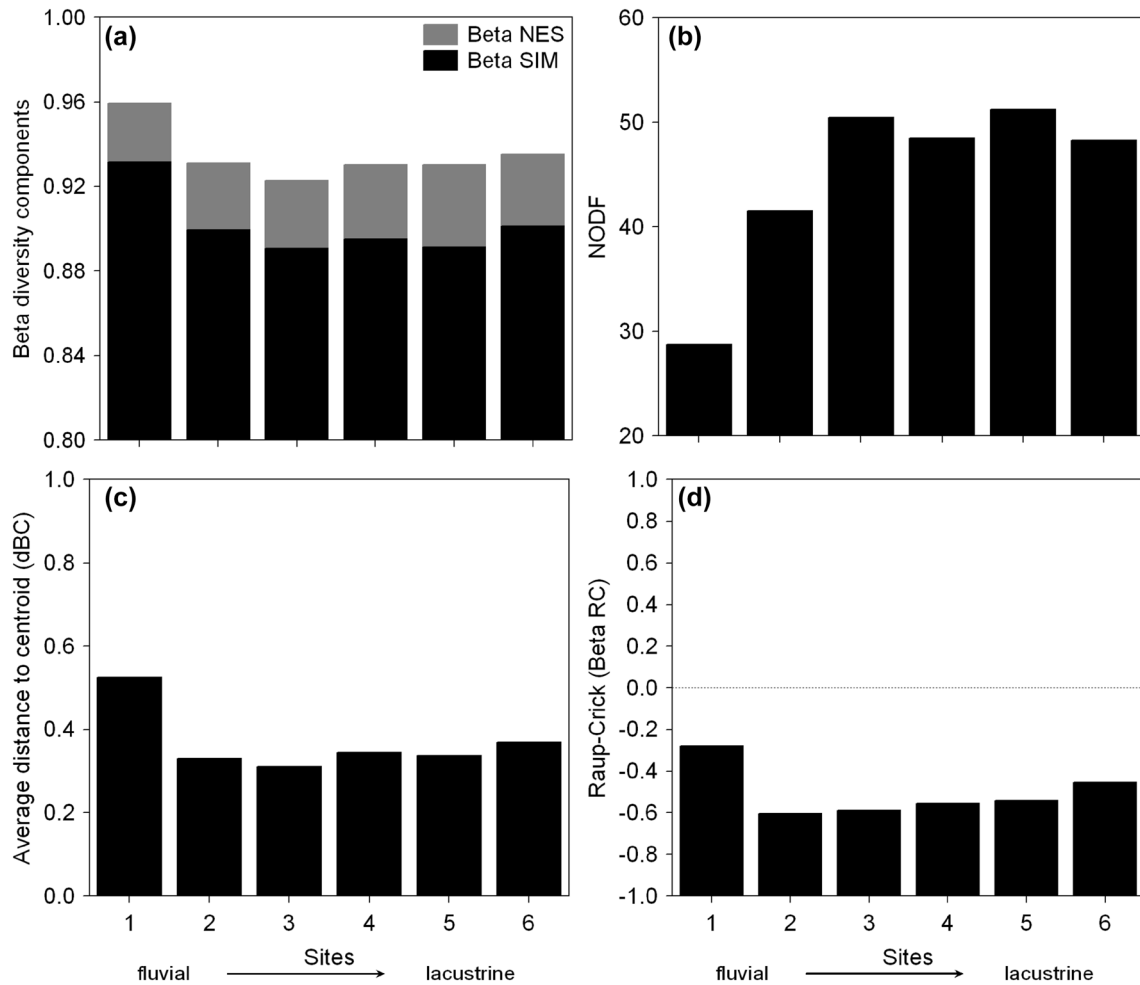
Fig. 2 Temporal beta diversity of zooplankton communities at each sampling site (1–6) in the Ribeirão das Lajes Reservoir
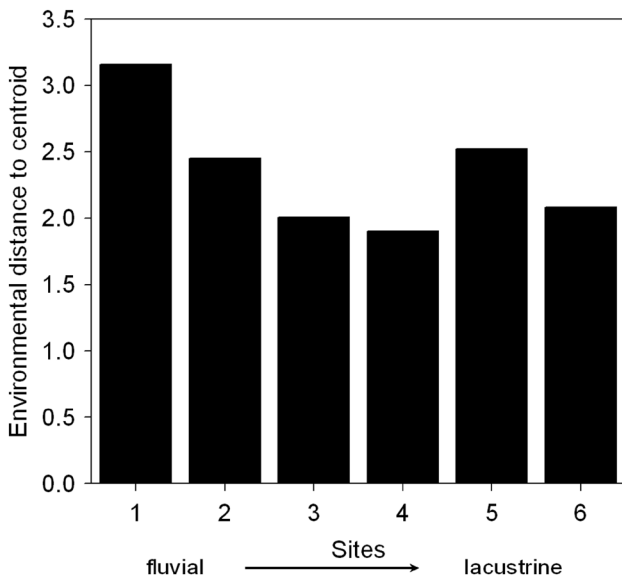
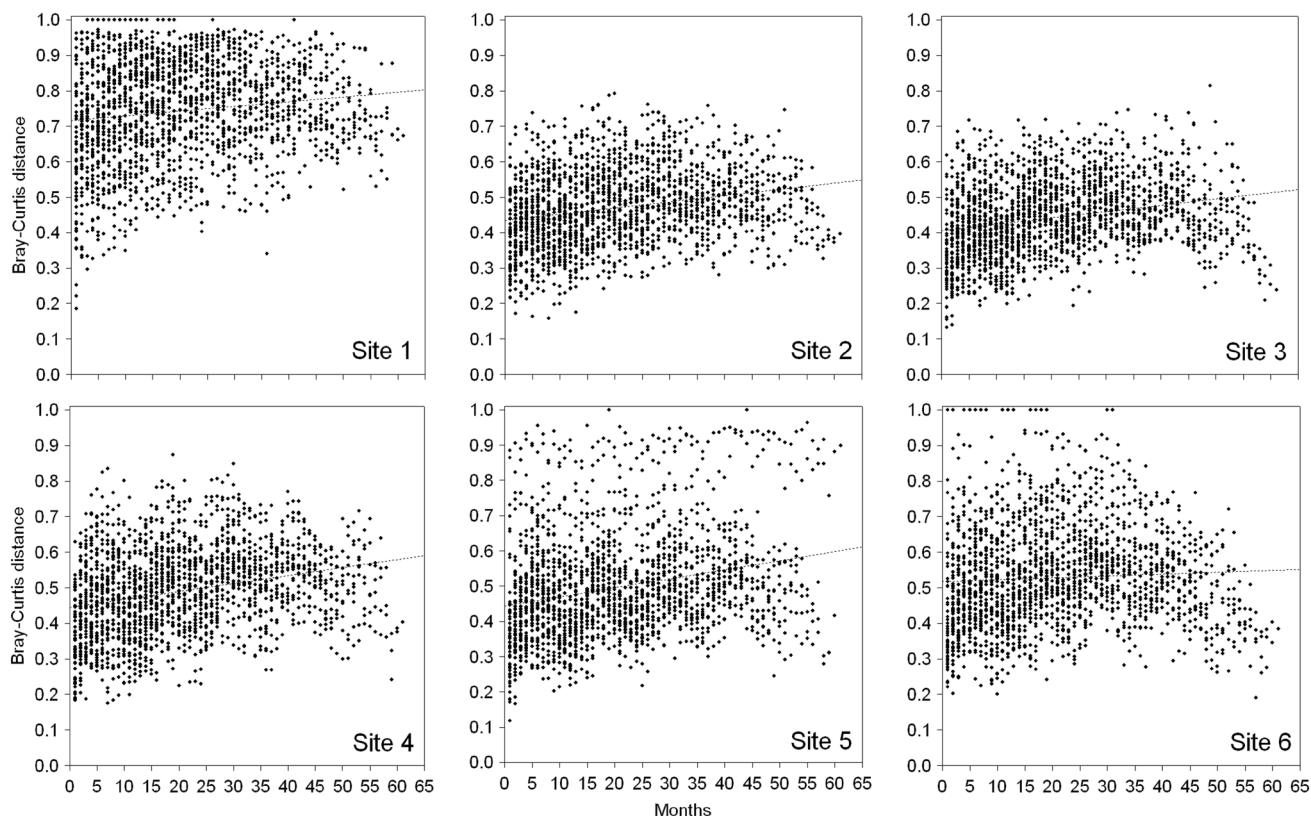**Fig. 3** Environmental variability at each sampling site (1–6) in the Ribeirão das Lajes Reservoir

Table 2 Spearman correlation coefficients between environmental variability (distance to centroid) and beta diversity measures ($n=6$). $P > 0.05$ in all cases

Measure of environmental variability	Beta diversity measures		
	ßSIM	dBC	ßRC
Distance to centroid	0.41	0.37	0.49

axis of the reservoir, except for the site located near the dam (site 6; Table 3). Thus, successive pairs of months and months separated by longer time lags tended to exhibit low and high changes in species composition, respectively. Except in the fluvial zone (site 1), environmental and hydrological distances were not significantly correlated with the temporal beta diversity matrices. Moreover, we found low coefficients of determination (Table 3). An abrupt decrease in beta diversity from the fluvial to the lacustrine zone was also detected when the intercepts of the models were compared (Figs. 4 and 5).

Table 3 Multiple regression results based in Bray–Curtis distance matrix. The results for other beta diversity measures were similar (see Table S2). Significant results are indicated in bold

| Site	Environmental	P	Hydrological	P	Time	P	R^2	P
1	**0.12**	0.05	− 0.03	0.47	**0.13**	0.00	**0.03**	0.00
2	− 0.06	0.44	0.03	0.60	**0.24**	0.00	**0.06**	0.00
3	0.02	0.79	0.11	0.06	**0.24**	0.00	**0.07**	0.00
4	0.12	0.10	**0.12**	0.04	**0.25**	0.00	**0.10**	0.00
5	− 0.03	0.71	0.00	1.00	**0.25**	0.00	**0.06**	0.00
6	0.08	0.38	0.12	0.05	0.04	0.38	**0.03**	0.00

Fig. 4 Relationship between Bray–Curtis distance and time lag at each sampling site (1–6)

Both fractions representing the total variation in community structure explained purely by environmental [a] and purely by temporal variables [c] were highly significant (Fig. 6) Thus, the results of the variation partitioning diverge from those of the multiple regression on distance matrices as both environmental and temporal matrices were significantly correlated with the zooplankton community data. However, the results of both methods (multiple regression on distance matrices and variance partitioning) were consistent in terms of effect sizes. Specifically, the matrix representing the temporal variables were much more important in predicting community structure than the environmental matrix (Fig. 6).

Discussion

We found high correlations between the different measures of beta diversity. Also, the analyses aiming to find variables correlated to beta diversity generated similar results (Table S2). Thus, our results were robust to the type of beta diversity metric, despite the debate on this issue (e.g. Baselga 2013).

Zooplankton temporal beta diversity in the Ribeirão das Lajes Reservoir was primarily driven by species turnover, instead of nestedness. This pattern (i.e. turnover component > nestedness component) appears to be ubiquitous in
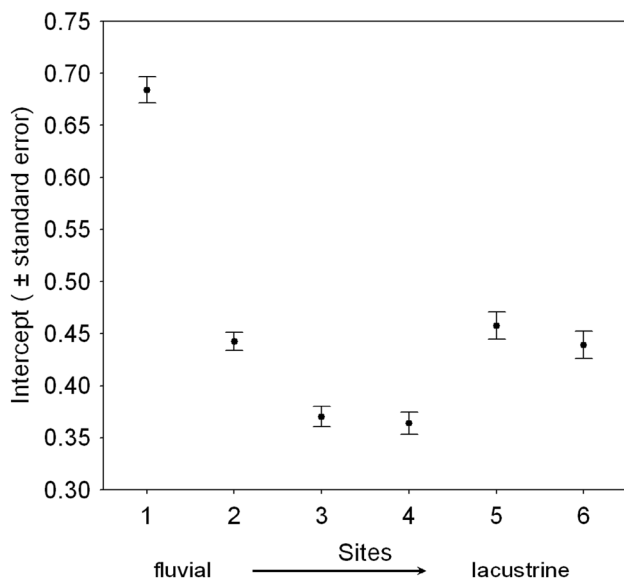
Fig. 5 Intercepts (±standard error) of the multiple regression models of Bray–Curtis distance matrices as function of time lags, environmental and hydrological distances for each sampling site in Ribeirão das Lajes Reservoir (sites 1–6)
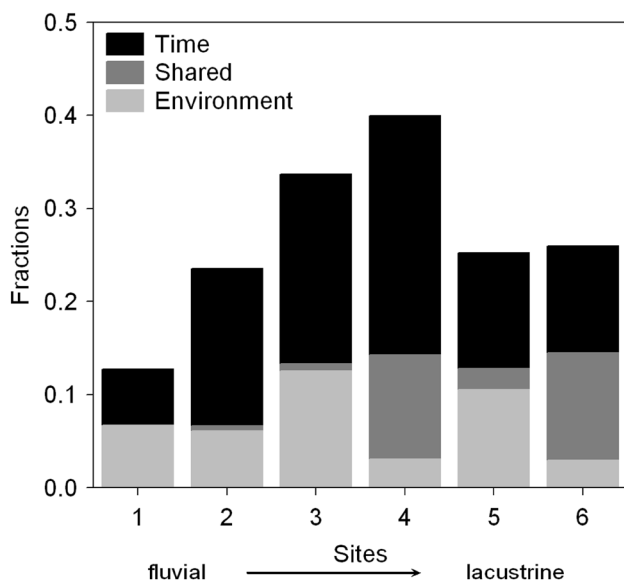
Fig. 6 Results of variation partitioning analyses. Shared: temporally autocorrelated environmental variables. *P* values associated with fractions [*a*], from site 1 to site 6, were 0.002, 0.001, 0.001, 0.030, 0.001, and 0.017, respectively; *P* values associated with fractions [*c*] were 0.006 (for site 1) and 0.001 (for sites 2, 3, 4, 5 and 6)

nature. For example, according to Soininen et al. (2018) turnover is "typically more than five times larger than nestedness". In our study, the dominance of a nestedness component of total beta diversity would indicate a decrease in local species richness over time. Lack of temporal trends in species richness associated with changes in species

composition over time was also found in other recent studies (Dornelas et al. 2014). Overall, this result is surprising since reservoirs are subject to constant impacts that are usually associated with biodiversity losses (e.g., eutrophication, introduction of alien species, abrupt changes in the hydrological level). The constant input of propagules coming from aquatic ecosystems upstream of the reservoir (especially via the watercourse) probably prevents zooplankton biodiversity losses (see discussion below).

Zooplankton beta diversity and environmental variability were higher in the fluvial region (site 1) than in the other regions of the reservoirs (sites 2–6). Three related mechanisms may explain these results. First, despite lack of hydrological data for each region of the reservoir, it is reasonable to assume that the variability of water flow is higher in the fluvial region. Thus, higher beta diversity in the fluvial region may derive from the higher temporal variability of flow in this region. Such a relationship has been experimentally shown by Larson and Passy (2013) that concluded that: "Our investigation revealed that the rates of species accumulation too increased with temporal heterogeneity in flow, which creates new niches throughout community development and promotes coexistence of species with diverse adaptations and requirements." On the other hand, Larson and Passy (2013) also demonstrated that beta diversity was lower at high flow conditions (as expected at the fluvial regions of reservoirs). Second, hydrological variability may also be related to environmental variability, which was also highest at site 1. Thus, the higher beta diversity in the fluvial region, compared to other regions of the reservoir, could also be explained by the higher temporal variability in the limnological characteristics. A growing number of studies have tested the relationship between beta diversity and environmental heterogeneity, especially when both are measured spatially (Bini et al. 2014; Astorga et al. 2014; Heino et al. 2015a, b). In studies focused on a temporal dimension, as in our case, more variable sites are thus likely to have high beta diversity due to changes in environmental factors, favoring different species compositions over time. Third, and probably more important, most of the species contributing to the regional diversity drift into the reservoir via its fluvial region. The faster rate of species accumulation in this region (Fig. 1), as well as the decrease in species richness along the main axis of the reservoir, strongly supports this inference. Even with unfavorable hydrological conditions for developing euplanktonic communities (Marzolf 1990), the fluvial region is the main "gateway" to the reservoir and, temporally, different species compositions can be detected, explaining the highest beta diversity in this region. Our inference about the importance of passive dispersal from upstream regions to the biodiversity of the reservoir is also consistent with the low rates of overland dispersal in zooplankton (Gray and Arnott 2012).

According to the matrix regression models, we found no evidence that environmental differences between months are positively related to beta diversity values in the inner regions of the reservoir (i.e., sites 2, 3, 4, 5 and 6). Thus, for these regions, the hypothesis of increased beta diversity due to the increase of environmental differences was not supported. Only the time lag matrix was significantly and positively correlated with the beta diversity matrix in most of the sites (1, 2, 3, 4 and 5). Changes in sampling methods and taxonomic determination can, for example, explain trends in long-term biodiversity studies (Straile et al. 2013). This explanation seems unlikely in our study because the same group of researchers, using the same procedures, carried out the biomonitoring program that resulted in our dataset. The basic interpretation of the correlation between beta diversity and time lag is that consecutive months tend to have more similar communities that a pair of months selected at random (i.e., beta diversity is temporally autocorrelated). According to Collins et al. (2000), significant correlations between beta diversity and time lag indicate that a community "is unstable and undergoing directional change". On the other hand, no significant results imply "fluctuation or stochastic variation over time"; negative relationships would imply that the community is "unstable and undergoing convergence". However, independently of the inference proposed by Collins et al. (2000) for the presence of temporal autocorrelation, we believe that the interpretations of this result are uncertain (e.g. absence of relevant predictors of community structure and ecological drift; Hatosy et al. 2013). We emphasize that significant relationships between zooplankton community structure and environmental variables were found when the analyses were based on a raw-data approach. However, in general, we found that the temporal variables were substantially more important than environmental variables.

Randomness, neutrality, unpredictability and stochasticity, or their antonyms, are recurrent concepts used in community ecology and, particularly, in studies of beta diversity (Vellend et al. 2014). As suggested by Brownstein et al. (2012), instead of examining whether the communities are stochastic or not, we should measure the stochasticity level of ecological communities (see also Vellend et al. 2014). Although originally developed for spatial scales, the approach proposed by Brownstein et al. (2012) can be easily adapted to time scales: (1) theoretically, for a zero time lag (i.e., at the intercept), beta diversity should be zero; (2) lower beta diversity values for short time lags would be expected; (3) however, high intercepts indicate large changes in communities even for time lags of zero ("nugget effect", in the geostatistical literature, see Legendre and Fortin 1989). Besides sampling error, an intercept greater than zero may be interpreted as a measure of stochasticity ("variance in composition of species truly inexplicable" according to Vellend et al. 2014). Using this approach, we observed a decrease in the values of the intercept along the main axis of the reservoir (Fig. 5). It is important to note that this pattern is also consistent with our first hypothesis and that, although less stochastic, the variations in beta diversity in the areas closest to the dam were unrelated to environmental distances between months (Fig. 6).

Increased beta diversity due to increased time lags is also a pattern consistent with those obtained by Dornelas et al. (2014), for different biological communities. To analyze changes in planktonic communities in reservoirs, however, one needs to adapt the concept of "shifting baseline syndrome", developed by Pauly (1995) for fisheries. What was the zooplankton community before damming? The answer to this question can be given considering studies conducted before and after damming. Planktonic samples obtained in lotic environments have, in general, high densities of protozoa and low densities of microcrustaceans or rotifers. After damming, however, protozoa densities tend to decline and the microcrustaceans and rotifers increase (e.g., Lodi et al. 2014). The "correct" reference for reservoirs, considering these abrupt changes in communities, would be therefore the species composition observed before the formation of these environments. Thus, changes in zooplankton composition found in this and other studies are certainly underestimated.

Our results suggest the importance of reservoir zonation variation on the dynamics of planktonic communities: a comparison between sites indicates that the fluvial region of the reservoir, where environmental variation was the highest, was also, in terms of species composition, the most variable over time. Our results evaluating compositional dissimilarities between pairs of months, however, emphasize the low predictability of temporal beta diversity (for similar results based on the spatial beta diversity see Heino et al. 2013). Taken together, these results indicate that monitoring beta diversity of planktonic communities, at least in the Ribeirão das Lajes Reservoir, may be useful to detect hydrological changes in the watershed. However, it is unlikely that it would help to detect small changes in water quality.

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