



Diatom diversity at multiple scales in urban reservoirs in Southern Brazil reveals the likely role of trophic state

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ARTICLE INFO

Keywords:

Beta diversity
Additive partitioning
Community variation
Nestedness
Turnover
Stochasticity

ABSTRACT

Diatoms grow under very specific physical and chemical conditions, and eutrophication may cause community variation. We aimed to describe spatial and temporal variation in diatom community diversity in two urban reservoirs of different trophic status at different spatial scales. We collected samples of epiphytic diatoms from aquatic macrophytes from six sites in each reservoir in the metropolitan region of Curitiba, Southern Brazil, in fall and in spring. We assessed the variation in cell density and taxa richness (considering the lower taxonomic level possible) between the reservoirs and periods using *t*-tests, and the differences in community composition using PERMANOVA. Principal coordinates analysis (PCoA) was used to observe the change in floras between reservoirs and periods. We also partitioned gamma diversity into alpha and beta diversities using Additive Partitioning. In this case, variation components at different spatial scales were generated for each period. Beta diversities at different scales were also divided into turnover and nestedness components. We identified 132 infrageneric taxa in each reservoir. Spatial and temporal variation in species diversity and composition occurred in both reservoirs at different scales. Even so variation between reservoirs is a component that cannot be expected by a null model, indicating a possible role of eutrophication in community variation. Community variation at different scales was higher in the more eutrophic reservoir, in line with the positive relationship between beta diversity and productivity. Turnover was always the main component of beta diversity considering all spatial and temporal community variation. Nestedness occurred particularly in community variation among time periods at a same location, in line with studies suggesting community stability in urban reservoirs. Taken together, our results highlight the key role of nutrient availability in determining species composition, community variation within reservoirs, and community variation over time.

1. Introduction

A major goal in community ecology is to explain biodiversity variation across space and time. Indeed, there is a great growth in the number of studies explaining variation patterns in the composition of communities (Melo et al., 2011). In aquatic ecosystems, factors such as productivity and environmental heterogeneity are often considered chiefly responsible for changes in biodiversity (Bini et al., 2014).

In modified systems, such as reservoirs, environmental changes related to trophic conditions affect communities (Yang et al., 2012; Wojciechowski et al., 2017a), and community variation is expected among reservoirs of different trophic levels (Silva et al., 2014). Indeed, changes in the structure of periphytic diatom communities are

commonly related to eutrophication processes (Mattila and Räsänen, 1998; Taniwaki et al., 2013). A decrease in nutrients concentration and an increase in water transparency toward the dam is also a common pattern within a reservoir (Ribeiro Filho et al., 2011), although it depends on morphometric characteristics and retention time. Anyway, community variation is expected to occur within and between reservoirs (Kennedy and Walker, 1990; Straškraba et al., 1993; Taniwaki et al., 2013). Periphytic algae are model organisms because they respond quickly to environmental heterogeneity, which results in changes in the community structure (Stenger-Kovacs et al., 2007; Pellegrini and Ferragut, 2012; Liu et al., 2013).

Some observational studies have investigated the spatial and/or temporal patterns of periphytic algae in urban aquatic environments,

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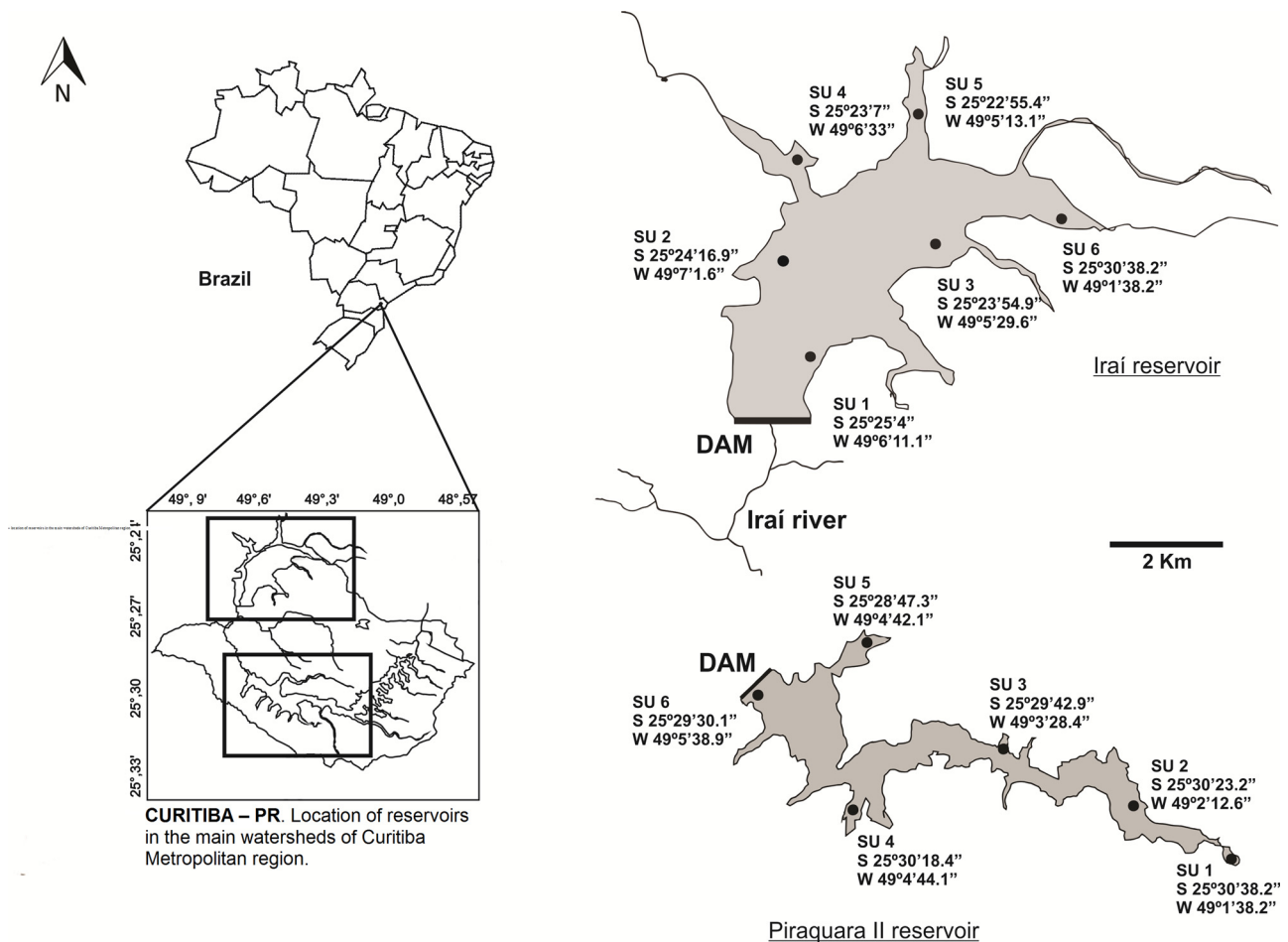


Fig 1. Location of the reservoirs and sample units (SU, ●).

such as reservoirs (Vercellino and Bicudo, 2006; Silva et al., 2010; Pellegrini and Ferragut, 2012; Taniwaki et al., 2013). In such impacted ecosystems, the general expectation is that eutrophication should be the main driver of biological diversity (Taniwaki et al., 2013; Vilar et al., 2014). In this context, the composition and biodiversity should vary between reservoirs with different trophic state. On the other hand, reservoirs are human-made ecosystems that usually cause spatial homogenization in abiotic (other than trophic state) and biotic features (Papastergiadou et al., 2010; Daga et al., 2015). Thus, empirical evidence of how aquatic communities vary between and within relatively stable environments such as reservoirs is still needed, particularly when different trophic levels are observed, as in many urban reservoirs (Silva et al., 2014).

Biodiversity is a broad concept that encompasses many facets of biological variability, for instance, taxonomic, genetic and functional (Naeem et al., 2016). Also, any dimension of the biodiversity is scale dependent. The total diversity of a study area (gamma diversity) comprises the local diversity of one sample unit (alpha diversity), and the variation of diversity among sample units (beta diversity), according to Whittaker (1960, 1972). By splitting biodiversity into a local component and the variation among locals, one can investigate how biodiversity varies at different scales. Indeed, McArthur et al. (1966) and later Allan (1975) have proposed an additive partitioning method to describe gamma diversity as composed by components of variation at different scales. Given that variation among sampling sites can occur at more than one scale (e.g. among sampling sites within a region; or among regions), the overall diversity index (e.g. we used taxa richness considering the lower taxonomic level, hereafter species richness) of a region (i.e. gamma diversity) can be described as the mean species

richness per sampling site (alpha diversity) and the variation among sampling sites considering several hierarchical scales (more than one beta diversity, see Crist et al., 2003). As a consequence, this method can be used as a strategy to identify the main source of variation in aquatic communities (e.g., within or between reservoirs as described above). Also, each component of gamma diversity can be compared to what could be expected in a partitioning according to a null model, indicating if the observed sources of variation in biological communities can be expected by chance (Flach et al., 2012).

In addition, the beta diversity at a given scale is the result of turnover – or real variation – and nestedness. Spatial turnover refers to the replacement of some species in a community by others, and nestedness occurs when less biodiverse communities are subsets of more biodiverse ones (Baselga, 2010). For example, higher habitat specificity and lower dispersion ability can favor turnover in communities (Barton et al., 2013). On the other hand, the increase in environmental impacts may be related to nestedness in communities, given that compositional variation among communities generated by species loss is a usual consequence of impacted areas (Karthick et al., 2011). Thus, investigating beta diversity helps to identify and understand patterns and processes which determine the diversity on local and regional scales (Soininen et al., 2007).

In this study, we investigated spatial and temporal variation of epiphytic diatom biodiversity in the water supply reservoirs of Iguaçú River sub-basin in the metropolitan region of Curitiba, Paraná. Firstly, we tested the hypothesis that there is a higher spatial and temporal variation in the composition of epiphytic diatoms between heterogeneous reservoirs than would be expected to exist by chance. If not rejected, we speculated that communities differ likely due to the clear

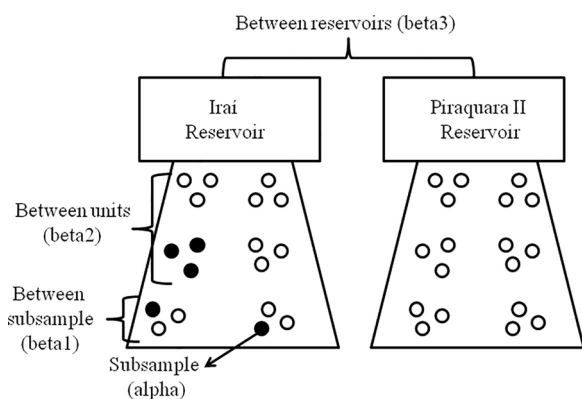


Fig. 2. Layout of partition of gamma diversity in each sampling period.

differences in trophic levels between studied reservoirs as detailed in methods. Complimentary, we expected that variation between reservoirs (beta diversity) should be the main component of gamma diversity when compared to variation within the reservoir. We also predicted that the relative importance of turnover and nestedness on beta diversity should depend on whether the variation is within or between reservoirs. We realize that eutrophication effects in reservoirs have already been described for a long time (Ryding and Rast, 1989; for effects specifically in microalgae see Yang et al., 2012; Taniwaki et al., 2013; Wojciechowski et al., 2017a). However, we emphasize that our focus was not on the well-known negative effects of eutrophication on species richness, or simply comparing the abundance and identity of taxa between reservoirs. Indeed, eutrophication proxies were not used directly as predictors (see methods). Instead, we innovated by investigating the likely effects of differences in reservoir trophic level on community variation at multiple scales, allowing us to discuss key questions in community assembly mechanisms in aquatic habitats (see Bini et al., 2014; Heino et al., 2015).

2. Materials and methods

2.1. Study sites

We sampled epiphytic diatoms in the urban reservoirs Piraquara II and Iraí, used for water supply. Both reservoirs belong to the environmental protection area of the Rio Iguagu watershed, located in the metropolitan region of Curitiba, Paraná, Brazil. Piraquara II (Fig. 1) was formed in 2008 by the impoundment of the Piraquara River (Consórcio Paranassan, 2000). This reservoir has a total area of 5.64 km², an average depth of 3.28 m, a water residence time of approximately 75 days, a drainage area of 58 km² and around 21.10⁶ mm³ of water (Bittencourt and Gobbi, 2006; Silva et al., 2010). It is predominantly located in a rural area, and its water body is influenced by diffuse pollution (Bittencourt and Gobbi, 2006). On the other hand, Iraí reservoir (Fig. 1) was formed by the impoundment of the Iraí river in 2000 (Consórcio Sogreah/Cobrape, 2000). It has 15 km² of area, a drainage area of 113 km², an average water residence time of 312 days and an average depth of 4.7 m (Bollmann et al., 2005) (Fig. 1). This reservoir receives four tributaries besides the Iraí river itself, which has a high load of domestic, industrial, and agricultural sewage (Consórcio Sogreah/Cobrape, 2000; Cetto et al., 2004).

The two reservoirs differ mainly in relation to their state of degradation: Piraquara II is considered “moderately degraded” and Iraí reservoir is considered “critically degraded to polluted” according to the water quality index classification of reservoirs from 1999 to 2008, performed by Instituto Ambiental do Paraná (Paraná Instituto Ambiental do Paraná, 2009). Average values from several samples collected by the sanitation company responsible for water capture clearly show that Iraí has higher levels of nutrients, and a lower index

of water quality (see Tables in Appendix A). Surely other limnological variables also differ between reservoirs (e.g. concentration of suspended solids and turbidity), but data abovementioned clearly indicate that limnological differences are most likely a consequence of the differences in trophic status. However, sampling by the sanitation company was neither carried out at the same sites, nor in the same sampling periods than this study, preventing us to make a direct link between communities and environmental conditions.

2.2. Sampling of diatoms and abiotic characterization of reservoirs

We sampled epiphytic diatoms from stems of emergent aquatic macrophytes (*Polygonum hydropiperoides* Michaux, *Ludwigia peruviana* (L.) H. Hara, *Alternanthera philoxeroides* (Mart.) Griseb.), depending on their occurrence and availability. Due to the spatial heterogeneity in the aquatic plant community, unfortunately, it was not possible to always sample diatoms from the same substrate. In Iraí reservoir, all samples were collected from the macrophyte *A. philoxeroides*. However, in Piraquara II reservoir three aquatic macrophytes species were used. Thus, we cannot disregard a possible effect of substrate on spatial and temporal differences in the epiphytic diatom communities. Nevertheless, we opted to accept this limitation, because it was the only viable strategy to compare the communities within and between the reservoirs during the sampling periods. We also believe that this fact may occur in environments with different trophic states (Silva et al., 2014). However, sampling different substrates did not bias our main results (see results below).

We selected six sample units in each reservoir in fall and spring to represent the dam area and places located upstream influenced by different tributaries. In each sample unit, three subsamples were obtained forming a spatially hierarchical sampling design (Fig. 2). Sampled stems of macrophytes were in the adult stage, with non-senescent leaves, and about 20 centimeters deep from the water surface. We cut from nine to twelve fragments, between the internodes, measuring about seven centimeters of length each, which were directly packed in bottles containing a known amount of *Transeau* solution (Bicudo and Menezes, 2006). We collected epiphytic diatoms by scraping them off the stems of aquatic macrophytes with steel blades encased in aluminum foil and jets of *Transeau* solution of the sample itself. An aliquote of 10 mL of epiphyton community of each subsample was oxidized using the technique described by Simonsen (1974), and modified by Moreira-Filho and Valente-Moreira (1981). Permanent slides were prepared with 0.5 mL using Naphrax[®]. Qualitative and quantitative analyses were performed using a light microscope Olympus CH-2 (objective lens 40X). Remaining aliquots and permanent slides were deposited in the Herbarium of the Federal University of Paraná (UPCB).

Species identification was based on classical and modern literature. Details for each identified taxon are given in Table B3 of Appendix B. We carried out the count of the valves on permanent slides (in each subsample) until the species accumulation curve reached the asymptote. The asymptote was reached when after counting 20 fields of view no new species were added. Fragmented valves which were not possible to identify (usually those with more than 50% of its surface broken) were not included in the analysis. Counting efficiency was based on Pappas and Stoermer (1996), being not less than 80% of reliability count. We calculated the relative densities of the valves of taxa per cm², as described in Battarbee (1986). Therefore the length and diameter of the macrophyte stems were measured with a sliding caliper, and the formula of the surface area of a cylinder (cm²) used to determine the sampled area and calculate the total abundance per sampled area. The coefficient of variation in sampled areas was low (c. 0.10) given that we tried to standardize them to minimize differences due to sampled areas.

Several limnological variables were determined by the Sanitation Company responsible for water management (Sanepar) during the same time period, but at different sites. We were kindly allowed to use these data to characterize the reservoirs according to their environmental

variables. In the field, the transparency of the water column (m, Secchi disk), the pH (pH CONSORT C535 meter) and the water temperature (°C, thermometer Incoterm) were measured. Estimations of total nitrogen (mg/L), total phosphorus (mg/L), pH, turbidity (NTU), COD (mg/L), dissolved oxygen (mg/L), dissolved solids (mg/L) were also supplied by Sanepar, as well as the trophic state index (Lamparelli, 2004). Water aliquots (1000 mL – in replicas) were collected at each sampling site for the determination of chlorophyll *a* (Appendix B). Aliquots were kept refrigerated in dark opaque packed bottles until they were filtered onto glass fiber filters using a vacuum pump. The filtered samples were kept frozen for two days until the procedure of extraction of chlorophyll *a*. The filters were macerated and kept refrigerated for 24 h with 90% acetone in individual tubes. Subsequently, we centrifugated the samples at 4000 rpm for 15 min; the supernatant was reserved and the absorbance was measured on a Hitachi 2001 spectrophotometer. We calculated the concentrations of chlorophyll *a* according to Jeffrey and Humphrey (1975). Considering the differences in several limnological variables, such data confirmed that the trophic level of Iraí reservoir was higher than of Piraquara II (see abiotic data available in Appendix A and chlorophyll *a* in Appendix B). Even so, given that the abiotic variables were not always determined at the same sites and time as diatom samples were collected due to financial and logistic constrains, we could not directly evaluate the effect of environmental proxies on diatom communities. In addition to these data collected during the same period as diatoms, averages estimates of nitrogen, phosphorus and water quality index (determined by Sanepar) considering twice-a-year samplings from 2010 to 2013 at different sites of the reservoirs also confirm that the main difference between the reservoirs is related to trophic state (Appendix B).

2.3. Data analyses

Our analyses were based on the assumption that differences between the reservoirs are mainly due to the trophic state, as shown above. However, we could not make direct analyses linking environmental variables and diatoms given that environmental data could not be collected at the same sites and time as diatom samples. Therefore, our discussion is based on “indirect gradient analyses” (Ramette, 2007).

Firstly, we used paired *t*-tests to verify the temporal variation (between fall and spring) in each reservoir, and non-paired *t*-tests to evaluate differences in species richness and density of diatom communities between reservoirs and in each sampling period. In this case, the three subsamples of each sampling unit were combined into a single value per sampling unit. As said in the previous subtopic, if Piraquara II reservoir has higher diversity and abundance indexes, we cannot rule out the possible effect of substrates (Biolo and Rodrigues, 2013), given that diatoms were sampled from more than one substrate in this reservoir. We did not compare differences in species richness and density within each reservoir, but only between reservoirs and periods. Indeed, our goal was to check for within reservoir variability only considering community composition and variation. Exploring upstream and downstream differences within each reservoir considering species richness and abundance would be related to a local goal not related to our study.

Instead, we then used Multivariate Permutation Analysis of Variance (PERMANOVA, Anderson, 2001) to check whether there were differences in the diatom community composition within the reservoirs (e.g., between sample units), between reservoirs and between periods, with 999 permutation. In this case, we used the relative density matrix of species, with log transformed data [$\log(x+1)$], as the unit for the subsample analysis. The “sample unit” factor (e.g., in which three subsamples were attested) was nested within the factors “reservoirs” and “periods” to assess whether there was significant variation in composition between sample units within the reservoirs. The factors “reservoirs” and “periods” were crossed to check if the differences between reservoirs were dependent on time periods. We applied the Principal Coordinates Analysis (PCoA), using the dissimilarity index

Bray-Curtis (Bray and Curtis, 1957) to observe the differences indicated in PERMANOVA. We have also used the “Dufrene-Legendre Indicator Species Analysis” to describe typical species for each reservoir and period (Dufrene and Legendre, 1997). An indicator value (IndVal) for each species in each reservoir and period is calculated based on their specificity (to what extent each species occurs only in a certain reservoir and period) and fidelity (to what extent each species occurs in all sampling units of a certain reservoir and period). Significance of IndVal for each species was calculated using 1000 random iterations.

Gamma diversity, which we considered as the total diversity of diatoms in the two reservoirs in one period, was partitioned into components at different hierarchical spatial scales through Additive Partitioning (McArthur et al., 1966; Allan, 1975; Crist et al., 2003). In this case, we considered alpha diversity as the average species richness in each subsample of each sample unit. Beta1 diversity was the variation of diversity between subsamples from a sample unit – thus a component that refers to the local variation of diatoms in the same sample unit. The component beta2 was the variation of diversity between sample units of the same reservoir, which indicates a variation in a larger spatial scale, but still a restricted spatial variation within a reservoir. Finally, we considered the variation between reservoirs as the beta3 component, which means variation at the highest spatial scale in our study – supposedly the most important component of gamma diversity (Fig. 2), given the known effect of a reservoirs’ trophic level on communities (Silva et al., 2014). This partition was performed for each sampling period in order to evaluate whether there was temporal variation in the importance of spatial components of gamma diversity.

The values observed for the alpha and beta components dependent on the number of species and the size of the sample unit, and also on the distance between them and on the dissimilarity of environmental conditions (Schmera and Erős, 2008). Therefore, we used a null model, which presupposes a random distribution of species at each site, to obtain an adequate evaluation and estimate the relative importance of each component assessed. For example, a certain component may be larger than others in absolute terms, but not differ from what would be expected by the null model (Flach et al., 2012). The null model used in Additive Partitioning was proposed by Crist et al. (2003), and consists of the random distribution of individuals among all sample units, annulling the ubiquity of intraspecific aggregation observed in communities. We calculated how many times the value of the component observed in the original data was higher than the values obtained by randomization. In this case, significant values are interpreted if i) only a few randomizations generated higher values than expected – then the value of the observed component is significantly higher than would be expected by the null model; or ii) when many randomizations generated higher values than the observed one – then the observed value of the component was significantly lower than would be expected by the null model. Thus, for each component, the proportion (*p*) in which the observed values were lower than would be expected by the null model was indicated after 999 permutations. If *p* = 0.001, for example, it means that there was only one value higher than or equal to what was observed in the original data; and if *p* = 0.999, it means that there were 999 randomly generated values higher than or equal to what was observed in the original data. Thus, we considered *p* lower than 0.050 or higher than 0.950 as those statistically significant.

Finally, we divided the beta diversity components into turnover and nestedness, through the similarity index of Sorensen according to Baselga (2010), which considers beta diversity as the overall variation between multiple samples. In this case, β_{sor} (total beta diversity), was divided into β_{sim} (turnover) and β_{nes} (nestedness) considering: variation between subsamples of a sample unit; variation between sample units of a reservoir; and variation among reservoirs. In the first case, 24 divisions of β_{sor} were generated – for each one of the six sample units of each reservoir in each period. In the second case, four divisions were generated: one division for each reservoir in each period. In these first two cases, we applied paired *t*-tests to evaluate if the importance of

Table 1

Results of *t*-tests comparing species richness and density in each reservoir between periods and in each period between reservoirs. Values of species richness and density for each sampling unit in each sampling period are available in Table B3 in Appendix B. Bold numbers indicate significant differences.

	Species Richness			Species Density		
	<i>t</i>	<i>df</i>	<i>p</i>	<i>t</i>	<i>df</i>	<i>P</i>
In Iraí between fall and spring	-1.69	5	0.150	0.81	5	0.455
In Piraquara II between fall and spring	6.17	5	0.002	6.83	5	0.001
In fall between Iraí and Piraquara II	2.11	10	0.061	-1.34	10	0.234
In spring between Iraí and Piraquara II	-0.06	10	0.949	2.10	10	0.089

turnover differed from the importance of nestedness. In the third case, there were only two possible divisions – one for each period, which prevented us from applying statistical tests.

We conducted all the statistical analyses in the R environment (R Core Team, 2010) using “vegan” (Oksanen et al., 2011; *adonis* and *adipart* function), and “betapart” (Baselga et al., 2013; *beta.multi* function) packages.

3. Results

A total of 174 infra-generic taxa of diatoms were found in the reservoirs. All species recorded, as well as some morphometric values, the reservoir and period in which they were detected and references used for identification are shown in Appendix B. Coincidentally, the total number of species was the same in Piraquara II and Iraí (134 species each). There was no significant difference per sample unit in species richness and density between the reservoirs in any period (Table 1). There was temporal variation in Piraquara II reservoir: its richness and density was higher in fall than in spring (Table 1). In this case, the mean species richness was 37 in spring and 64 in fall; and the mean species density was 253,166 in spring and 1,069,688 in fall. No temporal variation was observed in Iraí reservoir (Table 1).

The PERMANOVA results showed significant floristic variation within and between the reservoirs, depending on the sample period (Table 2). These results indicate that the epiphytic diatoms presented local and regional variability, as well as temporal variation. Typical species for each reservoir and period are given in Table B5 (Appendix B). There were several typical spring and fall species for both reservoirs (Table B5 in Appendix B). Among the species most related to Iraí reservoir, those from the genus *Achnanidium* were commonly found; whereas species from the genus *Eunotia* were frequently found as typical for Piraquara II reservoir (Table B5 in Appendix B). The PCoA diagram shows that the major differences between reservoirs occurred in the spring (Fig. 3). In this period, there was also more variation in species composition, as suggested by the higher dispersion of points in the multivariate space. Variations in species composition between periods were conspicuous in both Iraí and Piraquara II reservoir.

Results of gamma diversity partitioning were similar for both periods (Fig. 4). Alpha and beta3 diversity were higher and beta1 and

Table 2

Results of PERMANOVA comparing diatom species composition between reservoirs and periods, and among sample units (SU) within reservoirs and periods (see methods for the description of hierarchical design).

	<i>F</i>	<i>R</i> ²	<i>p</i>
1) Reservoir	9.74	0.102	0.001
2) Period	9.73	0.101	0.001
Interaction 1) X 2)	4.91	0.051	0.001
SU (Period:Reservoir)	4.55	0.047	0.001

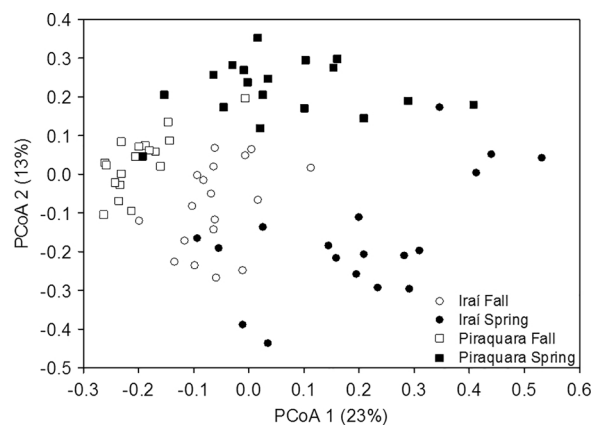


Fig. 3. Diagram of Principal Coordinates Analysis summarizing diatom species composition of Piraquara II and Iraí reservoirs during fall and spring.

beta2 diversity were lower than expected by the null model (Fig. 4). In absolute terms, beta2 diversity was the largest component, although the amount was considered lower than expected by randomized species occurrence.

The contribution of turnover was significantly greater than that of nestedness considering variation between subsamples (i.e. the smallest scale) and between sample units (i.e. larger scale but still within reservoirs) according to the paired *t*-tests (Fig. 5). Even so, variations on the smallest scale (i.e. between subsamples) show some pairs in which there is more nestedness than turnover. This suggests that nested communities were more commonly found between subsamples than between sample units. More turnover than nestedness was also observed in the variation between reservoirs in both sampling periods (Fig. 6). The importance of turnover compared to nestedness decreased when beta diversity division was between periods, especially in Piraquara II reservoir where nestedness was the most important component of temporal variation (Fig. 6).

4. Discussion

Spatial and temporal variation is commonly found in periphytic diatom communities, making it an important group for the investigation of the response of ecological communities to environmental gradients (Mattila and Räsänen, 1998; Soininen et al., 2004; Heino and Soininen, 2010; Taniwaki et al., 2013; Rimet et al., 2015). Here, we have shown the importance of different scales of variation in diatom communities in urban reservoirs of water supply, and suggest that nutrient availability is a key driver of beta diversity. Our suggestion is based on the set of environmental data showing clear differences in nutrient availability indicating the likely effect of trophic status; albeit we can never rule out effects of other variables that were different between reservoirs. Even so, the differences observed in suspended solid and turbidity, for instance (see tables in Appendix A and B), may also be a consequence of the trophic state of reservoirs. This is in line with another study describing macrophyte variation in the same urban reservoirs (Silva et al., 2014) and we could confirm by PERMANOVA, PCoA and IndVal. IndVal results also suggested several species characteristic for ecosystems of high trophic state in both spring and fall in Iraí and typical indicators of low trophic in Piraquara II (see Table B5 in Appendix B). We thus suggest that future studies could focus on physiological responses of such species related to trophic state. More than describing a known variation in community composition between reservoirs, our research innovated by comparing the variation scales to null models and by investigating the components which describe the variation of the communities. We also showed that despite temporal variation in community composition (PERMANOVA results and Fig. 3), the hierarchical sources of community variation were temporally stable

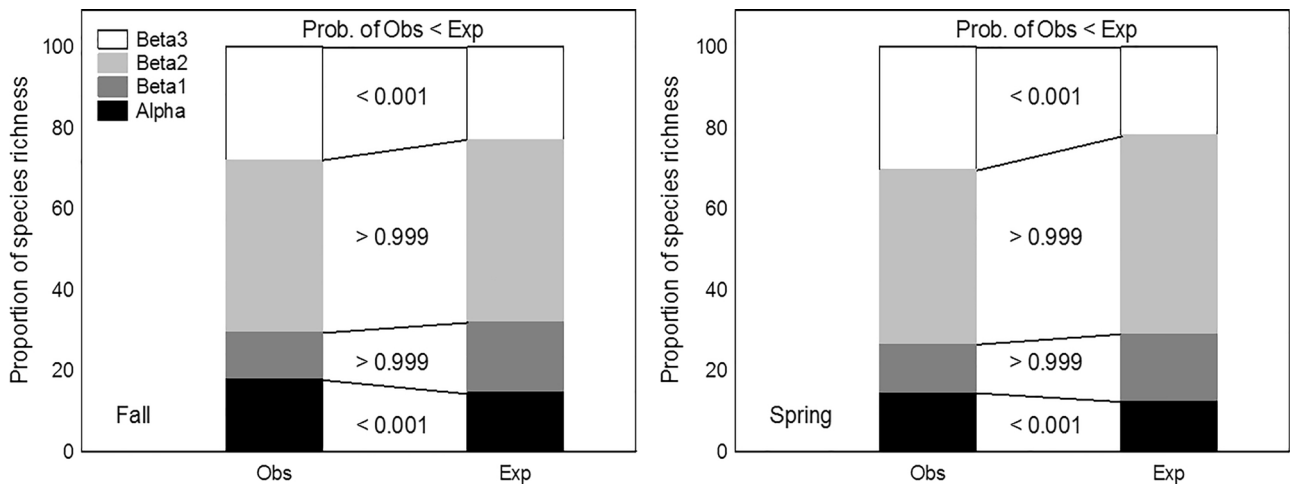


Fig. 4. Additive partitioning of gamma diversity for the two sampling periods, showing the importance of each component and the comparison with the null model. *P* values indicate the probability of a certain component to be less than expected in the null model.

in reservoirs (Additive Partitioning results and Fig. 4). Both in fall and spring 2013, variation between reservoirs of different trophic state was the main source for compositional variation.

It would be reasonable to expect greater diversity variation in environmentally variable sites, given the positive relationship between environmental heterogeneity and beta diversity (Heino et al., 2015). In accordance with our expectations, the composition of species in Iraí reservoir was more variable in both periods compared to Piraquara II reservoir (even though diatoms were collected from different macrophytes in Piraquara II). Iraí clearly has a higher trophic level in relation, and the positive relation between productivity and beta diversity described by Chase and Ryberg (2004); Chase (2010) and Bini et al. (2014) support our results. Indeed, new colonizations quickly occur in areas with high levels of nutrients (Moschini-Carlos, 1999), possibly producing changes in species composition of the periphytic algal communities. Under eutrophic conditions, it is possible to have less competitive exclusion due to less resource limitation (Cardinale, 2011). It is also important to note that tributaries are more numerous in Iraí reservoir. Limnologically different adjacent tributaries certainly influence beta diversity by carrying substances to the reservoir, such as nutrients or algal seedlings, resulting in changes in nutrient availability and exchange of species between sites (Lopes et al., 2014).

Unfortunately standardization of the natural substrate in both reservoirs was impossible: we have always sampled the macrophyte *A. philoxeroides* in Iraí reservoir; but in Piraquara II reservoir we had to sample *A. philoxeroides*, *P. hydrophipoides* and *L. peruviana* to represent

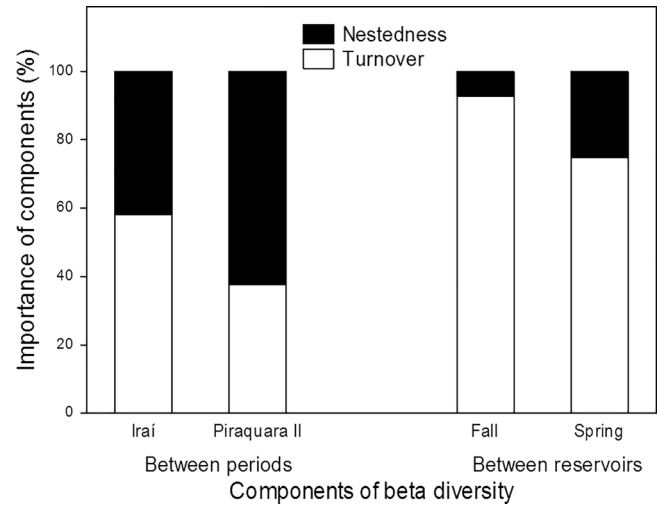


Fig. 6. Percentage of beta diversity between periods (for each reservoir) and between reservoirs (in each period) due to turnover and nestedness.

all sampling units. It has been shown that substrate can affect periphyton community composition (Biolo and Rodrigues, 2013). The higher compositional variation in the reservoirs in which only one substrate was sample reinforces our assumption on the likely positive effect of

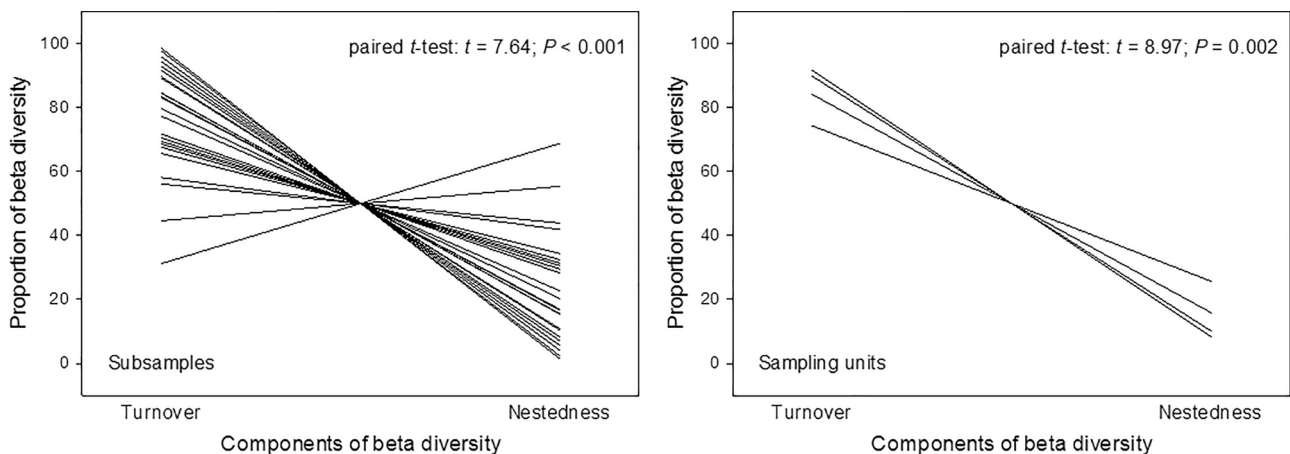


Fig. 5. Percentage of beta diversity between subsamples and between sample units due to turnover and nestedness. Results of paired *t*-tests are shown in the graphs.

eutrophication on community variation. At least, we generated evidence that the substrate was not as important as the differences between reservoirs. We emphasize that the relative contribution of the types of substrate and other ecological mechanisms should be evaluated in future studies.

Biological diversity varies at different spatial scales (Heino and Soininen, 2010; McGlenn and Hurlbert, 2012; Wetzel et al., 2012; Barton et al., 2013) and the identification of the main scale of variation is essential to support studies aimed at understanding the underlying reasons for community change (Crist et al., 2003; Soininen, 2004; Soininen et al., 2009; Flach et al., 2012; Wetzel et al., 2012). The variation between reservoirs was higher than expected by a null model for both sampling periods, highlighting the influence of reservoir identity – and likely of productivity level – in beta diversity (Chase 2010; Bini et al., 2014; Gaiser et al., 2014). On the other hand, variation within reservoirs (between subsample and between sample units) was lower than expected by the null model, indicating that the environmental changes at local scales, although significant (PERMANOVA results), do not contribute more to the total diversity than expected by stochasticity. This also highlights the importance of investigating larger scales of variation to understand community assembly in diatom communities. Our results suggest that reservoirs should be considered as sample units in future efforts to investigate the determinants of beta diversity of diatoms in urban reservoirs, and to improve predictability (see Soininen, 2004).

It is also important to note that the diversity of a subsample (alpha) was higher than expected by the null model. This indicates high coexistence of species and suggests high microhabitat specificity of diatoms in urban reservoirs (Stewart and Lamoureux, 2012). Diatoms probably share resources efficiently at a local scale, resulting in high species coexistence with a small niche breadth, increasing the local richness (Soininen and Heino, 2007). Evidences in the literature support our results. First, the niche breath for benthic diatoms is closely related to the availability of resources (Passy, 2008). It is also shown that epiphytic diatoms can express tolerance to low nutrient availability in lentic environments (Bennion et al., 2014). Studies performed in lotic environments also indicate greater influence of environmental factors at very local scales in determining the community structure when compared to larger spatial scales (Soininen, 2004). Thus, our results and the literature suggest that micro-habitat features (in a sample unit, not among them within a reservoir) are central for diatom communities (Heino and Soininen, 2010; Barton et al., 2013). Trade-offs related to tolerance, nutrient availability, growth form and/or colonization time (Passy, 2008) can also explain high local coexistence. For instance, species can tolerate lower quality environments (Faria et al., 2013) for a limited time to increase their colonization (Passy, 2008).

Beta diversity at different spatial scales was primarily ruled by turnover in our study, indicating high species replacement. Indeed, high turnover was observed even between periods in the same sample unit, indicating a temporal segregation in the distribution and occupancy of the species (McGlenn and Hurlbert, 2012). High turnover has also been demonstrated for diatoms by Wetzel et al. (2012). According to Barton et al. (2013), high turnover may be caused by low dispersion capacity of epiphytic diatoms. The higher temporal turnover in Iraí reservoir compared to Piraquara II is also in line with previous studies showing that species replacement occurs mainly due to higher stochasticity in more productive spaces/sites (Chase, 2010; Bini et al., 2014). Idiosyncrasies in dispersion and colonization are usual causes of high turnover, and those mechanisms are more common in more productive environments (Chase, 2010; Bini et al., 2014), in our study Iraí reservoir was clearly more productive than Piraquara II.

The contribution of nestedness was more evident in Piraquara II reservoir, characterized by a lower trophic level. Some studies suggest that nestedness in benthic communities may directly influence habitat homogeneity (Tornés and Ruhí, 2013; Petsch et al., 2015). Indeed, it is possible that Piraquara II has higher habitat homogeneity given the

lower number of adjacent tributaries, and lower trophic levels. Once again, this result is even more surprising given that diatoms in Piraquara II reservoir were sampled from different substrates. If we considered substrate identity as the main source of habitat heterogeneity (see also Biolo and Rodrigues, 2013), then we would expect turnover to be more important than nestedness in a reservoir in which more species of macrophytes were sampled as natural substrates, which is not the case. This result thus suggests that other environmental characteristics were more important than substrate identity for the composition of epiphytic diatom communities in the studied ecosystems. Surely, further studies are needed to elucidate the causes of environmental heterogeneity for epiphytic diatoms communities: limnological variables, landscape characteristics (such as adjacent rivers, catchment land use) or substrate identity and so on. Also substrate identity may not represent differences in complexity of substrates, another potential driver of diatom variation (Biolo and Rodrigues, 2013).

Our study also suggests that turnover is the main beta diversity component describing the significant variation between reservoirs that differ mainly in trophic levels. Therefore, the diatom communities from an environment degraded by eutrophication are not necessarily a subset of the communities from preserved environments. This is in line with the rationale that diatoms have a high degree of habitat specificity and strongly respond to environmental factors (Heino and Soininen, 2010; Rimet et al., 2015).

Compared to spatial variation, nestedness was relatively more important in temporal variation, although turnover was usually the highest component of beta diversity. This can be partly explained by the fact that urban supply reservoirs have controlled conditions, possibly causing higher stability in abiotic and biotic conditions (Papastergiadou et al., 2010; Silva et al., 2014) and decreasing species turnover over time. Associately, temporal dependence is commonly observed in ecological diatom communities (Soininen, 2008; Smol and Stoermer, 2010; Pellegrini and Ferragut, 2012), assuming that the composition of one period may have been highly dependent on the composition of the previous period (see also Wojciechowski et al., 2017b).

Urban reservoirs provide important environmental services to society and are economically important (Tundisi et al., 2015). Understanding biological diversity in these systems is particularly important, since reservoirs in urban areas usually have fast water degradation (Silva et al., 2014). By showing clear differences between two urban reservoirs of different trophic state, we indeed suggest that eutrophication is the main source of variation in epiphytic diatom communities (Virtanen and Soininen, 2016). Local variations within reservoirs were mainly in the reservoir with the higher trophic level: at intermediate and local scales, a more productive environment can cause larger variation, which can also be explained by the positive relationship between beta diversity and stochastic processes related to productivity (Chase 2010; Bini et al., 2014). Our results thus emphasize that the ecological determinants of epiphytic diatom communities dependent on the scales of observation. Nevertheless, we suggest that eutrophication is a process that affects biodiversity at multiple scales.

Acknowledgements

We are grateful to Sanepar for providing abiotic data and logistic support for samplings. Authors also acknowledge CNPq and CAPES for continuous support considering both student and researcher scholarships, and other financial resources. We are also grateful for two anonymous reviewers and the Limnologia's editor Michael Hupfer for valuable suggestions on a previous draft of this manuscript.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.limno.2018.04.001>.

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