Environmental Pollution 288 (2021) 117778

Contents lists available at ScienceDirect

Environmental Pollution

journal homepage: www.elsevier.com/locate/envpol

Homogenization of diatom assemblages is driven by eutrophication in tropical reservoirs[☆]

Stéfano Zorzal-Almeida [a,*], Elaine C. Rodrigues Bartozek [b,c], Denise C. Bicudo [b,c]

[a] Universidade Federal do Espírito Santo – UFES, Av. Fernando Ferrari, 519, Vitória, ES, Brazil
[b] Instituto de Botânica, Department of Ecology, Av. Miguel Estéfano 3687, 04301-902, São Paulo, SP, Brazil
[c] Universidade Estadual Paulista "Júlio de Mesquita Filho" – UNESP, Av. 24A, 1515, 13506-900, Rio Claro, SP, campus, Rio Claro, SP, Brazil

ARTICLE INFO

Keywords:
Beta diversity
Biodiversity
Nestedness
Trophic gradient

ABSTRACT

Eutrophication is one of the most widespread causes of biotic homogenization in freshwater ecosystems. Biotic homogenization can be characterized as reductions in local diversity (alpha) and occupation of available niches by more generalist species. Beta diversity is expected to decrease in more homogeneous communities, however, there is no consensus on how it responds to eutrophication. We used a space-for-time approach to analyze the process of biotic homogenization on diatom assemblages in response to eutrophication in tropical reservoirs ranging from oligotrophic to hypereutrophic conditions. Diatom assemblages were analyzed in phytoplankton and surface sediment from 12 reservoirs with different trophic levels. We calculated total beta diversity and turnover and nestedness components and used regressions to analyze their relationships with productivity differences (without distance effects). Total beta diversity had a positive influence of the trophic gradient, whereas turnover was not related to eutrophication. However, we found that eutrophication and lower species richness (alpha diversity) led to increasing rates of the nestedness component. We also observed that the homogenization process was not characterized by invasion of new species, but, on the contrary, by filtering nutrient-rich tolerant species also present in oligo-mesotrophic reservoirs and able to occupy available niches in the eutrophic reservoirs. These findings (increase in nestedness, decrease in alpha diversity, and development of tolerant species) suggest that biotic homogenization is leading to a simplification of diatom assemblages in tropical reservoirs, making assemblages from eutrophic and hypereutrophic reservoirs a subset of assemblages from oligotrophic and mesotrophic ones.

1. Introduction

Currently, biodiversity loss has been documented as one of the main consequences of anthropogenic stressors (Dudgeon et al., 2006; Reid et al., 2018). These losses are not simply characterized by reductions in local species richness (alpha diversity), but they also imply regional taxonomic simplification of the communities (Solar et al., 2015), which is demonstrated in lower beta diversity (i.e., variation in assemblage compositions among sites). Reductions in alpha and beta diversities may be followed by the spread of more generalist species and regional extinctions of rare and specialist species in response to environmental changes, a process known as biotic homogenization (Olden, 2006; Petsch, 2016), whose consequences include loss of ecosystem stability, thus reducing its resilience in coping with environmental disturbances (Hughes and Stachowicz, 2004).

Biotic homogenization in response to anthropogenic stressors has been reported for both terrestrial and freshwater ecosystems. For instance, removal of forested areas for agricultural use has led to the biotic homogenization of several animal and plant groups (Solar et al., 2015), as well as soil microbial communities (Rodrigues et al., 2012) in the Amazon region. In wetlands, the degradation and consequent habitat simplification has increased the similarity on plant, diatom, zooplankton, and macroinvertebrate communities (Lougheed et al., 2008). Urbanization can be also pointed out as one of the main causes of biotic homogenization, as it often produces a disturbed and homogeneous environment that leads to local extinction, subsequently leaving the environment more susceptible to invasion of alien species (Blair, 2001; McKinney, 2006). Schwartz et al. (2006) observed an association

---

[☆] This paper has been recommended for acceptance by Sarah Harmon.

[*] Corresponding author.

E-mail addresses: stefanozorzal@gmail.com (S. Zorzal-Almeida), elaine.bartozek@gmail.com (E.C.R. Bartozek), denisecbicudo@gmail.com (D.C. Bicudo).

https://doi.org/10.1016/j.envpol.2021.117778
Received 17 March 2021; Received in revised form 21 June 2021; Accepted 9 July 2021

between higher extinction rates of rare plant species in Californian flora and human population density, suggesting urban development as a cause of biotic homogenization.

In freshwater ecosystems, urbanization can promote water degradation, leading to eutrophication (Fontana et al., 2014; Zorzal-Almeida et al., 2018), which, when derived from nutrient enrichment (mainly nitrogen and phosphorus), can be a cause of biotic homogenization in these ecosystems (Donohue et al., 2009; Menezes et al., 2015; Wengrat et al., 2018). Reductions in environmental heterogeneity seem to be a key factor leading to this phenomenon, filtering species that succeed under more eutrophic conditions (Menezes et al., 2015). Contradictorily, beta diversity can be positively influenced by eutrophication at regional scales (Chase, 2010), whereas local diversity seems to be higher at intermediate levels of nutrient concentration (Svensson et al., 2007). Even though eutrophication has been suggested to both increase and decrease the turnover component (Chalcraft et al., 2008) and since the nestedness process cause species loss in response to some event that promotes disaggregation, it is reasonable to expect nestedness rates to increase with nutrient enrichment (Baselga, 2010).

Although diatom assemblages from tropical reservoirs have shown a process of biotic homogenization in response to eutrophication (Wengrat et al., 2018), it has not yet been analyzed whether the similarity among communities in eutrophic environments (1) is due to a sorting/selecting species that leads to a lower species richness, or (2) the local extinctions that generates a community composed by a subset of a richest community. Therefore, partitioning beta diversity into its components of turnover and nestedness (species substitution and species loss, respectively) could be an interesting way to solve that gap, since they help to access the processes that underly beta diversity. In addition, spatial data can be an alternative for the lack of long time series, often necessary in biotic homogenization studies. However, long time series (e.g., monitoring programs) demands greater human and financial efforts to maintain the research, which makes space-for time approach an interesting alternative. Accessing spatial patterns of biotic homogenization may give insights on how the process occur over time, which is in the core of the space-for-time approach (Blois et al., 2013). Despite its use in freshwater ecology (Thomaz et al., 2012), to our knowledge, no studies have explicitly used space-for-time approach to assess the effects of eutrophication on biotic homogenization.

We carried out samplings ranging a broad productivity gradient – from oligotrophic to hypereutrophic conditions – to investigate if the spatial biotic homogenization in a series of tropical reservoirs occurs in response to anthropogenic eutrophication. Our hypothesis is that eutrophication leads to the homogenization of diatom assemblages in tropical reservoirs. We predicted that (i) turnover rates should not increase with eutrophication, since species replacement is not expected in homogenization processes, (ii) the nestedness component should increase with higher eutrophication levels, and that (iii) homogenization leads to species loss, making diatom assemblages from more productive reservoirs a subset of those that are less productive. Finally, we made some considerations regarding using the space-to-time approach in diatom assemblage homogenization.

2. Material and methods

2.1. Study area

This study was conducted in 12 man-made reservoirs distributed in three watersheds of São Paulo State, southeastern Brazil (Fig. 1), encompassing an area lager than 31′000 km^2, located between 46°25′W - 48°22′W and 22°37′S - 23°39′S. Five of the reservoirs are components of the largest water supply system in the world (Cantareira System) and are connected via tunnels. All waters from the reservoirs flow into the Barra Bonita reservoir, located in the Tietê River, the largest river in the

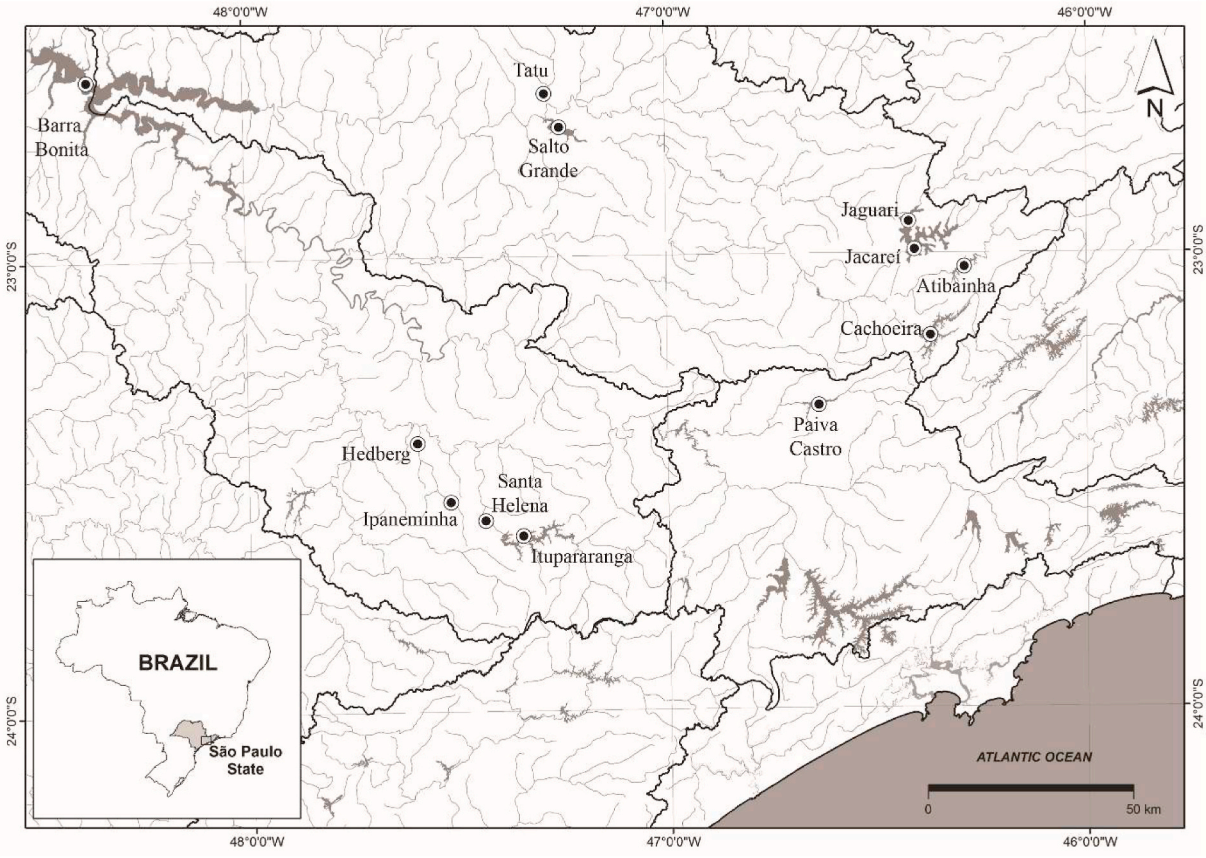

Fig. 1. Location of the reservoirs in the present study (modified from Bicudo et al., 2016).

region. The reservoirs are between 7 and 222 km apart from each other and located between 451 and 846 m above sea level with constructions varying from 1811 to 1982 (our sampling was not influenced by the reservoirs filling). Reservoirs mean depth ranges from 2.2 to 28.4 m and surface area from 0.11 to 241.27 km^2 (Zorzal-Almeida et al., 2017a). For more specific information about each reservoir, see Supplementary Material. The regional climate is characterized as humid subtropical zone and its annual cumulative precipitation ranges from 1300 to 1600 mm (Alvares et al., 2014). There are no relevant differences among their local climates. The land use of drainage basins comprises agriculture, cattle breeding, and urban areas. The reservoirs provide water for multiple uses, including water supply (e.g., Cantareira System), electrical generation, navigation, and recreation.

2.2. *Sampling design and procedures*

For physical and chemical characterizations, we selected from two to seven sampling sites at each reservoir depending on their size, number of main inflowing streams, and maximum depth (Table 1). Field samplings were conducted in one summer and one winter, and water samples were collected using a van Dorn bottle on the subsurface. Conductivity (µS cm^{-1}) and pH were measured *in situ* by using standard electrodes (Horiba U-50). Total phosphorous and total nitrogen (µg L^{-1}) were determined following the analytical procedures of Standard Methods (APHA, 2005), and chlorophyll-*a* (µg L^{-1}), corrected for phaeophytin using 90% ethanol (Sartory and Grobbelaar, 1984). Trophic State Index (TSI) was calculated using an adaptation of Carlson's TSI for tropical reservoirs (Lamparelli, 2004; Zorzal-Almeida et al., 2017b). Mean values among the sampling sites within each reservoir were used in our analyses.

We sampled diatom assemblages from both phytoplankton and surface sediments at the deepest region of each reservoir. During both the summer and winter, planktonic diatoms were sampled using a van Dorn bottle at three different depths (subsurface, mean depth, and 1 m above the sediment) and then integrated. Considering that sediments integrate temporal and spatial scales (Smol, 2008), we used a UWITEC gravity corer to sample surface sediment diatoms only in winter, since it corresponds to the dry season in Brazil, when sediments are more stable. The upper 2 cm of each sediment core (triplicate per sampling site) were extruded and then pooled together. Water and surface sediment diatom samples were oxidized using hydrogen peroxide (H_2O_2 35%) and hydrochloric acid (HCl 37%) (Battarbee et al., 2001), and permanent glass slides were prepared using Naphrax as a mounting medium. Diatoms were identified and quantified at a magnification of 1000× using a Zeiss Axioskop 2 microscope. To ensure the same counting effort among different samples, a minimum of 400 valves per slide were counted until reaching a counting efficiency of at least 90% (Pappas and Stoermer, 1996). Species relative abundances matrix resulting from diatom counting was converted into a presence matrix (0/1), while phytoplankton and surface sediment matrices were combined into a single matrix to represent the local assemblage. Both phytoplankton and surface sediment diatoms matrices were aggregated to access the reservoir total richness in a short time period. The sedimentation rates of other reservoirs from the same region indicate that the first 2 cm of the surface sediment represent about 1.8 year in oligotrophic reservoirs (Cardoso-Silva et al., 2015) and about 0.9 year in hypereutrophic reservoirs (Costa-Böddeker et al., 2012). Moreover, some paleolimnological studies have found that no significant changes in diatom community have occurred over the last years (Wengrat et al., 2019; Fontana et al., 2014; Costa-Böddeker et al., 2012). Therefore, we understand to be plausible to use surface sediment to complement the diatom flora in our studied systems, since it can also integrate spatial scales, as mentioned before (Smol, 2008). Bartozek et al. (2018) explored the floristic composition of diatom assemblages in these reservoirs in a previous study.

2.3. *Numerical analysis*

Firstly, we performed a Principal Component Analysis (PCA) with log-transformed (except pH) and standardized environmental variables to analyze the main patterns of the environmental data (pH, conductivity, total nitrogen, and total phosphorous). After that, chlorophyll-*a* values were regressed against the PCA axis that better represented a eutrophication gradient, which allowed assess how chlorophyll-*a* represents the eutrophication. To accomplish the homoscedastic assumption of linear regression, chlorophyll-*a* was Box-Cox transformed prior to the analysis (Box and Cox, 1964).

Using the diatom matrix, we estimated the total beta diversity of the diatom assemblages and its corresponding components of turnover and nestedness according to Baselga (2010). Geographic distance has been cited as an important factor affecting beta diversity of diatom assemblages (as previously demonstrated by Wetzel et al. (2012) and Zorzal-Almeida et al. (2017a) for tropical assemblages). To control and remove this effect, beta diversity, turnover and nestedness were firstly regressed against geographical distance (Euclidian distance based on geographical coordinates). The residuals of this linear regression were used to assess the effects of eutrophication in diatom beta diversity through linear regression. In this analysis, eutrophication distance was proxied by differences between mean chlorophyll-*a* of two reservoirs and regressed against its diatom beta diversity value (total, turnover, and nestedness). Finally, the effects of eutrophication on total richness were assessed using linear regression of log-transformed mean chlorophyll-*a* and total number of diatom species. For all regressions, homoscedasticity was assessed using the Breusch-Pagan test (Breusch and Pagan, 1979), and all models fit the assumptions. We used adjusted R^2 to quantify the variance explained in our models (Karch, 2020). All numerical analyses were performed on R v. 4.0.1 (R Core Team, 2020) using the packages *vegan* (Oksanen et al., 2019) and *betapart* (Baselga et al., 2018).

Table 1
Mean and standard deviation of abiotic variables, chlorophyll-a and trophic state (based on mean Trophic State Index – Lamparelli, 2004).

Reservoir	pH	Conductivity (µS cm^{-1})	TN (µg L^{-1}	TP (µg L^{-1})	Chlorophyll-*a* (µg L^{-1})	Trophic State (TSI)
Jacareí	7.2 (±0.1)	35.1 (±1.2)	202.8 (±63.0)	10.0 (±3.7)	4.1 (±0.3)	Oligotrophic
Paiva Castro	6.4 (±0.2)	42.0 (±3.4)	216.6 (±54.9)	13.0 (±1.7)	2.1 (±1.1)	Oligotrophic
Atibainha	6.5 (±0.2)	33.6 (±2.0)	334.3 (±48.4)	8.5 (±0.8)	2.6 (±0.6)	Oligotrophic
Cachoeira	6.7 (±0.1)	39.0 (±1.9)	286.6 (±82.7)	13.1 (±2.6)	2.4 (±0.5)	Oligotrophic
Santa Helena	7.1 (±0.3)	100.0 (±4.0)	544.5 (±66.2)	13.9 (±1.3)	4.5 (±2.9)	Oligotrophic
Tatu	6.4 (±0.2)	56.8 (±2.0)	596.7 (±158.6)	22.1 (±1.1)	2.5 (±1.6)	Oligotrophic
Jaguari	7.0 (±0.2)	36.1 (±0.4)	386.1 (±26.2)	19.9 (±6.4)	2.5 (±2.3)	Mesotrophic
Itupararanga	7.2 (±0.3)	98.3 (±7.0)	765.5 (±107.4)	26.2 (±12.1)	18.2 (±14.7)	Mesotrophic
Ipaneminha	7.1 (±0.1)	162.8 (±6.0)	918.6 (±22.0)	34.2 (±2.2)	12.6 (±2.2)	Mesotrophic
Hedberg	7.9 (±0.3)	134.3 (±1.9)	1298.7 (±256.1)	100.3 (±33.9)	46.1 (±54.6)	Eutrophic
Salto Grande	8.6 (±0.6)	313.1 (±23.2)	2337.7 (±723.1)	189.8 (±81.8)	180.1 (±130.3)	Eutrophic
Barra Bonita	8.2 (±0.3)	354.2 (±34.0)	5334.5 (±2451.3)	283.5 (±149.5)	82.9 (±31.4)	Hypereutrophic

3. Results and discussion

The reservoirs trophic state ranged from oligotrophic to hypereutrophic conditions, pH mean values ranged from slightly acidic (6.4) to alkaline (8.6), and mean conductivity ranged between 33.6 and 354.2 μS cm^{-1} (Table 1). Using these variables, PCA analysis summarized a total of 91.9% of data variability along the first axis (and 5.2% in the axis 2), and showed strong significant Pearson correlation with the analyzed variables (pH [$r = -0.92$], conductivity [$r = -0.96$], total phosphorous [$r = -0.98$], and total nitrogen [$r = -0.97$]), with higher values on the positive side of the axis (Fig. 2A). Then, the first axis (PC1) can be interpreted as eutrophication gradient, and chlorophyll-*a* exhibited a strong positive correlation with this axis (R^2 adj. $= 0.88$; Fig. 2B). Therefore, these results allow us to use chlorophyll-*a* values as a *proxy* of eutrophication levels in our analyses. The higher the chlorophyll-*a* level the higher the level of eutrophication.

Dispersal limitation has been pointed out as an important driver of beta diversity in aquatic ecosystems (Thompson and Townsend, 2006), and can be related to geographic distance between diatom assemblages (Virtanen and Soininen, 2012; Zorzal-Almeida et al., 2017a). We found a positive correlation between the beta diversity of diatom assemblages and geographical distance, possibly due to increasing rates of species substitution (turnover). Pairwise total diatom beta diversity between reservoirs varied from 0.13 to 0.83 (median = 0.55, Fig. 3A). The turnover component had the greatest contribution to beta diversity (0.00–0.65, median = 0.43). Our models showed positive correlation between total beta diversity and geographical distance between reservoirs (R^2 adj. $= 0.31$, $p < 0.01$, Fig. 3B), which also occurred for the turnover component (R^2 adj. $= 0.18$, $p < 0.01$, Fig. 3C). However, the nestedness component showed lower contribution to total beta diversity (0.00–0.42, median = 0.13) and did not show a significant correlation with the spatial distance (R^2 adj. $= 0.004$, $p > 0.05$, Fig. 3D). Species replacement seems to increase with larger geographical distances (Verleyen et al., 2009; Wetzel et al., 2012). Additionally, since we did not find the nestedness component and geographical distance to be correlated, it seems that in the metacommunity context, mass effect (see Leibold et al., 2004) showed less or no effect on diatom assemblages in tropical reservoirs. Jamoneau et al. (2017) found mass effects acting in river diatom community and related it to a decrease in turnover and an increase in nestedness rates, opposite to our findings. Despite rivers and reservoirs show different connectivity degrees, mass effects in reservoirs should not be completely ruled out, since some of them, as the reservoirs here studied, are arranged in a cascade system (Zorzal-Almeida et al., 2018).

Considering that both stochastic (dispersion limitation) and deterministic (productivity) processes are important co-factors for the variation in beta diversity (Virtanen and Soininen, 2012; Zorzal-Almeida et al., 2017a), we assessed the effect of eutrophication on beta diversity by isolating the effect of geographic distance (see comments above). We found positive correlation between total beta diversity and trophic difference (R^2 adj. $= 0.17$, $p < 0.01$) (Fig. 4A). At first sign, such finding seems to contradict the results of other works (e.g., Wang et al., 2019), however, these studies compared communities within reservoirs that have the same trophic state. In these cases, lower beta diversity in eutrophic conditions was expected due to reduced species richness and similarity among communities. We decided to assess the trophic gradient using the difference of trophic levels between reservoirs, and not as a direct measure of local eutrophication, as usual, and found, higher beta diversity in higher trophic difference between reservoirs, as expected.

Notwithstanding, it is also important in the process of biotic homogenization assessment to consider whether nestedness increases and species richness decreases along such gradient. In this way, our results showed that eutrophication increased the nestedness rates (R^2 adj. $= 0.39$, $p < 0.01$, Fig. 4C), indicating homogenization of diatom assemblages as a result of reduction in species richness along the trophic gradient (as discussed later). Nestedness is generally associated with species loss (Baselga, 2010), but the factors that underly nestedness are still poorly explored. For freshwater ecosystems, some evidence show that anthropogenic stressors filter the most sensitive species and favor the occupation of more generalist ones, resulting in lower species richness and higher nestedness rates (Gutiérrez-Cánovas et al., 2013; Petsch, 2016). Wang et al. (2019) found that although species turnover is frequently the dominant component of beta diversity, the nestedness component has more influence when total phosphorous levels increase. In contrast, turnover usually seems to be more related to species substitution in response to natural environmental gradients or increasing spatial scales (Baselga, 2010; Zorzal-Almeida et al., 2017a). We found that the turnover component was not related to eutrophic differences between reservoirs (R^2 adj. $= 0.02$, $p > 0.05$, Fig. 4B), suggesting that diatoms species replacement did not depend on productivity changes in reservoirs. These results show that our first and second predictions were correct. We hypothesized that eutrophication causes diatom assemblage homogenization, therefore, we expected to find enhanced nestedness as

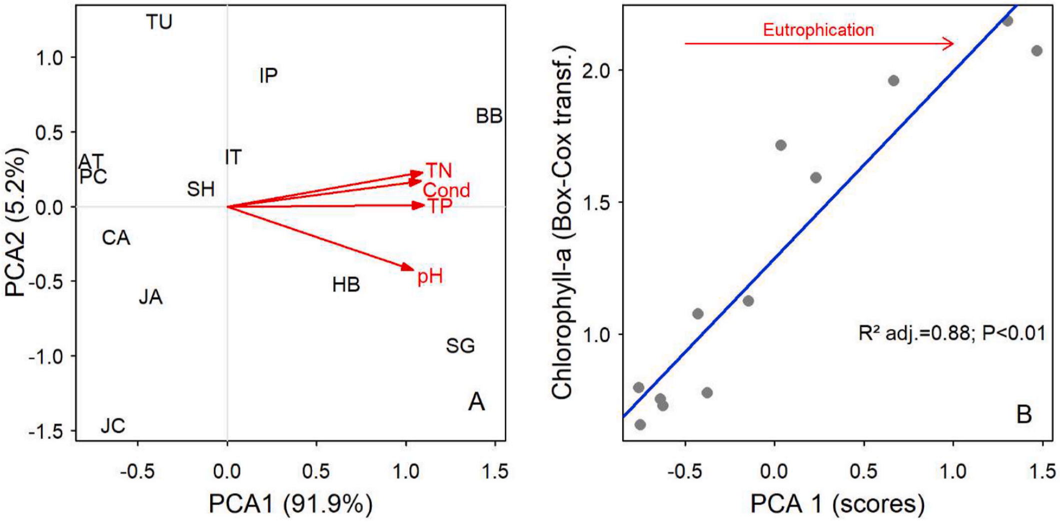

Fig. 2. Principal Components Analysis (PCA) for the environmental variables (A) and regression between the first axis of the PCA, representing the eutrophication process (arrow), and chlorophyll-*a* (B). Reservoirs: Atibainha (AT), Barra Bonita (BB), Cachoeira (CA), Hedberg (HB), Ipaneminha (IP), Itupararanga (IT), Jacareí (JC), Jaguari (JA), Paiva Castro (PC), Salto Grande (SG), Santa Helena (SH), Tatu (TU). Variables: Conductivity (Cond), total nitrogen (TN), total phosphorous (TP).

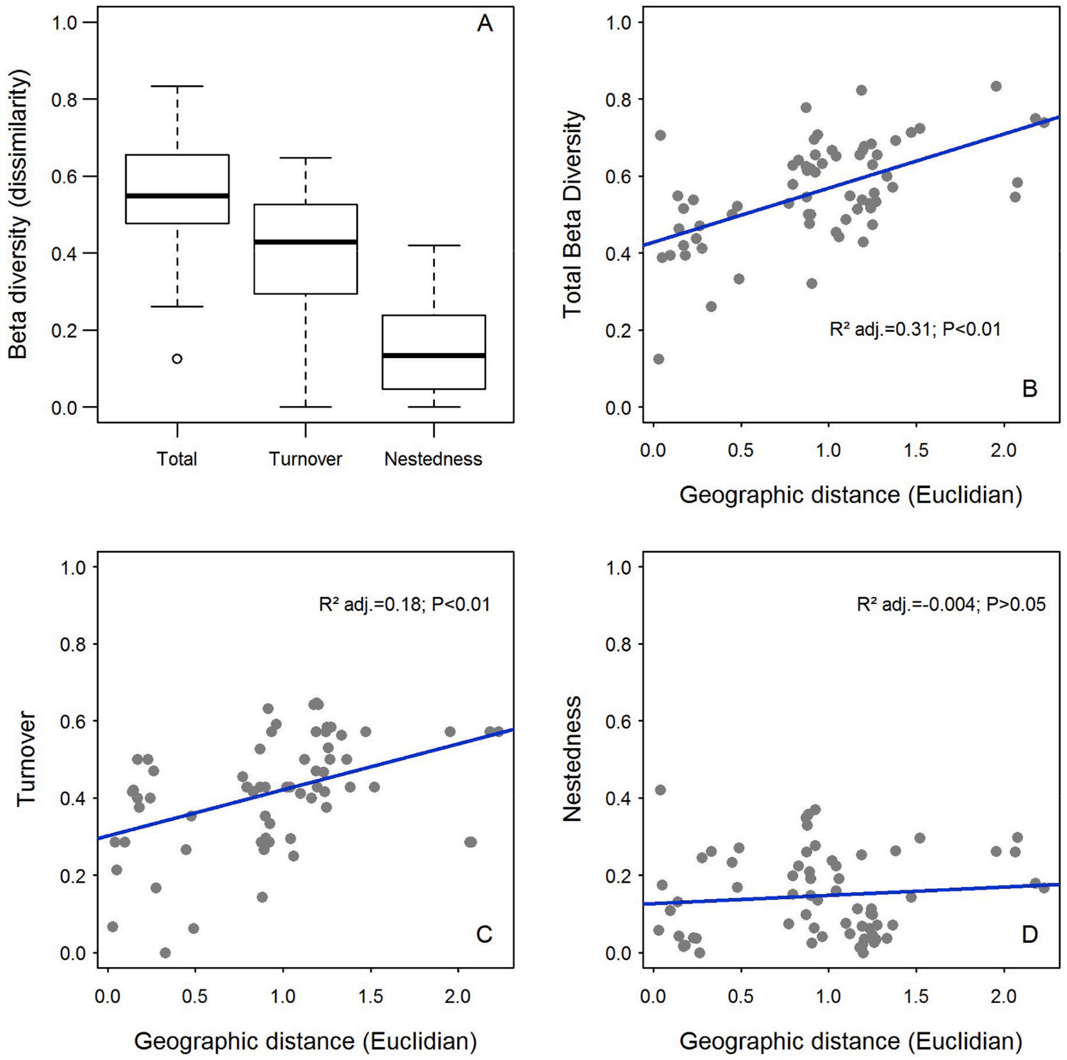

Fig. 3. Boxplot of total beta diversity, and it turnover and nestedness components (A). Regression of Total Beta Diversity (B) and its components Turnover (C) and Nestedness (D) in function of geographic distance (Euclidian distance) between sampling sites.

eutrophication increases, as well as no change in the turnover component, since tolerant diatom species are selected in nutrient-rich environments (Xue et al., 2019), making them a subset of the assemblages found in less productivity environments. Homogenization in response to eutrophication had been reported for periphytic diatoms (Vilar et al., 2014), aquatic invertebrates (Donohue et al., 2009), and lake fish communities (Menezes et al., 2015), demonstrating a potential loss of regional biodiversity.

Losses of sensitive species and maintenance of tolerant ones due to anthropogenic impacts can lead to biota homogenization (Solar et al., 2015; Petsch, 2016). Nestedness occurs when eutrophic conditions select the same tolerant species in different places, if not, the species substitution component may have greater importance in beta diversity (Gianuca et al., 2017). Our results demonstrate that the nestedness component may have been influenced by the selection of tolerant *Aulacoseira* species in eutrophic reservoirs (Table 2), such as *A. granulata*, *A. granulata* var. *angustissima*, and *A. ambigua*. These species have preference for nutrient-rich environments and exhibit broad tolerance range (Bicudo et al., 2016), corroborating the hypothesis of community homogenization. The environmental gradient shows the existence of species with broad environmental tolerance, in our case, eutrophication. For instance, we found species that indicate eutrophication (*Aulacoseira ambigua* and *Cyclotella meneghiniana*; van Dam et al., 1994; Lobo et al., 2014; Bicudo et al., 2016) with important relative contribution to the diatom assemblages in oligotrophic (e.g., Santa Helena) and mesotrophic (e.g. Ipaneminha) environments (Table 2). These results also clarify that the biotic homogenization process analyzed in our study was not characterized by invasive species, which we consider to be those that do not occur in richest communities. We were not able to conclude if these species are indeed invasive in the full pool of species. Disturbances caused by anthropogenic stressors, such as organic pollution by sewage, can locally extinct sensitive species and make the niche available for invasive species (McKinney, 2006; Blair, 2001). However, our results suggest that homogenization was not characterized by invasive species due to the turnover component patterns, which would be expected to increase in response to this homogenization mechanism: new species would be introduced into the eutrophic environment (species replacement) and would not be a subset of larger communities (nestedness).

Since biotic homogenization is often related to decreasing species richness in the communities (Solar et al., 2015), our third prediction expected to find less diatom species in environments with higher productivity. We found that species richness (alpha diversity) was negatively influenced by the eutrophication process (R^2 adj. $= 0.56$, $p < 0.01$, Fig. 4D). Increasing productivity rates and consequent eutrophication of freshwater ecosystems have been pointed out a factor that may lead to lower species richness (Declerck et al., 2007; Wengrat et al., 2018), especially resulting from species extinction (see discussion above).

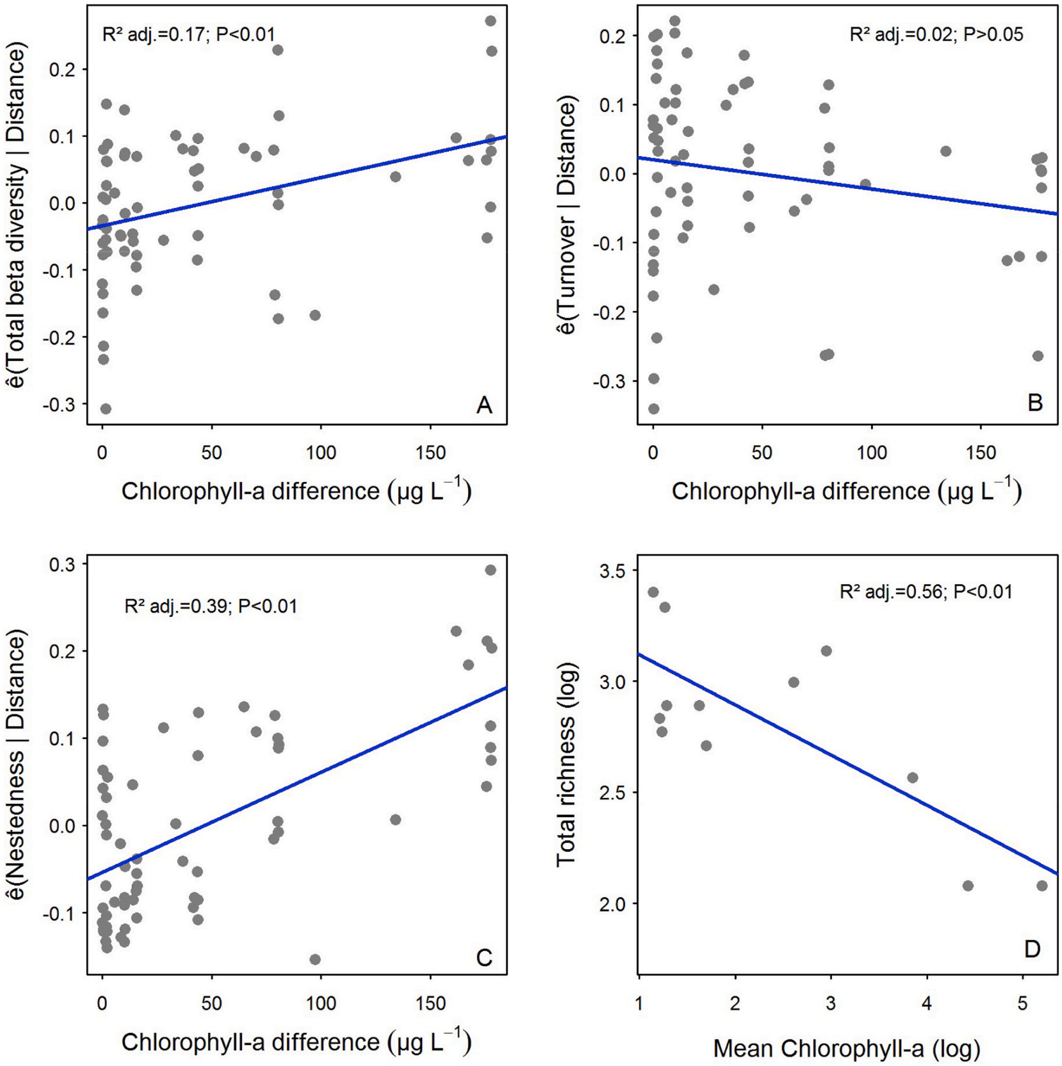

Fig. 4. Regression plot of the residuals of Total Beta Diversity (A) and its components Turnover (B) and Nestedness (C) in function of chlorophyll-a between sampling sites, controlled for geographical distance, and regression plot between total richness and mean chlorophyll-a in each reservoir (D).

Gianuca et al. (2017) found that higher nutrients levels cause strong reduction in local richness and diversity and in unconnected environments, in these cases, nestedness was the dominant component in beta diversity, in agreement with our results. These authors also found that the interaction between nutrient addition and dispersion affects the contribution of the nestedness and turnover components to beta diversity. In tropical reservoirs, dispersion mechanisms also seem to limit diatoms (Zorzal-Almeida et al., 2017a), which supports our decision to control the effects of geographic distance on beta diversity.

Wengrat et al. (2018) used diatom assemblages from sediment cores collected in reservoirs of the same study area and found homogenization of diatom assemblages during the eutrophication process over time. Our results corroborate such findings by using a spatial rather than a temporal approach. The biotic homogenization process, *sensu* Olden (2006), must be assessed over time and among different communities. Our results show that the space-for-time approach is efficient at assessing the homogenization of diatom assemblages caused by eutrophication in tropical reservoirs. This approach has been used in evolutionary (Wogan and Wang, 2018) and ecological contexts (Faber et al., 2018), suggesting that relationships between communities and environment across space could create a significant model to represent changes in species communities over time (Blois et al., 2013). Thus, our findings suggest that the space-for-time approach is feasible for the assessment of biotic homogenization in aquatic ecosystems. For further studies, we suggest applying the approach to assess other biotic communities (e.g., zooplankton or macrophytes) as well as other aquatic ecosystems.

4. Conclusions

We conclude that eutrophication can cause homogenization of the diatom assemblages in tropical reservoirs, leading to a lower number of species and selecting more tolerant species, which are a subset of communities from less impacted environments. Despite being recognized as one of the main threats to aquatic ecosystems for decades, eutrophication remains relevant and challenging in terms of diversity loss. The space-for-time approach is a viable alternative to understand the biotic homogenization of different aquatic communities and has the potential to infer on the process on a broader spatial scale.

Authors' contributions

ECRB, SZA and DCB contributed to conceptualization, writing - review & editing. ECRB and SZA also contributed in formal analysis and roles/writing - original draft.

Table 2
Maximum relative abundance of the three more representative species in each studied reservoir, considering all counting data of the phytoplankton and surface sediment.

Reservoir	Taxa
Atibainha	*Spicaticribra kingstonii* J.R.Johansen, Kociolek & R.L.Lowe (67.2%)
	Aulacoseira tenella (Nygaard) Simonsen (54.7%)
	Discostella stelligera (Cleve & Grunow) Houk & Klee (43.9%)
Barra Bonita	*Au. granulata* (Ehrenberg) Simonsen (51.6%)
	Au. granulata var. *angustissima* (O.Müller) Simonsen (45.4%)
	Cyclotella meneghiniana Kützing (40.74%)
Cachoeira	*D. stelligera* (Cleve & Grunow) Houk & Klee (49.9%)
	Au. tenella (Nygaard) Simonsen (25.6%)
	Navicula notha J.H.Wallace (13.1%)
Hedberg	*Au. ambigua* (Grunow) Simonsen (55.2%)
	Au. granulata var. *angustissima* (O.Müller) Simonsen (24.8%)
	Au. granulata (Ehrenberg) Simonsen (19.9%)
Ipaneminha	*D. stelligera* (Cleve & Grunow) Houk & Klee (42.3%)
	Eunotia intricans Lange-Bertalot & Metzeltin (28.6%)
	Au. granulata (Ehrenberg) Simonsen (22.4%)
Itupararanga	*Au. ambigua* (Grunow) Simonsen (63.6%)
	Fragilaria aquaplus Lange-Bertalot & S.Ulrich (18.2%)
	D. stelligera (Cleve & Grunow) Houk & Klee (15.0%)
Jacareí	*Au. tenella* (Nygaard) Simonsen (52.6%)
	Ac. catenatum (Bily & Marvan) Lange-Bertalot (17.5%)
	C. meneghiniana Kützing (12.9%)
Jaguari	*Au. tenella* (Nygaard) Simonsen (35.7%)
	Cyclotella meneghiniana Kützing (16.4%)
	D. stelligera (Cleve & Grunow) Houk & Klee (14.9%)
Paiva Castro	*Au. tenella* (Nygaard) Simonsen (34.2%)
	D. stelligera (Cleve & Grunow) Houk & Klee (20.0%)
	Ac. catenatum (Bily & Marvan) Lange-Bertalot (15.8%)
Salto Grande	*Au. granulata* var. *angustissima* (O.Müller) Simonsen (63.7%)
	Au. ambigua (Grunow) Simonsen (47.6%)
	Au. granulata (Ehrenberg) Simonsen (13.8%)
Santa Helena	*Punctastriata lancettula* (Schumann) P.B.Hamilton & Siver (81.8%)
	Au. ambigua (Grunow) Simonsen (7.5%)
	Achnanthidium sp. (6.3%)
Tatu	*Nitzschia australodesertorum* E.A.Lehmkuhl, T.Ludwig & C.E.M. Bicudo (20.2%)
	Ac. catenatum (Bily & Marvan) Lange-Bertalot (18.4%)
	Ac. minutissimum (Kützing) Czarnecki (13.2%)

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

This study was carried out within the framework of the AcquaSed project, supported by funds from Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP, AcquaSed Project, n° 2009/53898-9). SZA and ECRB thank their doctoral fellowship (FAPESP 2013/23703-7 and 2013/14337-7, respectively). Funding was also provided by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, Grant 310176/2019-0 to DCB).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.envpol.2021.117778.

References

Alvares, C.A., Stape, J.L., Sentelhas, P.C., et al., 2014. Köppen's climate classification map for Brazil. Meteorol. Z. 22, 711–728. https://doi.org/10.1127/0941-2948/2013/0507.

APHA, 2005. Standard Methods for Examination of Water and Wastewater. American Public Health Association WWA, Washington, D.C.

Bartozek, E.C.R., Zorzal-Almeida, S., Bicudo, D.C., 2018. Surface sediment and phytoplankton diatoms across a trophic gradient in tropical reservoirs: new records for Brazil and São Paulo State. HOEHNEA 45, 69–92. https://doi.org/10.1590/2236-8906-51/2017.

Baselga, A., 2010. Partitioning the turnover and nestedness components of beta diversity. Global Ecol. Biogeogr. 19, 134–143. https://doi.org/10.1111/j.1466-8238.2009.00490.x.

Baselga, A., Orme, D., Villeger, S., Bortoli, J., Leprieur, F., 2018. Betapart: Partitioning Beta Diversity into Turnover and Nestedness Components. R package version 1.5.1. https://CRAN.R-project.org/package=betapart.

Battarbee, R.W., Jones, V., Flower, R.J., et al., 2001. Diatoms. In: Smol, J.P., Birks, H.J.B., Last, W.M. (Eds.), Tracking Environmental Change Using Lake Sediments. Kluwer Academic Publishers, London, pp. 155–203.

Bicudo, D.C., Tremarin, P.I., Almeida, P.D., et al., 2016. Ecology and distribution of *Aulacoseira* species (Bacillariophyta) in tropical reservoirs from Brazil. Diatom Res. 31, 199–215. https://doi.org/10.1080/0269249X.2016.1227376.

Blair, R.B., 2001. Creating a homogeneous avifauna. In: Marzluff, J.M., Bowman, R., Donnelly, R. (Eds.), Avian Ecology and Conservation in an Urbanizing World. Springer, Boston, pp. 459–486.

Blois, J.L., Williams, J.W., Fitzpatrick, M.C., Jackson, S.T., Ferrier, S., 2013. Space can substitute for time in predicting climate-change effects on biodiversity. Proc. Natl. Acad. Sci. Unit. States Am. 110, 9374–9379. https://doi.org/10.1073/pnas.1220228110.

Box, G.E.P., Cox, D.R., 1964. An analysis of transformations. J. Roy. Stat. Soc. 26, 211–252. https://doi.org/10.1111/j.2517-6161.1964.tb00553.x.

Breusch, T.S., Pagan, A.R., 1979. A simple test for heteroscedasticity and random coefficient variation. Econometrica 47, 1287–1294. https://doi.org/10.2307/1911963.

Cardoso-Silva, S., Ferreira, P.A.L., Moschini-Carlos, V., et al., 2015. Temporal and spatial accumulation of heavy metals in the sediments at Paiva Castro Reservoir (São Paulo, Brazil). Environ. Earth Sci. 75, 9. https://doi.org/10.1007/s12665-015-4828-2.

Chalcraft, D.R., Cox, S.B., Clarck, C., Cleland, E.E., Suding, K.N., Weiher, E., Pennington, D., 2008. Scale-dependent responses of plant biodiversity to nitrogen enrichment. Ecology 89, 2165–2171. https://doi.org/10.1890/07-0971.1.

Chase, J.M., 2010. Stochastic community assembly causes higher biodiversity in more productive environments. Science 328, 1388–1391. https://doi.org/10.1126/science.1187820.

Costa-Böddeker, S., Bennion, H., Jesus, T.A., et al., 2012. Paleolimnologically inferred eutrophication of a shallow, tropical, urban reservoir in southeast Brazil. J. Paleolimnol. 48, 751–766. https://doi.org/10.1007/s10933-012-9642-1.

Declerck, S., Vanderstukken, M., Pals, A., Muylaert, K., de Meester, L., 2007. Plankton biodiversity along a gradient of productivity and its mediation by macrophytes. Ecology 88, 2199–2210. https://doi.org/10.1890/07-0048.1.

Donohue, I., Jackson, A.L., Pusch, M.T., Irvine, K., 2009. Nutrient enrichment homogenizes lake benthic assemblages at local and regional scales. Ecology 90, 3470–3477. https://doi.org/10.1890/09-0415.1.

Dudgeon, D., Arthington, A.H., Gessner, M.O., et al., 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. Biol. Rev. 81, 163–182. https://doi.org/10.1017/S1464793105006950.

Faber, J., Quadros, A.F., Zimmer, M., 2018. A Space-For-Time approach to study the effects of increasing temperature on leaf litter decomposition under natural conditions. Soil Biol. Biochem. 123, 250–256. https://doi.org/10.1016/j.soilbio.2018.05.010.

Fontana, L., Albuquerque, A.L.S., Brenner, M., et al., 2014. The eutrophication history of a tropical water supply reservoir in Brazil. J. Paleolimnol. 51, 29–43. https://doi.org/10.1007/s10933-013-9753-3.

Gianuca, A.T., Declerck, S.A.J., Lemmens, P., de Meester, L., 2017. Effects of dispersal and environmental heterogeneity on the replacement and nestedness components of β-diversity. Ecology 98, 525–533. https://doi.org/10.1002/ecy.1666.

Gutiérrez-Cánovas, C., Millán, A., Velasco, J., Vaughan, I.P., Ormerod, S.J., 2013. Beta diversity along natural and anthropogenic stress gradients. Global Ecol. Biogeogr. 22, 796–805. https://doi.org/10.1111/geb.12060.

Hughes, A.R., Stachowicz, J.J., 2004. Genetic diversity enhances the resistance of a seagrass ecosystem to disturbance. Proc. Natl. Acad. Sci. Unit. States Am. 101, 8998–9002. https://doi.org/10.1073/pnas.0402642101.

Jamoneau, A., Passy, S.I., Soininen, J., Leboucher, T., Tison-Rosebery, J., 2017. Beta diversity of diatom species and ecological guilds: response to environmental and spatial mechanisms along the stream watercourse. Freshw. Biol. 63, 62–73. https://doi.org/10.1111/fwb.12980.

Karch, J., 2020. Improving on adjusted R-squared. Collabra: Psychology 6, 45. https://doi.org/10.1525/collabra.343.

Lamparelli, M.C., 2004. Grau de trofia em corpos d'água do estado de São Paulo: avaliação dos métodos de monitoramento. Dissertation, Universidade de São Paulo.

Leibold, M.A., Holyoak, M., Mouquet, N., et al., 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecol. Lett. 7, 601–613. https://doi.org/10.1111/j.1461-0248.2004.00608.x.

Lobo, E.A., Wetzel, C.E., Schuch, M., Ector, L., 2014. Diatomáceas epilíticas como indicadoras da qualidade da água em sistemas lóticos subtropicais e temperados. EDUNISC, Santa Cruz do Sul.

Lougheed, V.L., McIntosh, M.D., Parker, C.A., Stevenson, R.J., 2008. Wetland degradation leads to homogenization of the biota at local and landscape scales. Freshw. Biol. 53, 2402–2413. https://doi.org/10.1111/j.1365-2427.2008.02064.x.

McKinney, M.L., 2006. Urbanization as a major cause of biotic homogenization. Biol. Conserv. 127, 247–260. https://doi.org/10.1016/j.biocon.2005.09.005.

Menezes, R.F., Borchsenius, F., Svenning, J.C., et al., 2015. Homogenization of fish assemblages in different lake depth strata at local and regional scales. Freshw. Biol. 60, 745–757. https://doi.org/10.1111/fwb.12526.

Oksanen, J., Blanchet, F.G., Friendly, M., et al., 2019. Vegan: Community Ecology Package. R package version 2.5-6. https://CRAN.R-project.org/package=vegan.

Olden, J.D., 2006. Biotic homogenization: a new research agenda for conservation biogeography. J. Biogeogr. 33, 2027–2039. https://doi.org/10.1111/j.1365-2699.2006.01572.x.

Pappas, J.L., Stoermer, E.F., 1996. Quantitative method for determining a representative algal sample count. J. Phycol. 32, 393–696. https://doi.org/10.1111/j.0022-3646.1996.00693.x.

Petsch, D.K., 2016. Causes and consequences of biotic homogenization in freshwater ecosystems. Int. Rev. Hydrobiol. 101, 113–122. https://doi.org/10.1002/iroh.201601850.

R Core Team, 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Reid, A.J., Carlson, A.K., Creed, I.F., et al., 2018. Emerging threats and persistent conservation challenges for freshwater biodiversity. Biol. Rev. 94, 849–873. https://doi.org/10.1111/brv.12480.

Rodrigues, J.L.M., Pellizari, V.H., Mueller, R., et al., 2012. Conversion of the Amazon rainforest to agriculture results in biotic homogenization of soil bacterial communities. Proc. Natl. Acad. Sci. Unit. States Am. 110, 988–993. https://doi.org/10.1073/pnas.1220608110.

Sartory, D.P., Grobbelaar, J.E., 1984. Extraction of chlorophyll a from freshwater phytoplankton for spectrophotometric analysis. Hydrobiologia 114, 177–187. https://doi.org/10.1007/BF00031869.

Schwartz, M.W., Thorne, J.H., Viers, J.H., 2006. Biotic homogenization of the California flora in urban and urbanizing regions. Biol. Conserv. 127, 282–291. https://doi.org/10.1016/j.biocon.2005.05.017.

Smol, J.P., 2008. Pollution of Lakes and Rivers: a Paleoenvironmental Perspective, second ed. Blackwell Publishing, Oxford.

Solar, R.R.C., Barlow, J., Ferreira, J., et al., 2015. How pervasive is biotic homogenization in human-modified tropical forest landscapes? Ecol. Lett. 18, 1108–1118. https://doi.org/10.1111/ele.12494.

Svensson, J.R., Lindegarth, M., Siccha, M., et al., 2007. Maximum species richness at intermediate frequencies of disturbance: consistency among levels of productivity. Ecology 88, 830–838. https://doi.org/10.1890/06-0976.

Thomaz, S.M., Agostinho, A.A., Gomes, L.C., et al., 2012. Using space-for-time substitution and time sequence approaches in invasion ecology. Freshw. Biol. 57, 2401–2410. https://doi.org/10.1111/fwb.12005.

Thompson, R., Townsend, C., 2006. A truce with neutral theory: local deterministic factors, species traits and dispersal limitation together determine patterns of diversity in stream invertebrates. J. Anim. Ecol. 75, 476–484. https://doi.org/10.1111/j.1365-2656.2006.01068.x.

van Dam, H., Mertens, A., Sinkeldam, J., 1994. A coded checklist and ecological indicator values of freshwater diatoms from The Netherlands. Neth. J. Aquat. Ecol. 28, 117–133. https://doi.org/10.1007/BF02334251.

Verleyen, E., Vyverman, W., Sterken, M., et al., 2009. The importance of dispersal related and local factors in shaping the taxonomic structure of diatom metacommunities. Oikos 118, 1239–1249. https://doi.org/10.1111/j.1600-0706.2009.17575.x.

Vilar, A.G., van Dam, H., van Loon, E.E., Vonk, J.A., van Der Geest, H.G., Admiraal, W., 2014. Eutrophication decreases distance decay of similarity in diatom communities. Freshw. Biol. 59, 1522–1531. https://doi.org/10.1111/fwb.12363.

Virtanen, L., Soininen, J., 2012. The roles of environment and space in shaping stream diatom communities. Eur. J. Phycol. 47, 160–168. https://doi.org/10.1080/09670262.2012.682610.

Wang, R., Xu, M., Yang, H., et al., 2019. Ordered diatom species loss along a total phosphorus gradient in eutrophic lakes of the lower Yangtze River basin, China. Sci. Total Environ. 650, 1688–1695. https://doi.org/10.1016/j.scitotenv.2018.09.328.

Wengrat, S., Padial, A.A., Jeppesen, E., et al., 2018. Paleolimnological records reveal biotic homogenization driven by eutrophication in tropical reservoirs. J. Paleolimnol. 60, 299–309. https://doi.org/10.1007/s10933-017-9997-4.

Wengrat, S., Bennion, H., Ferreira, P.A.L., et al., 2019. Assessing the degree of ecological change and baselines for reservoirs: challenges and implications for management. J. Paleolimnol. 62, 337–357. https://doi.org/10.1007/s10933-019-00090-4.

Wetzel, C.E., Bicudo, D.C., Ector, L., et al., 2012. Distance decay of similarity in neotropical diatom communities. PloS One 7, 1–8. https://doi.org/10.1371/journal.pone.0045071.

Wogan, G.O.U., Wang, I.J., 2018. The value of space-for-time substitution for studying fine-scale microevolutionary processes. Ecography 41, 1456–1468. https://doi.org/10.1111/ecog.03235.

Xue, H., Zheng, B., Meng, F., Wang, Y., Zhang, L., Cheng, P., 2019. Assessment of aquatic ecosystem health of the wutong river based on benthic diatoms. Water 11, 727. https://doi.org/10.3390/w11040727.

Zorzal-Almeida, S., Bicudo, D.C., Lamparelli, M.C., Faustino, S.B., Ferragut, C., Bicudo, C. E.M., 2017b. Avaliação do Índice de Estado Trófico e sua aplicação na represa Guarapiranga em longa série temporal. In: Bicudo, C.E.M., Bicudo, D.C. (Eds.), 100 anos da represa Guarapiranga: lições e desafios. CRV, Curitiba, pp. 401–428.

Zorzal-Almeida, S., Bini, L.M., Bicudo, D.C., 2017a. Beta diversity of diatoms is driven by environmental heterogeneity, spatial extent and productivity. Hydrobiologia 800, 7–16. https://doi.org/10.1007/s10750-017-3117-3.

Zorzal-Almeida, S., Salim, A., Andrade, M.R.M., Nascimento, M.N., Bini, L.M., Bicudo, D. C., 2018. Effects of land use and spatial processes in water and surface sediment of tropical reservoirs at local and regional scales. Sci. Total Environ. 644, 237–246. https://doi.org/10.1016/j.scitotenv.2018.06.361.