



Eutrophication changes community composition and drives nestedness of benthic diatoms from coastal streams

A eutrofização altera a composição da comunidade e leva ao aninhamento de diatomáceas bentônicas em riachos costeiros

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Abstract: Aim: We evaluated changes in periphyton biomass and the composition of benthic diatom communities along a gradient of urbanization in 10 coastal streams located on the coastal plain of southernmost Brazil. **Methods:** At each coastal stream, we obtained limnological variables and periphytic material from the stolon of the aquatic macrophyte *Hydrocotyle ranunculoides* for further analyses of chlorophyll *a* and diatoms. **Results:** Total phosphorus was the only limnological variable selected by the statistical models, showing a positive relationship with periphyton biomass and a negative relationship with diatom species richness in these streams. Species composition (for both presence-absence and abundance data) was also explained by total phosphorus. Further, we observed a nested distribution of diatom species along the streams, in which poorer communities of streams with higher concentrations of phosphorus are subsets of richer communities from streams with lower concentrations of the nutrient. **Conclusions:** Our study shows that water quality modifications caused by eutrophication are leading to the loss of species and changes in the structure of biological communities in ecotones such as coastal streams.

Keywords: gradient of urbanization; washouts; lotic ecosystem; ecotones; Brazil.

Resumo: Objetivo: Avaliamos as mudanças na biomassa do perifíton e na composição das comunidades de diatomáceas bentônicas ao longo de um gradiente de urbanização em 10 riachos costeiros localizados na planície costeira do extremo sul do Brasil. **Métodos:** Em cada riacho coletamos variáveis limnológicas e o material perifítico do estolão da macrófita aquática *Hydrocotyle ranunculoides* para posterior análises de clorofila *a* e de diatomáceas. **Resultados:** Fósforo total foi a única variável limnológica selecionada pelos modelos, mostrando uma relação positiva com a biomassa e negativa com a riqueza de espécies de diatomáceas nesses riachos. A composição de espécies (para dados de presença e ausência e de abundância) também foi explicada pelas concentrações de fósforo total. Além disso, observamos uma distribuição aninhada de espécies ao longo dos riachos, de forma que as comunidades mais pobres de riachos com maiores concentrações de fósforo são subconjuntos de comunidades mais ricas com menores concentrações do nutriente. **Conclusões.** Evidenciamos em nosso estudo que as modificações na qualidade da água causadas pela eutrofização estão levando à perda de espécies e mudanças na estrutura de comunidades em ecótonos como os riachos costeiros.

Palavras-chave: gradiente de urbanização; sangradouros, ecossistema lótico, ecótonos, Brasil.



1. Introduction

Freshwater ecosystems are biodiversity hotspots, supporting more species per area than terrestrial ecosystems and accounting for approximately 10% of all known species (Strayer & Dudgeon, 2010). However, these ecosystems are also among the most threatened environments on the planet, presenting declines in biodiversity superior to terrestrial ecosystems (Sala et al., 2000; Strayer & Dudgeon, 2010), as a consequence of human-induced disturbances such as landscape modification for land use, the introduction of invasive species, damming of rivers, and water pollution by nutrient enrichment and other sources (Dudgeon et al., 2006; Vörösmarty et al., 2010; Petsch, 2016; Dudgeon, 2019). Given the threats faced by freshwater ecosystems, it is pivotal to better understand the effects of anthropogenic impacts on freshwater biota to enhance conservation strategies and ecosystem management policies (Vörösmarty et al., 2010; Jacobson et al., 2017).

Different phenomena are responsible for the degradation of streams in urban areas, which is commonly referred to as the “urban stream syndrome”. Among the main symptoms of streams draining urban areas are (i) changes in stream hydrology (Walsh et al., 2005; Grimm et al., 2008), as increased frequency of erosive and overland flow (Walsh et al., 2005); (ii) reduction of the diversity of aquatic species, which may result in biotic homogenization (e.g., Barnum et al., 2017); and (iii) anthropogenic eutrophication, which in urban areas occurs mainly due to disposal of domestic sewage (with high concentrations of nutrients) without proper treatment (Walsh et al., 2005; Tromboni & Dodds, 2017).

Anthropogenic eutrophication, resulting from excessive nutrient loading – mostly nitrogen and phosphorus – is among the most severe impacts threatening freshwater ecosystems around the world (Smith, 2003; Smith & Schindler, 2009; Dodds & Smith, 2016). Among its consequences are the increase in primary producer biomass and the occurrence of toxin-producing cyanobacterial blooms, resulting in the degradation of water conditions, reduction of species diversity, and changes in species composition (Smith & Schindler, 2009; Wojciechowski et al., 2017), with a predominance of generalist and tolerant species and local extinction of sensitive ones (Chen et al., 2016; Jacobson et al., 2017). If sensitive species are selectively removed along a eutrophication gradient and only tolerant species are able to

establish, a nested distribution pattern could be expected, in which communities with fewer species form a subset of richer communities (Patterson & Atmar, 1986; Baselga, 2010). This pattern can be explained by habitat quality and its abiotic characteristics, in addition to area and isolation (Wright et al., 1997). In fact, nestedness was already observed along gradients of anthropogenic impacts, such as presence of heavy metals in water (Gutiérrez-Cánovas et al., 2013), and experimental habitat homogenization (Schneck et al., 2011). Nutrient enrichment has also been described as a factor leading to nestedness of phytoplankton and zooplankton communities in experimental microcosms (Di Carvalho & Wickham, 2019), zooplankton in streams (Gutierrez et al., 2020), and diatoms in streams (Jamoneau et al., 2017) and reservoirs (Zorzal-Almeida et al., 2021).

The coastal plain of southernmost Brazil harbors several coastal streams (or washouts; *sangradouros* in Figueiredo & Calliari, 2006), that are considered marine-freshwater ecotones, essential for the establishment of freshwater, estuarine and marine biological communities (Figueiredo & Calliari, 2006; Bastos et al., 2013). These channels drain coastal lakes and wetlands through the foredunes arriving at the sea surf zone (Figueiredo & Calliari, 2006), being responsible for the transport of a considerable amount of organic matter, sediment, and nutrients from the continent to the marine environment (Baumgarten et al., 2007). Studies about *sangradouros* geology and genesis classify these ecosystems as (i) permanent, that are permanently connected to the sea; (ii) intermittent, that can occasionally lose connection with the sea and; (iii) ephemeral, which originated momentarily due to heavy rains and soon disappear (Pereira da Silva, 1998). Moreover, these ecosystems are strongly influenced by precipitation and evaporation (Figueiredo & Calliari, 2006). Studies about these ecosystems show that in urbanized areas they are mostly impacted by eutrophication (Albertoni & Palma-Silva, 2006; Baumgarten et al., 2007). However, there is a scarcity of studies on the effects of eutrophication gradients on these streams and their biodiversity.

In streams, benthic algae, especially diatoms, are among the most important primary producers and account for an important portion of species diversity (Biggs, 1996). Diatoms respond quickly to environmental changes and are commonly used in studies evaluating human-induced impacts on aquatic environments, such as those related to

urbanization (Jüttner et al., 2012; Chen et al., 2016; Mbao et al., 2020) and eutrophication (Hering et al., 2006; Vilmi et al., 2015; Licursi et al., 2016; Zorzal-Almeida et al., 2021). The composition of diatom communities usually presents substantial changes in response to eutrophication, resulting mostly from the dominance of some tolerant taxa (Chen et al., 2016; Xiao et al., 2018).

In this context, we aimed to evaluate the effects of eutrophication, as a consequence of a gradient of urbanization, on benthic algal biomass and diatom communities from coastal streams, important marine-freshwater ecotones. Specifically, we expected to find a reduction in diatom species richness and an alteration in diatom community composition along the eutrophication gradient, causing a nested pattern of species distribution.

2. Material and Methods

2.1. Study area

We sampled 10 coastal streams (intermittent and permanent ones) in the Coastal Plain of Rio Grande do Sul State, southern Brazil (Figure 1). The Coastal Plain of Rio Grande do Sul was formed in the Holocene from the deposition of sediments in events of marine transgressions and regressions, which formed a complex system of coastal lakes and wetlands (Schwarzbold & Schäfer, 1984). The

average annual temperature and precipitation of the region are 18 °C and 1200 mm, respectively (Cordazzo & Seeliger, 1995). The climate of the region is subtropical super-humid mesothermic (Vieira, 1983). The 10 coastal streams in which the samplings were carried are located in Cassino beach, Rio Grande (in the extreme south of Brazil), and are distributed along a remarkable urbanization gradient on 16.8 km of shore extension. Streams 1, 2, and 3 corresponded to a less urbanized area and consequently to less anthropogenic influence concerning sewage disposal. Streams 4 to 10 are located in an area of strong urban influence, although in regions with distinct degrees of urbanization. We sampled periphyton and obtained limnological variables on the same day in all streams (17 March 2016). In each stream, we selected a point with no shading near the foredunes and away from the sea surf zone.

2.2. Limnological variables

We obtained data on dissolved oxygen (DO), electrical conductivity (COND), pH, salinity (SAL), and total dissolved solids (TDS) using an *in-situ* Horiba U-50 multi-parameter probe. In addition, we sampled 500 ml of surface water at each stream for analyses of total nitrogen (TN; Allen et al., 1974) and total phosphorus (TP; Valderrama, 1981; Baumgarten et al., 1996).

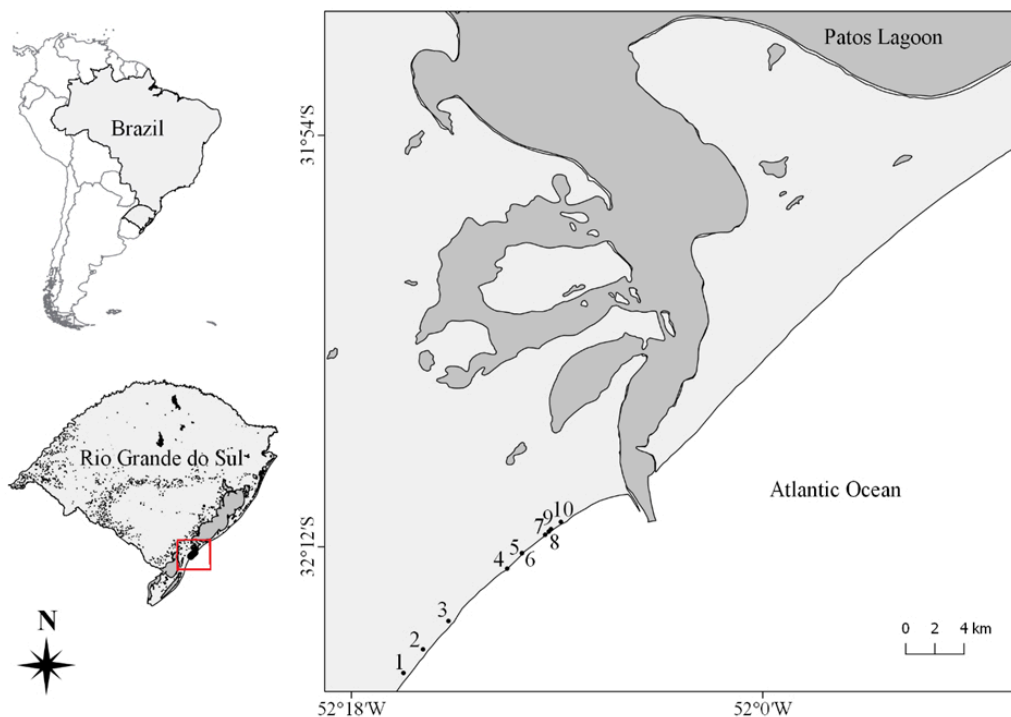


Figure 1. Location of the 10 studied coastal streams in the Coastal Plain of Rio Grande do Sul State, Brazil.

2.3. Sampling of benthic algae and diatom counts

We sampled the benthic material from stolons of the aquatic plant *Hydrocotyle ranunculoides* L f., an herb belonging to the Araliaceae family associated with the foredune streams (Souza & Lorenzi, 2008). This substrate was chosen because it was found in all streams. We scraped the stolons with a soft brush and washed them with distilled water. Three stolons of similar sizes were scraped to obtain material for chlorophyll-*a* analysis and other three for community analysis. Immediately after sampling, we preserved the material for diatom community analysis with 4% formalin. Chlorophyll-*a* concentrations were determined according to Mackinney (1941), adapted by Paranhos (1996) and Chorus & Bartram (1999). We measured the scraped area of the stolons (using a pachymeter) to obtain the concentration of chlorophyll-*a* per unit area as a measure of benthic algal biomass (in $\mu\text{g cm}^{-2}$). The aliquots reserved for the analyses of diatom communities were oxidized according to Simonsen (1974) adapted by Moreira-Filho & Valente-Moreira (1981). After this, we mounted permanent slides using Naphrax[®] (Brunel Microscopes Ltd., Chippenham, UK). To evaluate the species composition of the diatom communities we counted 300 valves from each stream using an optical microscope with a magnification of 1000 \times . All specimens were identified to the lowest possible taxonomic level, usually species, using specialized bibliography such Metzeltin et al. (2005), Metzeltin & García-Rodríguez (2012) and Round et al. (1990).

2.4. Data analyses

We calculated the Trophic State Index for each stream using total phosphorus, according to Lamparelli (2004). To assess sampling sufficiency, we constructed a species accumulation curve using the rarefaction method (accumulation of individuals). We used multiple linear regressions to evaluate the influence of limnological variables on chlorophyll-*a* and on diatom species richness. To produce a minimum adequate model for each response variable, we performed a manual selection by sequentially removing non-significant explanatory variables until only significant variables remained in the final model. Five explanatory variables were included in the regressions (pH, DO, SAL, TN, and TP), all of which have variance inflation factor (VIF) smaller than 4 (Zuur et al., 2009). Chlorophyll *a* was log-transformed to improve normality. Regression residuals meet the

assumptions of homogeneity of variance, normality, and independence.

To explore differences in the composition of diatom communities among the coastal streams, we performed Nonmetric Multidimensional Scaling (NMDS) analyses on presence-absence and logarithmically transformed abundance data using Sørensen and Bray-Curtis dissimilarity coefficients (Legendre & Legendre, 1998), respectively, followed by the adjustment of environmental variables (*envfit* function available in the R *vegan* package; Oksanen et al., 2017). We used Permutational Multivariate Analysis of Variance (PERMANOVA; Anderson, 2001) using the same dissimilarity coefficients described above and 999 permutations to verify which environmental variables influence the composition of communities. Finally, we used the Nestedness metric based on Overlap and Decreasing Fill (NODF; Almeida-Neto et al., 2008) to calculate nestedness. NODF values range from 0 to 100, with NODF = 100 representing perfectly nested communities. We calculated NODF only for rows (sites) since we aimed to test the occurrence of a nested pattern in species composition among streams. We generated two null models (with 999 permutations) to test the significance of the observed nestedness metric: 1) rows equiprobable and columns equiprobable (total number of species is preserved, but species richness and frequency of occurrence are not); 2) rows equiprobable and columns fixed (species frequencies are preserved, but site frequencies are not) (Wright et al., 1997; Gotelli, 2000; Jonsson, 2001). Spearman's coefficient was applied to evaluate the correlation between the TP concentrations and the nestedness order of the coastal streams. We ran all analyses in the R environment (R Core Team, 2017), using the packages *car* (Fox & Weisberg, 2011) and *vegan* (Oksanen et al., 2017).

3. Results

The coastal streams varied strongly in their limnological characteristics, mainly in relation to nutrients and dissolved oxygen (Table 1). The most striking gradient was of total phosphorus, so that the streams more distant from the urban area had six times lower concentrations of total phosphorus than the streams at the urbanized area (Table 1). Thus, the streams varied from mesotrophic to hypereutrophic environments.

We found 71 taxa of diatoms, ranging from 15 to 34 taxa per stream (Table 1). However, the species accumulation curve did not reach an asymptote

Table 1. Data obtained from 10 coastal streams on southernmost Brazil.

Coastal stream	Cond (mS cm ⁻¹)	DO (mg L ⁻¹)	TDS (g L ⁻¹)	Sal (‰)	TP (µg L ⁻¹)	TN (mg L ⁻¹)	Chl- <i>a</i> (µg cm ⁻²)	S	TS
S1	0.37	8.8	0.242	0.2	113.29	0.24	0.16	27	ME
S2	0.55	8.7	0.352	0.3	120.88	0.45	0.03	32	ME
S3	0.34	7.0	0.223	0.2	177.01	7.91	0.05	34	EU
S4	0.77	12.2	0.499	0.4	500.16	0.02	0.29	24	SU
S5	0.41	7.1	0.254	0.2	506.22	0.13	0.20	26	SU
S6	0.79	2.5	0.508	0.4	621.52	0.89	0.31	26	SU
S7	1.03	6.0	0.659	0.5	591.18	0.20	0.13	22	SU
S8	0.87	5.3	0.559	0.4	685.24	2.34	0.44	15	HY
S9	0.22	12.7	0.137	0.1	255.90	0.05	0.06	27	EU
S10	0.74	6.3	0.474	0.4	430.37	1.67	0.18	31	SU

Cond = electrical conductivity; DO = dissolved oxygen; TDS = total dissolved solids; Sal = salinity; TP = total phosphorus; TN = total nitrogen; Chl-*a* = periphyton chlorophyll *a*; S = diatom species richness; TS = trophic state; ME = mesotrophic; EU = eutrophic; SU = supereutrophic; HY = hypereutrophic.

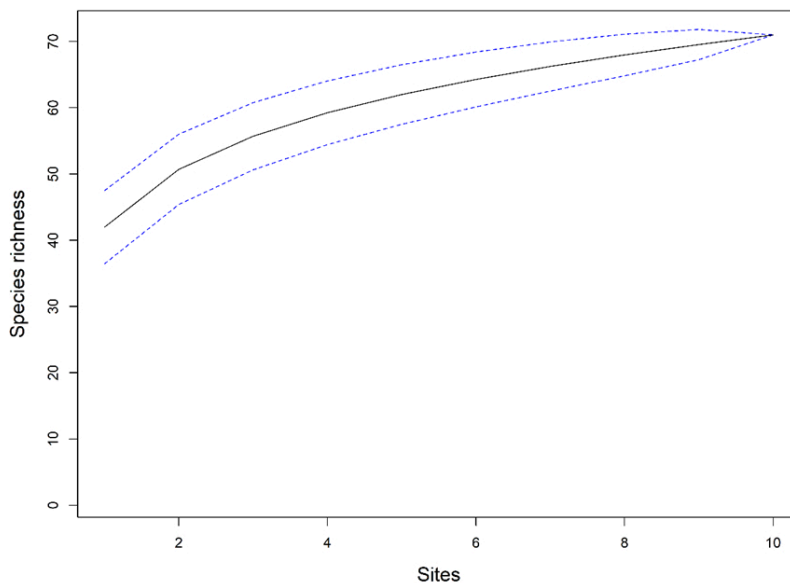


Figure 2. Diatom's species accumulation curve constructed by using the rarefaction method (black line with 95% confidence interval).

(Figure 2), indicating that species richness should be even greater. The more abundant species was *Nitzschia palea*, followed by *Gomphonema parvulum* and *Nitzschia amphibia* (Table 2). These species dominated in eutrophic streams, whereas species such as *Capartogramma crucicola*, *Cocconeis placentula*, and *Nupela* sp1 were commonly found in streams away from urban areas (streams 1, 2, and 3; Table 2).

Benthic algal biomass measured as chlorophyll-*a* and diatom species richness were explained only by total phosphorus concentrations. Whereas chlorophyll-*a* presented a positive relationship with total phosphorus ($P = 0.006$; adjusted $R^2 = 0.58$; Figure 3a), diatom species richness presented a

negative relationship with it ($P = 0.013$; adjusted $R^2 = 0.50$; Figure 3b).

We also found a significant nested pattern among diatom communities ($\text{NODF}_{\text{FOVS}} = 59.16$; $P = 0.001$ for null model 1; $P = 0.035$ for null model 2; Figure 4). The nestedness of diatom communities strongly correlated with total phosphorus ($\rho = -0.83$; $P = 0.005$), such that communities in streams with higher phosphorus concentrations were nested subsets of communities in streams with lower concentrations.

Finally, the streams presented distinct communities along the eutrophication gradient for both presence-absence (Figure 5A) and abundance (Figure 5B) data. Corroborating this result,

Table 2. List of diatom taxa found in 10 coastal streams on southernmost Brazil, indicating the relative abundance of each species and the streams where each species occurred.

Taxa	Abbreviation	Abundance (%)	Stream
<i>Achnantheidium minutissimum</i> (Kützing)	sp.1	0.03	2
<i>Achnantheidium reimeri</i> (Camburn)	sp.2	0.03	10
<i>Amphora copulata</i> (Kützing)	sp.3	0.57	3,4,5,10
<i>Anomoeoneis sphaerophora</i> (Kützing) Pfitzer	sp.4	0.47	1,3,8,9
<i>Aulacoseira ambigua</i> (Grunow) Simonsen	sp.5	0.03	6
<i>Capatogramma crucicola</i> (Grunow ex Cleve) Ross	sp.6	0.57	1,3
<i>Cocconeis placentula</i> (Ehrenberg)	sp.7	1.63	1,2,3,10
<i>Cyclotella meneghiniana</i> (Kützing)	sp.8	5.33	1,2,3,4,6,7,8,9, 10
<i>Diadesmis confervaceae</i> (Kützing)	sp.9	1.80	1,2,4,5,9,10
<i>Diploneis crabro</i> (Ehrenberg) Ehrenberg	sp.10	0.03	7
<i>Diploneis subovalis</i> (Cleve)	sp.11	0.20	4,8,10
<i>Discostella stelligera</i> (Cleve & Grunow) Houk & Klee	sp.12	0.10	4
<i>Encyonema neomesianum</i> (Krammer)	sp.13	0.60	1,2,4,10
<i>Eunotia bidens</i> (Ehrenberg)	sp.14	0.03	10
<i>Eunotia bilunaris</i> (Ehrenberg) Schaarschmidt	sp.15	1.03	2,3,4,5,9,10
<i>Eunotia</i> sp. 1	sp.16	0.23	1,3
<i>Eunotia</i> sp. 2	sp.17	0.07	1,3
<i>Eunotogramma</i> sp. 1	sp.18	0.03	3
<i>Fallacia meridionalis</i> (Metzeltin, Lange-Bertalot & García Rodríguez)	sp.19	1.10	5,6,7
<i>Frustulia crassinervia</i> (Brébisson ex W. Smith) Lange-Bertalot & Krammer	sp.20	0.13	4,10
<i>Gogorevia</i> sp.	sp.32	0.40	1,2,3
<i>Gomphonema acuminatum</i> (Ehrenberg)	sp.21	0.47	1,2,3
<i>Gomphonema gracile</i> (Ehrenberg)	sp.22	5.76	1,2,3,4,5,7,8,9, 10
<i>Gomphonema lagenula</i> (Kützing)	sp.23	2.03	2,3,5,6,8,9,10
<i>Gomphonema laticollum</i> (Reichardt)	sp.24	2.30	2,3,4,10
<i>Gomphonema parvulum</i> (Kützing) Kützing	sp.25	12.25	1,2,3,4,5,6,7,8, 9, 10
<i>Gomphonema turris</i> (Ehrenberg)	sp.26	0.07	5
<i>Gomphonema</i> sp. 1	sp.27	0.07	2
<i>Gyrosigma acuminatum</i> (Kützing) Rabenhorst	sp.28	2.06	1,2,6,7
<i>Gyrosigma scalproides</i> (Rebenhorst) Cleve	sp.29	0.03	9
<i>Hippodonta hungarica</i> (Grunow) Lange-Bertalot, Metzeltin & Witkowski	sp.30	0.60	1,3,5,6,9,10
<i>Lemnicola hungarica</i> (Grunow) Round & Basson	sp.31	0.57	1,2,5,6,10
<i>Navicula longicephala</i> (Hustedt)	sp.33	0.20	5,6
<i>Navicula recens</i> (Lange-Bertalot) Lange-Bertalot	sp.34	2.76	1,2,3,4,5,6,7,8, 9,10
<i>Navicula riediana</i> (Lange-Bertalot & Rumrich)	sp.35	0.83	2,3,7,9
<i>Navicula subrhynchocephala</i> (Hustedt)	sp.36	4.70	1,2,3,4,5,6,7,8, 9, 10
<i>Navicula</i> sp. 1	sp.37	0.80	2,6,7,9
<i>Navicula</i> sp. 2	sp.38	1.57	1,2,3,4,5,6,7,8,9
<i>Navicula</i> sp. 3	sp.39	0.17	1,3,5
<i>Navicula</i> sp. 4	sp.40	0.03	6
<i>Nupela</i> sp. 1	sp.41	0.10	1,2
<i>Nitzschia amphibia</i> (Grunow)	sp.42	7.09	2,3,4,5,6,7,8,9, 10
<i>Nitzschia acicularioides</i> (Kützing)	sp.43	0.03	9
<i>Nitzschia dissipata</i> (Kützing) Rabenhorst	sp.44	5.19	2,3,5,6,7,8,9,10
<i>Nitzschia inconspicua</i> (Grunow)	sp.45	0.70	3,5,6,7,8,9
<i>Nitzschia palea</i> (Kützing) W. Smith	sp.46	21.38	1,2,3,4,5,6,7,8, 9,10
<i>Nitzschia</i> sp. 1	sp.47	1.23	5,8,9,10
<i>Nitzschia</i> sp. 2	sp.48	0.17	6,9
<i>Nitzschia</i> sp. 3	sp.49	0.20	3,5
<i>Pinnularia acrosphaeria</i> (Smith)	sp.50	0.17	1,7
<i>Pinnularia gibba</i> (Ehrenberg) Ehrenberg	sp.51	0.13	7,10

Table 2. Continued...

Taxa	Abbreviation	Abundance (%)	Stream
<i>Placoneis uruguayensis</i> (Metzeltin, Lange-Bertalot & García Rodríguez)	sp.52	0.07	6,10
<i>Placoneis</i> sp. 1	sp.53	0.40	1,2,6,9
<i>Placoneis</i> sp. 2	sp.54	0.03	6
<i>Placoneis</i> sp. 3	sp.55	0.07	6,10
<i>Placoneis</i> sp. 4	sp.56	0.03	5
<i>Placoneis</i> sp. 5	sp.57	0.03	3
<i>Planothidium delicatulum</i> (Kützing) Round & Bukhtivarova	sp.58	1.50	2,4,6,7,9,10
<i>Planothidium</i> sp. 1	sp.59	0.03	2
<i>Psammothidium subatomoides</i> (Hustedt) Bukhtivarova & Round	sp.60	0.57	1,2,3,5,9
<i>Pseudostaurosira brevistriata</i> (Grunow) D.M Williams & Round	sp.61	0.27	2,3,7
<i>Pseudostaurosira trainorii</i> (Morales)	sp.62	1.50	3,4,10
<i>Pseudostaurosira</i> sp. 1	sp.63	0.10	3,4
<i>Pseudostaurosira</i> sp. 2	sp.64	0.13	4,10
<i>Rhopalodia gibberula</i> (Ehrenberg) Otto Muller	sp.65	0.57	2,3,5, 7,9,10
<i>Sellaphora pupula</i> (Kützing) Mereschkovsky	sp.66	0.37	1,2,4,5,7,9,10
<i>Sellaphora</i> sp. 1	sp.67	0.17	1,6
<i>Staurophora</i> sp. 1	sp.68	0.03	8
<i>Staurosira construens</i> (Ehrenberg)	sp.69	0.30	3,4
<i>Staurosirella pinnata</i> (Ehrenberg) D.M. Williams & Round	sp.70	1.27	4
<i>Ulnaria ulna</i> (Nizsch)	sp.71	4.50	1,2,3,4,5,6,7,9,10

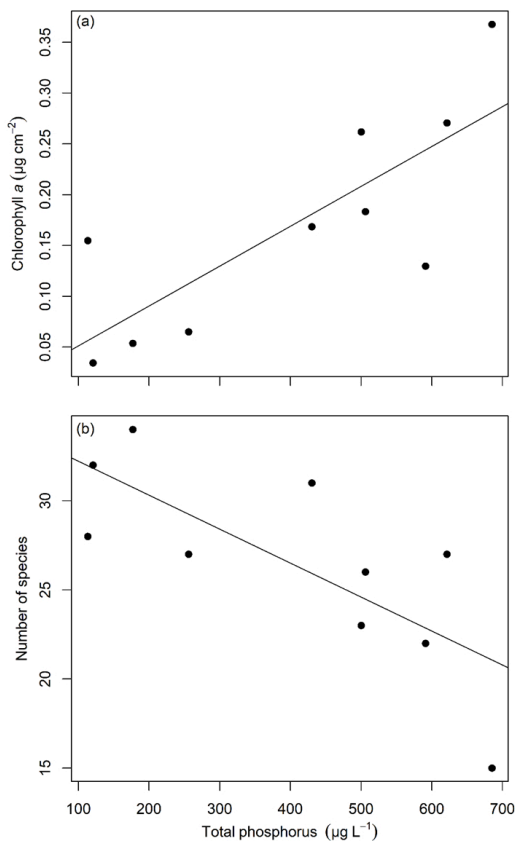


Figure 3. (a) Periphytic biomass represented by chlorophyll-*a* and (b) species richness of diatoms in relation to the concentrations of total phosphorus in the sampled coastal streams.

PERMANOVA analyses showed that differences in species composition among streams are explained by salinity (presence-absence: $R^2 = 0.17$, $P = 0.013$; abundance: $R^2 = 0.16$, $P = 0.025$), pH (presence-absence: $R^2 = 0.20$, $P = 0.001$; abundance: $R^2 = 0.20$, $P = 0.002$) and total phosphorus (presence-absence: $R^2 = 0.16$, $P = 0.014$; abundance: $R^2 = 0.15$, $P = 0.021$).

4. Discussion

In adequate concentrations, nitrogen and phosphorus are essential for the health of aquatic ecosystems (Søndergaard et al., 2017). However, at high levels, these nutrients can have negative effects on water quality, resulting in a eutrophication process (Søndergaard et al., 2017). Eutrophication is among the main causes of species losses and changes in the composition of aquatic communities worldwide (Allan & Flecker, 1993; Strayer & Dudgeon, 2010). Those changes affect ecosystem functioning by changing, for example, the quality and quantity of primary consumer food sources and the decomposition of detritus (Dodds & Smith, 2016). Our results showed that eutrophication increased benthic algal biomass in the studied marine-freshwater ecotones, but reduced diatom species richness and changed community composition by selectively removing



Figure 4. Nestedness order of the composition of diatom communities among the 10 coastal streams in southernmost Brazil. Black lines indicate species occurrence, line numbers indicate the streams, column numbers indicate species (respective species names are in Table 2).

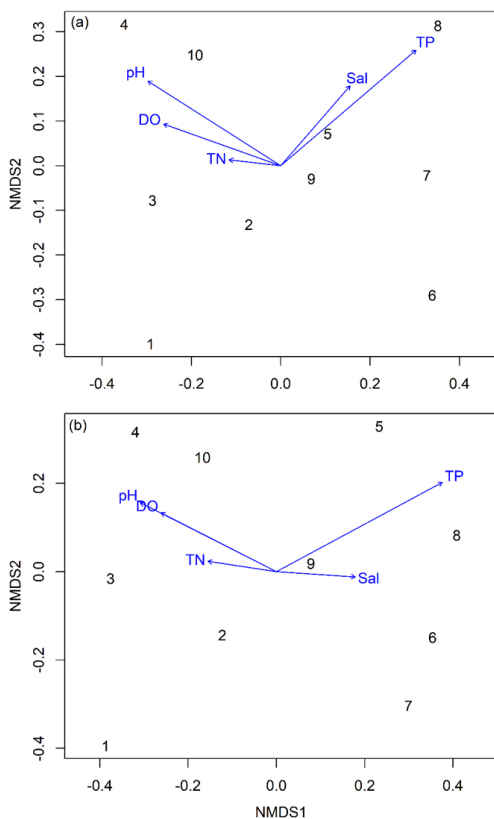


Figure 5. NMDS of benthic diatom communities using (a) presence-absence data and (b) abundance data. The numbers represent the 10 sampled streams; DO = dissolved oxygen; TN = total nitrogen; TP = total phosphorus; pH = potential of hydrogen; Sal = salinity.

less tolerant species, as indicated by the observed nested distribution.

Studies in urban freshwater ecosystems have increased in the last decades (Grimm et al., 2000),

mainly after the elaboration of the urban stream syndrome concept (Walsh et al., 2005). Our results are in accordance with this concept since we found that streams within urban areas are more prone to eutrophication, which leads to lower species richness than in streams less influenced by urbanization. The excessive increase of nutrients due to urbanization has already been shown to occur in other Brazilian regions (Tromboni & Dodds, 2017), as well as the negative impacts generated by sewage from urban areas for the biodiversity in several regions of the world (Barnum et al., 2017; Cunningham & Gharipour, 2018).

In flowing waters, both phosphorus and nitrogen are recognized as playing important roles in the eutrophication process (Dodds & Smith, 2016), despite phosphorus being usually considered the most important limiting nutrient in freshwater environments and thus, the main responsible for eutrophication (Hecky & Kilham, 1988; Schindler, 2012). Empirical evidence shows that stream benthic algal communities strongly respond to both nitrogen and phosphorus (Dodds & Smith, 2016). However, in our study, only total phosphorus (in addition to pH and salinity) explained the observed changes.

The observed decrease in species richness contradicts part of the literature on nutrient enrichment. For instance, in a meta-analysis, Hillebrand et al. (2007) found that species richness of primary producers increases with nutrient enrichment in freshwater ecosystems, results corroborated by Schneider et al. (2013) and Soininen et al. (2016) for stream benthic diatoms. However, our study sites presented high

levels of nutrient concentrations, such that the minimum total phosphorus values we found equal the maximum values from Schneider et al. (2013), which, in turn, are 6-fold smaller than the maximum phosphorus concentration found in our study. Thus, the reduction in diatom species richness and the nested distribution of communities related to the gradient of phosphorus concentrations among the studied streams suggest that the high levels of eutrophication resulted in harsh environmental conditions in which only a subset of generalist and eutrophic-tolerant species from the regional species pool were able to persist (Goldenberg Vilar et al., 2014). On the other hand, the less eutrophic streams harbored both sensitive and generalist/tolerant species, resulting in higher species richness than in eutrophic streams. For example, *Gomphonema parvulum* and different species of the genus *Nitzschia* are widely known to be tolerant to and indicators of anthropogenic eutrophication in lotic environments (Bere & Tundisi, 2010; Bere & Tundisi, 2011; Moresco et al., 2015). These species occurred in all streams, but were more abundant in those streams with the highest concentrations of phosphorus. In contrast, species such as *Capartogramma crucicola* and *Cocconeis placentula*, considered to have a low tolerance to eutrophication (e.g., Silva-Benavides, 1996; Lobo et al., 2004; Salomoni et al., 2006), occurred more frequently in the streams with low nutrient concentrations in our study. Moreover, we identified one species of the genus *Nupela* in streams 1 and 2 (with the lowest phosphorus concentrations) and several authors emphasize the preference of this genus of oligotrophic environments (Wojtal, 2009) or with moderated nutrient concentrations (Potapova et al., 2003).

Further, the observed changes in the species composition of benthic diatom communities along the eutrophication gradient is an expected result, since this group is known for rapidly responding to changes in physical and chemical characteristics of water (Hering et al., 2006; Jyrkänkallio-Mikkola et al., 2017). In addition to phosphorus, pH and salinity also affected the organization of communities in the studied streams. These two variables were probably important because of the characteristics of the studied ecosystems. Many of the coastal streams in the study region are formed in lakes and wetlands located behind the foredunes (Figueiredo & Calliari, 2005), thus being responsible for the drainage of these systems and of pluvial waters towards the sea, carrying

a considerable amount of organic matter and sediment (Figueiredo & Calliari, 2005, 2006). Moreover, these streams are constantly affected by seawater, increasing their salinity.

One main caveat of our study is that it was based on only one sampling at each coastal stream. This snapshot sampling did not capture seasonal changes in the nutrient loads of the streams, related either to variation in rainfall or to variation on the discharge of sewage. The latter is mostly related to the increased population during austral summer since this neighborhood attracts thousands of tourists every year (Silva, 2012). Further, during summer, the high evaporation rates reduce the volume and the number of these streams (Figueiredo & Calliari, 2006). Thus, despite the snapshot sampling and the reduced dataset, our sampling at the beginning of March was able to capture the synergistic effects of reduced water volume and increased nutrient inputs in the streams.

It is known that the science of eutrophication in lotic environments is not as advanced as in lentic environments (Dodds & Smith, 2016), especially when considering these coastal freshwater-marine ecotones. Therefore, we showed in this study the importance of such environments to biological diversity, as shown by the elevated number of diatom species found. We also found that modifications in water quality caused by eutrophication due to the urbanization process are leading to the local loss of species and changes in the composition of biological communities. It is fundamental that more studies on these coastal ecotones evaluate their biodiversity and how anthropogenic impacts are affecting their functioning.

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References

- Albertoni, E.F., & Palma-Silva, C., 2006. Macroinvertebrados associados a macrófitas aquáticas flutuantes em canais urbanos de escoamento pluvial (Balneário Cassino, Rio Grande, RS). *Neotrop. Biol. Conserv.* 1(2), 90-100.

- Allan, J.D., & Flecker, A.S., 1993. Biodiversity conservation in running waters: identifying the major factors that threaten destruction of riverine species and ecosystems. *Bioscience* 43(1), 32-43. <http://dx.doi.org/10.2307/1312104>.
- Allen, S., Grimsha, W.N., Parkinson, J.A., & Quarmby, C., 1974. *Chemical analysis of ecological materials*. London: Blackwell Scientific Publishers.
- Almeida-Neto, M., Guimarães, P., Guimarães Junior, P.R., Loyola, R.D., & Ulrich, W., 2008. A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos* 117(8), 1227-1239. <http://dx.doi.org/10.1111/j.0030-1299.2008.16644.x>.
- Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecol.* 26, 32-46. <https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x>.
- Barnum, T.R., Weller, D.E., & Williams, M., 2017. Urbanization reduces and homogenizes traits diversity in stream macroinvertebrate communities. *Ecol. Appl.* 27(8), 2428-2442. PMID:28872731. <http://dx.doi.org/10.1002/eap.1619>.
- Baselga, A., 2010. Partitioning the turnover and nestedness components of beta diversity. *Glob. Ecol. Biogeogr.* 19(1), 134-143. <http://dx.doi.org/10.1111/j.1466-8238.2009.00490.x>.
- Bastos, R.F., Condini, M.V., & Garcia, A.M., 2013. Fish species list of coastal streams in Southern Brazil, with notes on austral distribution limits of marine and freshwater endangered species. *Pan-Am. J. Aquat. Sci.* 8, 347-351.
- Baumgarten, M.G.Z., Millão, D., Costa, P.G., Attisano, K.K., Costa, N.B.D., Gutierrez, F.B., Giordano, S.B., & Araújo, E.A.C., 2007. Praia do Cassino (Rio Grande -RS): qualidade da água dos sangradouros da área central – antes (2003) e depois (2005) da instalação de estação de tratamento de esgotos (ETE). *Cad Ecol Aquat* 2, 1-12.
- Baumgarten, M.G.Z., Rocha, J.M.B., & Niencheski, L.F.H., 1996. *Manual de análises em oceanografia química*. Rio Grande: Editora da FURG.
- Bere, T., & Tundisi, J.G., 2010. Epipsammic diatoms in streams influenced by urban pollution, São Carlos, SP, Brazil. *Braz. J. Biol.* 70(4), 921-930. PMID:21180895. <http://dx.doi.org/10.1590/S1519-69842010000500002>.
- Bere, T., & Tundisi, J.G., 2011. Diatom-based water quality assessment in streams influence by urban pollution: effects of natural and two selected artificial substrates, São Carlos-SP, Brazil. *Braz. J. Aquat. Sci. Tech.* 15(1), 54-63. <http://dx.doi.org/10.14210/bjast.v15n1.p54-63>.
- Biggs, B.J.F., 1996. Patterns in benthic algae of streams. In: Stevenson, J., Bothwell, M.L. & Lowe, R.L., eds. *Algal ecology: freshwater benthic ecosystems*. San Diego: Elsevier. <http://dx.doi.org/10.1016/B978-012668450-6/50031-X>.
- Chen, X., Zhou, W., Pickett, S.T.A., Li, W., Han, L., & Ren, Y., 2016. Diatoms are better indicators of urban stream conditions: a case study in Beijing, China. *Ecol. Indic.* 60, 265-274. <http://dx.doi.org/10.1016/j.ecolind.2015.06.039>.
- Chorus, I., & Bartram, J., 1999. *Water Resources*. In Chorus, I. & Bartram, J., eds. *Toxic cyanobacteria in water: a guide to their public health consequences, monitoring and management*. New York: E & FN Spon. <http://dx.doi.org/10.4324/9780203478073>.
- Cordazzo, V.C., & Seeliger, U., 1995. *Guia Ilustrado da vegetação Costeira no Extremo Sul do Brasil*. Rio Grande: Editora da FURG.
- Cunningham, C., & Gharipour, M., 2018. Pipe dreams: urban wastewater treatment for biodiversity conservation. *Urban Sci.* 2(1), 2-18. <http://dx.doi.org/10.3390/urbansci2010010>.
- Di Carvalho, J.A., & Wickham, S.A., 2019. Simulating eutrophication in a metacommunity landscape: an aquatic model ecosystem. *Oecologia* 189(2), 461-474. PMID:30523402. <http://dx.doi.org/10.1007/s00442-018-4319-8>.
- Dodds, W.K., & Smith, V.H., 2016. Nitrogen, phosphorus and eutrophication in streams. *Inland Waters* 6(2), 155-164. <http://dx.doi.org/10.5268/IW-6.2.909>.
- Dudgeon, D., 2019. Multiple threats imperil freshwater biodiversity in the Anthropocene. *Curr. Biol.* 29(19), 960-967. PMID:31593677. <http://dx.doi.org/10.1016/j.cub.2019.08.002>.
- Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.-I., Knowler, D.J., Lévêque, C., Naiman, R.J., Prieur-Richard, A.H., Soto, D., Stiassny, M.L.J., & Sullivan, C.A., 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. *Biol. Rev. Camb. Philos. Soc.* 81(2), 163-182. PMID:16336747. <http://dx.doi.org/10.1017/S1464793105006950>.
- Figueiredo, S.A., & Calliari, L.J., 2005. Sangradouros: distribuição espacial, variação sazonal, padrões morfológicos e implicações no gerenciamento costeiro. *Gravel* 3, 45-57.
- Figueiredo, S.A., & Calliari, L.J., 2006. Washouts in the central and northern litoral of Rio Grande do Sul state, Brazil: distribution and implications. *J. Coast. Res.* 39, 366-370.
- Fox, J., & Weisberg, S., 2011. *An {R} Companion to Applied Regression*. 2nd ed. Thousand Oaks: Sage.
- Goldenberg Vilar, A.G., Van Dam, H., Van Loon, E.E., Vonk, J.A., Van Der Geest, H.G., & Admiraal, W., 2014. Eutrophication decrease distance decay of similarity in diatom communities. *Freshw. Biol.* 59(7), 1522-1531. <http://dx.doi.org/10.1111/fwb.12363>.

- Gotelli, N.J., 2000. Null model analysis of species co-occurrence patterns. *Ecology* 81(9), 2606-2621. [http://dx.doi.org/10.1890/0012-9658\(2000\)081\[2606:NMAOSC\]2.0.CO;2](http://dx.doi.org/10.1890/0012-9658(2000)081[2606:NMAOSC]2.0.CO;2).
- Grimm, N.B., Faeth, S.H., Golubiewski, N.E., Redman, C.L., Wu, J., Bai, W., & Briggs, J.M., 2008. Global change and the ecology of cities. *Science* 319(5864), 756-760. PMID:18258902. <http://dx.doi.org/10.1126/science.1150195>.
- Grimm, N.B., Morgan Grove, J., Pickett, S.T.A., & Redman, C.L., 2000. Integrated approaches to long-term studies of urban ecological systems. *Bioscience* 50(7), 571-584. [http://dx.doi.org/10.1641/0006-3568\(2000\)050\[0571:IATLTO\]2.0.CO;2](http://dx.doi.org/10.1641/0006-3568(2000)050[0571:IATLTO]2.0.CO;2).
- Gutierrez, M.F., Simões, N.R., Frau, D., Saigo, M., & Licursi, M., 2020. Responses of stream zooplankton diversity metrics to eutrophication and temporal environmental variability in agricultural catchments. *Environ. Monit. Assess.* 192(12), 1-17. PMID:33242179. <http://dx.doi.org/10.1007/s10661-020-08766-5>.
- Gutiérrez-Cánovas, C., Millán, A., Velasco, J., Vaughan, I.P., & Ormerod, S.J., 2013. Contrasting effects of natural and anthropogenic stressors on beta diversity in river organisms. *Glob. Ecol. Biogeogr.* 22(7), 796-805. <http://dx.doi.org/10.1111/gcb.12060>.
- Hecky, R.E., & Kilham, P., 1988. Nutrient limitation of phytoplankton in freshwater and marine environments: a review of recent evidence on the effects of enrichment. *Limnol. Oceanogr.* 33(4 Pt 2), 796-822. <http://dx.doi.org/10.4319/lo.1988.33.4part2.0796>.
- Hering, D., Johnson, R.K., Kramm, S., Schmutz, S., Szoszkiewicz, K., & Verdonschot, P.F.M., 2006. Assessment of European streams with diatoms, macrophytes, macroinvertebrates and fishes: a comparative metric-based analysis of organism response to stress. *Freshw. Biol.* 51(9), 1757-1785. <http://dx.doi.org/10.1111/j.1365-2427.2006.01610.x>.
- Hillebrand, H., Gruner, D.S., Borer, E.T., Bracken, M.E., Cleland, E.E., Elser, J.J., Harpole, W.S., Ngai, J.T., Seabloom, E.W., Shurin, J.B., & Smith, J.E., 2007. Consumer versus resource control of producer diversity depends on ecosystem type and producer community structure. *Proc. Natl. Acad. Sci. USA* 104(26), 10904-10909. PMID:17581875. <http://dx.doi.org/10.1073/pnas.0701918104>.
- Jacobson, P.C., Hansen, G.J.A., Bethke, B.J., & Cross, T.K., 2017. Disentangling the effects of a century of eutrophication and climatic warming on freshwater lake fish assemblages. *PLoS One* 12(8), e0182667. PMID:28777816. <http://dx.doi.org/10.1371/journal.pone.0182667>.
- Jamoneau, A., Passy, S.I., Soininen, J., Lebourcier, T., & Tison-Rosebery, J., 2017. Beta diversity of diatoms species and ecological guilds: response to environmental and spatial mechanisms along the stream watercourse. *Freshw. Biol.* 63(1), 62-73. <http://dx.doi.org/10.1111/fwb.12980>.
- Jonsson, B.G., 2001. A null model for randomization tests of nestedness in species assemblages. *Oecologia* 127(3), 309-313. PMID:28547100. <http://dx.doi.org/10.1007/s004420000601>.
- Jüttner, I., Chimonides, P.J., & Ormerod, S.J., 2012. Developing a diatom monitoring network in an urban river-basin: initial assessment and site selection. *Hydrobiologia* 695(1), 137-151. <http://dx.doi.org/10.1007/s10750-012-1123-z>.
- Jyrkänkallio-Mikkola, J., Meier, S., Heino, J., Laamanen, T., Pajunen, V., Tolonen, K.T., Tolkkinen, M., & Soininen, J., 2017. Disentangling multi-scale environmental effects on stream microbial communities. *J. Biogeogr.* 44(7), 1512-1523. <http://dx.doi.org/10.1111/jbi.13002>.
- Lamparelli, M.C., 2004. Graus de trofia em corpos d'água do Estado de São Paulo: avaliação dos métodos de monitoramento [Tese de doutorado em Ciências]. São Paulo: Departamento de Ecologia, Universidade de São Paulo.
- Legendre, P., & Legendre, L., 1998. *Numerical ecology*. Amsterdam: Elsevier.
- Licursi, M., Gómez, N., & Sabater, S., 2016. Effects of nutrient enrichment on epipellic diatom assemblages in a nutrient-rich lowland stream, Pampa region, Argentina. *Hydrobiologia* 766(1), 135-150. <http://dx.doi.org/10.1007/s10750-015-2450-7>.
- Lobo, E.A., Callegaro, V.L.M., Hermany, G., Bes, D., Wetzel, C.E., & Oliveira, C.A., 2004. Use of epilithic diatoms as bioindicators from lotic systems in Southern Brazil, with special emphasis on eutrophication. *Acta Limnol. Bras.* 16(1), 25-40.
- Mackinney, G., 1941. Absorption of light by chlorophyll solutions. *J. Biol. Chem.* 140(2), 315-322. [http://dx.doi.org/10.1016/S0021-9258\(18\)51320-X](http://dx.doi.org/10.1016/S0021-9258(18)51320-X).
- Mbao, E.O., Gao, J., Wang, Y., Sitoki, L., Pan, Y., & Wang, B., 2020. Sensitivity and reliability of diatom metrics and guilds in detecting the impact of urbanization on streams. *Ecol. Indic.* 116, 106506. <http://dx.doi.org/10.1016/j.ecolind.2020.106506>.
- Metzeltin, D., & García-Rodríguez, F., 2012. *Las Diatomeas Uruguayas*. Montevideo: DIRAC.
- Metzeltin, D., Lange-Bertalot, H., & García-Rodríguez, F., 2005. *Diatoms of Uruguay – Taxonomy Biogeography, Diversity*. Königstein: A.R.G. Gantner Verlag.
- Moreira-Filho, H., & Valente-Moreira, I.M., 1981. Avaliação taxonômica e ecológica das diatomáceas (Bacillariophyceae) epífitas em algas pluricelulares obtidas nos litorais nos estados do Paraná, Santa Catarina e São Paulo. *Bol Mus Mun* 47, 1-17.
- Moresco, C., Gubiani, E.A., & Rodrigues, L., 2015. Periphytic diatoms as indicators in a tropical stream:

- from urban to rural environments. *Acta Sci. Biol. Sci.* 37(4), 427-437. <http://dx.doi.org/10.4025/actascibiols.v37i4.27426>.
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., & Wagner, H., 2017. *vegan: Community Ecology Package*. R Package version 2.4-3 [online]. Retrieved in 2022, January 4, from <http://CRAN.R-project.org/package=vegan>
- Paranhos, R., 1996. *Alguns métodos para análise de água*. Rio de Janeiro: UFRJ. Cadernos Didáticos.
- Patterson, B.D., & Atmar, W., 1986. Nested subsets and the structure of insular mammalian and archipelagos. *Biol. J. Linn. Soc. Lond.* 28(1-2), 65-82. <http://dx.doi.org/10.1111/j.1095-8312.1986.tb01749.x>.
- Pereira da Silva, R., 1998. Ocorrência, distribuição e características morfodinâmicas dos sangradouros na zona costeira do Rio Grande do Sul: trecho Rio Grande – Chuí, RS [Dissertação de mestrado em Geociências]. Porto Alegre: Universidade Federal do Rio Grande do Sul.
- Petsch, D.K., 2016. Causes and consequences of biotic homogenization in freshwater ecosystems. *Int. Rev. Hydrobiol.* 101(3-4), 113-122. <http://dx.doi.org/10.1002/iroh.201601850>.
- Potapova, M.G., Ponader, K.C., Lowe, R.L., Clason, T.A., & Bahls, L.L., 2003. Small-celled *Nupela* species from North America. *Diatom Res.* 18(2), 293-306. <http://dx.doi.org/10.1080/0269249X.2003.9705593>.
- R Core Team, 2017. *R: A language and environment for statistical computing* [online]. Vienna: R Foundation for Statistical Computing. Retrieved in 2022, January 4, from www.R-project.org
- Round, F.E., Crawford, R.M., & Mann, D.G., 1990. *The diatoms: biology and morphology of the genera*. Cambridge: Cambridge University Press.
- Sala, O.E., Stuart Chapin 3rd, F., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L.R., Sykes, M.T., Walker, B.H., Walker, M., & Wall, D.H., 2000. Global biodiversity scenarios for the year 2010. *Science* 287(5459), 1770-1774. PMID:10710299. <http://dx.doi.org/10.1126/science.287.5459.1770>.
- Salomoni, S.E., Rocha, O., Callegaro, V.L., & Lobo, E.A., 2006. Epilithic diatoms as indicators of water quality in the Gravataí river, Rio Grande do Sul, Brazil. *Hydrobiologia* 559(1), 233-246. <http://dx.doi.org/10.1007/s10750-005-9012-3>.
- Schindler, D.W., 2012. The dilemma of controlling cultural eutrophication of lakes. *Proc Royal Soc B.* 279(1746), 4322-4333. PMID:22915669. <http://dx.doi.org/10.1098/rspb.2012.1032>.
- Schneck, F., Schwarzbold, A., & Melo, A.S., 2011. Substrate roughness affects stream benthic algal diversity, assemblage composition, and nestedness. *J. N. Am. Benthol. Soc.* 30(4), 1049-1056. <http://dx.doi.org/10.1899/11-044.1>.
- Schneider, S.C., Kahlert, M., & Kelly, M.G., 2013. Interactions between pH and nutrients on benthic algae in streams and consequences for ecological status assessment and species richness patterns. *Sci. Total Environ.* 444(1), 73-84. PMID:23266552. <http://dx.doi.org/10.1016/j.scitotenv.2012.11.034>.
- Schwarzbold, A., & Schäfer, A., 1984. Gênese e morfologia das lagoas costeiras do Rio Grande do Sul, Brasil. *Amazoniana* 9, 87-104.
- Silva, L.C. 2012. *O desenvolvimento do turismo no balneário Cassino: um problema de gerenciamento costeiro integrado* [Dissertação de mestrado em Gerenciamento Costeiro]. Rio Grande. Universidade Federal do Rio Grande - FURG.
- Silva-Benavides, A.M., 1996. The epilithic diatom flora of a pristine and a polluted river in Costa Rica, Central America. *Diatom Res.* 11(1), 105-142. <http://dx.doi.org/10.1080/0269249X.1996.9705368>.
- Simonsen, R., 1974. The diatom plankton of the Indian Ocean Expedition of RV Meteor. *Forsch Ergeb.* 19, 1-107.
- Smith, V.H., & Schindler, W.D., 2009. Eutrophication science: where do we go from here? *Trends Ecol. Evol.* 24(4), 201-207. PMID:19246117. <http://dx.doi.org/10.1016/j.tree.2008.11.009>.
- Smith, V.H., 2003. Eutrophication of freshwater and coastal marine ecosystems: a global problem. *Environ. Sci. Pollut. Res. Int.* 10(2), 126-139. PMID:12729046. <http://dx.doi.org/10.1065/espr2002.12.142>.
- Soininen, J., Jamoneau, A., Rosebery, J., & Passy, S.I., 2016. Global patterns and drivers of species and trait composition in diatoms. *Glob. Ecol. Biogeogr.* 25(8), 940-950. <http://dx.doi.org/10.1111/geb.12452>.
- Søndergaard, M., Lauridsen, T.L., Johansson, L.S., & Jeppesen, E., 2017. Nitrogen or phosphorus limitation in lakes and its impact on phytoplankton biomass and submerged macrophyte cover. *Hydrobiologia* 795(1), 35-48. <http://dx.doi.org/10.1007/s10750-017-3110-x>.
- Souza, V.C., & Lorenzi, H., 2008. *Botânica Sistemática*. São Paulo: Instituto Plantarum.
- Strayer, D.L., & Dudgeon, D., 2010. Freshwater biodiversity conservation: recent progress and future challenges. *J. N. Am. Benthol. Soc.* 29(1), 344-358. <http://dx.doi.org/10.1899/08-171.1>.
- Tromboni, F., & Dodds, W.K., 2017. Relationships between land use and stream nutrient concentrations in a highly urbanized tropical region of Brazil: thresholds and riparian zones. *Environ. Manage.*

- 60(1), 30-40. PMID:28405753. <http://dx.doi.org/10.1007/s00267-017-0858-8>.
- Valderrama, J.C., 1981. The simultaneous analysis of total nitrogen and total phosphorus in natural waters. *Mar. Chem.* 10(2), 109-122. [http://dx.doi.org/10.1016/0304-4203\(81\)90027-X](http://dx.doi.org/10.1016/0304-4203(81)90027-X).
- Vieira, E.F. 1983. Rio Grande: geografia física, humana e econômica. Porto Alegre: Sagra.
- Vilmi, A., Karjalainen, S.M., Landeiro, V.L., & Heino, J., 2015. Freshwater diatoms as environmental indicators: evaluating the effects of eutrophication using species morphology and biological indices. *Environ. Monit. Assess.* 187(5), 243. PMID:25864081. <http://dx.doi.org/10.1007/s10661-015-4485-7>.
- Vörösmarty, C.J., McIntyre, P.B., Gessner, M.O., Dudgeon, D., Prusevich, A., Green, P., Glidden, S., Bunn, S.E., Sullivan, C.A., Liermann, C.R., & Davies, P.M., 2010. Global threats to human water security and river biodiversity. *Nature* 467(7315), 555-561. PMID:20882010. <http://dx.doi.org/10.1038/nature09440>.
- Walsh, C.J., Roy, A.H., Feminella, J.W., Cottingham, P.D., Groffman, P.M., & Morgan 2nd, R.P., 2005. The urban stream syndrome: current knowledge and the search for a cure. *J. N. Am. Benthol. Soc.* 24(3), 706-723. <http://dx.doi.org/10.1899/04-028.1>.
- Wojciechowski, J., Heino, J., Bini, L.M., & Padial, A.A., 2017. Temporal variation in phytoplankton beta diversity patterns and metacommunity structures across subtropical reservoirs. *Freshw. Biol.* 62(4), 751-766. <http://dx.doi.org/10.1111/fwb.12899>.
- Wojtal, A.Z., 2009. *Nupela marvanii* sp. nov., and *N. lapidosa* (Krasske) Lange-Bertalot in Poland with notes on the distribution and ecology of the genus of *Nupela* (Bacillariophyta). *Fottea*. 9(2), 233-242. <http://dx.doi.org/10.5507/fot.2009.024>.
- Wright, D.H., Patterson, B.D., Mikkelsen, G.M., Cutler, A., & Atmar, W., 1997. A comparative analysis of nested subset patterns of species composition. *Oecologia*. 113(1), 1-20. PMID:28307284. <http://dx.doi.org/10.1007/s004420050348>.
- Xiao, W., Liu, X., Irwin, A.J., Laws, E.A., Wang, L., Chen, B., Zeng, Y., & Huang, H., 2018. Warming and eutrophication combine to restructure diatoms and dinoflagellates. *Water Res.* 128, 206-216. PMID:29107905. <http://dx.doi.org/10.1016/j.watres.2017.10.051>.
- Zorzal-Almeida, S., Bartozek, E.C.R., & Bicudo, D.C., 2021. Homogenization of diatom assemblages is driven by eutrophication in tropical reservoirs. *Environ. Pollut.* 288, 117778. PMID:34280747. <http://dx.doi.org/10.1016/j.envpol.2021.117778>.
- Zuur, A., Ieno, E.N., Walker, N.J., Saveliev, A.A., & Smith, G.M., 2009. Mixed effects models and extensions in Ecology with R. New York: Springer. <http://dx.doi.org/10.1007/978-0-387-87458-6>.

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