



UNIVERSIDADE FEDERAL DE MINAS GERAIS
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Vida Silvestre



Gabriel Estevão Nogueira Aguilã

Meu passado me condena! A autocorrelação temporal do fitoplâncton em um sistema lacustre neotropical

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Orientadora: Paulina Maria Maia Barbosa

Coorientador: Diego Guimarães Florêncio Pujoni

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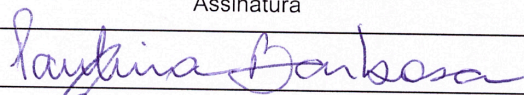
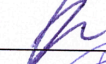
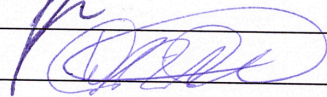
Gabriel Estevão Nogueira Aguilá

No dia 21 de fevereiro de 2020, às 14:00 horas, na sala 236, bloco I3 do Instituto de Ciências Biológicas da Universidade Federal de Minas Gerais, teve lugar a defesa de dissertação de mestrado no Programa de Pós-Graduação em Ecologia, Conservação e Manejo da Vida Silvestre, de autoria do(a) mestrando(a) Gabriel Estevão Nogueira Aguilá, intitulada: “**Meu passado me condena! A autocorrelação temporal do fitoplâncton em um sistema lacustre neotropical**”. Abrindo a sessão, o(a) orientador(a) e Presidente da Comissão, Doutor(a) Paulina Maria Maia Barbosa, após dar a conhecer aos presentes o teor das normas regulamentares do trabalho final, passou a palavra para o(a) candidato(a) para apresentação de seu trabalho. Estiveram presentes a Banca Examinadora composta pelos Doutores: Ricardo Ribeiro de Castro Solar (UFMG), Diego Marcel Parreira de Castro (UFMG) e demais convidados. Seguiu-se a arguição pelos examinadores, com a respectiva defesa do(a) candidato(a). Após a arguição, apenas os senhores examinadores permaneceram no recinto para avaliação e deliberação acerca do resultado final, sendo a decisão da banca pela:

- Aprovação da dissertação, com eventuais correções mínimas e entrega de versão final pelo orientador diretamente à Secretaria do Programa, no prazo máximo de 30 dias;
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- Reformulação da dissertação com indicação de nova defesa em data estabelecida a critério do Colegiado em observância às Normas Gerais da Pós-graduação na UFMG e ao Regimento do PPG-ECMVS;
- Reprovação

Nada mais havendo a tratar, o Presidente da Comissão encerrou a reunião e lavrou a presente ata, que será assinada por todos os membros participantes da Comissão Examinadora.

Belo Horizonte, 21 de fevereiro de 2020.

Comissão Examinadora	Assinatura
Doutor(a) Paulina Maria Maia Barbosa	
Doutor(a) Ricardo Ribeiro de Castro Solar	
Doutor(a) Diego Marcel Parreira de Castro	

Dedico essa dissertação a todos os organismos
planctônicos que se sacrificaram em prol de
avanços na ecologia.

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“Pensar globalmente, agir localmente” David Brower

Meu passado me condena! A autocorrelação temporal do fitoplâncton em um sistema lacustre neotropical

Resumo

Sabe-se que a estrutura da metacomunidade de plâncton responde a fatores locais (i.e., biótico e abiótico) e à conectividade dos ambientes. Muitos estudos buscam quantificar a influência de fatores locais e regionais na determinação da abundância de populações coexistentes por meio da adequação de modelos de metacomunidade, como species-sorting e neutral a dados reais. A maioria dos estudos testou hipóteses nesse sentido a partir de uma perspectiva espacial, na qual foram avaliadas estruturas comunitárias em áreas vizinhas, bem como variáveis ambientais importantes, e a importância da proximidade e similaridade ambiental dos fragmentos na previsão da estrutura da comunidade é quantificada pela aplicação de métodos de partição de variância. No entanto, como os ambientes aquáticos não são estáveis ao longo do tempo, o trade-off entre as dinâmicas species-sorting e neutral também pode ser testado a partir de uma perspectiva temporal. Portanto, este estudo teve como objetivo quantificar a influência das limitações ambientais e estocásticas da população fitoplanctônica em um conjunto de lagos naturais não conectados, onde a comunidade foi amostrada mensalmente por oito anos. Nossa hipótese é que, apesar de sua alta taxa de rotatividade, as populações fitoplanctônicas têm uma autocorrelação temporal expressiva, que pode ser interpretada como dinâmica neutra. Essa interpretação vem do fato de que uma população pode persistir no ambiente, mesmo que esse ambiente não seja adequado às necessidades da espécie. Assim, espera-se que a autocorrelação seja tão importante quanto, ou ainda mais importante, que o efeito ambiental para explicar a estrutura da comunidade. Para testar nossa hipótese, realizamos a partição de variância total separadamente para cada uma das 21 espécies de fitoplâncton mais abundantes, avaliando a importância das dimensões temporal (i.e., abundância no último mês), espacial (i.e., lagos vizinhos) e ambientais. Nossa hipótese foi corroborada, com a dimensão temporal tendo maior importância sobre todas as outras dimensões. Sugerimos que esses organismos estejam "dispersando temporalmente", com fortes relações fonte-sumidouro ao longo do tempo, superando os filtros ambientais.

Palavras-chave: Plâncton; lagos não conectados; autocorrelação temporal; coerência temporal; dispersão temporal.

My past condemns me! The temporal autocorrelation of phytoplankton in a neotropical lake system

Abstract

Plankton metacommunity structure is known to respond to both local factors (i.e., biotic and abiotic) and patch connectivity. Many studies are seeking to quantify the influence of local and regional factors in determining the abundance of coexisting populations through the adequacy of metacommunity models such as species-sorting and neutral to real data. Most studies tested hypotheses in this regard from a spatial perspective, where community structures in neighboring patches were evaluated, as well as important environmental variables, and the importance of patches proximity and environmental similarity in predicting community structure is quantified by applying variance partition methods. However, as aquatic environments are not stable over time, the trade-off between species-sorting and neutral dynamics can also be tested from a temporal perspective. Therefore, this study aimed to quantify the influence of environmental and stochastic limitations of the phytoplankton population on a set of unconnected natural lakes, where the community was sampled monthly for eight years. Our hypothesis is that although its high turnover rate, phytoplankton populations have an expressive temporal autocorrelation, that may be interpreted as neutral dynamics. This interpretation comes from the fact that a population can persist in the environment, even if this environment may not be suitable for the species needs. Thus, it is expected that the autocorrelation can be as important as, or even more important than the environmental effect to explain community structure. To test our hypothesis, we performed the total variance partition separately for each of the 21 most abundant phytoplankton species, assessing the importance of the temporal (i.e. abundance in the last month), spatial (i.e. neighboring lakes), and environmental dimensions. Our hypothesis was corroborated, with the temporal dimension having the greatest importance over all other dimensions. We suggest that these organisms are “dispersing temporally”, with strong source-sink relationships over time, outperforming environmental filters.

Key-words: Plankton; unconnected lakes; temporal autocorrelation; temporal coherence; temporal dispersion.

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1. Introdução Geral

Através de uma iniciativa pioneira e visão estratégica, em 1999, o governo federal, criou o Programa de Pesquisa Ecológica de Longa Duração (PELD). Este programa é formado por uma rede de sítios de referência no Brasil para a pesquisa científica no tema de Ecologia de Ecossistemas e segue um movimento internacional voltado para a obtenção de séries temporais de longa duração dos ecossistemas do mundo inteiro (International Long Term Ecological Research Program - ILTER Seeliger *et al.*, 2002). As informações coletadas no PELD abrangem longas séries temporais sobre os ecossistemas e suas biotas associadas, sendo de extrema importância para um país que é considerado o mais diverso do mundo. Estes sítios, além de importantes para a pesquisa, são cruciais na formação de recursos humanos especializados.

Pouco tempo depois de seu estabelecimento, emergiram realizações positivas de cunho científico, social e político, através de abordagens integradoras. Desta forma, as informações obtidas sobre ecossistemas e biodiversidade em um longo prazo, começaram a subsidiar as tomadas de decisão em relação às medidas de conservação e gerenciamento de bacias hidrográficas. Isso só foi possível, devido à boa comunicação entre os meios social, científico, privado e governamental. Além disso, os programas de educação ambiental iniciaram um papel importante na integração social e política (Barbosa *et al.*, 2004).

O programa PELD conta atualmente com 30 sítios, presentes nos mais diversos ecossistemas do país. Dentre eles, o Site 4 – Mata Atlântica e sistema lacustre do médio Rio Doce, como o próprio nome já diz, abrange um dos biomas mais ameaçados do Brasil, a Mata Atlântica. Considerado o hotspot mais prioritário para a conservação da biodiversidade em toda a região neotropical, abriga o maior remanescente de Mata Atlântica no estado de Minas Gerais, o Parque Estadual do Rio Doce (PERD), totalizando 36.000ha de florestas, além do terceiro maior sistema lacustre do país reconhecido como um sítio RAMSAR (RAMSAR, 2010). Sob constante pressão, este remanescente sofre com inúmeros impactos, como: supressão vegetal, urbanização, plantações de monoculturas, introdução de espécies não nativas e extração mineral (Oliveira *et al.*, 2019). Dado sua importância, este site foi selecionado com o propósito de monitorar e pesquisar suas comunidades biológicas em longo prazo, permitindo que estratégias de conservação mais eficazes fossem desenvolvidas.

A comunidade fitoplanctônica é composta por um conjunto de algas microscópicas fotossintetizantes, unicelulares de curto ciclo de vida que habitam ecossistemas aquáticos. Estes organismos podem ser encontrados isolados ou em colônias, vivendo em suspensão na coluna d'água, geralmente próximo a superfície, onde a penetração de luz é maior (Margalef, 1978) Além disso, estes organismos apresentam dispersão passiva, dependendo de outros meios para se deslocar entre ambientes (e.g. através de animais, vento). As algas apresentam uma ampla diversidade de formas e estruturas morfológicas que influenciam, por exemplo, nas suas adaptações à flutuabilidade (Litchman e Klausmeier, 2008; Reynolds, 2006). Os grupos mais comuns em água doce são: Bacillariophyta, Chlorophyta, Cryptophyta, Chrysophyta, Cyanophyta, Dinophyta e Euglenophyta.

Por se tratarem de organismos produtores, responsáveis pela produção da maior parte do oxigênio atmosférico e por participarem do ciclo biogeoquímico de muitos elementos, essa comunidade é considerada de grande importância ecológica, sendo base das cadeias tróficas nos ecossistemas aquáticos (Falkowski *et al.*, 2004; Field *et al.*, 1998). Em alguns lagos do sistema de lagos do PERD esta comunidade vem sendo avaliada, desde a década de 1980, sob diferentes aspectos, buscando compreender melhor a ecologia destes organismos e sua participação na dinâmica dos ambientes.

Os primeiros estudos publicados com essa comunidade na região foram de cunho experimental, com medições das taxas fotossintéticas (i.e., produtividade primária) e como estes organismos respondiam às variações nas características abióticas. Foi verificado que estes ambientes apresentam uma produtividade primária menor que a esperada para ambientes tropicais cercados por florestas nativas, fato este explicado pela limitação de nutrientes (Tundisi *et al.*, 1985 in Saijo & Tundisi). A biomassa fitoplanctônica e a produtividade aumentam durante o período de mistura, porque há um aumento das concentrações de nutrientes na zona limnética (Henry *et al.*, 1989 in Saijo & Tundisi, 1985). Outro estudo realizado com essa comunidade buscou compreender como as variações de temperatura na coluna d'água influenciavam sua distribuição tendo sido constatado que, estes gradientes determinam não somente as variáveis físicas e químicas, mas também, a estrutura vertical da comunidade planctônica (Matsumura-Tundisi *et al.*, 1989 in Saijo & Tundisi, 1985) .

Com o início do PELD, foram medidas de forma simultânea, a produção bacteriana e do fitoplâncton em sete lagos, durante o período de 1999 a 2001. Em alguns momentos, foi observado que durante o período chuvoso, a produção fitoplanctônica reduzia enquanto a bacteriana apresentava um aumento. Durante o período de mistura a disponibilidade de

nutrientes na coluna d'água aumenta. Desta forma o período chuvoso (verão) foi caracterizado como estação heterotrófica beneficiando o bacterioplâncton, enquanto o período seco (inverno) como estação autotrófica beneficiando o fitoplâncton (Petruccio *et al.*, 2006).

Em outra publicação foi investigada a relação entre o tamanho dos organismos da comunidade fitoplanctônica no lago Dom Helvécio, e as variações relacionadas aos mecanismos sazonais, no período de 2001 a 2004. Não foi identificada nenhuma influência significativa das variações sazonais sobre o biovolume destes organismos, porém, a distribuição das classes de tamanho sob as diferentes condições de estabilidade foram distintas, com predomínio de organismos de menor tamanho nos períodos de estratificação e de organismos maiores no período de mistura. Este resultado mostrou que a constância da densidade do fitoplâncton em função da sazonalidade, não significa uma comunidade estável, e sim, que essas alterações causam mudanças significativas na estrutura dessa comunidade (Barros *et al.*, 2006). Neste mesmo lago, foi investigado o papel da atelomixia (i.e., microdesestratificações na coluna d'água) na substituição de assembleias fitoplanctônicas durante um ciclo hidrológico completo no ano de 2002. Foram identificadas mudanças na estruturação desta comunidade, moldadas por variações sazonais e diárias de temperatura da água, influenciando nos padrões de estratificação, profundidade de penetração da luz e disponibilidade de nutrientes. Assim, ficou claro que a temperatura é tão importante para a ecologia do fitoplâncton em ambientes tropicais, quanto em ambientes temperados (Souza *et al.*, 2008).

Outro estudo investigou o papel das alterações climáticas, sazonais e antropogênicas sobre as características físicas, químicas e biológicas do lago Dom Helvécio, utilizando dados limnológicos coletados ao longo de três décadas (i.e., 70, 80 e 1999 a 2006). Mudanças na diversidade dos organismos planctônicos foram relacionadas às alterações sazonais e à introdução de espécies de peixes não nativos (Maia-Barbosa *et al.*, 2010). Outra pesquisa, trabalhando com dois lagos monomíticos de características distintas, Carioca e Dom Helvécio, observou os efeitos de distúrbios e fatores ambientais abióticos sobre a biomassa de desmídias, durante o período de 2002 a 2006. Foi constatado que a estabilidade física dos lagos favoreceu a dominância destes organismos em lagos monomíticos tropicais, embora, outros fatores abióticos determinaram sua composição e abundância de grupos funcionais (Barbosa *et al.*, 2013). Através deste resultado, outro estudo utilizando o mesmo período, buscou compreender se as diferenças morfométricas entre estes dois lagos promoviam a seleção de estratégias de vida distintas das desmídias. Observou-se, que, na lagoa Carioca,

ambiente raso e turvo, as espécies dominantes foram classificadas como oportunistas, enquanto, na lagoa Dom Helvécio ambiente profundo e claro, as espécies dominantes foram classificadas como ruderais, compostas por desmídias que possuem braços e espinhos que conferem vantagem adaptativa em ambientes estratificados (Barbosa *et al.*, 2013).

No último e mais recente trabalho publicado, através de experimentos com mesocosmos em um dos lagos, foi investigado como mudanças nas condições ambientais afetam a produção primária bruta da comunidade fitoplanctônica, durante um período de 12 dias entre janeiro e fevereiro de 2015. Observou-se que na camada superior do lago, o efeito da fotoinibição sobre estes organismos, era principalmente durante a depleção de nutrientes e a alta disponibilidade de luz na estação chuvosa. Foram constatadas fortes evidências que os nutrientes, matéria orgânica e luz afetam as taxas metabólicas, demonstrando que as taxas de respiração da comunidade estavam muito relacionadas à atividade dos organismos autotróficos (Brighenti *et al.*, 2018).

Dado esse panorama histórico, vimos que a produtividade primária, composição e a estruturação da comunidade fitoplanctônica são fortemente influenciadas pelos gradientes ambientais e as variações de temperatura ao longo do dia e do ano. Desta forma, estes processos contribuem para a seleção das espécies dominantes nos diferentes ambientes, influenciando conseqüentemente, no seu metabolismo. Entretanto, ainda há a necessidade de estudar a dinâmica dessa comunidade numa perspectiva da paisagem. Por isso, neste estudo, buscamos compreender a dinâmica de um conjunto de comunidades fitoplanctônicas, na região do médio Rio Doce, metacomunidade, sob uma perspectiva espacial e temporal, identificando os principais fatores ambientais e atributos espécie-específicos que atuam em conjunto para determinar a estruturação desta comunidade. Assim, este estudo trás uma nova abordagem, considerando a abundância das espécies em tempos distintos, propondo uma nova perspectiva para estudos de metacomunidades, e considerando a autocorrelação temporal, muitas vezes negligenciada.

Neutral dynamics drives phytoplankton metacommunity structure in a tropical lake system: a temporal perspective

2. Introduction

Holt et al. (2003) stated that an “important challenge for ecologists is to assess the interplay of temporal variation and spatial heterogeneity in determining species’ abundances and constraints on species coexistence in local communities”. This statement highlights that community dynamics can only be understood when we consider the temporal and spatial dimensions of the interaction between species and physical habitat, which is the main focus of metacommunity studies. Metacommunity theory is relatively recent in ecology (Letters, 2004). Most current studies seek to evaluate the evidence for environment or dispersal drivers in shaping local communities, which in summary reduce to quantify how much the species-sorting or neutral dynamics fit to the data, as well as possible predictors that explain the dominance of one model over the other (Viana *et al.*, 2016; Arrieira *et al.*, 2017; Soininen & Teittinen, 2019). The principle that differentiates these two models is that the competitive capacities of species are distinct or similar, causing the local community to be mainly structured by environmental filtering (i.e., species-sorting) or by dispersion and demographic stochasticity (i.e., neutral) (Hubbell, 2001; Holyoak *et al.*, 2005).

Due to the rapid turnover of planktonic species and high propagule production rates, it was initially thought that the species-sorting model was the most appropriate for this community. However, several recent articles have challenged this understanding and demonstrated a trade-off between these two paradigms (i.e., species-sorting vs neutral). It is already known that the adequacy of metacommunity models to real data depends on both the characteristics of the environment and species traits (Devercelli *et al.*, 2016; Bortolini *et al.*, 2019). Regarding environmental characteristics, it has been observed that communities of protists and flagellate algae are mainly structured by environmental factors in isolated lakes, however in highly connected environments, stochastic processes prevailed over the environmental filter (Lansac-Tôha *et al.*, 2016). Regarding species traits, studies have found distinct influences of environmental and spatial dimensions in the structuring process, varying according to morphophysiological traits and dispersal capacities (Zhao *et al.*, 2017; Pujoni *et al.*, 2019). Other studies have shown that not only traits, but the abundance may affect how populations respond to environmental gradients and spatial variables (Segovia *et al.*, 2017).

Regarding the methodology employed in the studies, the vast majority have made this comparison between species-sorting and neutral dynamics in a spatial perspective. In these studies, several environments of the same region are evaluated for the structure of its community and its environmental characteristics (Soininen *et al.*, 2007; Nabout *et al.*, 2009; Meier & Soininen, 2014). Variance partition methods are applied to test whether community similarity is mainly due to the patches' proximity (i.e., neutral dynamics), or the similarity of their environmental characteristics (i.e., species-sorting dynamics). Some studies included measurements of the same environment over different time periods, because seasonality would promote a new dimension of environmental variation that could also be assessed. These studies made the partition between three components namely, the environmental, the spatial and the temporal dimensions (Padiál *et al.*, 2014; Pujoni *et al.*, 2019). The inclusion of samples from the same environment raises the discussion about pseudoreplication, as there would be temporal autocorrelation between these measurements (Pujoni *et al.*, 2019). However, the presence of this temporal autocorrelation could be interpreted similarly to presence of spatial autocorrelation, which is an indication of neutral dynamics. Thus, if the environment changes over time, but the abundance of the species remains similar to the previous month, this demonstrates that the stochastic population dynamics are overcoming the response to the environmental gradients. Thus, we can assess trade-off from a temporal perspective by interpreting dispersive-demographic relationships over time.

Phytoplankton organisms are known as good indicators of environmental change, being considered the first level for the biological response, responding to disturbances in hours or days (Munawar & Munawar, 1987; Racault *et al.*, 2017 and Stefanidou *et al.*, 2019). However, it is also known that different groups do not respond to changes at the same speed. In a study that evaluated the marine phytoplankton community for 60 years, it was shown that dinoflagellates followed the speed of climate change, while diatoms responded more slowly (Chivers *et al.*, 2017). This difference in response to environmental changes caused the restructuring of this community, leading to numerous ecosystem changes. Studies that evaluated founder effects in microorganism communities reported that the way colonization in environments occurred (i.e., sequential or simultaneous), along with environmental variables (i.e., constant or variable), influenced the community for generations, even when environments were ephemeral or assessed on small spatial scales (Tucker & Fukami, 2014; Ventura *et al.*, 2014 and Toju *et al.*, 2018). These studies have shown that although its high

turnover rates, microorganism communities may have a temporal autocorrelation that uncouples populations' and abiotic variables' time series.

Given this current panorama of studies with the planktonic community and its metacommunity dynamics, knowing that the two paradigms (i.e., species-sorting and neutral) may coexist in natural communities, our work aimed to evaluate the adequacy of these paradigms in a temporal perspective. Our first hypothesis is that although its high turnover rate, phytoplankton populations have an expressive temporal autocorrelation, that may be interpreted as neutral dynamics. Our second hypothesis is that this temporal autocorrelation may explain an equal to or even greater fraction of community structure in comparison to environmental gradients. As a prediction, we expect that the explanation of variance for species abundance in the previous month over the abundance of species in the current month will be as equal as or even greater than the explanation of variance given by environmental variables. In this study we decided to apply the extreme decomposition principle, analyzing each species individually and analyzing the result together as described in Pujoni *et al.* (2019).

3. Methods

2.1 Study area

The data used in this study was collected in four unconnected lakes belonging to the system of lakes in the middle section of the Doce River basin, southeastern Minas Gerais, Brazil (19°29'24''S – 19°48'18''S, 42°28'18''W – 42°38'30''W - Figure 1). It is the third-largest lake system in Brazil, with over 300 water bodies (Maillard *et al.*, 2012). In this region is located the Rio Doce State Park, the largest remnant of Atlantic Forest in the state of Minas Gerais. This unit and its surroundings were selected as one of the sites of the Brazilian Long-term Brazilian Ecological Research Program (ILTER), and in 2010 was recognized as a RAMSAR site (RAMSAR, 2010). The climate in the region is predominantly mesothermal, with two well-defined seasons: dry winter - from April to September and rainy summer - from October to March.

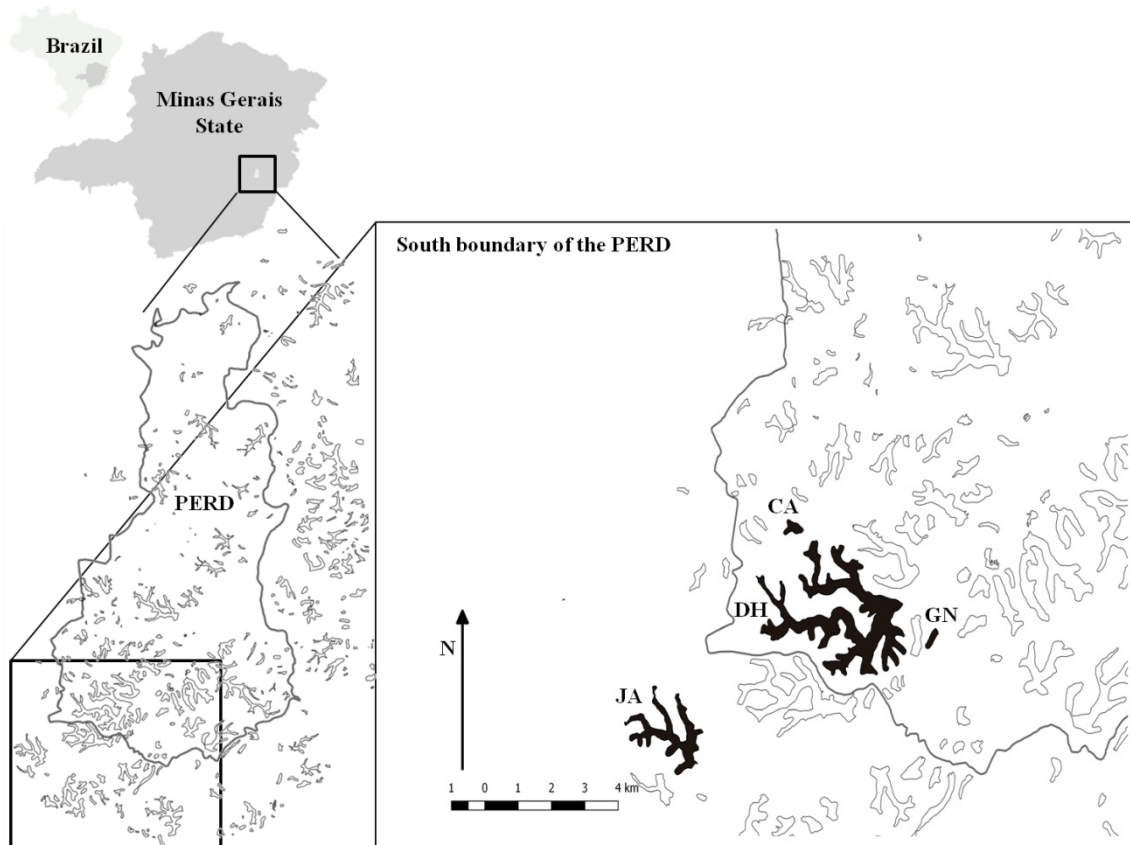


Figure 1: Rio Doce State Park (PERD) and the four highlighted black lakes (JA - Jacaré, CA - Carioca, DH - Dom Helvécio, GA - Gambazinho). The boundaries of the PERD and the entire lake complex are outlined in gray lines.

2.2 Variables collected and analyzed

The sampling of biotic and abiotic variables was made with a monthly frequency in the limnetic region of the lakes between 1999 and 2009. Vertical profiles of the temperature and pH were made and community and nutrients samples were taken in four depths defined by Secchi disc (subsurface, 10%, 1% and aphotic zone). Phytoplankton samples were collected with a Van Dorn bottle at the respective depths, fixed with acetic lugol and stored away from light. Details of sampling methodology can be found in Barros *et al.* (2013) and Maia-Barbosa *et al.* (2014). The data used is available in the data repository of the Sibbr-GBIF (www.site.com.br). During the monitoring period, 329 taxa were identified and we selected the 21 most abundant that represented 95% of the total community abundance.

The physical and chemical variables selected for characterization of the environments were: Secchi disc depth (m), temperature, pH, total phosphorus and nitrogen concentrations ($\mu\text{g/L}$), orthophosphate - PO_4 ($\mu\text{g/L}$) and dissolved inorganic nitrogen ($\mu\text{g/L}$). From the

temperature profile, we calculated the standard deviation that was used as a measure of thermal stratification strength (Fiedler, 2010).

2.3 Statistical analysis

Abiotic variables were averaged by depth and standardized to zero mean and unit variance. We applied Hellinger's transformation to species densities and also averaged by depth. We performed the total variance partition of each of the 21 species separately between the environmental and temporal dimensions through a partial redundancy analysis (pRDA). The pure explanation fraction (i.e., coefficient of determination) of each dimension as well as the joint explanation fractions were estimated according to the methodology described by (Borcard *et al.*, 2018). To perform the analysis, we replaced the spatial component (MEM's) with the abundance of the respective species at the previous time, that is, last month, to represent the temporal dimension (i.e., neutral dynamics) (matrix 1). The measured physical and chemical variables representing the environmental dimension were evaluated in the current month (matrix 2) and the previous month (matrix 3), in order to observe the environmental oscillations over time and their relationship with species abundances. The selected lakes were also evaluated using three dummy variables, representing possible environmental variables not considered (matrix 4). Thus, we extracted ten adjusted fractions of variation in addition to the residuals: Lake - purely environmental, Env - purely environmental, Env.Lag - purely environmental last month and Sp.Lag - purely temporal, in addition to the intersections: Sp.Lag)Lake – co-structured temporally and environmentally, Lake)Env – environmentally structured, Env)Env.Lag – fraction of the current environmental variation, structured by the values of the previous month, Env.Lag)Lake – co-structured by temporal and environmental variation, Env.Lag)Sp.Lag – time-structured variation, Sp.Lag)Env – co-structured temporally and environmentally. All analyses were performed in the *software* R version 3.4.4 (R Core team, 2018) using the package: “vegan” (Oksanen *et al.*, 2019).

4. Results

4.1 Study lakes characterization

The region has a clear seasonal variation in temperature and rainfall (Figure 2 - A). The four lakes evaluated are landlocked and have no connection to any other lake or river.

Carioca lake is warm monomictic and has the lowest Secchi depth and the highest total phosphorus and PO₄ concentrations in the mixing period (Table 1). Dom Helvécio lake has a dendritic shape and is the largest and deepest lake. Due to these characteristics, it maintains a chemical stratification, even when the temperature profile is uniform, which is indicative of meromixis because its hypolimnion remains isolated from top layers during the whole year, which also contributes to its oligotrophic condition (i.e. morphometric oligotrophy). Lake Gambazinho lake is the most oligotrophic and has the higher Secchi disk transparency, allowing the sunlight to reach its bottom, heating up the whole water column during the summer. For this reason the lake is thermally and chemically uniform in both winter and summer, which classify this lake as polymictic. The three described lakes are located within the PERD and are surrounded by rainforest. The Jacaré lake is located outside the PERD, suffering numerous anthropogenic pressures, such as the presence of eucalyptus plantations in its surroundings. This lake also has a dendritic shape but smaller surface area when compared to Dom Helvécio. It has a very variable environment regarding stratification patterns, light penetration depth and nutrients concentrations (Figure 2D).

In all four lakes, it is possible to note that the photic zone decreases during mixing. It is also possible to note some pulses of total phosphorus during the summer, which is caused by allochthonous material carried by the rainwater. This material is deposited at the bottom of the lakes where decomposition take place. The nutrients mineralized by the bacteria are resuspended when the lake mixes.

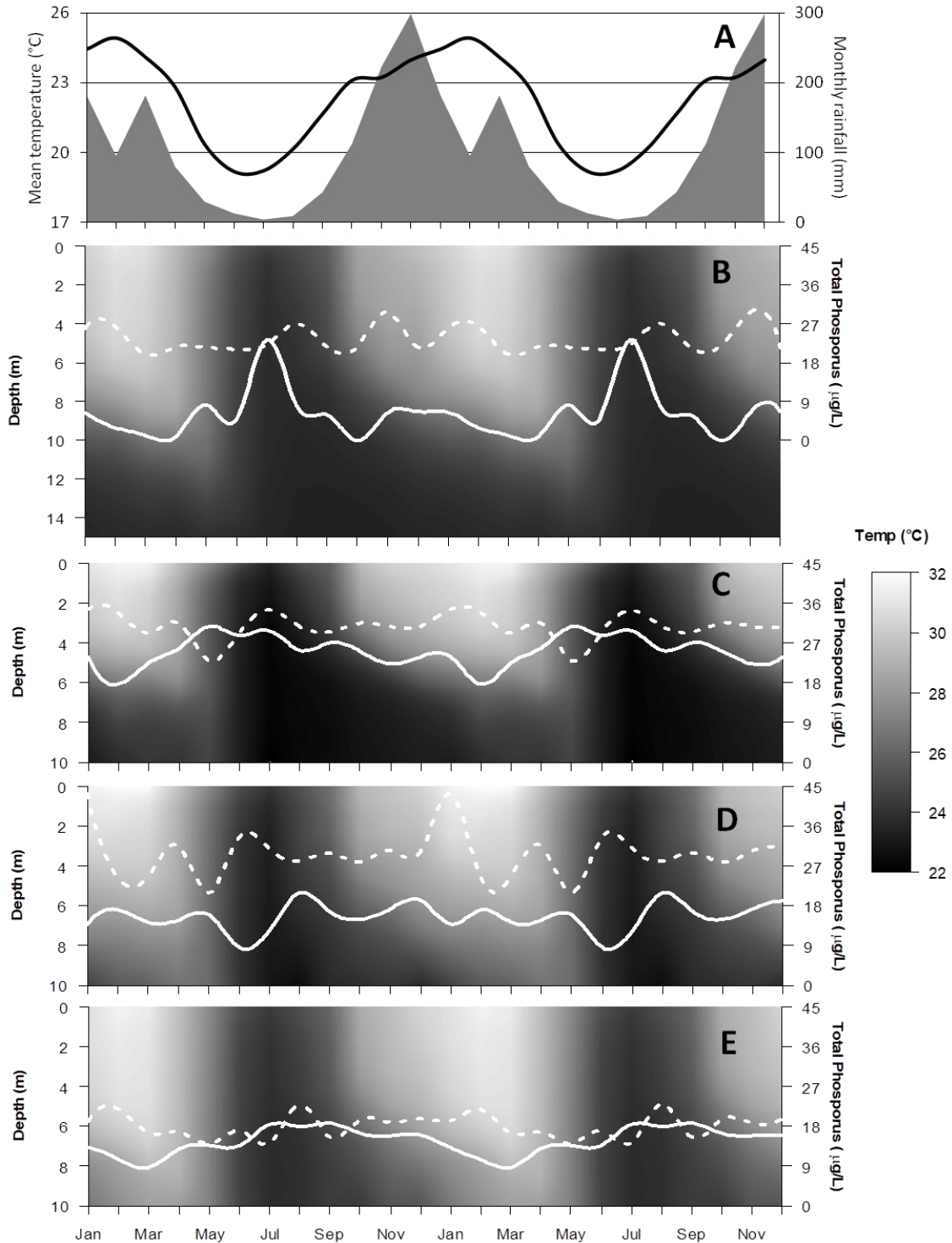


Figure 2: Representation of average seasonality for the meteorological and limnological variables. We calculated the averages for the same month using the whole time series (1999 - 2009). This seasonal component has been doubled (i.e., two identical averaged years) to make it easier to see the change from December to January. Caption: 2A - Seasonal and interannual variation in temperature (black line) and rainfall (shaded area). 2B - Dom Helvécio lake (data below 14m is not shown because temperature is constant), 2C - Carioca lake, 2D - Jacaré lake and 2E - Gambazinho lake. The solid white line indicates the boundary of the photic zone (3x Secchi disc depth) and the dotted white line indicates the total phosphorus concentration.

	Lakes							
	CA		DH		GN		JA	
	Dry	Rain	Dry	Rain	Dry	Rain	Dry	Rain
Area (Km²)	0.12		3.81		0.01		1.0	
Depth.Max*(m)	11.8		39.2		10.3		9.3	
Shorel. Dev.**	1.28		4.93		1.13		2.9	
Secchi (m)	1.20 ± 0.36	1.59 ± 0.46	2.73 ± 0.82	2.86 ± 0.49	2.15 ± 0.50	2.30 ± 0.64	2.37 ± 0.67	2.30 ± 0.97
Stabil (°C)	0.87 ± 0.57	2.47 ± 0.65	1.28 ± 0.92	2.44 ± 0.75	0.27 ± 0.23	1.12 ± 0.58	0.46 ± 0.24	1.33 ± 0.41
pH	6.18 ± 0.94	6.12 ± 0.76	5.97 ± 0.82	6.41 ± 0.80	5.80 ± 0.79	5.79 ± 0.66	6.11 ± 0.78	6.42 ± 0.85
P.tot (µg/L)	32.27 ± 19.53	24.90 ± 12.27	25.56 ± 19.18	18.14 ± 9.98	20.09 ± 13.25	17.20 ± 7.50	26.20 ± 14.16	25.04 ± 13.64
N.tot (µg/L)	434.38 ± 277.62	567.20 ± 416.12	505.40 ± 297.78	499.67 ± 261.46	338.53 ± 188.66	404.05 ± 315.79	432.86 ± 183.57	553.95 ± 329.27
PO4 (µg/L)	5.46 ± 4.70	4.23 ± 3.13	3.67 ± 2.92	3.76 ± 2.79	2.62 ± 1.40	2.98 ± 2.32	3.50 ± 2.15	4.69 ± 3.41
DIN (µg/L)	129.68 ± 121.96	160.99 ± 249.44	156.05 ± 139.23	125.26 ± 153.92	69.90 ± 66.40	100.12 ± 195.10	150.82 ± 100.32	205.27 ± 272.97

Table 1: Variation of the abiotic characteristics of the lakes according to the dry and rain periods over the years. The values represent the mean ± standard deviation of each variable in the respective periods. Caption: CA - Carioca, DH - Dom Helvécio, GN - Gambazinho and JA - Jacaré; Secchi - Depth of light penetration into water column equal to 10%, Stabil - Lake stability calculated by standard deviation of temperature, pH, P.tot - Total phosphorus (µg/L), N.tot - Total nitrogen (µg/L), PO4 - Orthophosphate (µg/L) and DIN - Dissolved Nitrogen (µg/L). *Depth maximum **Shoreline development.

4.2 Analysis of variance partition for species

By evaluating the variance partition of the 21 species individually, we found that the explanatory values obtained for the purely temporal dimension “Sp.Lag” and the intersection between this and the purely environmental dimension “Lake” were the highest, with averages of 20% and 22% respectively (Table 2). Of the 21 species evaluated, 11 presented variance explanation values for “Sp.Lag” and “Lake” added, above 40%, as follows: *Pseudanabaena granulata*, *Planktolyngbya limnetica*, *Aphanocapsa elachista*, *Merismopedia sp.*, *Staurastrum smithii*, *Limnothrix redekei*, *Cylindrospermopsis raciborskii*, *Cryptomonas sp.*, *Elakatothrix sp.*, *Monoraphidium sp.* and *Staurastrum chaetoceras*. On the other hand, we observed lower purely environmental explanation for the 21 species, with average values: “Lake” (2%), “Env” (1%) and “Env.Lag” (1%). The average residual fraction among all species was 42%.

Species	Sp.Lag	Lake	Env	Env.Lag	Sp.Lag∩ Lake	Sp.Lag∩ Env	Sp.Lag∩ Env.Lag	Lake∩ Env	Lake∩ Env.Lag	Env∩ Env.Lag	Residual	3 rd 4 th Order
<i>Pseudanabaena galeata</i>	21%	2%	2%	2%	24%	3%	3%	0%	0%	0%	31%	11%
<i>Planktolyngbya limnetica</i>	12%	1%	0%	0%	56%	0%	1%	0%	0%	0%	8%	18%
<i>Chlorella sp.</i>	19%	2%	1%	0%	7%	2%	3%	0%	0%	1%	48%	12%
<i>Cosmarium asphaerosporum</i>	9%	5%	2%	2%	19%	1%	0%	0%	0%	0%	43%	22%
<i>Aphanocapsa elachista</i>	8%	5%	0%	0%	62%	0%	1%	0%	0%	0%	25%	5%
<i>Merismopedia sp.</i>	28%	2%	1%	1%	15%	0%	0%	1%	0%	0%	52%	4%
<i>Cosmarium bioculatum</i>	37%	0%	0%	0%	0%	0%	2%	0%	0%	2%	56%	5%
<i>Staurodesmus crassus</i>	19%	0%	1%	0%	15%	0%	0%	1%	0%	1%	35%	26%
<i>Coelastrum sphaericum</i>	6%	7%	0%	1%	22%	0%	1%	1%	1%	0%	38%	18%
<i>Staurastrum smithii</i>	34%	0%	1%	0%	23%	0%	0%	0%	0%	0%	25%	12%
<i>Synechococcus sp.</i>	0%	0%	0%	2%	0%	0%	0%	0%	0%	2%	98%	0%
<i>Teilingia granulata</i>	14%	5%	0%	0%	22%	0%	0%	0%	0%	0%	45%	16%
<i>Limnothrix redekei</i>	23%	2%	0%	0%	34%	0%	1%	0%	0%	0%	33%	7%
<i>Cylindrospermopsis raciborskii</i>	34%	2%	1%	0%	18%	0%	0%	1%	0%	0%	37%	8%
<i>Cryptomonas sp.</i>	26%	2%	1%	1%	25%	2%	1%	0%	1%	0%	43%	3%
<i>Elakatothrix sp.</i>	20%	3%	0%	0%	26%	0%	0%	0%	0%	0%	39%	14%
<i>Cosmarium contractum</i>	5%	5%	4%	2%	23%	0%	0%	1%	1%	0%	30%	22%
<i>Cosmarium moniliforme</i>	22%	0%	0%	0%	16%	0%	4%	0%	0%	1%	50%	9%
<i>Monoraphidium sp.</i>	11%	5%	1%	0%	43%	0%	1%	0%	1%	1%	35%	5%
<i>Sphaeroszma sp.</i>	22%	0%	0%	0%	5%	0%	2%	0%	0%	1%	62%	6%
<i>Staurastrum chaetoceras</i>	43%	0%	0%	0%	4%	2%	3%	0%	0%	1%	44%	5%
Mean	20%	2%	1%	1%	22%	1%	1%	0%	0%	0%	42%	11%

Tabela 2: Explanation of the variance of the 21 species partitioned abundance in environmental and temporal dimensions (ordered from most to least abundant). Caption: Lake - purely environmental, Env - purely environmental, Env.Lag - purely environmental last month and Sp.Lag - purely temporal, beyond the intersections: Sp.Lag∩Lake – co-structured temporally and environmentally, Lake∩Env – environmentally structured, Env∩Env.Lag – fraction of the current environmental variation, structured by the values of the previous month, Env.Lag∩Lake – co-structured by temporal and environmental variation, Env.Lag∩Sp.Lag – time-structured variation, Sp.Lag∩Env – co-structured temporally and environmentally. Third and fourth order interactions averaged less than 11% and are not shown.

5. Discussion

Our hypotheses that phytoplankton populations from isolated lakes have an expressive temporal autocorrelation that may overcome the environmental filter were corroborated. Although it is known that algae species respond to abiotic gradients, the structure of the phytoplankton community has some type of inertia, showing a delayed response to environmental changes. Therefore, stochastic demographic effects were the possible cause of this persistence in our study area. We believe that our study shows a real pattern because environmental variables that are known to be important for structuring the phytoplankton community were included in the analysis, mainly the thermal stratification, measured by the standard deviation of the temperature profile and the light penetration, measured by the Secchi disc disappearance depth. These variables have already been highlighted by several studies as the essential drivers in tropical environments (Bouvy *et al.*, 2006; Figueredo e Giani, 2001; Talling, 1987).

The lakes we have studied have environmental differences among them that are justified mainly by their distinct morphometric and/or historical characteristics (i.e., anthropogenic pressures). Carioca lake is the second smallest among the four studied lakes, and develops a very strong thermal stratification, mainly due to its darker color. The brown color of its water is explained by the high concentration of chromophoric dissolved organic carbon released by the organic matter (i.e., leaf litter) carried by the rain (Granéli *et al.*, 2012). *Pseudanabaena galeata* is the dominant species representing half of the total abundance. This species is described as indicative of frequently stirred up and inorganically turbid shallow lakes by Padisák *et al.* (2009) and it shows small decreases in abundance in the onset of stratification (between September and November) when light penetration increases. In this period, *Cosmarium asphaerosporum*, the second most dominant species, can dominate, as it has a competitive advantage in clear and stratified environments. However, it does not persist more than three months, and is rapidly replaced again by *P. galeata* which dominates until the onset of the next year's stratification. *Coelastrum sphaericum*, the third most dominant species, is reported as an indicator of shallow, mixed and highly enriched systems and showed density peaks in the winter, in periods when *P. galeata* was not dominating. However, it is far less expressive than *P. galeata* and dominated only three months in the whole period, once in March and twice in August.

The Dom Helvécio, the largest and deepest lake in the system, is clearer than Carioca, because the organic matter carried by the rain during summer sinks to the hypolimnion and are mineralized, losing most of its chromophoric properties. This lake also develops a strong stratification, with a thermocline deeper than Carioca's, and although it can be thermally homogeneous in winter, we can classify it as meromictic, with an isolated hypolimnion. There is no long-term dominance in this lake, and the four most abundant species combined correspond to half of the total abundance, with the first three representing, on average, 14% of the relative abundance each. *Chlorella* sp., which is an indicator of shallow and well mixed oligotrophic environments (Padisák *et al.*, 2009), dominated during mixing events. *Pseudanabaena galeata* started to be reported in this environment from 2005, representing more than 20% of the total abundance since then. It dominates specially in the onset of mixing periods (between March and May). *Cosmarium asphaerosporum* dominated during summer, when lake is stratified, being replaced by *Staurodesmus crassus* in some few periods. Both species are known to indicate the same kind of stratified environments (Padisák *et al.*, 2009).

Gambazinho is the smallest and clearest of the four studied lakes and has a polymictic pattern. The two species that dominate this lake community are the Cyanobacterias *Pseudanabaena galeata* and *Planktolyngbya limnetica*, which together represent more than 80% of the total abundance and are both indicative of turbid and mixed environments (Padisák *et al.*, 2009). The former, was only recorded in this lake after 2005 (same year in Dom Helvécio lake), when it dominated since then, alternating in some months with *P. limnetica*. One explanation why these shade adapted species dominate in this clear environment, is because they are located in deeper depths, thus avoiding photoinhibition (i.e., deep chlorophyll maximum). It is worth to mention that desmids constitutes only a small fraction of the phytoplankton community, mainly because the stratification period in this lake is not long enough to sustain a population burst. The Jacaré lake is the second largest of the studied lakes, and varied greatly from stratified to fully mixed. *Aphanocapsa elachista*, which is an indicator of shallow and nutrient rich environments, represented on average half of the counts, dominating during both mixing and stratified moments. *Chlorella* sp. and *Merismopedia* sp., were the second most abundant species, dominating during mixing events. *Merismopedia* sp. is known to have a very broad and generalist habitat template.

As we can notice from the described above, when we look at the broader long-term scale, the dominance of certain species in certain types of environments is quite predictable, accordingly to the already described species' ecology. This may indicate, at first sight, that the

environmental filter is determining the phytoplankton community structure, and that species-sorting is the dominant paradigm to explain community structure variation. However, the environmental dimension explained only a small fraction of the total variability, showing that when we analyze more refined scales and short-term processes, this predictability is almost lost. In our data, many species were dominating not only during favorable environmental conditions, but also during unfavorable ones, weakening the correlation between the species density and the abiotic gradient, and thus the environmental fraction. One possible explanation for this paradox is that real communities are never in equilibrium, because environment is always changing (Scheffer *et al.*, 2003). However, species may have a delayed response because unfavorable conditions may affect only its growth rate and not its mortality rate. One population may reach very high densities at times when the environment is favorable, decreasing slowly when conditions become unfavorable, until favorable conditions are restored. So it may take very long for one population to respond even when the environmental turnover is fast. This fact reinforces the importance of long-term studies, because if we sample a patch only once, it is very likely that we will capture a transition phase between two stable conditions, finding species in high densities associated with unexpected abiotic conditions. This may lead to misinterpretation that species may be adapted to certain environment condition.

This uncoupling between community structure and local conditions have already been described and studied in a spatial perspective, leading to the description of the mass-effect metacommunity paradigm, which settle a source-sink dynamics (Letters, 2004). With this type of dynamics, a population may be maintained in high densities by immigration even in habitats where they tend to be excluded, whether due to intolerance to abiotic conditions or interspecific competition (Holt *et al.*, 2003). This demonstrates the importance of dispersal in the metacommunity structuring processes, which can often mask environmental filters. This same source-sink dynamics can be seen in a temporal perspective, where a species with high abundance would be able to persist through unfavorable environments, establish a form of “Time escape”, thus remaining as the dominant species for long periods.

Transposing the interpretation of a neutral dynamics from a spatial perspective to a temporal perspective requires some modifications. In a spatial perspective, species dispersal is limited essentially by their dispersal abilities, geographical barriers and environmental filters. However in a temporal perspective species are limited mainly by their rate of response to environmental change. If the unfavorable conditions affect species mortality, so the response

may be more abrupt, however, if it decreases only the reproduction rate, so the response may be slow and thus “Temporal dispersal” may take place. In both cases, neutral dynamics are efficiently evaluated when dispersive-demographic factors exceed environmental filters and are therefore considered crucial for community structuring.

Although the temporal dimension is the focus on this study, we would like to highlight that there is still evidence that the spatial component has also an important role in structuring this plankton metacommunity (Pujoni *et al.*, 2019). An interesting case is the Cyanobacteria *Pseudanabaena galeata* which was recorded between 1999-2004 only in the Carioca lake. From 2005 onwards, high abundances were also observed in both Dom Helvécio and Gambazinho lakes. It is very possible that this synchrony occurred due to dispersal events. However, since we have no clear evidence of this process, we can only presume it occurred. In recent years, some authors have drawn attention to biotic homogenization (Solar *et al.*, 2015; Richardson *et al.*, 2018 and Finderup Nielsen *et al.*, 2019), synergistic effect of various changes, such as climate change (Wagner & Adrian, 2011) and biological invasions (Human & Gordon, 1997; Lososová *et al.*, 2016), causing major changes in the structure and functioning of ecosystems (Kunte, 2008; Petsch, 2016 and Defriez *et al.*, 2016). Results such as those presented in this study show the difficulty in predicting and dealing with species invasion in new environments, which can reduce the density of native populations, decreasing diversity and the quality of the environment. With climate change interfering, among other factors, in hydrological cycles, interannual rainfall changes even more, and all these changes may compromise the dynamics and climate of a region, such as the Middle Rio Doce. If any of these dominant species obtains, even at some point, the favoring of environmental characteristics, a biotic homogenization between the lakes may occur, compromising the functioning and environmental quality of these lakes (Hambright & Zohary, 2000; Borics *et al.*, 2012 and Burson *et al.*, 2018).

Our results raise interesting discussions about possible implications for experimental ecology. Many studies are based on the assumption that when we measure, at the same time, the species density and the corresponding environmental characteristics of the environment, we can thus infer about its niche (Peterson *et al.*, 2011; Chucholl, 2017 and Langdon *et al.*, 2019). When a species is not present in a certain environment at a certain time, we infer that it is not suitable for that species, and likewise, when we find a species with high abundance, we consider it to be very well adapted to those conditions. Most of the time, we do not take into account the temporal and/or spatial autocorrelation dimension in our studies and neglecting

this feature may lead to important misinterpretations. Therefore, we emphasize the importance of considering the necessity to repeated measures in order to describe a real patterns. We also highlight the importance of ecophysiological studies carried out both *in situ* and *in vitro* to complement our knowledge about the species niche limits (Gómez-Aparicio *et al.*, 2006; Martínez *et al.*, 2015).

We conclude that in this phytoplankton metacommunity, we can link the “macro” and long-term structure of the community to the environmental conditions, demonstrating that species are not equivalent competitors in all kinds of environments. This result favor species-sorting explanation over neutral dynamics. However, the “micro” and sort-term structure cannot be predicted by environmental variation, and the population inertia (i.e., density in the previous month) explains much better the community structure. We suggest that this temporal autocorrelation may be interpreted as time escape through source-sink dynamics. We strongly recommend that further works include this temporal dimensions to improve understanding of the metacommunity dynamics.

6. Conclusão Geral

Nossos resultados mostraram que nos estudos de dinâmica da metacomunidade fitoplanctônica a dimensão temporal precisa ser considerada para evitar associações espúrias, permitindo modelagens mais robustas que direcionem melhor as estratégias de conservação. Principalmente porque, estes organismos, possuem dinâmica caótica e têm curto ciclo de vida, e ainda assim, apresentaram uma surpreendente expressiva autocorrelação temporal neste estudo. Enfatizamos que a interação entre as espécies em estudos de metacomunidades deve, sempre que possível, ser considerada, pois como observado, a dominância de algumas espécies pode impedir o crescimento de outras.

Constatamos que os organismos fitoplanctônicos são sim, bons indicadores de alterações ambientais, porém, essas respostas em relação ao meio não são tão diretas e imediatas, como costumeiramente determinamos. Além disso, reforçamos a importância de estudos de longo prazo, que permitem a realização de sínteses baseadas num conjunto robusto de dados, proporcionando a compreensão da dinâmica de comunidades e suas influências nos processos ecológicos. Desta forma, podemos separar os fatores aleatórios dos determinísticos sobre os organismos, permitindo que medidas de conservação mais adequadas sejam adotadas, preservando a biodiversidade e seus importantes serviços ambientais.

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