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Efeitos da disponibilidade de nutrientes e da dominância de cianobactérias sobre a diversidade, estrutura e funcionamento de comunidades planctônicas: uma abordagem integrada e multidimensional da biodiversidade

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O presente trabalho em nível de doutorado foi avaliado e aprovado por banca examinadora composta pelos seguintes membros:

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Certificamos que esta é a **versão original e final** do trabalho de conclusão que foi julgado adequado para obtenção do título de doutor em Ecologia.

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Prof. Dr. Mauricio Mello Petrucio
Orientador

Florianópolis, 2020.

Este trabalho é dedicado ao meu melhor amigo, Gustavo Inácio (*in memorian*) que em pouco tempo e com muito amor, polinizou o mundo.

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RESUMO

Atualmente, a diversidade biológica diminui a uma taxa muito mais acelerada em ambientes aquáticos continentais do que nos marinhos ou terrestres. Desde o início dos anos 90, diversos estudos foram desenvolvidos a fim de trazer uma maior compreensão sobre como os ecossistemas respondem a essas reduções na diversidade biológica e como tais mudanças afetam o funcionamento dos ecossistemas, bem como a provisão de bens e serviços a humanidade. Estudos recentes demonstraram que tais respostas são comumente mediadas pelos atributos (i.e., características) funcionais das espécies e que os efeitos da biodiversidade no funcionamento do ecossistema também dependem de tais atributos. No entanto, apesar dos esforços da ciência, ainda não temos uma clara compreensão de como tais respostas principalmente em longo prazo, se traduzem diretamente em mudanças nas taxas de diferentes processos ecossistêmicos na natureza. Nesta tese de doutorado, tive como objetivo avaliar os efeitos da disponibilidade de nutrientes e da dominância de cianobactérias — duas importantes perturbações antrópicas nos ambientes aquáticos — na estrutura e composição do plâncton (fitoplâncton e zooplâncton), e sobre duas importantes funções dos ecossistemas aquáticos: a eficiência no uso de nutrientes limitantes (fósforo e nitrogênio) pelo fitoplâncton, e o controle descendente que o zooplâncton exerce sobre as algas (controle *top-down*). Para tal, estruturei essa tese de doutorado em três capítulos onde busco explorar os mecanismos ecológicos subjacentes a relação entre a biodiversidade e o funcionamento do ecossistema (B-EF) usando uma combinação de abordagens experimentais e observacionais, além de diferentes técnicas taxonômicas e funcionais para estimativa da diversidade biológica. No primeiro capítulo, utilizando uma série temporal de 8 anos, eu e meus coautores avaliamos a relação entre múltiplos aspectos da diversidade biológica e a eficiência no uso de recursos limitantes pelo fitoplâncton em uma lagoa que apresenta uma prolongada e persistente dominância de cianobactérias, e está passando por um processo de eutrofização. Além disso, também avaliamos o efeito da disponibilidade de recursos na estrutura da comunidade fitoplanctônica, assim como na eficiência no uso de nutrientes pela comunidade. No segundo capítulo, utilizando um subconjunto da base de dados utilizada no capítulo anterior, avaliamos a importância relativa das abordagens baseadas no tamanho e na identidade taxonômica das espécies para explicar a força do controle *top-down* do zooplâncton sobre as algas. Além disso, também tentamos separar o mecanismo subjacente a relação entre o tamanho do corpo do zooplâncton e o controle *top-down* das algas. Por fim, no terceiro capítulo, utilizando um subconjunto de dados de um experimento *outdoor* realizado durante 66 dias em Heverlee na Bélgica, eu e meus coautores avaliamos como a diversidade de tamanho e composição do zooplâncton respondem a um gradiente de adição de nutrientes, e como tais respostas afetam o controle *top-down* das algas. Com os três capítulos, demonstramos que diante de perturbações ambientais (aumento de nutrientes e dominância de cianobactérias), as abordagens funcional e taxonômica se complementam na explicação da variação do controle top-down das algas. Nossos resultados indicam claramente que o tamanho do corpo do zooplâncton explica uma parte substancial e independente da variação do controle *top-down*, o que está de acordo com diversos estudos que demonstram a importância do papel do tamanho do corpo do zooplâncton no controle da biomassa do fitoplâncton. No entanto, ao contrário do esperado, a riqueza de espécies também desempenhou um importante papel, indicando que a diversidade taxonômica pode representar adequadamente alguns atributos não avaliados que também influenciam o funcionamento do ecossistema. Além disso, nós demonstramos que diferentes aspectos da diversidade podem ter respostas e efeitos divergentes no funcionamento do ecossistema dependendo da perturbação ambiental, o que destaca a importância de se considerar múltiplos aspectos da biodiversidade — diversidade taxonômica e funcional — nas pesquisas B-EF. No geral, os resultados obtidos ilustraram o potencial das abordagens funcionais para revelar as respostas da biodiversidade às mudanças ambientais e seus efeitos nos ecossistemas. Além disso, dada a falta de grandes herbívoros em ambientes tropicais e a evidência de que a dominância de cianobactérias aumentará em ecossistemas de água doce no futuro, os resultados aqui destacam a preocupação com o fluxo de energia em ambientes aquáticos que apresentam prolongados períodos de dominância de cianobactérias.

Palavras-chave: Biodiversidade, Funcionamento do ecossistema, Diversidade funcional, Efeito de seleção, Complementaridade, Eutrofização

ABSTRACT

Given the unprecedented and growing threats to inland waters — eutrophication, cyanobacterial blooms, over-exploitation, and climate change — from multiple human activities, biodiversity is decreasing at faster rates in freshwater ecosystems than in marine or terrestrial. Since the early 1990s, hundreds of studies attempted to explain how ecosystems respond to biodiversity loss and how changes in biodiversity scale up to affect ecosystem functioning, as well as the provision of goods and services to humans. Recent studies have demonstrated that such biodiversity responses are commonly trait-mediated and the effects of communities on ecosystem functioning also depend on species traits. However, it remains unclear to what extent such biodiversity responses translate into changes in the rates of many ecosystem processes in naturally assembled communities. In this doctoral dissertation, I aimed at evaluating the effects of nutrient availability and cyanobacteria dominance on structure and composition of plankton communities (phytoplankton and zooplankton), and on two important ecosystem functions in aquatic systems: phytoplankton resource use efficiency (RUE) of limiting nutrients — phosphorus and nitrogen — and zooplankton top-down control of algae. For this, I structured this doctoral dissertation in three chapters to explore the mechanisms that underlie biodiversity-ecosystem functioning (B-EF) relationships, using a combination of experimental and fieldwork approaches, together with multiple aspects of biodiversity (i.e., taxonomic and functional diversity). In the first chapter, I and my coauthors analyzed the relationship between different measures of phytoplankton diversity, temporal turnover and RUE using 8-years monitoring data set from a cyanobacteria-dominated subtropical lake, which is now experiencing a shift in the trophic state from oligo-mesotrophic to eutrophic. Additionally, we aimed at evaluating the effect of resource availability on phytoplankton community structure and RUE. In the second chapter, using 1-year monitoring data set from the same lake, we evaluated the relative importance of size-based and taxon-based approaches in explaining the strength of zooplankton top-down control on algae, and also aimed at disentangling the mechanism by which zooplankton body size drives such ecosystem function. Finally, in the third chapter, we used an experimental metacommunity approach that simulated typical gradients of productivity and plant structural complexity to test how zooplankton body size diversity and composition responded to such gradients and whether and how such trait responses impacted top-down control of algae. Through these three chapters, we demonstrated that under environmental changes (i.e., nutrient increase and prolonged cyanobacteria dominance) approaches based on body size and taxonomic richness complement each other in explaining variation in zooplankton top-down control. Our results clearly indicate that zooplankton body size explains a substantial and independent part of the variance in top-down control, which corroborates several studies demonstrating the role of zooplankton body size to control phytoplankton biomass. But contrary to our expectations, species richness also plays a role, indicating that species richness may adequately represent some unmeasured traits that also influence ecosystem functioning. Moreover, we demonstrated that different aspect of biodiversity might have divergent responses and divergent effects on ecosystem functioning depending on environmental perturbation, which highlight the importance of considering multiple aspects of biodiversity — taxonomic and functional approaches — in B-EF research. Overall, our results illustrated the potential for trait-based approaches to reveal biodiversity responses to environmental change and their generalizable effects on ecosystems. Furthermore, given the lack of large grazers in tropical and subtropical regions, and the evidence that Cyanobacteria dominance will increase in freshwater ecosystems under the predicted future climate, the results herein highlight the concern about the energy flow in aquatic systems dominated by Cyanobacteria.

Keywords: Biodiversity, Ecosystem functioning, Functional diversity, Selection effect, Complementarity, Eutrophication

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SUMÁRIO

1. INTRODUÇÃO GERAL

1.1 O DECLÍNIO GLOBAL DA DIVERSIDADE BIOLÓGICA

Nos dias atuais, é de comum consenso que a diversidade biológica do planeta está em declínio (McCann, 2000). Nos últimos 70 mil anos, *Homo sapiens* alterou a ecologia global a uma velocidade sem precedentes na história evolutiva, modificando abruptamente a flora e a fauna, levando à extinção milhares de espécies, de mamíferos a seres vivos microscópicos (Vitousek et al., 1997; Collen et al., 2013; Ceballos et al., 2015; Tilman et al., 2017). Nas últimas décadas, cientistas de diferentes áreas têm reunido esforços para tentar compreender como os ecossistemas respondem a essas reduções na diversidade biológica, objetivando melhores predições sobre o cenário futuro diante das mais variadas ameaças antrópicas (e.g*.,* perda e degradação de habitats, sobre-exploração de espécies, introdução de espécies exóticas, poluição, mudanças climáticas), assim como suas complexas interações e alterações associadas (Craig et al., 2017). Porém, apesar dos esforços, ainda não temos uma clara compreensão dos efeitos, principalmente em longo prazo, de modificações provocadas e/ou aceleradas pelo homem na diversidade de espécies e nos diferentes processos que ocorrem no ecossistema — metabolismo, decomposição, produção de biomassa, controle ascendente e descendente, dentre outras. Consequentemente ainda pouco se sabe sobre o impacto dessas alterações na provisão dos serviços ecossistêmicos essenciais à sociedade — provisão de alimento, água potável, combustíveis, energia, regulação do clima, controle de erosão, recreação, inspiração, dentre outros.

Atualmente, a diversidade biológica diminui a uma taxa muito mais acelerada em ambientes aquáticos continentais que nos marinhos ou terrestres (Collen et al., 2013). De acordo com o relatório Planeta Vivo 2020 (WWF, 2020), uma em cada três espécies de água doce se encontra ameaçada de extinção. No entanto, o mais alarmante é essa taxa ser subestimada por só levar em consideração espécies de vertebrados. Além disso, apesar da importância crucial da água doce para a vida, os ambientes aquáticos continentais apresentam as maiores taxas de degradação do habitat por poluição (WWF, 2020), uma das principais ameaças a biodiversidade e aos múltiplos usos desses ecossistemas (BPBES, 2020). Entre as principais formas de poluição, o enriquecimento de nutrientes, principalmente fósforo (P) e nitrogênio (N), associado às atividades humanas (eutrofização artificial) é a alteração antrópica mais estudada em ambientes de água doce (e.g., Vanni et al., 1987; Abrams, 1993; Hulot et al., 2000; Jeppesen et al., 2000; Kozlowsky-Suzuki & Bozelli, 2002; Jeppesen et al., 2003; Vakkilainen et al., 2004; Hessen et al., 2006; Moss et al., 2011; Decaestecker et al., 2015; Melo et al., 2019).

A eutrofização artificial ocorre mediante aporte de compostos orgânicos nos ecossistemas aquáticos provenientes de atividades agrícolas, urbanas e industriais. O aumento da carga de nutrientes altera a estrutura das comunidades aquáticas (Vanni et al., 1987; Hulot et al., 2000; Jeppesen et al., 2000; Kozlowsky-Suzuki & Bozelli, 2002) e o funcionamento do ecossistema (Abrams, 1993; Jeppesen et al., 2003; Melo et al., 2019), levando ao comprometimento da qualidade da água doce e consequentemente a redução da disponibilidade hídrica. Dessa forma, além dos custos ecológicos e sociais, os custos econômicos da eutrofização com políticas de resposta (e.g., tratamento de água potável para remoção de nutrientes, toxinas de algas e macrófitas) são altos (Pretty et al., 2003; Dodds et al., 2009). Segundo o relatório Riscos Globais 2020 (*Global Risks Report*) publicado pelo Fórum Econômico Mundial (FEM), o declínio significativo na qualidade e quantidade de água doce disponível está entre as 5 principais ameaças à prosperidade global na próxima década. Assim, diante do crescente desbalanço entre a disponibilidade e a demanda hídrica, compreender como a biodiversidade responde às crescentes ameaças antrópicas e afetam o funcionamento desses ecossistemas aquáticos é fundamental para uma gestão eficiente dos recursos hídricos (Daam et al., 2019).

1.2 BIODIVERSIDADE E FUNCIONAMENTO DO ECOSSISTEMA

Nos últimos 30 anos, a percepção científica da diversidade biológica passou por uma grande mudança de paradigma (Naeem, 2002). Antes considerada como variável dependente das propriedades e processos ecossistêmicos, a diversidade biológica era vista como mero resultado da atuação de fatores abióticos (e.g., disponibilidade de recursos) e bióticos (e.g., competição e predação). Embora a percepção da diversidade como um impulsionador dos processos do ecossistema tenha sido sugerida por Charles Darwin em 1859, o interesse em avaliar os efeitos da diversidade no funcionamento do ecossistema (B-EF), principalmente nos terrestres, aumentou somente nas últimas três décadas (Gamfeldt & Hillebrand, 2008). O marco inicial se deu em 1991 em uma conferência realizada na Alemanha para avaliar o conhecimento sobre as consequências da redução do número de espécies no funcionamento dos ecossistemas. O encontro resultou em um livro (Schulze & Mooney, 1993) e diversas outras publicações durante os anos 90 (e.g., Naeem et al., 1994, Tilman & Downing, 1994; Naeem et al., 1995;

Tilman et al., 1996; Chapin et al., 1997; Naeem & Li, 1997). Esses estudos, juntamente com as críticas em relação a validade das abordagens experimentais e interpretação dos resultados (Aarssen, 1997; Huston, 1997; Wardle, 1998; 1999; 2000), serviram de base para o refinamento não apenas do desenho experimental e dos métodos de análise empregados nos estudos B-EF, como também dos modelos propostos para explicar os mecanismos ecológicos subjacentes a relação entre a biodiversidade e os processos ecossistêmicos (Hooper & Vitousek 1997; Tilman et al., 1997; Loreau, 1998a; 1998b; Hector, 1998; Hector et al., 1999; Norberg, 2000; Loreau & Hector, 2001).

O efeito positivo da biodiversidade no funcionamento, estabilidade e serviços do ecossistema tem sido atribuído principalmente a dois mecanismos ecológicos: efeito de seleção (efeito de amostragem) (Hooper & Vitousek 1997; Tilman, 1997; Loreau, 1998a) e complementaridade (Loreau, 1998b; Norberg, 2000; Loreau & Hector, 2001) — o último reconhecido como o principal em ecossistemas terrestres (Hooper et al., 2005; Cardinale et al., 2007). Relações positivas podem surgir do efeito de seleção (Figura 1a) quando uma comunidade contém espécies com um conjunto de atributos funcionais particulares que proporcionam uma elevada habilidade competitiva (diferença de aptidão), permitindo melhor performance da comunidade no ambiente (Carroll et al., 2011; Godoy et al., 2020). Isso ocorre, pois, comunidades mais diversas têm maior probabilidade de conter espécies mais competitivas em seu *pool* regional; acompanhada de elevadas taxas de crescimento, tais espécies tendem a dominar a comunidade (Aarssen, 1997; Huston, 1997; Hector, 2002). Por outro lado, a complementaridade total (Figura 1b) ou parcial (Figura 1c) ocorre quando diferenças funcionais ou genéticas entre as espécies (relacionadas a diferenças em nicho ecológico) reduzem a competição interespecífica, aumentando a performance da comunidade no ambiente (Carroll et al., 2011; Turnbull et al., 2012; Godoy et al., 2020). Nesse cenário, a coexistência é possível pois as espécies podem diferir de três formas: no uso do recurso (partição de nicho), na capacidade de alterar o ambiente (facilitação abiótica), e/ou na forma de interagir com outras espécies (Barry et al., 2018). Especificamente, a partição de nicho (i.e., complementaridade de recursos) pode ocorrer mediante uso de diferentes tipos de recursos (e.g., uso de nutrientes, luz, água, dentre outros), em diferentes proporções, escalas de tempo (particionamento espacial) e/ou espaço (particionamento temporal) (Chesson, 2000; Barry et al., 2018). A partição de nicho é comumente considerada a principal causa do efeito positivo da biodiversidade no funcionamento do ecossistema.

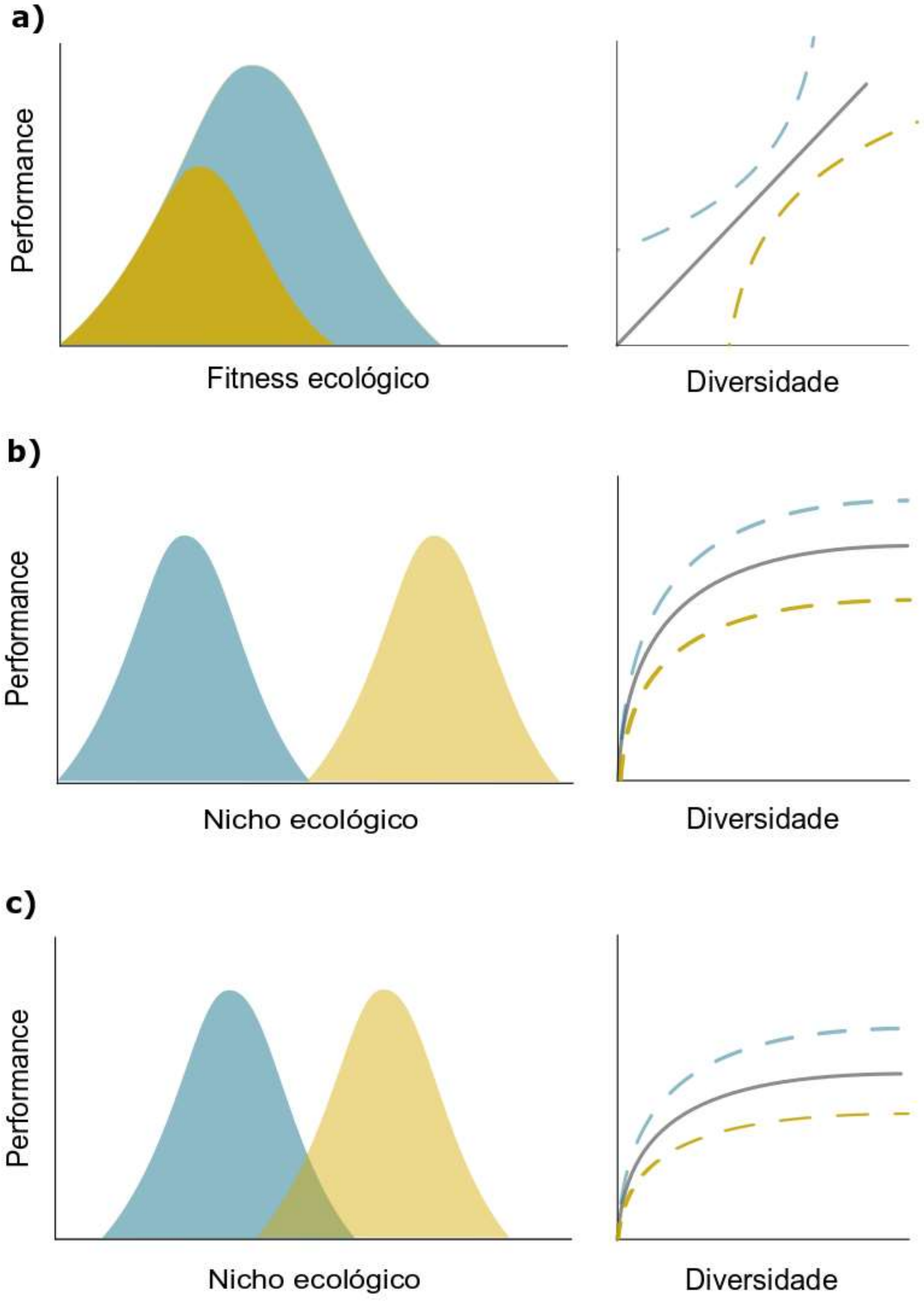

Figura 1 Modelo conceitual exemplificando a relação entre a performance dos organismos, a diversidade biológica, e os mecanismos subjacente a relação, diferença de aptidão (fitness) (**a**) e diferença de nicho ecológico (**b** e **c**). Figura adaptada de Schmid et al., 2002.

No entanto, apesar das tentativas de separar os efeitos desses dois mecanismos (e.g., Loreau & Hector, 2001; Fridley, 2001; Cardinale et al., 2006; Ye et al., 2013; Gianuca et al., 2016), os efeitos de seleção e a complementaridade não devem ser entendidos como explicações opostas, mas sim como mecanismos que atuam simultaneamente (Ye et al., 2013; Gianuca et al., 2016). Por exemplo, se uma comunidade contém duas ou mais espécies competitivamente superiores e dominantes que não coexistem simultaneamente, porém são altamente complementares no tempo (*complementary dominant species*), o efeito de seleção (i.e., poucas espécies com efeitos dominantes) predomina, mas a importância relativa da complementaridade aumenta com o tempo (Fridley, 2001; Allan et al., 2011). Nesse caso, ambos, mecanismos — efeito de seleção e complementaridade, atuam nas relações B-EF, o que dificulta a separação de seus efeitos. Além disso, estudos que quantificam a complementaridade geralmente confundem o seu efeito (consequência) com as possíveis causas (i.e., partição de nicho, facilitação abiótica e interações tróficas), falhando em demonstrar como a perda de espécies compromete o funcionamento do ecossistema (Barry et al., 2018). No entanto, separar as causas da complementaridade e entender como elas interagem entre si e geram os padrões observados nas relações B-EF é uma tarefa complexa, já que a partição de recursos, a facilitação abiótica e as interações tróficas ocorrem simultaneamente na natureza (mas veja Barry et al., 2018).

1.3 O TAMANHO DO CORPO COMO UM IMPORTANTE ATRIBUTO FUNCIONAL

Nos ambientes aquáticos, o tamanho do corpo é considerado um importante atributo funcional por ser intimamente associado com diferentes processos fisiológicos dos organismos (e.g., taxa de crescimento, reprodução, respiração, herbivoria, dentre outras), influenciando o papel ecológico que eles desempenham no ecossistema (*effect-trait*) e suas respostas a diferentes distúrbios antrópicos (*response-trait*) (Peters, 1983; Brown et al., 2004; Woodward et al., 2005; White et al., 2007; Reiss et al., 2009; Woodward et al., 2011; Yvon-Durocher et al., 2011). Dessa forma, medir o tamanho do corpo é uma maneira conveniente de obter informações sobre o nicho ecológico em um único parâmetro por duas razões. Primeiro, o tamanho do corpo é um parâmetro facilmente obtido na natureza (ou na literatura), excluindo a necessidade da observação direta de múltiplas características (Woodward et al., 2005). Segundo, o uso de um único atributo funcional remove os efeitos de possíveis sinais contrastantes entre características que podem cancelar umas às outras ou então introduzir efeitos de confusão na análise (Butterfield & Suding, 2013).

Nas relações consumidor-recurso, diferenças no tamanho do corpo podem permitir a partição de nicho na comunidade, pois geralmente limitam fisicamente o tamanho da partícula de alimento que pode ser ingerida pelos consumidores (Burns, 1968; Neil, 1975). Especificamente para organismos filtradores como o zooplâncton, o tamanho do corpo determina o fluxo de alimento ingerido e, portanto, está diretamente relacionado com as taxas de filtração da comunidade (Hansen, 1997). O tamanho do corpo do zooplâncton tem um papel fundamental na determinação do controle descendente (*top-down*) das algas (Jeppesen et al., 2003; Ye et al., 2013; Thompson et al., 2015; Gianuca et al., 2016b; Wong et al., 2016) — um processo ecossistêmico chave para manutenção de diversos serviços fornecidos pelos ambientes aquáticos, como provisão de água potável e alimento, serviços culturais e recreacionais. No entanto, esses resultados são baseados em espécies que apresentam maior tamanho corporal (e.g*., Daphnia magna*), comumente encontradas em ambientes temperados (Jeppesen et al., 2003; Thompson et al., 2015; Gianuca et al., 2016b). Dessa forma, permanece incerto se o tamanho do corpo teria o mesmo impacto no funcionamento de ecossistemas tropicais e subtropicais onde a comunidade zooplanctônica é composta basicamente por organismos de pequeno porte e a diversidade de tamanho é reduzida (Lacerot et al., 2013).

A relação entre o tamanho do corpo do zooplâncton e o controle *top-down* das algas pode ser explicada através dos mecanismos descritos acima (subseção 1.2). Em um estudo recente, Gianuca et al. (2016*b*) propôs a separação desses dois mecanismos (efeito de seleção e complementaridade) com base na importância relativa do tamanho médio da comunidade e da diversidade de tamanho. No efeito de seleção, espécies de maior tamanho corporal são competitivamente superiores a espécies de menor tamanho (Brooks & Dodson, 1965; Mourelatos & Lacroix, 1990) e portanto, apresentam elevadas taxas de herbivoria sobre uma ampla faixa de tamanho de algas (células grandes e pequenas). Nesse cenário, as espécies grandes melhoram a performance da comunidade no ambiente e dessa forma, o tamanho médio da comunidade é responsável pela relação positiva entre a diversidade e o controle *top-down* (Gianuca et al., 2016b). Por outro lado, quando há partição de nicho com base no tamanho do corpo, a complementaridade entre espécies zooplanctônicas grandes e pequenas é o principal mecanismo responsável pela relação positiva entre a diversidade e o *controle top-down* das algas (Ye et al., 2013). Nesse cenário alternativo, a variedade de recursos permite que espécies zooplanctônicas de maior tamanho corporal apresentem maiores taxas de herbivoria sobre algas grandes, enquanto espécies de menor tamanho apresentam maiores taxas de herbivoria sobre algas pequenas (Hansen et al., 1994; Cyr & Curtis, 1999). Aqui, a diversidade de tamanho da comunidade é responsável pela relação positiva entre a diversidade e o controle *top-down*. No entanto, alguns estudos apontam que as taxas de filtração podem estar mais relacionadas ao modo de alimentação (Geller & Müller, 1981; Hansen et al., 1994; Hansen, 1997; Sommer et al., 2000, 2001, 2002) do que ao tamanho do corpo (DeMott, 1989). Além disso, grandes cladóceros podem apresentar uma razão específica entre o tamanho da presa e o tamanho do corpo menor do que de copépodes de tamanho médio, que por sua vez podem ingerir tamanhos de presas maiores do que de cladóceros grandes (Geller & Müller, 1981).

1.4 RELAÇÃO ENTRE A DISPONIBILIDADE DE NUTRIENTES, DOMINÂNCIA DE CIANOBACTÉRIAS E ZOOPLÂNCTON

Nas últimas décadas, florações de cianobactérias aumentaram em magnitude e frequência em ecossistemas aquáticos continentais ao redor do mundo (Sukenik et al., 2015). O principal motivo foi o efeito combinado de enriquecimento de nutrientes (eutrofização artificial) e mudanças climáticas, como aumento da temperatura superficial da água e mudanças nos padrões de precipitação (Paerl et al., 2011; Kosten et al., 2012; Yang et al., 2016; Walls et al., 2018). A eutrofização artificial tem um efeito seletivo na comunidade fitoplanctônica, favorecendo a proliferação de cianobactérias em detrimento de outras espécies (Reynolds, 1987; Downing et al., 2001; Paerl & Huisman, 2008; 2009; Soares et al., 2013). Esta relação positiva entre o aumento da carga de nutrientes e a dominância de cianobactérias desenvolve prolongadas florações, aumentando o risco de liberação de toxinas nesses ambientes. No entanto, florações de cianobactérias não se restringem a sistemas eutróficos; podem ocorrer em ambientes que apresentam baixas concentrações de nutrientes (oligotróficos) (Chislock et al., 2014; Cottingham et al., 2015; Tonetta et al., 2015), tornando a relação cianobactéria-nutriente complexa. A maioria dos estudos empíricos sobre esta relação foca principalmente nos efeitos do aumento de P sobre a composição e estrutura do fitoplâncton (Rose et al., 2017). Porém, pouco se sabe sobre os efeitos desse aumento a longo prazo na performance dessas comunidades (e.g., eficiência de uso dos nutrientes limitantes), assim como os possíveis efeitos de retroalimentação na disponibilidade de nutrientes dos ambientes aquáticos.

Além de representarem uma séria ameaça à saúde de seres humanos e outros animais (Carmichael et al., 2001), devido à forte influência da qualidade do alimento na fisiologia do indivíduo (captação, incorporação e excreção) (Frost et al., 2005), florações de cianobactérias desencadeiam uma série de modificações na composição, estrutura e dinâmica das comunidades aquáticas (Ersoy et al., 2017; Josué et al., 2019). Para o zooplâncton, qualidade do fitoplâncton varia de acordo com o estado trófico do ambiente, podendo limitar não apenas o crescimento e a reprodução (Elser et al., 2000; 2001; Jensen et al., 2004), como também a performance (e.g., taxa de pastejo, respiração, excreção, dentre outras) desses organismos nos ecossistemas aquáticos (Hessen & Andersen, 1990), principalmente de grandes cladóceros (Hawkins & Lampert, 1989). Geralmente, cianobactérias são reconhecidas como um recurso alimentar inadequado para o zooplâncton devido ao seu baixo valor nutricional (Elert et al., 2013) e a produção de toxinas (Infante & Riehl, 1984; Fulton & Paerl, 1987*a*, 1988; Wilson et al., 2006 Ger et al., 2016). Além disso, a complexa morfologia (filamentos e colônias) de algumas espécies pode reduzir as taxas de filtração do zooplâncton (Fulton & Paerl, 1987*b*), comprometendo o importante controle que esses organismos exercem sobre as algas (controle *top-down*) nos ambientes aquáticos (Wilson et al., 2006). No entanto, relações positivas entre o zooplâncton, incluindo grandes cladóceros como *Daphnia magna*, e as cianobactérias já podem ser explicadas por processos evolutivos que influenciam a performance do zooplâncton, bem como pela resistência do fitoplâncton ao pastejo (Schaffner et al., 2019) e/ou pelo comportamento de alimentação seletiva que algumas espécies de zooplâncton apresentam (Rose et al., 2017; Ger et al., 2018; Leitão et al., 2018; Leitão et al., 2020).

Além do efeito indireto, através do fitoplâncton, sobre o zooplâncton, a disponibilidade de nutrientes também pode apresentar um efeito direto sobre a composição e estrutura da comunidade, alterando o papel funcional desses organismos nos ecossistemas aquáticos (Hulot et al., 2000). O crescimento de espécies de zooplâncton que apresentam maior tamanho corporal é fortemente reduzido em condições oligotróficas associadas a baixas concentrações de P (Hessen & Andersen, 1990; Andersen & Hessen 1991; Sommer, 1992; Urabe et al., 1997; DeMott et al., 1998; Schulz & Sterner 1999; Guo et al., 2019; Hartnett, 2019). Isso ocorre porque organismos de grande tamanho corporal geralmente apresentam uma maior demanda energética, e por isso não conseguem sobreviver em ambientes oligotróficos. Geralmente, esse filtro ambiental (i.e., baixa concentração de nutrientes) leva a exclusão de espécies zooplanctônicas grandes, favorecendo a dominância de espécies pequenas, levando a redução tanto da diversidade de tamanho, quanto do tamanho médio da comunidade (Dodson et al. 2000; Gianuca et al. 2017). Por outro lado, estudos demonstram que na ausência de peixes e cianobactérias, o aumento da carga de nutrientes, principalmente P, favorece o aumento do tamanho médio da comunidade (Dodson et al. 2000). No entanto, ainda não está claro se a eutrofização também aumenta a diversidade de tamanho da comunidade ou se leva apenas a dominância de espécies grandes e à exclusão competitiva de espécies pequenas, sendo necessário mais estudos sobre o efeito da estrutura de tamanho no funcionamento do ecossistema em resposta ao aumento de nutrientes nos ecossistemas aquáticos.

1.5 O CASO PECULIAR DA LAGOA DO PERI

1.5.1 Caracterização da área

A lagoa costeira subtropical do Peri é a maior lagoa de água doce do litoral de Santa Catarina (aproximadamente 5,07 km^2 de área) (CECCA, 1997; Baptista & Nixdorf, 2014), localizada na costa sudeste da ilha de Florianópolis (27° 43′ S; 48° 30′ W; Figura 2). A lagoa está inserida em uma área de preservação ambiental (Parque Municipal da Lagoa do Peri – PMLP) que recentemente passou por uma recategorização em seu enquadramento para Unidade de Conservação Monumento Natural Municipal (MONA) da Lagoa do Peri pela Lei Municipal 10.530/2019. Sua área é delimitada por uma bacia hidrográfica (aproximadamente 20,1 Km^2, profundidade média e máxima igual a 4,2 m e 11,0 m, respectivamente) rodeada nas porções Norte, Oeste e Sul por formações de Mata Atlântica, em diferentes estágios secundários de vegetação (Teive et al., 2008, Cardoso et al., 2008), além de uma área de reflorestamento de espécies exóticas em suas margens (*Pinus ellioti* e *Eucaliptus*). Apesar da proximidade com o mar, a lagoa não sofre influência das oscilações da maré, pois se encontra aproximadamente a 3 metros acima do nível do mar, no entanto mantém contato intermitente com o oceano através de um canal (rio Sangradouro) de sentido único (Teive et al., 2008; Baptista & Nixdorf, 2014). Apresenta como principais tributários os rios Cachoeira Grande e Ribeirão Grande, situados ao Sul e a Oeste da bacia, respectivamente (Figura 2), que juntamente com a densa vegetação desempenham um importante papel na regularização do fluxo e controle da qualidade de água da lagoa.

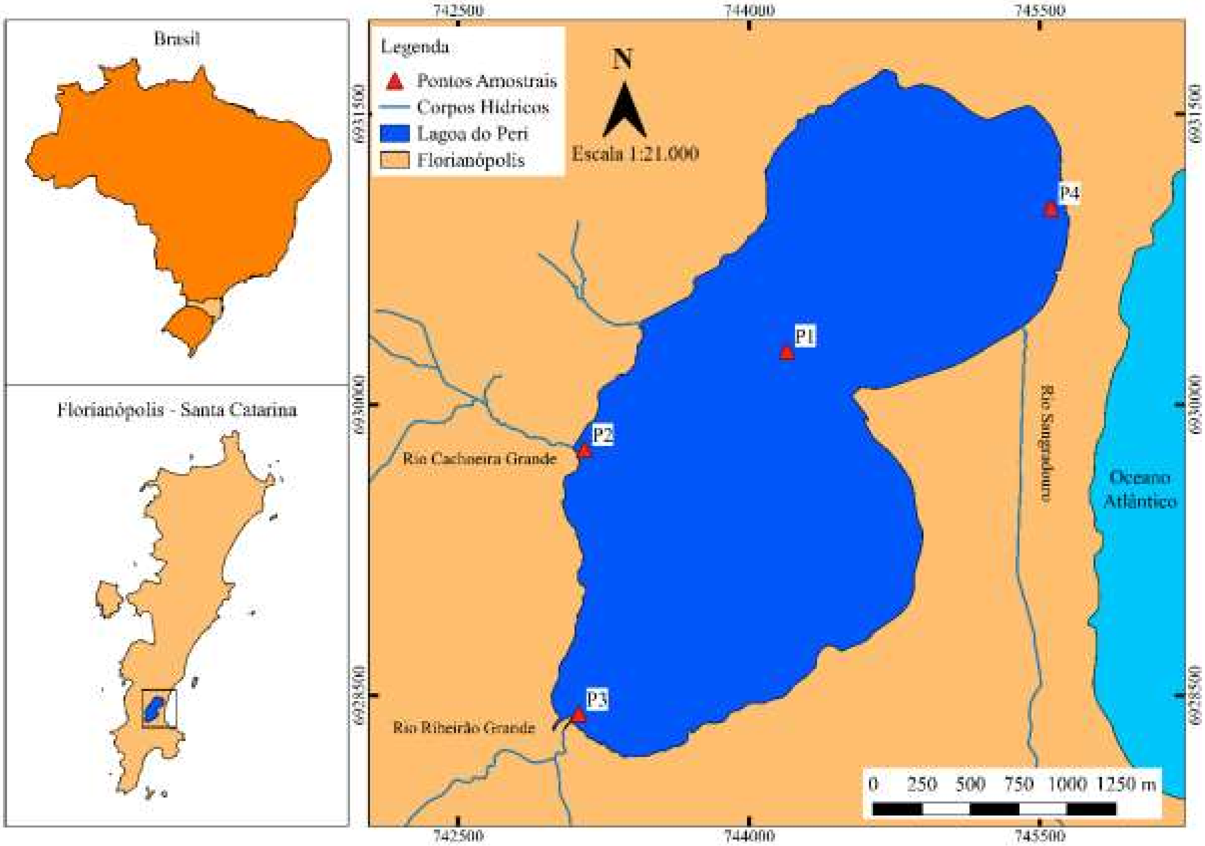

Figura 2 Mapa da Lagoa do Peri, Santa Catarina, Brasil, ilustrando os pontos de amostragem (P1, P2, P3 e P4) onde foram coletados dados observacionais para elaboração dos capítulos 1 e 2. Projeção: Mercator Transversal Universal. DATUM: SIRGAS 2000. Shapefile: Secretaria de Desenvolvimento Sustentável do Estado de Santa Catarina, 2012; Agência Nacional de Águas, 2012 e Infraestrutura e Planejamento Urbano de Florianópolis, 2012.

Além de sua importância ecológica (e.g., conservação da biodiversidade e da geodiversidade, preservação e restauração de matas ciliares, dentre outros) e social (e.g., promoção de atividades de pesquisa, ecoturismo e educação ambiental, preservação do patrimônio histórico, cultural e arqueológico, dentre outros), desde o ano de 2000 o manancial hídrico da Bacia da Lagoa do Peri vem sendo utilizado pela Companhia Catarinense de Águas e Saneamento (Casan) para o abastecimento público de água para a população das regiões Leste e Sul da ilha de Florianópolis. No entanto, desde o último ano observa-se severa redução do volume de água na lagoa, preocupando a comunidade científica e a população local sobre a degradação do manancial e a iminência de um colapso no abastecimento de água da região. Além disso, acompanhada a esta redução do volume de água, foi observado um aumento na densidade de cianobactérias potencialmente tóxicas, sendo constatada uma concentração superior às concentrações anteriores (Grellmann, 2006; Hennemann & Petrucio, 2011; Tonetta et al., 2013; Baptista & Nixdorf, 2014). Florações de cianobactérias merecem especial atenção e monitoramento, pois além de comprometerem biodiversidade local — i.e., alterar a composição, estrutura e dinâmica das comunidades aquáticas — também podem comprometer o abastecimento de água potável para população (Pretty et al., 2003; Dodds et al., 2009).

1.5.2 O estado da arte sobre os estudos na Lagoa do Peri

Devido à topografia da região e, principalmente, à intensa ação do vento, a Lagoa do Peri apresenta homogeneidade espacial (horizontal e vertical) em todas as estações do ano (Hennemann & Petrucio 2011), sendo classificada como um sistema de circulação polimítica (Tonetta et al., 2013). Com uma zona eufótica geralmente menor que a zona de mistura, a lagoa é caracterizada como um ambiente limitado por luz (Laudares-Silva, 1999), meso-eutrófica para a transparência e concentração de clorofila-*a*, e oligotrófica para a concentração de nutrientes (Hennemann & Petrucio 2011), com potencial limitação de P (Hennemann et al., 2015). No entanto, recentemente tem se constatado um aumento da concentração de clorofila-*a* na água (Hennemann et al., 2016) e de matéria orgânica e nutrientes “aprisionados” no sedimento (Hennemann et al. 2015), que somadas a prolongada dominância de cianobactéria observada nas últimas décadas (Tonetta et al., 2015) são fortes indicativos de que a lagoa está passando por um processo de eutrofização. Além disso, mudanças climáticas, como o aumento de temperatura e alterações nos regimes de precipitação, potencialmente contribuem para liberação de matéria orgânica e nutrientes do sedimento para a coluna d’água, e consequentemente para o aumento da produtividade primária na lagoa (Lemes-Silva et al. 2020).

Além dos fatores climáticos, muitas espécies de cianobactéria capazes de fixar nitrogênio atmosférico (N_2) ou então de acessar o P imobilizado nos sedimentos ou em águas profundas são potenciais fontes de N e P para os ambientes de água doce (Agawin et al., 2007; Elser et al., 2007; Cottingham et al., 2015). Em ambientes oligotróficos, como a Lagoa do Peri, essas espécies contribuem significativamente para o aumento da quantidade desses nutrientes na água, facilitando o crescimento de outras espécies de fitoplâncton, assim como o processo de transição para um estado eutrófico através da redução da resiliência (*sensu* Holling, 1973) do ecossistema (Cottingham et al., 2015). Desde meados de 1990, vem sendo registrada na Lagoa do Peri a presença da cianobactéria fixadora de N_2, *Raphidiopsis raciborskii* (Woloszynska) Aguilera, Berrendero Gómez, Kastovsky, Echenique & Salerno (basionym *Cylindrospermopsis raciborskii* (Woloszynska 1912) Seenayya et Subba Raju, 1972) (Aguilera et al., 2019), assim como o aumento da sua abundância relativa e dos prolongados períodos de dominância (Laudares-Silva, 1999; Grellmann, 2006; Hennemann & Petrucio, 2011; Tonetta et al., 2013; Baptista & Nixdorf, 2014). Devido a sua alta afinidade por uma ampla variedade de recursos e grande capacidade de armazenamento de P, essa cianobactéria apresenta uma elevada habilidade competitiva, principalmente em ambientes que apresentam limitação de P. Entre 2004 e 2005 registrou-se na lagoa a dominância de *R. raciborskii*, assim como a presença de outras espécies de cianobactéria potencialmente tóxicas, como *Microcystis irregulare*, *Pseudoanabaena galeata* e *Limnothrix planctonica* (Laudares-Silva, 1999; Grellmann, 2006). Entre junho de 2009 e janeiro de 2011, Tonetta et al. (2013) observaram uma alternância de dominância entre a espécie *R. raciborskii* e *Limnothrix redekei*, em que *L. redekei* foi dominante apenas nos meses de novembro/2009 e dezembro/2009. Essa alternância de dominância foi associada ao aumento da temperatura e da concentração de P na lagoa, e diminuição na velocidade do vento. Além desses táxons, os autores registraram uma alta frequência de ocorrência (< 80%) das espécies de cianobactéria filamentosas *Planktolyngbya brevicellularis* e *Planktolyngbya limnetica* durante o período de estudo. Além disso, em uma recente nota técnica emitida no dia 23 de novembro de 2020 pelo Laboratório de Ficologia da Universidade Federal de Santa Catarina, foi constatada floração da alga verde *Botryococcus sp.*, sendo mais um forte indicativo de que a Lagoa do Peri está passando por um processo de eutrofização.

2 OBJETIVOS

2.1 Objetivo geral

Nessa tese eu proponho que a disponibilidade de nutrientes e a dominância de cianobactérias alteram a biodiversidade e o funcionamento dos ecossistemas aquáticos, principalmente através de seus efeitos sobre a estrutura e composição das comunidades planctônicas. Especificamente, proponho que os mecanismos — efeito de seleção e complementaridade — subjacentes as relações B-EF atuam de forma complementar, e que a importância relativa de cada mecanismo varia de acordo com a escala de tempo. Além disso, sugiro que o uso de uma abordagem baseada em atributos funcionais tanto de resposta (i.e., como a comunidade responde a mudança) quanto de efeito (i.e., como esta comunidade alterada afeta os processos ecossistêmicos), como o tamanho do corpo, trazem uma melhor compreensão sobre os padrões de organização das comunidades biológicas e da relação das mesmas com o funcionamento dos ecossistemas aquáticos diante de gradientes de perturbação que influenciem este atributo funcional. Para avaliar tais hipóteses, exploro os mecanismos ecológicos subjacentes a relação entre a biodiversidade e o funcionamento dos ecossistemas aquáticos utilizando uma combinação de abordagens experimentais e observacionais, além de diferentes técnicas taxonômicas e funcionais para estimativa da diversidade biológica. Estruturo esta tese de doutorado em três capítulos (Figura 3) nos quais respondo a diferentes perguntas, detalhadas a seguir.

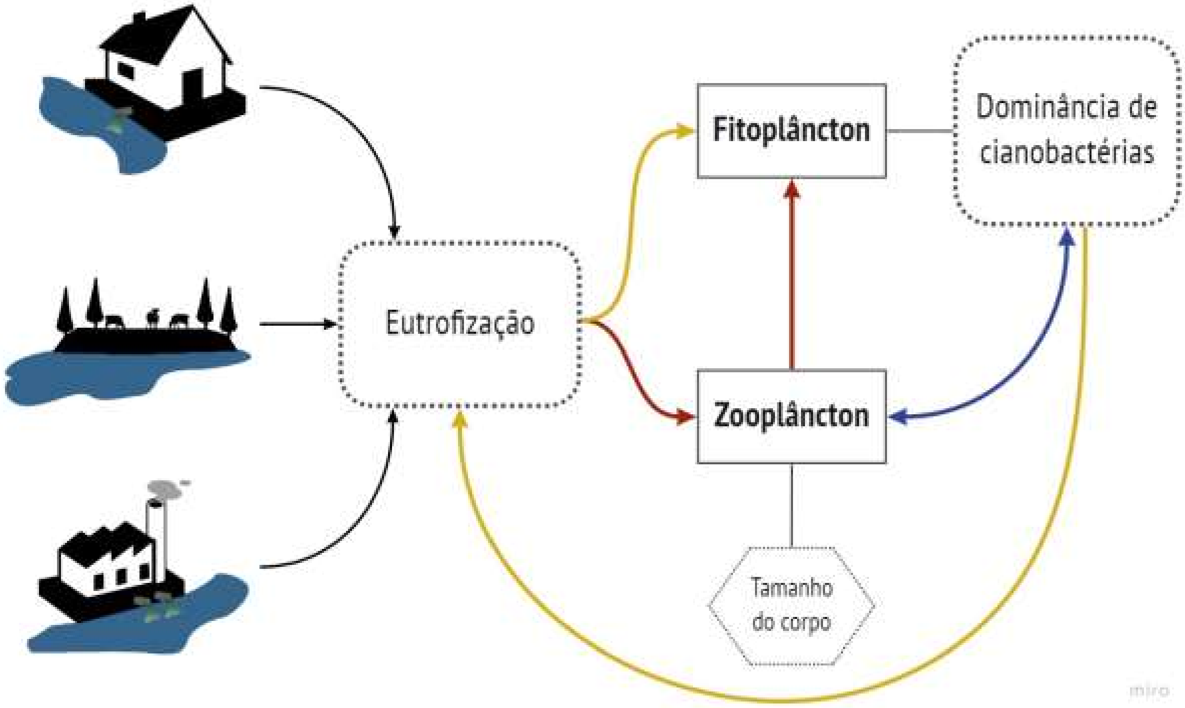

Figura 3 Fluxograma da estrutura da dissertação de doutorado. Linha continua amarela representa o primeiro capítulo, linha continua azul representa o segundo capítulo, e linha continua vermelha representa o terceiro capítulo.

2.2 Objetivos específicos

Capítulo 1: Negative biodiversity effects caused by cyanobacteria dominance decreases resource use efficiency overtime

Nesse capítulo, eu e meus coautores avaliamos a relação entre múltiplos aspectos da diversidade biológica (riqueza, uniformidade e *turnover* funcional) e a eficiência no uso de recursos limitantes (nitrogênio e fósforo) pelo fitoplâncton em uma lagoa que está passando por um processo de eutrofização (Figura 3; linha continua amarela) para responder as seguintes perguntas:

i. Como a diversidade e composição do fitoplâncton respondem ao aumento de nutrientes na lagoa?

ii. Como é a relação entre a diversidade (riqueza e uniformidade), o *turnover* entre grupos funcionais (relação diversidade-*turnover*) e o uso de N e P (relação diversidade-funcionamento do ecossistema)?

iii. Qual é a importância relativa de possíveis mudanças na biodiversidade e no *turnover* entre grupos funcionais para eficiência no uso de N e P?

iv. Quais são os possíveis efeitos a longo prazo do aumento de nutrientes para o funcionamento do ecossistema?

Para tal, utilizamos uma série temporal de 8 anos (2009 – 2018) de coletas mensais de dados abióticos e bióticos no ponto de amostragem P1 (Figura 2) provenientes do programa de monitoramento da Lagoa do Peri realizados pelo Laboratório de Ecologia de Águas Continentais (LIMNOS). Especificamente, neste capítulo testamos as seguintes hipóteses: (**H_1**) comunidades fitoplanctônicas dominas por cianobactérias exibem taxas de turnover mais lentas do que comunidades mais uniformes (i.e., menor evenness, mais lento *turnover* temporal); (**H_2**) a uniformidade do fitoplâncton é negativamente relacionada a RUE (i.e., menor evenness, maior RUE); (**H_3**) variações na composição dos RFGs predizem melhor a variação em RUE do que riqueza de espécies ou a uniformidade; (**H_4**) o aumento de nutrientes reduz RUE ao longo do tempo.

Capítulo 2: Grazing efficiency asymmetry drives zooplankton top-down control on phytoplankton in a lake dominated by non-toxic cyanobacteria

Nesse capítulo, eu e meus coautores avaliamos a importância da diversidade de tamanho e composição do zooplâncton para o controle *top-down* das algas em uma lagoa que apresenta prolongada dominância de cianobactérias (Figura 3; linha continua azul) para responder as seguintes perguntas:

i. Qual é a importância relativa do tamanho do corpo do zooplâncton e da riqueza de espécies para o controle top-down das algas?

ii. Qual é o principal mecanismo (efeito de seleção ou complementaridade) pelo qual o tamanho do corpo opera a relação entre a diversidade e controle *top-down* das algas nesses ambientes?

Aqui, avaliamos dados abióticos e bióticos correspondentes a um período de 12 meses consecutivos (abril 2011 – março 2012) de coleta de campo em quatro pontos de amostragem (P1-P4; Figura 2) na Lagoa do Peri. Especificamente, neste capítulo testamos as seguintes hipóteses: (**H_1**) abordagens baseadas no atributo funcional tamanho do corpo aumentam nossa capacidade de explicar o controle *top-down* das algas em comparação com a abordagem mais tradicional baseada em táxons; (**H_2**) a complementaridade no uso de recursos entre espécies que variam no tamanho do corpo é o principal mecanismo que liga o tamanho do corpo ao controle *top-down* do fitoplâncton, como sugerido por Ye et al. (2013).

Capítulo 3: Trait-based zooplankton community assembly and the functioning of aquatic ecosystems along a productivity gradient.

Nesse último capítulo, eu e meus coautores avaliamos como a diversidade de tamanho e composição do zooplâncton em condições experimentais respondem a um gradiente de adição de nutrientes, e como tais respostas afetam o controle *top-down* das algas (Figura 3; linha continua vermelha) para responder as seguintes perguntas:

i. Como a diversidade de tamanho e composição do zooplâncton respondem a um gradiente de adição de fósforo?

ii. Essa resposta é modificada pela presença de macrófitas artificiais?

iii. Qual é a importância relativa do tamanho médio da comunidade e da diversidade de tamanho para o controle *top-down* das algas?

iv. Qual é a importância relativa das mudanças na diversidade de tamanho e composição do zooplâncton em resposta à adição de fósforo em comparação com o efeito da adição de fósforo *per se* para o controle *top-down* das algas?

Para tal, utilizamos um subconjunto dos dados de um experimento *outdoor* de montagem de metacomunidades (ARENA) realizado durante 66 dias em Heverlee na Bélgica no ano de 2005. Esse banco de dados foi disponibilizado pelo Dr. Steven Declerck (NIOO-KNAW, Holanda) e pelo Dr. Luc De Meester (KU Leuven, Bélgica).

CAPÍTULO I

Manuscrito a ser submetido ao periódico *Freshwater Biology*

Negative biodiversity effects caused by cyanobacteria dominance decreases resource use efficiency over time

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ABSTRACT

1. In freshwater ecosystems, eutrophication and cyanobacterial blooms are global scale pressures increasingly affecting biodiversity and many functions (i.e., resource use efficiency - RUE) in aquatic ecosystems. However, despite the cumulative knowledge over the last decades, it remains unclear to what extent human-driven modifications in biodiversity translates into change in the rates of specific ecosystem processes in naturally assembled communities.
2. Here, we analyzed the relationships between different measures of phytoplankton diversity (richness, evenness, and functional diversity), temporal turnover of phytoplankton Reynolds functional groups (RFGs) and RUE of phosphorus (TP) and nitrogen (TN), over 8 years in a cyanobacteria-dominated subtropical lake. We also aimed at evaluating the resource availability effects on phytoplankton and RUE.
3. As hipothesized, we found slower temporal turnover rates of RFGs and higher RUE when Cyanobacteria dominated phytoplankton. However, contrary to our expectations, changes in phytoplankton biomass predicted variation in RUE better than species richness, evenness or functional diversity. Finally, we found no significant nutrient effects on phytoplankton community structure and composition, but we demonstrated a strong negative effect of TP and TN on RUE, indicating a progressively lower efficiency in resource use with increasing supply of TP and TN.
4. Our findings point out that nutrient increasing along with prolonged Cyanobacteria dominance might have negative effects on biodiversity and ecosystem functioning over time.
5. We emphasize that future studies should evaluate the long-term effects of multiple biodiversity measures, such as evenness and community turnover, on ecosystem processes in order to achieve effective restoration management in highly disturbed aquatic ecosystems.

INTRODUCTION

The primary hypothesis of diversity-productivity relationships posits that more diverse communities result in more efficient use of the limiting resources and therefore allows greater biomass production (Cardinale et al., 2006; Cardinale et al., 2012; Gross & Cardinale, 2007; Hector et al., 1999; Naeem et al., 1994; Tilman, Lehman, & Thomson, 1997). The positive relationship between diversity and productivity often observed in terrestrial ecosystems has mainly been attributed to two well-known mechanisms: selection effect (aka sampling effect) (Hooper & Vitousek 1997; Loreau, 1998a; Tilman, 1997) and resource-use complementarity (Loreau, 1998b; Loreau & Hector, 2001; Norberg, 2000). The latter is often recognized as the main mechanism driving diversity-productivity relationships in plant communities (Cardinale et al., 2007; Hooper et al., 2005). Positive relationships may arise from selection effect when a community contains highly productive species with a set of certain functional traits (i.e., dominant traits) that enable them to better exploit limiting resources (aka *fitness* difference). This occur because more diverse communities are more likely to contain such species (Aarssen, 1997; Hector, 2002; Huston, 1997). On the other hand, complementarity takes place when a community contains a greater number of coexisting species with niche differences (i.e., reduced niche overlap) that allow for a more complete and efficient use of the limiting resources compared with less diverse communities. Yet, observational studies and experiments aimed at quantifying the relative importance of each mechanism have yielded mixed results (van der Plas, 2019), and it remains unclear to what extent an increase in species diversity translates into changes in the rates of specific ecosystem processes in naturally assembled communities.

In phytoplankton communities, most research has largely focused on the effect of species richness on resource use efficiency (RUE) (Chai et al., 2020; Lehtinen et al., 2017; Ptacnik et al., 2008; Striebel, Behl, & Stibor, 2009), but the impact of other components of species diversity, such as evenness, on RUE is still poorly understood. Recent studies indicated that phytoplankton evenness has stronger effects on ecosystem functioning than species richness (Filstrup et al., 2014; Filstrup et al., 2019; Hodapp et al., 2015; Lehtinen et al., 2017), providing additional information that will be independent of variance in the number of species (Wilsey et al. 2005), especially in highly disturbed ecosystems where a single dominant taxa tends to dominate (Hillebrand, Bennett, & Cadotte, 2008). However, a negative (e.g., Filstrup et al., 2014) and positive (e.g., Tian et al., 2017) phytoplankton evenness-RUE relationship has been recorded associated to Cyanobacteria dominance. Cyanobacterial can use TP more efficiently than others phytoplankton taxa. Indeed, the relative abundance of few cyanobacteria species generally increase with nutrient concentrations (Jeppesen et al. 2000; Paerl & Huisman, 2008; Reynolds, 1987; Soares et al., 2013). Yet, recent studies revealed the ability of some cyanobacteria species to dominate phytoplankton communities even under low nutrient concentrations (Tonetta et al., 2015) or extreme nutrient ratios (Chislock, Sharp, & Wilson, 2014), and it is still unclear whether cyanobacteria dominance in oligotrophic lakes would have a similar impact on RUE.

Some cyanobacteria can fix atmospheric nitrogen (i.e., N_2-fixing) playing an important role in biogeochemical cycles, primary productivity (Litchman et al., 2015; Reynolds, 2006) and lake trophic state (Cottingham et al., 2015). For instance, N_2-fixing cyanobacteria release high rates of nitrogen in biologically available forms (e.g., ammonium) promoting the growth of other phytoplankton species and, thus, the coexistence of N_2-fixing and non-N_2-fixing phytoplankton species (Agawin et al., 2007). The nitrogen release by Cyanobacteria is also an important determinant of nutrient dynamic, especially in low-nutrient systems (Cottingham et al., 2015). Specifically, Cyanobacteria have the potential to alter N and P availability (Elser et al., 2007), and shift freshwater ecosystems from a low-nutrient and clear-water state to a high-nutrient and turbid-water state (Cottingham et al., 2015). In this case, measures of species dominance should complement measures of species richness and contribute to deepening our understandings of diversity-productivity relationship in lakes undergoing eutrophication processes.

In general, the effect of biodiversity on productivity relies on the niche differences among species within a community (Schimid et al., 2002), which is better represented by functional traits (Violle et al. 2007). Over the last three decades, an increasing number of studies have been highlighting the importance of considering functional traits in B-EF research, rather than species richness as the sole measure of species diversity (Abonyi, Horváth, & Ptacnik, 2018; Lavorel & Garnier, 2002; Pinheiro-Silva, et al., 2020; Schimid et al., 2002; Violle et al., 2007) since traits impact ecological fitness via their effects on individual performance (Litchman et al., 2015; Violle et al., 2007). Further, changes in organismal performance (e.g., growth, reproduction, and survival) should be related to changes in trait values mainly linked to resource acquisition and utilization (Schimid et al., 2002), since they link ecological processes at individual-level with biogeochemical cycles (Litchman et al., 2015). For example, several physiological traits related to resource acquisition and utilization of N_2-fixing cyanobacteria are distinct from those of non-N_2-fixing phytoplankton species (Berman-Frank et al., 2007). Such adaptations are key factors in the success (e.g., high growth reproduction and survival rates) of N_2-fixing cyanobacteria across a wide range of climate conditions from temperate to tropical and subtropical regions (Padisák, 1997; Wiedner et al., 2007).

Considering phytoplankton, Reynolds functional groups (RFGs, supported by Kruk et al. 2017) are sensitive to environmental variation, and in this sense, this trait-based approach has been increasingly applied to explain and predict the response of phytoplankton to environmental conditions in aquatic systems (Bortolini et al. 2019; Crossetii et al. 2014; Nabout, Nogueira, & Oliveira, 2006; Rangel et al. 2016). This method classifies phytoplankton taxa based on morphological traits (e.g., dimensions, volumes and surface ratios) strongly correlated with physiological capabilities (Kruk et al., 2010), such as growth rates (Tang, 1995), RUE (Sommer, 1984), and vulnerability to grazing by filter-feeding zooplankton (e.g., Burns, 1968; Lampert, 1987) and has been largely applied to improve understanding and to make better predictions of compositional responses to environmental change (Bortolini at al., 2016; Moresco et al., 2020; Pineda et al., 2020; Rodrigues et al., 2018). Following this reasoning, one may expect that RFGs composition should play an important role in determining resource use efficiency by phytoplankton across a wide range of environmental gradients.

Another critical debate in B-EF research relies on the effect of species diversity on the stability of the ecosystem processes, especially under anthropogenic perturbations such as eutrophication (Lehman & Tilman, 2000; Loreau & Mazancourt, 2013; McCann, 2000; Steiner et al., 2005; Tilman, Reich, & Knops, 2006; Tilman & Downing, 1994). There is an emerging consensus that more diverse communities have stronger capacity to be more temporally stable than less diverse ones (Tilman & Downing, 1994), and thus display slower species turnover with time (Ptacnik et al., 2008; Shurin et al., 2007). However, previous studies that have investigated diversity-community turnover relationships in phytoplankton communities (Filstrup et al., 2014; Ptacnik et al., 2008) found controversial results. While species richness reduces temporal turnover and increases phytoplankton RUE across a wide range of environmental gradients (Ptacnik et al. 2008), there can be an opposing relationship between phytoplankton evenness, temporal turnover, and RUE in nutrient-enriched lakes (Filstrup et al 2014). Specifically, phytoplankton communities dominated by Cyanobacteria had slower inter and intraannual turnover rates and displayed the highest RUE, strengthening cyanobacteria dominance over time. This outcome suggest that cyanobacteria-dominated lakes have a strong tendency to maintain itself in that state (Filstrup et al 2014). Therefore, based on the study of Filstrup et al. (2014) and the abovementioned potential of trait-based approaches for understanding biodiversity and ecosystem functioning responses to environmental change, we hypothesised that: (H_1) phytoplankton communities dominated by Cyanobacteria display slower temporal turnover rates of RFGs than more even communities (i.e., lower evenness, slower temporal turnover rates), (H_2) phytoplankton evenness is negatively correlated with RUE (lower evenness, higher RUE), (H_3) variations in RFG composition predict variations in RUE better than species richness or evenness, and (H_4) nutrient increasing reduces RUE over time.

To test these hypotheses, we analyzed the direction and strength of relationships between phytoplankton diversity (species richness, evenness, and functional diversity), temporal turnover of RFGs and RUE of limiting nutrients (nitrogen and phosphorus) over 8 years in a cyanobacteria-dominated lake, which is currently going through a trophic state shift, from oligo-mesotrophic to eutrophic (Hennemann, Simonassi, & Petrucio, 2015; Tonetta & Petrucio, 2020). We used monthly monitoring data set to answer the following questions: (Q_1) How does phytoplankton diversity and composition respond to increasing nutrients? (Q_2) What is the relationship between biodiversity metrics (richness, evenness, and functional diversity), temporal turnover of RFGs (biodiversity-community turnover relationship) and RUE (biodiversity-ecosystem functioning relationship)? (Q_3) What is the relative importance of possible changes in biodiversity and temporal turnover of RFGs in determining RUE? (Q_4) What are the possible long-term effects of nutrient increasing on RUE?

MATERIAL AND METHODS

Study area

Phytoplankton and abiotic variables were sampled monthly from Peri Lake (27° 44’ S, 48° 31’ W), a coastal shallow lake located in the south of the Florianópolis Island, in the state of Santa Catarina, Brazil (Fig. 1). The water body has a surface area of 5.07 km^2, a drainage basin of 20 km^2 approximately, and average and maximum depth of 4.2 m and 11.0 m, respectively. The lake has no marine influence (freshwater year-round) and is surrounded by Atlantic Rain Forest in its north, south, and west areas, and by restinga vegetation (i.e., coastal forest and scrub on sandy soils) in its east. It is located within a protected area with restricted human occupation, which makes Peri Lake the main freshwater source for public water supply of Florianópolis Island. The climate of the region is wet subtropical (Cfa, according to the Köppen climate classification) with an annual average air temperature ranging from 16.5 to 20ºC during the winter and from 23.0 to 26.5ºC in the summer season (Lemes-Silva & Petrucio, 2018; Tonetta, Staehr, & Petrucio, 2017), precipitation mostly concentrated during the spring and summer (mean = 276 mm; Lemes-Silva, Hennemann, & Petrucio, 2020), and a strong influence of winds throughout the year.

Peri lake is classified as a well-mixed water body strongly limited by light (Laudares-Silva, 1999), meso-eutrophic for transparency of the water column (Secchi depth ranged from 0.80 to 1.35 m) and chlorophyll-a concentration, and oligotrophic for nutrients (Hennemann & Petrucio 2011), with potential P limitation (Hennemann et al., 2015). However, recent studies have demonstrated that Peri lake is now experiencing a change toward a more eutrophicated state (Hennemann et al., 2015; Tonetta & Petrucio, 2020), mainly due to increasing concentrations of chlorophyll-a in the water (Hennemann et al., 2016), nutrients in sediments (Hennemann et al. 2015), and cyanobacteria dominance over last decades (Tonetta et al., 2015).

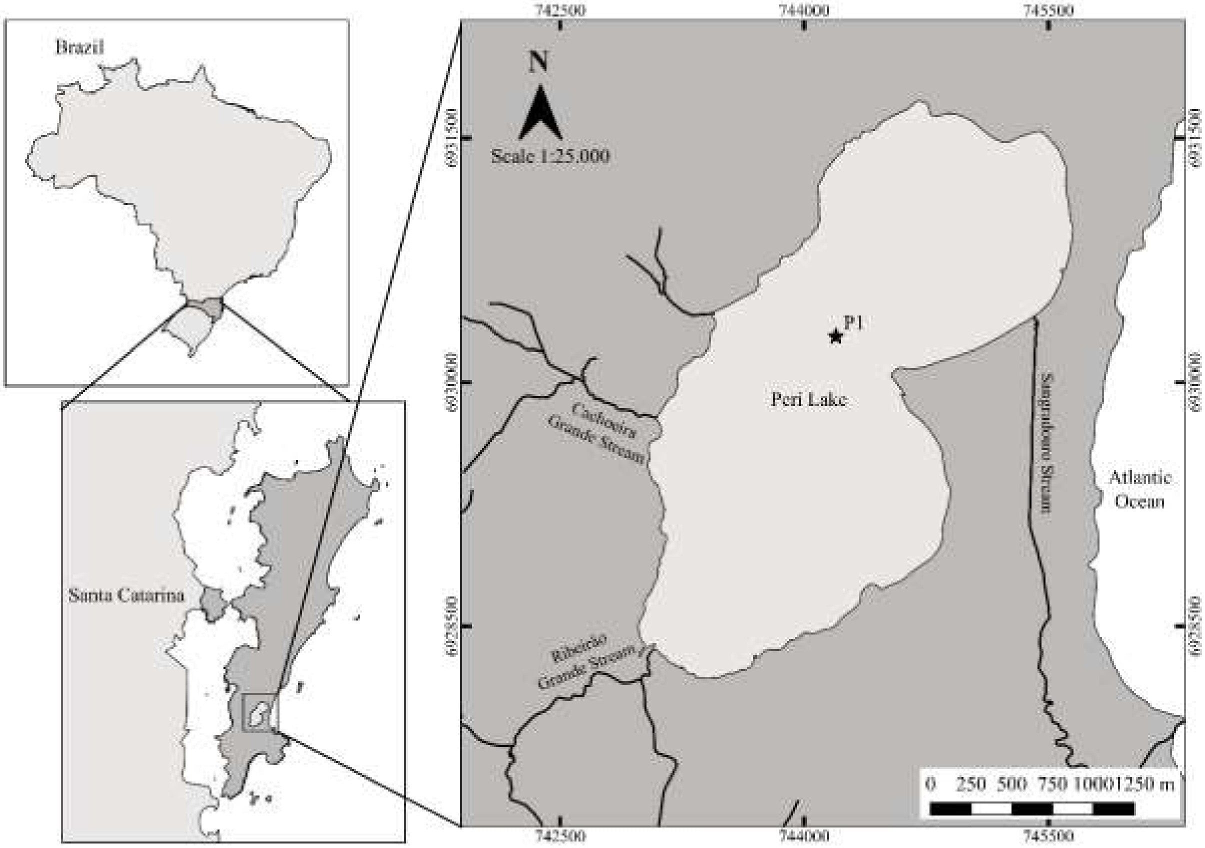

Figure 1 Peri Lake, Santa Catarina State, Brazil, showing the sampling site (P1). Projection: Universal Transverse Mercator. DATUM: SIRGAS 2000. Shapefile Data: Secretariat of Sustainable Development of the State of Santa Catarina, 2012; National Water Agency, 2012 and Infrastructure and Urban Planning of Florianopolis, 2012

Sampling and laboratory analysis

Water samples were collected from the subsurface of the water column in the pelagic zone of Peri Lake (P1; Fig. 1) for 81 months from July 2009 to July 2018, excluding 28 months (February 2011, June 2013 to August 2013, and January 2014 to December 2015) in which phytoplankton were not sampled. Water temperature (±0.2ºC accuracy and 0.1ºC resolution), dissolved oxygen (±0.2 mg l^{-1} accuracy and 0.1 mg l^{-1} resolution) and pH (±0.004 accuracy and 0.001 resolution) were measured *in situ* with a multiparameter meter (model YSI 85, YSI, Inc., Yellow Springs, Ohio, USA). Water transparency was evaluated using a Secchi disk and the euphotic zone (Z_{EU}; m) was estimated as 2.7 times the Secchi disk depth. Total phosphorus and nitrogen (TP and TN; Valderrama 1981) concentrations were determined in laboratory from filtered and unfiltered frozen water samples kept in polyethylene bottles at −20°C. Chlorophyll-a concentrations (Chl*a*) were obtained by filtering 500-ml water samples through glass fiber filters Millipore AP40 using method and equations described by Lorenzen (1967).

Total phytoplankton samples were directly collected with bottles (100 ml) from the subsurface of the water column and preserved in 1% acetic Lugol. In the laboratory, the individuals (cells, colonies, filaments) were counted using an inverted microscope following Utermöhl (1958) and Lund, Kipling, & Le Cren (1958). Samplings were standardized for all months, and the counting and the identification of species of each community were performed by the same team. Phytoplankton density was calculated according to Apha (2005) and biovolume was calculated by multiplying the density of each taxon by its respective volume. The cell volume was calculated from geometric models, according to the shape of the cells (Sun & Liu, 2003). The carbon content (C) was estimated from the biovolume (*V*) using a conversion formula: C = a *V* b, where a = 0.1204; b = 1.051 (Rocha & Duncan, 1985). In order to obtain the carbon biomass of the populations (µg C L^{-1}), the mean carbon content of each species was multiplied by the density.

Phytoplankton diversity metrics

Species richness (S) was considered as the total number of taxa present in each sampling month. Phytoplankton evenness was calculated as the Probability of Interspecific Encounter (PIE, bits; Hurlbert, 1971) for each sampling month using the *mobr* package (McGlinn et al., 2019) in R. PIE is based on Simpson's (1949) dominance index and represents the probability that two individuals sampled at random from a community are of different species (Hurlbert, 1971). The index is maximal and equal to 1 when species are more evenly distributed. PIE was calculated based on relative carbon biomasses of phytoplankton taxa.

The phytoplankton organisms were grouped according to Reynolds Functional Groups (RFGs), using the criteria of Reynolds et al. (2002), Padisák, Crossetti, & Naselli-Flores (2009) and Kruk et al. (2017). Then, functional diversity (FD) and functional redundancy (FR) was calculated as the number of RFGs per sampling (Reynolds et al., 2002; Silva, Pelicice, & Rodrigues, 2020) and the number of taxa in each RFGs (i.e., within-group richness) (Fonseca & Ganade, 2001; Kruk et al., 2016), respectively.

Phytoplankton resource use efficiency

The RUE is the ratio of production rate to uptake rate (Hodapp, Hillebrand, & Striebel, 2019). However, since the rate of biomass production is difficult to obtain, in aquatic ecosystems RUE is commonly estimated based on standing stock measures (i.e., realised productivity), such as biomass values or chlorophyll-a concentrations (e.g., Abonyi et al., 2018; Filstrup et al., 2014; Ptacnik et al., 2008; Ye et al., 2019), divided by available resource (i.e., potential productivity). Here, RUE was used as a proxy of ecosystem functioning and quantified as phytoplankton carbon biomass per unit of total phosphorus (RUE_P) and total nitrogen (RUE_N).

Statistical analysis

To detect possible outliers, normality of distributions, heterogeneity of variance, collinearity, dependence and interactions in the data set we applied the protocol for data exploration proposed by Zuur, Ieno, & Elphick (2010). To deal with the small amount of missing values in the data set ($n = 4$), median imputation technique was applied (Legendre & Legendre, 1998). We used a nonparametric Kruskal-Wallis H test to compare variations of the chemical, physical and biotic variables among the years with statistical significance sets around p-value < 0.05. When a significant difference was detected, a pairwise test for multiple comparisons of ranked data (Dunn post hoc test) with a Bonferroni correction was performed using the R package PMCMRplus (Dinno, 2017). Additionally, spearman pairwise correlations (rs) were applied to measure the strength and direction of the relationships among environmental variables related to eutrophic conditions (lake depth, euphotic zone depth, OD, pH, TP, TN, and chlorophyll *a* concentrations).

To explore possible cumulative changes in phytoplankton composition over time, a temporal turnover measure (D) proposed by Shimadzu, Dornelas, & Magurran (2015) was calculated using the raw data to compare monthly assemblages against the assemblage of the first month of the time series (i.e., single baseline). D is an asymmetric measure based on community dynamics resulting from processes (e.g., local immigration, extinction and population growth) that can be decomposed into two key ecological components: change in community composition (D_1) and change in community size *sensu* its mean abundance (D_2). To quantify the rate of change in functional composition, temporal turnover was calculated based on relative carbon biomasses of RFGs (functional group-based turnover). D_1 is a function of species proportions and ranges from 0 when there is no turnover to negative values ($D_1 \leq 0$) when there is any change in the relative biomass distribution of species. D_2 is dependent only on the amount of change in total biomass between two (or more) samples in time. Negative values indicate that overall biomass has decreased, while positive values indicate that overall biomass has increased over time. Taken together, D and D_2 can provide a more sensitive indicator of changes in species composition through time (Shimadzu et al. 2015).

To determine both the direction and strength of diversity-turnover-productivity relationships, and the effects of nutrient availability on phytoplankton community structure (i.e., biomass, richness, evenness, functional diversity and temporal turnover of RFGs) we conducted linear mixed-effect models (LMM*s*; Laird & Ware, 1982) using the 'lme' function from the R package *nlme* (Pinheiro et al., 2015). Additionally, we also tested the effect of light limitation on RUE by using euphotic zone depth (Z_{EU}) as predictor in LMMs (Table 3). In all models, years were included as random term, together with a first order autoregressive (AR1) structure to accommodate the lack of independence between sampling events (and thus residuals). Prior to the analyses, phytoplankton biomass, nutrient concentrations (TP and TN), and RUE were log-transformed (natural logarithm) to obtain the best fit of residuals (i.e., normality and homoscedasticity). The most parsimonious model was selected based on the lowest Akaike's information criterion (AIC). The importance of alternative models was ranked by their AIC differences (ΔAIC) to the most parsimonious model, where only models with ΔAIC < 2 were considered (Burnham & Anderson, 2002). The variance explained by each model was determined using two types of adjusted-R^2 proposed for mixed-effect models (Nakagawa & Schielzeth, 2013), namely marginal and conditional R^2 (R^2m and R^2c, respectively). R^2m represents the variance explained by fixed term, while R^2c represents the variance explained by both fixed and random terms. To detect possible temporal structure left in the residuals, a visual inspection using 'acf' function from R package *stats* (R Core Team, 2019) was performed. We checked the model's goodness of fit using a visual examination of standard diagnostic plots (Zuur et al., 2009). All analyses were performed using the statistical environment R, version 3.6.1 (The R Development Core Team, 2019).

RESULTS

Environmental variables

Basic environmental information for Peri Lake over the last decade is given in Table 1. We observed a significant decrease in average lake depth (Fig. S1b), especially from 2013 onwards, which has decreased from 9.63 m (±0.65 m) to 7.36 m (±0.11 m) in 2018 ($\chi^2 = 30.66$, $p < 0.001$). Secchi depth showed a sharp decrease over time (Fig. S1b), ranging from 0.96 m

(±0.10 m) in 2009 to 0.71 m (±0.11 m) in 2018 ($\chi2 = 41.771$, $p < 0.001$), as well the euphotic zone (Fig. S1c, ranging from 2.97 m (±0.24 m) in 2010 to 1.89 m (±0.29) in 2018 ($\chi^2 = 41.771$, $p < 0.001$). Chl*a* concentration (Fig. S1d) was high (average = 30.51±11.30 µg L^{-1}) during the study period, ranging from 16.87 µg L^{-1} (±3.21 µg L^{-1}) in 2009 to 44.90 µg L^{-1} (±6.02 µg L^{-1}) in 2013. Additionally, we also observed that the last years sampled had higher chl*a* concentrations than initial years (2009 and 2010) (Fig. S1c; $\chi^2 = 49.595$, $p < 0.001$). Despite the low nutrient concentrations (TP: average = 14.53±5.9 µg L^{-1}, TN: average = 663.40±336.17 µg L^{-1}), TP (Fig. S1e) and TN (Fig. S1f) showed increasing trends over time. Specifically, TP and TN maximum ranges increased along sampling years (Table 1; TP: $\chi^2 = 28.162$, $p < 0.001$, and TN: $\chi^2 = 36.941$, $p < 0.001$). During most of the study period, TN:TP ratios were greater than 50 (Table 1).

Spearman correlation analysis (Fig. S2) showed a moderate but significantly positive (rs = 0.41, p = 0.001) correlation between TP and TN. Moreover, TP was significantly negatively correlated with euphotic zone depth (Zeu; rs = - 0.32, p = 0.014), whereas TN showed a negative correlation with euphotic zone depth (rs = - 0.49, $p < 0.001$) and a positive correlation with chl*a* concentrations (rs = 0.39, p = 0.002). Moreover, Chl*a* concentrations was significantly positively related to lake depth (rs = 0.27, p = 0.036) and negatively related to euphotic zone depth (rs = -0.44, p = 0.001); water temperature was significantly negatively related to DO (rs = -0.64, $p <0.001$); pH was significantly positively related to CE (rs = 0.31; p = 0.018).

Table 1 Statistical summary showing mean values, standard deviation (SD), minimum (Min) and maximum (Max) of lake depth, Secchi depth, euphotic zone depth (Z_{EU})water temperature (WT), pH, dissolved oxygen (DO), total nitrogen (TN), total phosphorus (TP), TN:TP ratio and chlorophyll *a* (Chl*a*) concentrations in Peri Lake from July 2009 to July 2018.

Year		**Depth**	**Secchi**	**Z_{EU}**	**WT**	**pH**	**DO**	**TN**	**TP**	**TN:TP**	**Chl*a***
2009	Mean±SD	8.92±0.86	0.96±0.10	2.59±0.28	2.59±0.28	22.23±4.15	7.12±0.26	761.01±197.75	12.25±2.43	64.82±22.13	16.87±3.2
	Min	8.00	0.80	2.16	2.16	17.90	6.64	372.50	9.70	27.18	13.10
	Max	10.00	1.10	2.97	2.97	28.50	7.38	939.17	16.14	86.61	21.40
2010	Mean±SD	8.17±1.05	1.11±0.09	2.99±0.24	2.99±0.24	22.41±3.37	7.06±0.53	383.92±157.88	10.73±3.13	35.96±11.21	19.63±4.1
	Min	7.00	0.90	2.43	2.43	18.70	5.72	162.77	7.61	20.95	10.68
	Max	10.00	1.20	3.24	3.24	28.70	7.72	758.15	16.84	55.12	24.23
2011	Mean±SD	7.65±1.16	0.88±0.21	2.38±0.58	2.38±0.58	21.65±4.06	7.21±1.13	346.97±95.50	14.71±3.08	24.68±9.03	24.08±6.2
	Min	6.50	0.70	1.89	1.89	14.70	5.66	126.37	9.79	7.67	8.01
	Max	10.50	1.40	3.78	3.78	27.30	9.64	451.05	21.19	41.02	29.37
2012	Mean±SD	8.20±1.28	0.78±0.14	2.09±0.38	2.09±0.38	23.25±4.12	6.76±0.60	985.90±367.61	16.87±9.94	67.45±25.82	32.93±8.8
	Min	6.00	0.60	1.62	1.62	17.30	5.48	419.10	7.68	20.84	18.16
	Max	10.00	1.00	2.70	2.70	29.00	7.96	1481.35	44.25	102.37	47.53
2013	Mean±SD	9.78±0.56	0.84±0.18	2.27±0.49	2.27±0.49	23.43±2.45	6.51±0.56	643.05±266.45	11.34±3.56	67.63±40.79	45.09±6.8
	Min	9.00	0.50	1.35	1.35	19.40	5.68	108.91	6.36	8.06	36.31
	Max	10.50	1.05	2.84	2.84	26.50	7.30	899.41	15.90	125.54	55.00
2016	Mean±SD	7.43±0.23	0.65±0.16	1.77±0.44	1.77±0.44	22.24±4.75	6.81±1.11	742.18±296.68	14.23±7.07	58.96±30.53	36.27±9.2
	Min	7.20	0.40	1.08	1.08	14.80	3.94	336.14	8.00	18.13	24.03
	Max	8.10	1.00	2.70	2.70	28.35	7.98	1163.78	34.74	123.98	54.47
2017	Mean±SD	7.36±0.22	0.70±0.11	1.90±0.28	1.90±0.28	22.82±3.57	6.83±0.72	833.53±268.42	19.92±3.82	42.23±14.07	31.06±11.0
	Min	7.00	0.55	1.49	1.49	17.70	5.83	414.20	12.92	23.95	6.94
	Max	7.70	0.80	2.16	2.16	28.20	8.34	1300.68	26.81	79.57	48.06
2018	Mean±SD	7.36±0.11	0.71±0.11	1.93±0.29	1.93±0.29	22.87±3.82	6.88±0.67	811.23±307.36	16.04±3.84	50.66±15.33	24.26±4.1
	Min	7.20	0.60	1.62	1.62	17.00	5.52	402.29	11.28	28.29	18.16
	Max	7.50	0.90	2.43	2.43	26.03	7.66	1364.89	23.05	73.89	31.51

Phytoplankton community structure and composition

We recorded 101 phytoplankton taxa into 17 RFGs (Table S1). We observed higher values of taxa richness in 2011 (average = 15±2), and lower values in 2013 (average = 9±1) and 2017 (average = 9±2). The distribution of species across RFGs was relatively uneven (Fig. 2). Among the 101 taxa registered, **J** (21 taxa), **N** (11 taxa), **X1** (10 taxa) and **MP** (8 taxa) had the highest species richness. Species equitability (i.e., evenness) was relatively high in the initial year, but we observed decreasing trend in last years sampled. The mean value of the evenness index (PIE) varied from 0.73 (±0.09) in 2011 (i.e., lowest dominance) to 0.37 (±0.20) in 2018 (i.e., highest dominance).

Phytoplankton biomass showed a sharp decrease over time (Fig. 3a), especially from 2014 onwards. The relative contribution of RFGs to overall phytoplankton biomass did not change during the study period (Fig.3b), with exception of the years 2011, 2012 and 2013, in which we observed a major contribution of other RFGs, especially **S1** and **N** . In particular, RFG **SN** (represented by the nitrogen-fixing cyanobacteria, *R. raciborskii*) was the most important during the entire study period, and represented 49% of total average biomass, followed by RFG **S1** (20.62%, represented by shade-adapted Cyanobacteria genera, *Planktolyngbya*, *Limnothrix* and *Pseudoanabaena*) (Fig. S3a), RFG **N** (13.13%, *Cosmarium* and *Staurastrum*) (Fig. S3b), and RFG **C** (6.29%, *Aulacoseira ambigua*) (Fig. S3c).

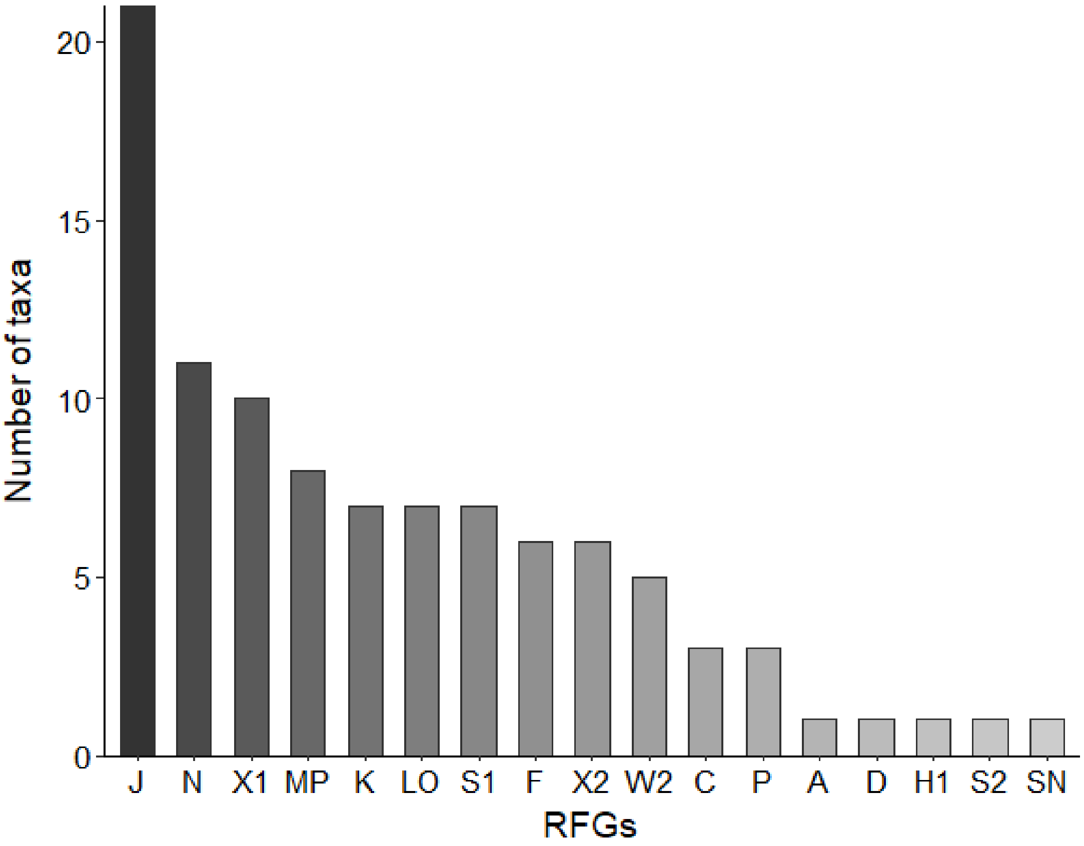

Figure 2 The frequency distribution of phytoplankton taxa per Reynolds functional groups (RFGs) in Peri Lake from July 2009 to July 2018.

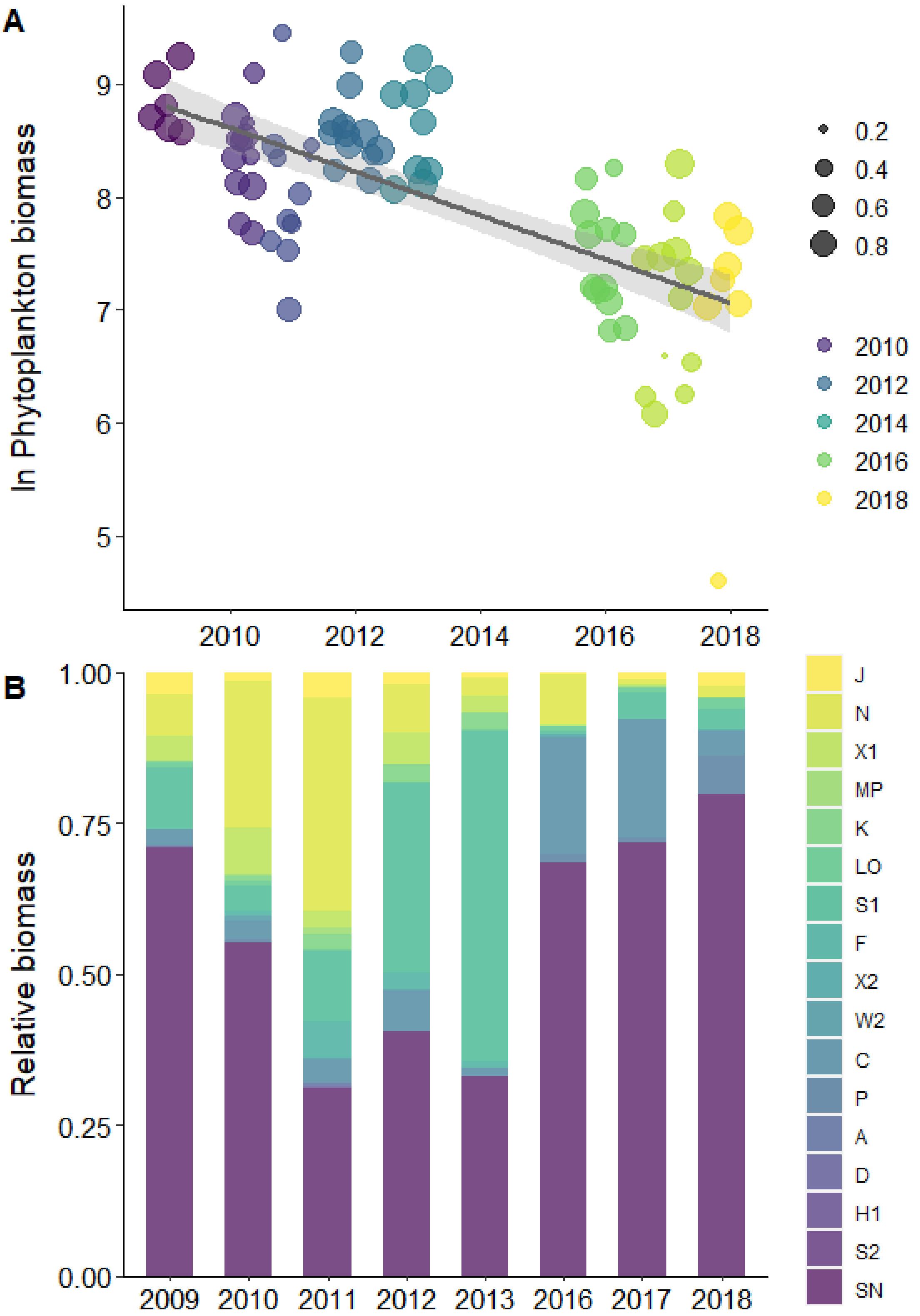

Figure 3 Interannual variation of **A**) phytoplankton biomass and **B**) the relative biomass contribution (%) of phytoplankton by Reynolds functional groups (RFGs) in Peri Lake from July 2009 to July 2018. In **A**, the confidence interval of 95% is provided, and the size of dots reflects the proportion of Cyanobacteria calculated as total biomass of Cyanobacteria to total phytoplankton biomass.

Temporal turnover of RFGs (D) revealed high intra- and interannual variability in community structure over the study period relative to July 2009 (Fig. 4a). When considering each ecological component of temporal turnover separately (Fig. 4b), we found no changes in phytoplankton community composition (D_1, dotted grey line), but we observed significant changes in the overall phytoplankton biomass (D_2, two-dash grey line) overtime. Specifically, the overall phytoplankton biomass has been shrinking since 2009.

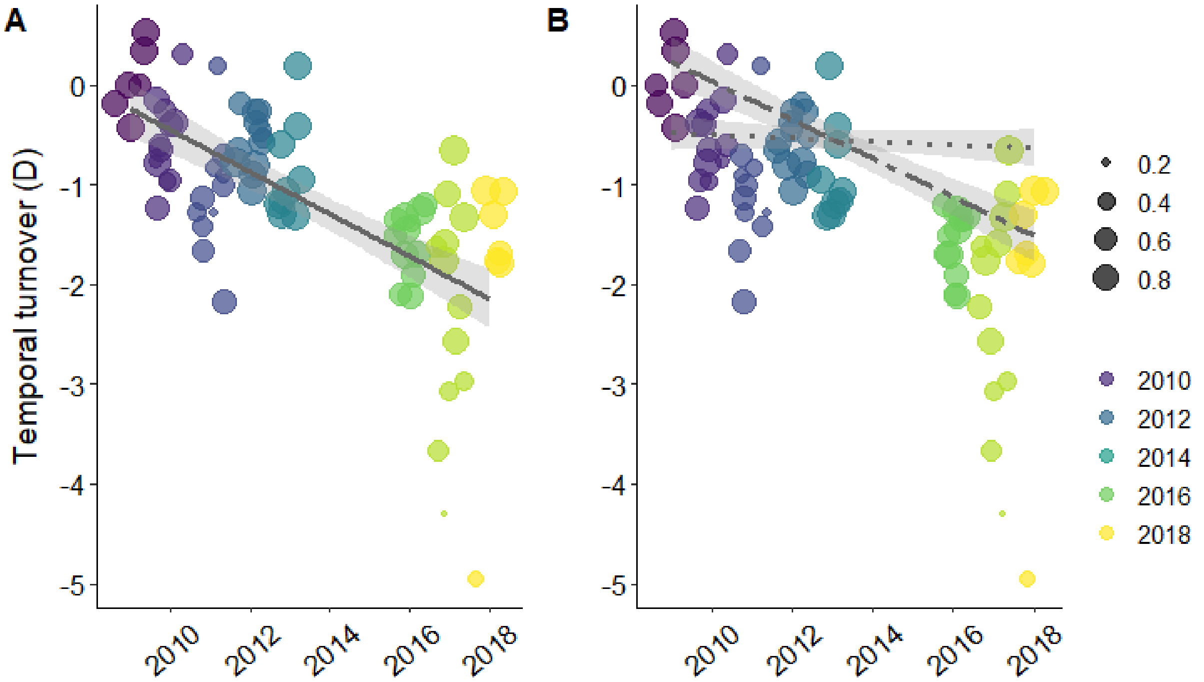

Figure 4 Scatter plots illustrating the interannual variations of **A**) phytoplankton temporal turnover **B**) and its ecological components in Peri Lake from July 2009 to July 2018. In B, the solid grey line represents the temporal turnover measure (D), the dotted grey line represents the compositional change (D_1), and the two-dash grey line represents the community biomass change (D_2). The confidence interval of 95% is provided. The size of dots reflects the proportion of Cyanobacteria calculated as total biomass of Cyanobacteria to total phytoplankton biomass.

Diversity-temporal turnover relationships

Mixed-effect models revealed that temporal turnover of RFGs (D) was positively related with changes in species richness (Fig. 5a; Table 2), but negatively related with changes in evenness (Fig. 5b; Table 2). Such pattern was consistent across all years. However, both measures explained low amounts of variation ($R^2m = 0.093$ and $R^2m = 0.079$, respectively), and a larger proportion of the evenness-turnover relationship was explained by the random term ($R^2c = 0.620$).

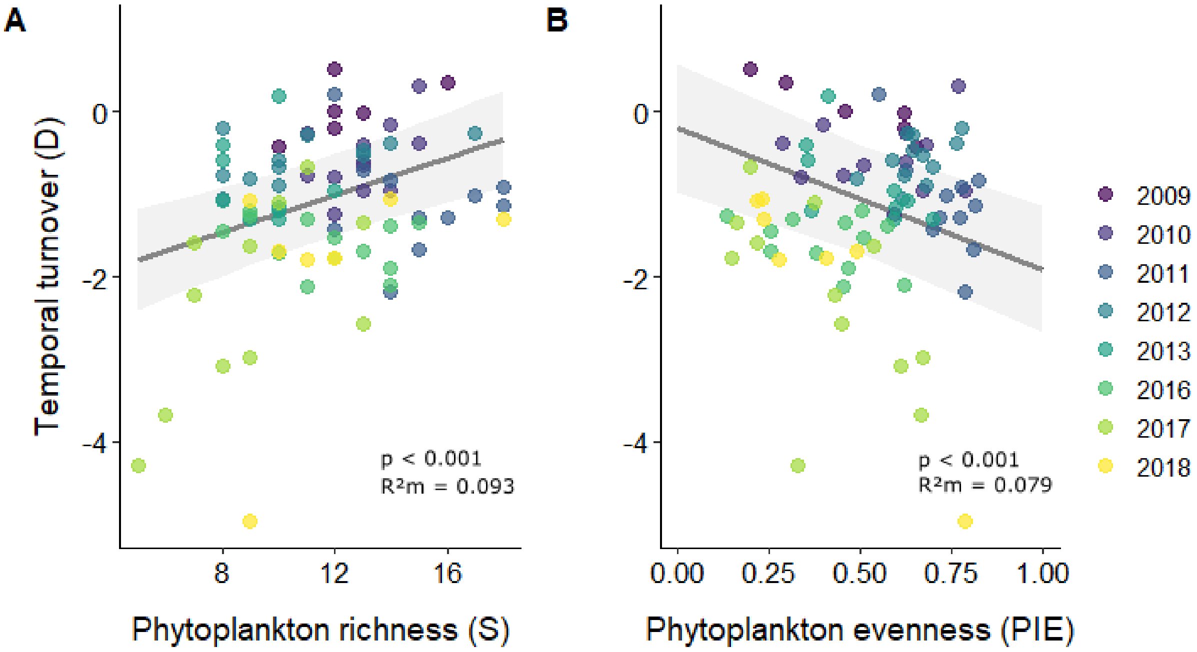

Figure 5 **A**) Phytoplankton species richness (S) and **B**) phytoplankton evenness (PIE) explaining temporal turnover in Peri Lake. The solid line represents the fitted values of the overall model, and it is based on linear mixed-effect model (random intercept and fixed slope). The confidence interval of 95%, p-value and marginal adjusted-R^2 (R^2m) of the overall model are provided.

Diversity-ecosystem functioning relationships

Mixed-effect models revealed that both RUE_P (Fig. 6) and RUE_N (Fig. 7) significantly increased with increasing species richness and functional diversity (Table 2). In contrast, RUE_P and RUE_N were negatively correlated with evenness. Moreover, RUE displayed a strong positive relationship with temporal turnover of RFGs (Table 2), which in turn reflect changes in phytoplankton biomass (Fig. 4b). Specifically, more efficiency in resource use by phytoplankton was associated with high values of biomass (D_2; RUE_P: $R^2m = 0.873$; RUE_N: $R^2m = 0.709$).

Considering AIC differences, temporal changes in phytoplankton biomass (ΔAIC = 0) was the most important driver of RUE, followed by evenness and species richness. Functional diversity had the lowest relative importance to explain variations in RUE (Table 2).

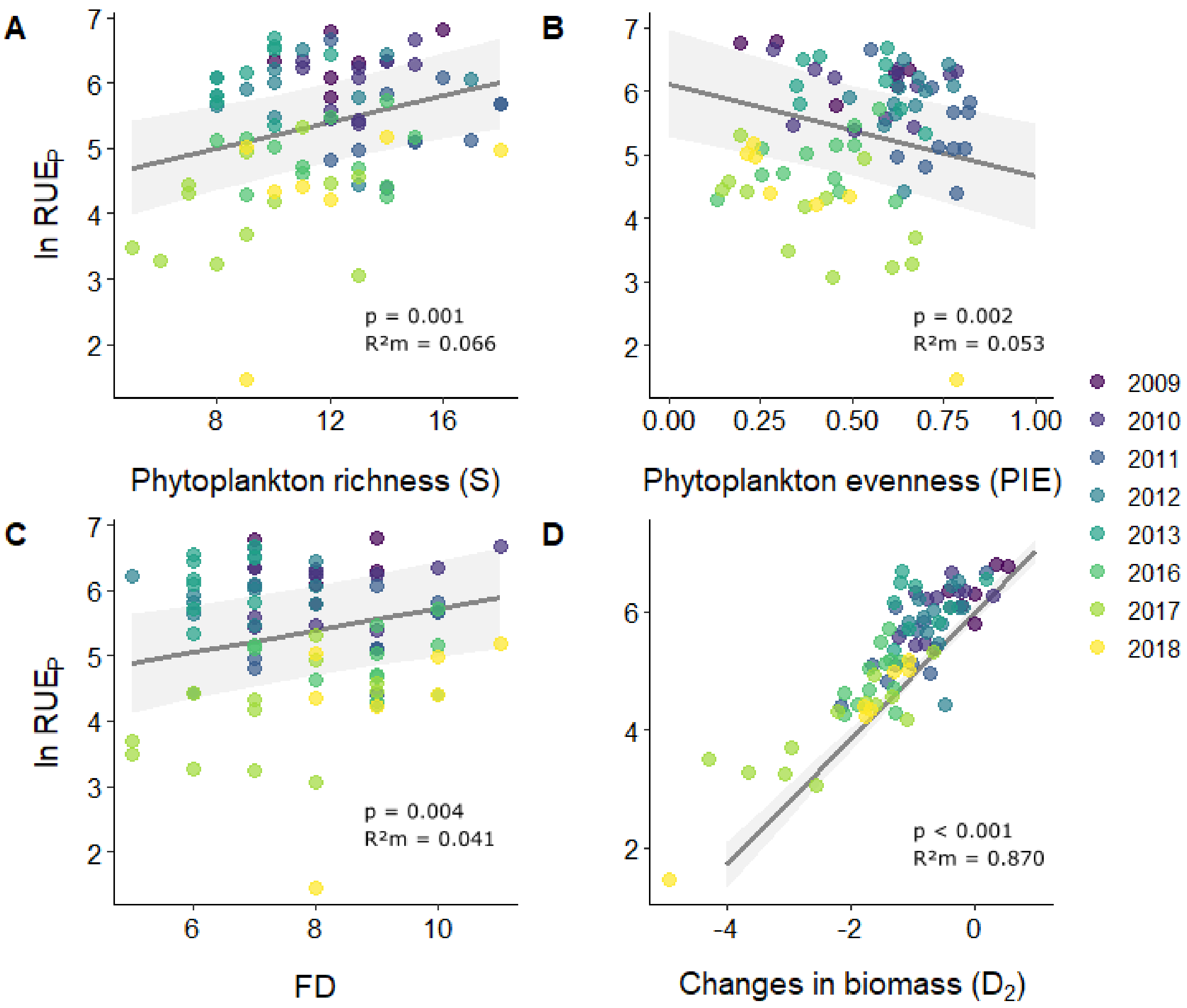

Figure 6 **A**) Phytoplankton species richness (S), **B**) phytoplankton evenness (PIE), **C**) phytoplankton functional diversity (FD), and **D**) biomass change in phytoplankton community (D_2) explaining resource use efficiency for phosphorus (RUE_P) in Peri Lake. The solid line represents the fitted values of the overall model, and it is based on linear mixed-effect model (random intercept and fixed slope). The confidence interval of 95%, p-value and marginal adjusted-R^2 (R^2m) of the overall model are provided.

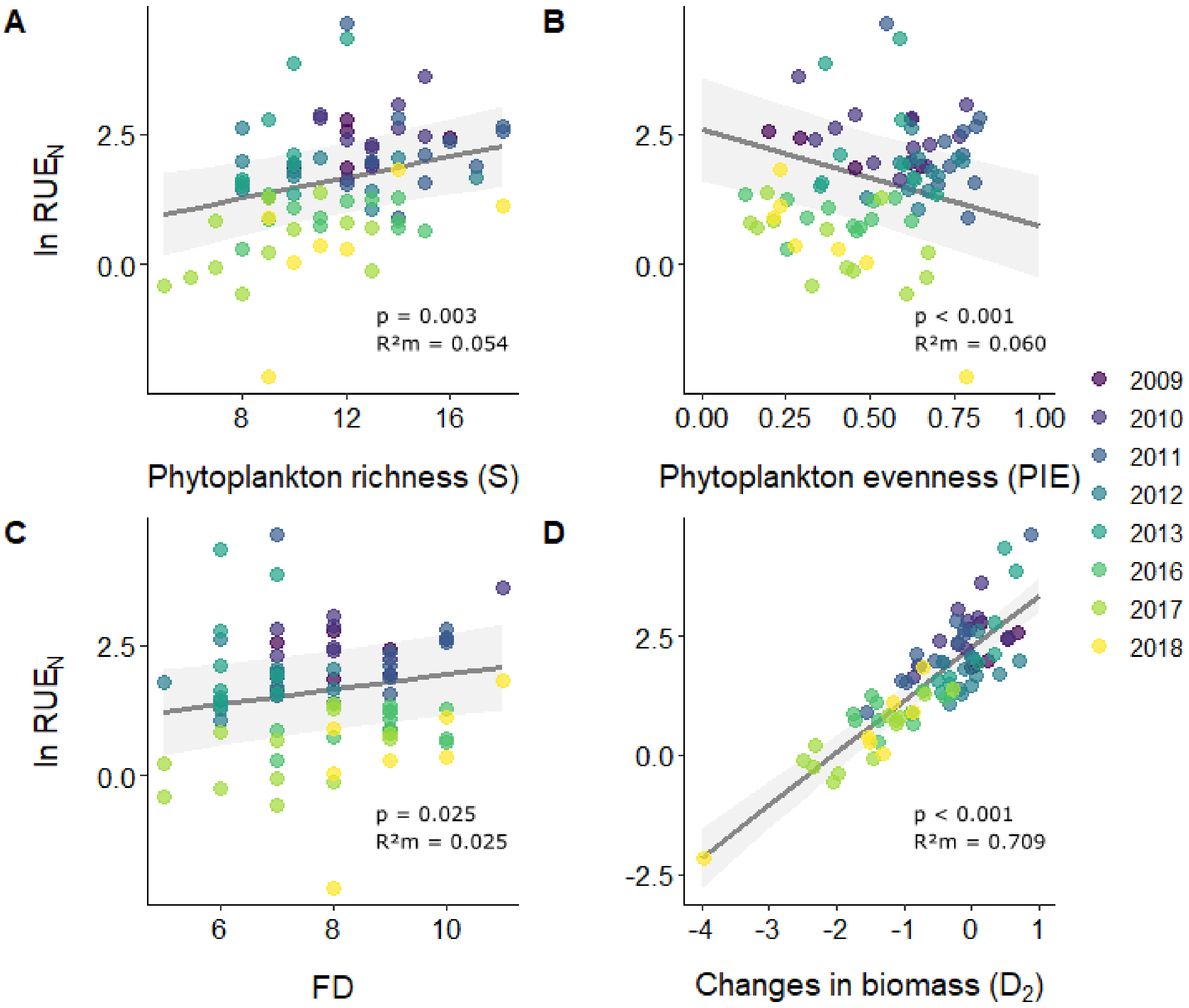

Figure 7 **A**) Phytoplankton species richness (S), **B**) phytoplankton evenness (PIE), **C**) phytoplankton functional diversity, and **D**) biomass change in phytoplankton community (D_2) explaining resource use efficiency for nitrogen (RUE_N) in Peri Lake. The solid line represents the fitted values of the overall model, and it is based on linear mixed-effect model (random intercept and fixed slope). The confidence interval of 95%, p-value and marginal adjusted-R^2 (R^2m) of the overall model are provided.

Effects of resource availability on community structure and ecosystem functioning

Phytoplankton biomass was not related to nutrient availability (Fig. S4). Likewise, phytoplankton species richness, PIE, FD and temporal turnover of RFGs were not explained by nutrient concentrations (Fig. S5). On the other hand, RUE significantly decreased with increasing TP (Fig. 8a; Table 3; $R^2m = 0.149$) and TN (Fig. 8b; Table 3; $R^2m = 0.326$), and slightly increased with increasing Z_{EU} (Fig. S6), indicating that eutrophication conditions (nutrient increasing and light limitation) reduce RUE. However, Z_{EU} explained low amounts of variation (RUE$_P$: R^{2}m = 0.036; RUE$_N$: R^{2}m = 0.097), with a larger proportion being explained by the random term (RUE$_P$: R^{2}m = 0.548; RUE$_N$: R^{2}m = 0.514).

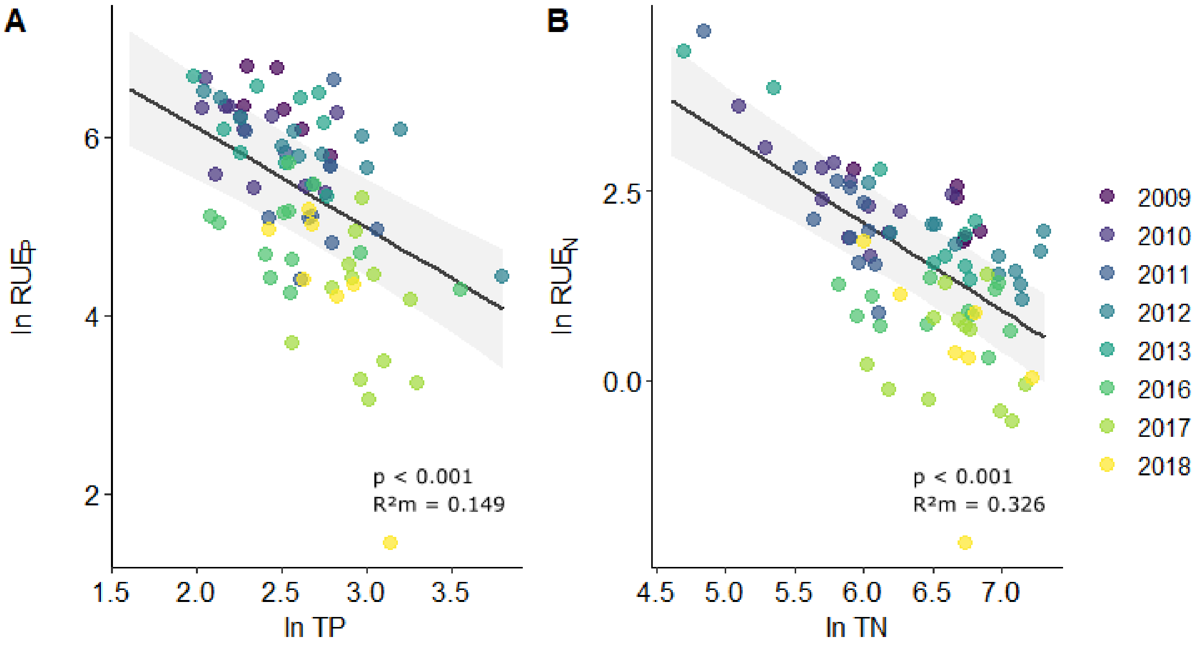

Figure 8 Total phosphorus (log-transformed; lnTP, µg L^{-1}) and total nitrogen (log-transformed; lnTN, µg L^{-1}) explaining phytoplankton resource use efficiency for **A**) phosphorus (RUE$_P$) and **B**) nitrogen (RUE$_N$), respectively, in Peri Lake. The solid line represents the fitted values of the overall model, and it is based on linear mixed-effect model (random intercept and fixed slope). The confidence interval of 95%, p-value and marginal adjusted-R^2 (R^{2}m) of the overall model are provided.

Table 2 Linear mixed-effect models (LMMs) of relationships among response variables (D, RUE_P and RUE_N) and predictors. In all models, years were included as random term, together with a first order autoregressive (AR1) structure to accommodate the lack of independence between sampling events. d.f. refers to degrees of freedom; R^2m and R^2c refer to marginal (only fixed terms) and conditional (fixed and random terms) adjusted R^2, respectively; RUE_P and RUE_N refer to phytoplankton resource use efficiency (log-transformed) of total phosphorus and total nitrogen, respectively; D refers to temporal turnover of Reynolds Functional Groups (RFGs); D_1 refers to compositional change in phytoplankton community; D_2 refers to biomass change in phytoplankton community; PIE refers to phytoplankton evenness; S refers to phytoplankton richness; FD refers to number of RFGs.

Models	**d.f.**	**Intercept**	**Coefficient**	**logLink**	**AICc**	**Δ AICc**	**R^2m**	**R^2c**
Response variable: D								
PIE	5	-0.20	-1.708	-77.67	166.1	0	0.079	0.620
S	5	-2.36	0.113	-78.8	168.5	2.3	0.093	0.093
Response variable: RUE_P								
D_2	5	5.97	1.064	-27.0	64.8	0	0.870	0.886
PIE	5	6.12	-1.454	-81.7	174.3	109.5	0.053	0.714
S	5	4.20	0.099	-83.9	178.5	113.7	0.066	0.566
FD	5	4.06	0.165	-84.5	179.8	115.0	0.041	0.653
D_1	5	5.33	-0.073	-87.1	185.1	120.3	0.001	0.580
Response variable: RUE_N								
D_2	5	2.26	1.101	-50.4	111.5	0	0.709	0.767
PIE	5	2.60	-1.858	-88.1	186.9	75.4	0.060	0.673
S	5	0.47	0.100	-92.6	196.0	84.5	0.054	0.490
FD	5	0.50	0.144	-94.0	198.7	87.2	0.025	0.570
D_1	5	1.52	-0.234	-94.6	200.1	88.6	0.007	0.520

Table 3 Linear mixed-effect models (LMMs) of relationships among response variables (RUE_P and RUE_N) and predictors. In all models, years were included as random term. d.f. refers to degrees of freedom; R^2m and R^2c refer to marginal (only fixed terms) and conditional (fixed and random terms) adjusted-R^2, respectively; RUE_P and RUE_N refer to phytoplankton resource use efficiency (log-transformed) of total phosphorus and total nitrogen, respectively; TP refers to total phosphorus; TN refers to total nitrogen; Z_{EU} refers to euphotic zone depth.

Models	**d.f.**	**Intercept**	**Coefficient**	**logLink**	**AICc**	**Δ AICc**	**R^2m**	**R^2c**
Response variable: RUE_P								
TP	5	8.33	-1.123	-73.1	156.9	0	0.149	0.510
Z_{EU}	5	4.57	0.353	-85.6	181.9	25.0	0.036	0.548
Response variable: RUE_N								
TN	5	9.02	-1.157	-72.9	156.6	0	0.326	0.599
Z_{EU}	5	0.23	0.617	-91.7	194.2	37.6	0.097	0.514

DISCUSSION

In this study we assessed the nature of the relationships (direction and strength) between many aspects of biodiversity (species richness, evenness, and functional diversity), temporal turnover of RFGs and RUE. Diversity components (S and PIE) affected temporal turnover in divergent ways. Specifically, temporal turnover of RFGs was positively related to species richness, but negatively related to phytoplankton evenness; this latter results is in agreement with our fisrt hypothesis (**H_1**), and indicates that phytoplankton communities dominated by few taxa had slower temporal turnover rates of RFGs. Similarly, our analysis revealed opposing relationships between RUE and diversity components (S, PIE and FD). Particularly, RUE displayed a positive correlation with richness and functional diversity, but a negative correlation with evenness; this latter results is in agreement with our second hypothesis (**H_2**), and suggests that the dominance of a highly productive species, such as *Raphidiopsis raciborskii*, can enhance resource use efficiency by phytoplankton in aquatic ecosystems. Additionally, we found no changes in phytoplankton community composition, but we observed significant changes in the overall phytoplankton biomass over time, indicating that all RFGs displayed the same trend in biomass. Specifically, phytoplankton biomass showed a sharp decrease over the last decade in Peri Lake. Contrary to our expectations, changes in phytoplankton biomass predicted variation in RUE better than species richness, evenness or functional diversity. We thus found no support for our third hypothesis (**H_3**) that variations in RFG composition could provide better predictions of RUE than species richness or evenness. We also demonstrated a strong negative effect of TP and TN on both measures of RUE (RUE_P and RUE_N), indicating a progressively lower efficiency in resource use with increasing supply of TP and TN, supporting our last hypothesis (**H_4**). Our overall results contradict established paradigms for terrestrial plants, but are in clear concordance with those of most recent studies aimed at testing B-EF relationships in phytoplankton communities. This contrasting results can be explained by the dominance toward better adapted species, such as Cyanobateria, at the expense of other phytoplankton species less competitive (Kosten et al., 2012). Below we discuss in detail the implications of these findings.

Diversity-temporal turnover relationships

We found that phytoplankton communities with greater number of species displayed slower temporal turnover rates than less diverse ones. The positive diversity-stability relationship reported here has been previously documented by many B-EF studies (Craven et al., 2018; Gross et al., 2014; Ptacnik et al., 2008). Yet, by using temporal turnover based on RFGs our result provides additional insights: phytoplankton communities with larger number of species display slower temporal turnover rates between RFGs (i.e., higher persistence). On the other hand, we also found slower rates of temporal turnover associated with dominance (i.e., low evenness) of a highly productive and opportunistic taxa (*Raphidiopsis raciborskii*). This result notably contrasts with positive diversity-stability relationships previously reported (Craven et al., 2018; Gross et al., 2014; Ptacnik et al., 2008), but supports the findings found by Filstrup et al. (2014) in hypereutrophic lakes. The authors found a negative phytoplankton evenness-RUE relationship resulted from the increased relative abundance of Cyanobacteria species that can use TP more efficiently under low light conditions than other phytoplankton taxa.

For instance, filamentous Cyanobacteria may cause alternate stable states of the algal community (i.e., one dominated by Cyanobacteria and one dominated by non-Cyanobacteria) in shallow and turbid lakes, such as Peri Lake, mainly due to differences in physiology between Cyanobacteria and other phytoplankton taxa (Scheffer et al., 1997). In particular, *Raphidiopsis raciborskii* is an invasive cyanobacteria (Padisak, 1997) with specific properties including N_2 fixation, high affinity for ammonia, nitrate (Burford, McNeale, & Mckenzie-Smith, 2006; Kenesi et al., 2009) and phosphate (Wu et al., 2009), large phosphorus storage capacity (Isvanovics et al., 2000), and high tolerance to low light conditions (Burford et al., 2006; Wojciechwski, Fernandes, & Fonseca, 2016). Such adaptations are key factors in the success of this cyanobacterium across a wide range of environments (Padisák, 1997; Wiedner et al., 2007). Therefore, Cyanobacteria dominance can reduce species turnover by competitively excluding or inhibiting other phytoplankton taxa, self-reinforcing its dominance (Filstrup et al., 2014). Furthermore, less diverse communities show reduced capacity for species turnover (Meyer et al., 2016). Our findings similarly suggest that Cyanobacteria dominance reduces temporal community turnover, promoting its persistence over time. Yet, by calculating community turnover based on RFGs, our study additionally suggests that this pattern is also consistent between functional groups (RFGs).

Diversity-ecosystem functioning relationship

Both RUE_P and RUE_N were positively correlated with species richness, which is largely in line with the evidence that RUE is enhanced with increasing species richness (Chai et al., 2020; Filstrup et al., 2014; Ptacnik et al. 2008; Striebel et al. 2009; Tian et al., 2017), but displayed a strong inverse relationship with evenness. The RUE-evenness relationship has yielded mixed results (Chai et al., 2020; Filstrup et al., 2014; Lehtinen et al., 2017; Tian et al., 2017). Our results contrasts with studies showing positive evenness-RUE relationships (Chai et al., 2020; Tian et al., 2017), but reveal the same pattern found by previous empirical studies (Filstrup et al., 2014; Hodapp et al., 2015; Lehtinen et al., 2017). Using data from 131 hypereutrophic lakes along seven years, Filstrup et al. (2014) demonstrated that RUE increases when phytoplankton communities are dominated (calculated as Pielou's evenness) by Cyanobacteria. Other recent studies have similarly suggested that phytoplankton communities dominated by few genera may result in higher production of biomass per unit of nutrients (Hodapp et al., 2015; Lehtinen et al., 2017). This outcome suggests that environmental conditions allowed a few dominant species also more efficient in resource use outcompete other phytoplankton species (Hodapp et al., 2015). Lower values of evenness associated with dominance of Cyanobacteria were observed in this study (ranged from 0.13 to 0.82) and in others lakes (ranged from 0 to 0.75) studied by Filstrup et al. (2014) compared with values observed by Tian et al. (2017) in a mesotrophic lake (ranged from 0.58 to 0.92). Despite the positive correlation between Cyanobacteria biomass and RUE found by Tian et al. (2017), this group was not dominant in phytoplankton community. These differences in evenness values likely explain the controversial results between abovementined studies.

This outcome relates to the ongoing debate on the underlying mechanism driving diversity-productivity relationships; efficiency in resource use (i.e., selection effects) (Hooper & Vitousek 1997; Loreau, 1998a; Tilman, 1997) and/or resource partitioning (i.e., complementarity) (Loreau, 1998b; Loreau & Hector, 2001; Norberg, 2000). The idea that niche partitioning enhances resource use efficieny in phytoplankton communities have been previously reported (Cardinale, 2011; Chai et al. 2020; Ye et al. 2019). In contrast, we observed that phytoplankton communities dominated by a highly productive species, such as *Raphidiopsis raciborskii*, can maintain high levels of ecosystem processes (RUE) via selection effect. The importance of dominant effects is commonly observed in many B-EF experiments (Filstrup et al., 2014; Hillebrand et al., 2008; Hodapp et al., 2015), and is supported by the theoretical prediction that ecosystem functions can be mediated by species niches via asymmetry in resource use efficiency (aka *fitness* difference). The rationale is that when a dominant species performs better than the mean of the community, the rates of key ecosystem processes will increase as far as evenness decreases (Hillebrand et al., 2008). This result has been previously demonstrated in zooplankton communities (Gianuca et al., 2016; Pinheiro-Silva et al., 2020), where zooplankton body size enhanced top-down control on phytoplankton via selection effects.

In our study, changes in phytoplankton biomass was the best predictor for RUE compared with richness, evenness or functional diversity, in contrast to our expectations. This finding indicates that variations in RUE is mainly due to changes in phytoplankton biomass, and not RFGs composition. Changes in phytoplankton biomass are often thought to be a result of changes in nutrient load, light availability (Braga & Becker, 2020) and water level (Naselli-Flores & Barone, 2005; Mac Donagh et al., 2009;Wang et al., 2011). As a consequence of both climate change and increased water demands, variations in water level has become an important disturbance to freshwater ecosystems (Yang et al., 2016). In shallow lakes, such variations can drive shifts between clear-water and turbid states (Scheffer & Jeppesen, 2007), indicating that high water levels can dilute the concentration of particles, including phytoplankton (Yang et al., 2016). In the present study, we observed a significant decrease in average lake depth from 2013 onwards, as well the euphotic zone depth, which decreased more than 60% (1.08 meters) over the last years. Yet, contrary to previous findings (Braga & Becker, 2020; Yang et al., 2016) we observed a sharp reduction of phytoplankton biomass under such environmental conditions.

A potential explanation for these differences in outcome is the negative feedback between light limitation and cyanobacteria growth. Some cyanobacteria such as *R. raciborskii*, can survive under low levels of light, since this cyanobacterium is a highly productive species with traits that allow to better exploit limiting resources in shallow, turbid lakes. However, they are unable to attain intensive cell division, showing lower growth rates when compared to high light availability (Wojciechwski, Fernandes, & Fonseca, 2016). The rationale is that, at extremely low irradiances, respiratory losses exceed photosynthetic carbon incorporation, and thus, biomass slowly declines (Tilzer, 1987). Moreover, light requirements in nitrogen-fixing species are higher than in heterocyst-free strains (Tilzer, 1987), and the existence of different trade-offs among strains and between Cyanobacteria species are important factors in determining the success of Cyanobacteria when exposed to different conditions of light limitation (Marinho, Souza, & Lürling, 2013). In this study, we did not evaluate the presence of heterocysts, but it is an interesting topic for a future study.

Effects of resource availability on community structure and ecosystem functioning

During most of the study period, TN:TP ratios were greater than 50, indicating that P more frequently limited primary producers than N and potentially favoring N_2-fixing Cyanobacteria (Litchman et al., 2015; Reynolds, 2006). We found no significant effect of nutrients on phytoplankton biomass and composition, but we demonstrated a strong negative effect of TP and TN on phytoplankton RUE, suggesting that biodiversity and ecosystem processes respond differently to nutrient enrichment (Filstrup et al., 2014). This latter result is consistent with previous studies (Frank et al., 2020; Gamfeldt & Hillebrand, 2011), and indicates that phytoplankton is less efficiency in resource use when nutrients become more abundant (Gamfeldt & Hillebrand, 2011). As discussed above, light intensity is a fundamental driver of ecosystem processes, affecting the rate of primary production (Reynolds, 1987). In oliotrophic lakes, productivity is generally limited by light and not by nutrients (Karlsson et al., 2009); therefore, light limitation might have strong effects on resource use efficiency.

CONCLUSION

It is well-known that multiple aspect of biodiversity might have divergent responses and divergent effects on ecosystem functioning depending on environmental perturbation (Hillebrand et al., 2011). Here, we demonstrated the importance of temporal changes in phytoplankton structure to ecosystem functioning. Specifically, changes in phytoplankton biomass drive diversity-RUE relationship. Despite the strong negative correlation between RUE and evenness, indicating that single or few dominant and highly productive species enhance efficiency in resource use, our findings indicate that phytoplankton biomass and RUE are both decreasing over time. Specifically, phytoplankton is becoming less efficient in the conversion of resources into new biomass over time, which might explain the sharp decrease of phytoplankton biomass over the last years in Peri Lake. Together with the strong negative effect of both nutrients (TP and TN) and light availability on RUE, our findings suggest that resource use efficiency by phytoplankton might progressively decline over time with increasing supply of nitrogen and phosphorus and decreasing of water level.

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CONFLICT OF INTEREST

We declare that there is no conflict of interest.

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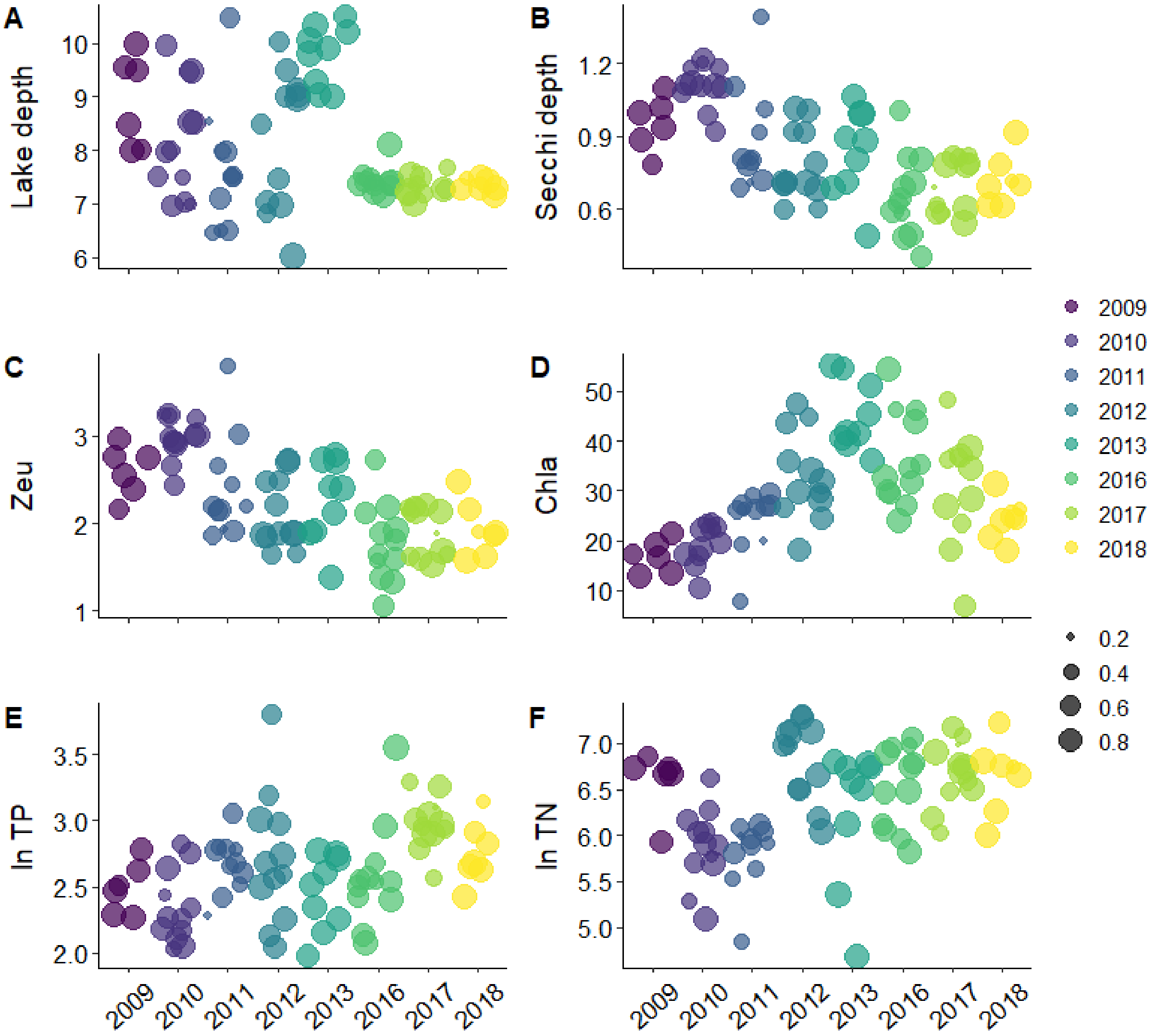
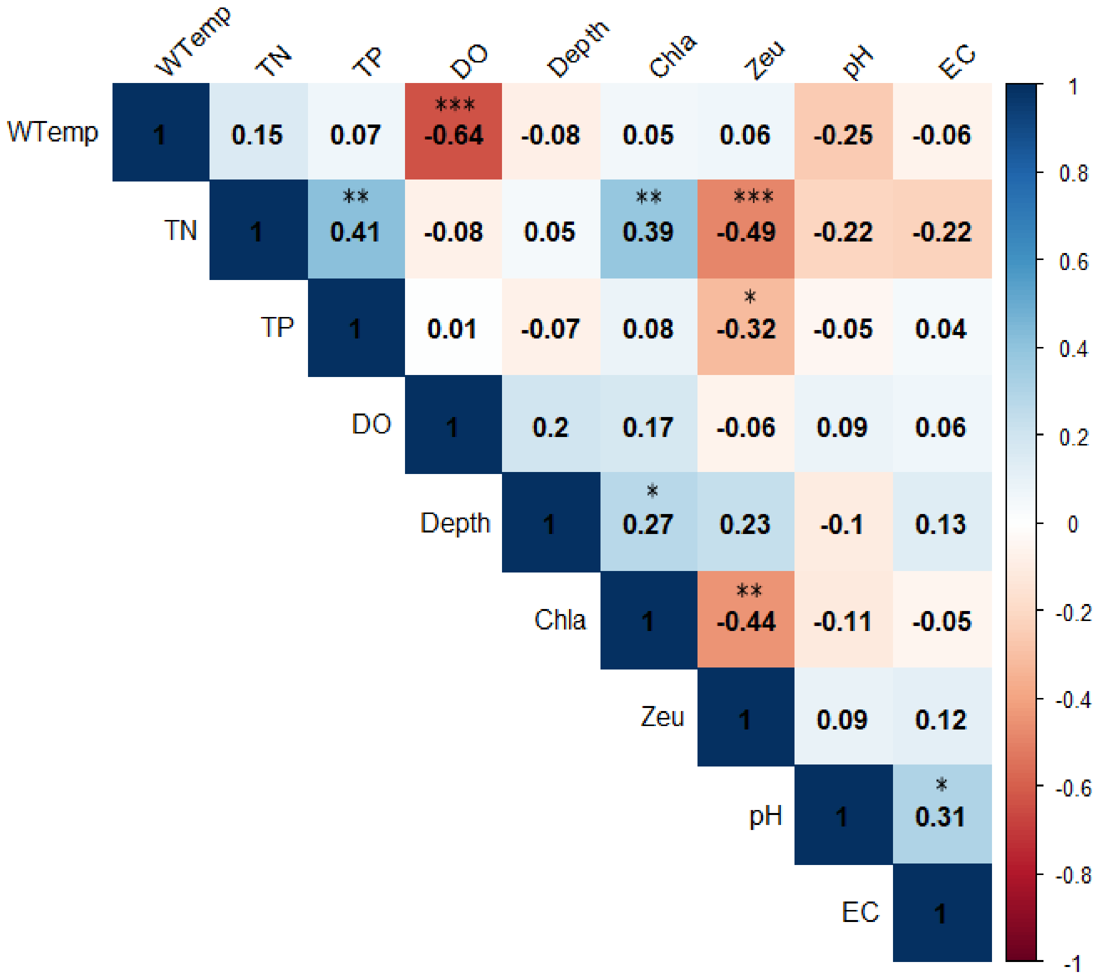


Figure S1 Scatter plots illustrating the interannual variations of **A**) lake depth, **B**) Secchi depth, **C**) euphotic zone depth, **D**) chlorophyll a concentrations, **E**) total phosphorus, and **F**) total nitrogen in Peri Lake from July 2009 to July 2018. Gray lines derived from Loess-fits to visualize the trend of abiotic variables across years. The size of dots reflects the proportion of Cyanobacteria calculated as total biomass of Cyanobacteria to total phytoplankton biomass.



	WTemp	TN	TP	DO	Depth	Chla	Zeu	pH	EC
WTemp	1	0.15	0.07	*** -0.64	-0.08	0.05	0.06	-0.25	-0.06
TN		1	** 0.41	-0.08	0.05	** 0.39	*** -0.49	-0.22	-0.22
TP			1	0.01	-0.07	0.08	* -0.32	-0.05	0.04
DO				1	0.2	0.17	-0.06	0.09	0.06
Depth					1	* 0.27	0.23	-0.1	0.13
Chla						1	** -0.44	-0.11	-0.05
Zeu							1	0.09	0.12
pH								1	* 0.31
EC									1

Figure S2 Spearman correlation matrix between water temperature (WTemp), total nitrogen (TN), total phosphorus (TP), dissolved oxygen (DO), lake depth (Depth), chlorophyll a concentrations (Chla), euphotic zone (Zeu), pH and electrical conductivity (EC). Correlation coefficient (rs) is shown. Blue-tinted sqares represent positive correlations, while red-tinted squares represent negative correlations. The boldness of the colour represent the strength of the relationship between variables, with stronger correlations having bolder colours. The number of asterisks denote the significance of the correlation: * refers to 0.05>p=0.01, ** refers to 0.01<p=0.001, *** refers to p<0.001.

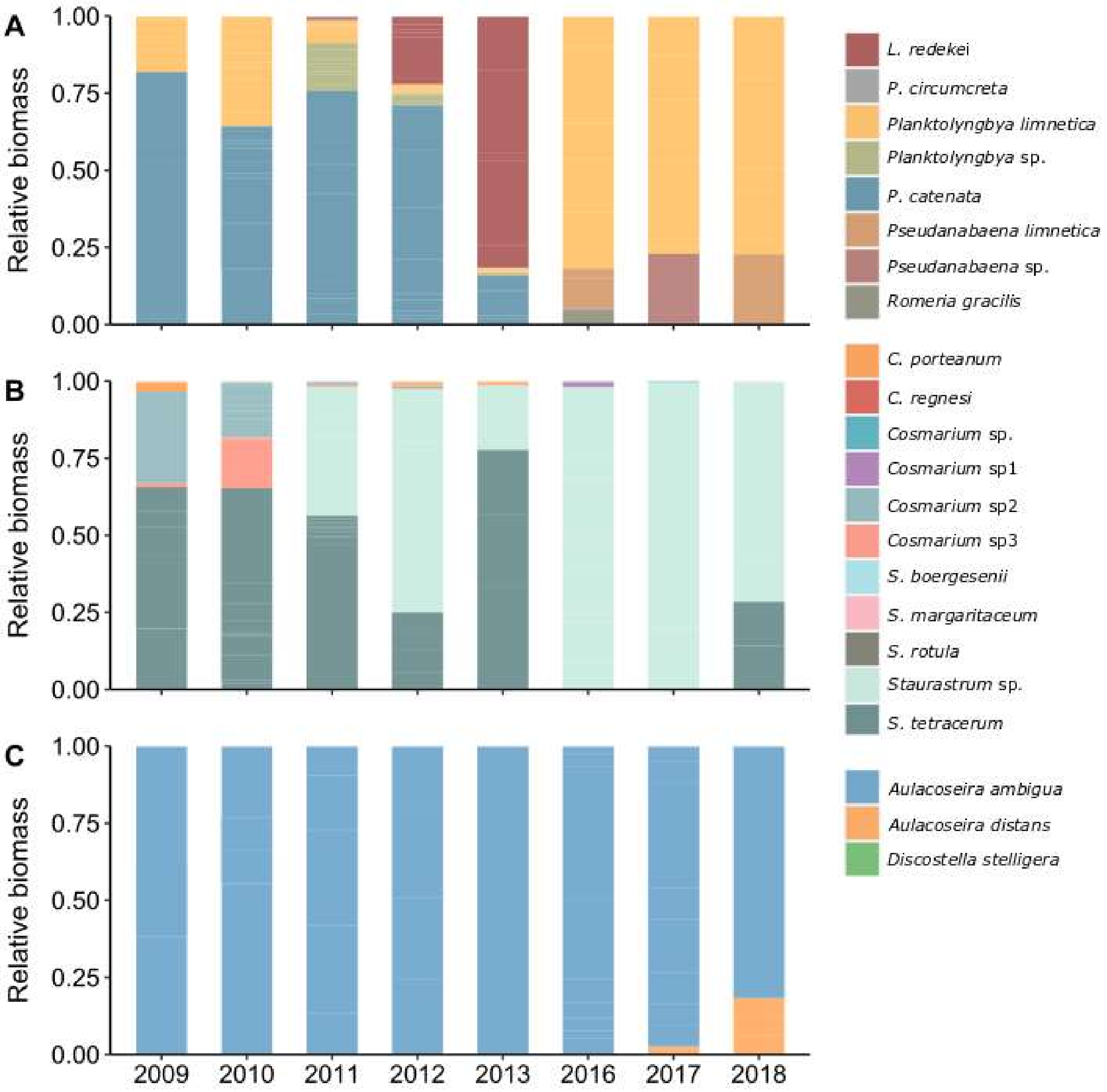


Figure S3 Interannual variation of the relative biomass contribution of the dominant Reynolds functional groups (RFGs) to total phytoplankton biomass in Peri Lake from July 2009 to July 2018. **A**) RFG S1, **B**) RFG N, and **C**) RFG C.

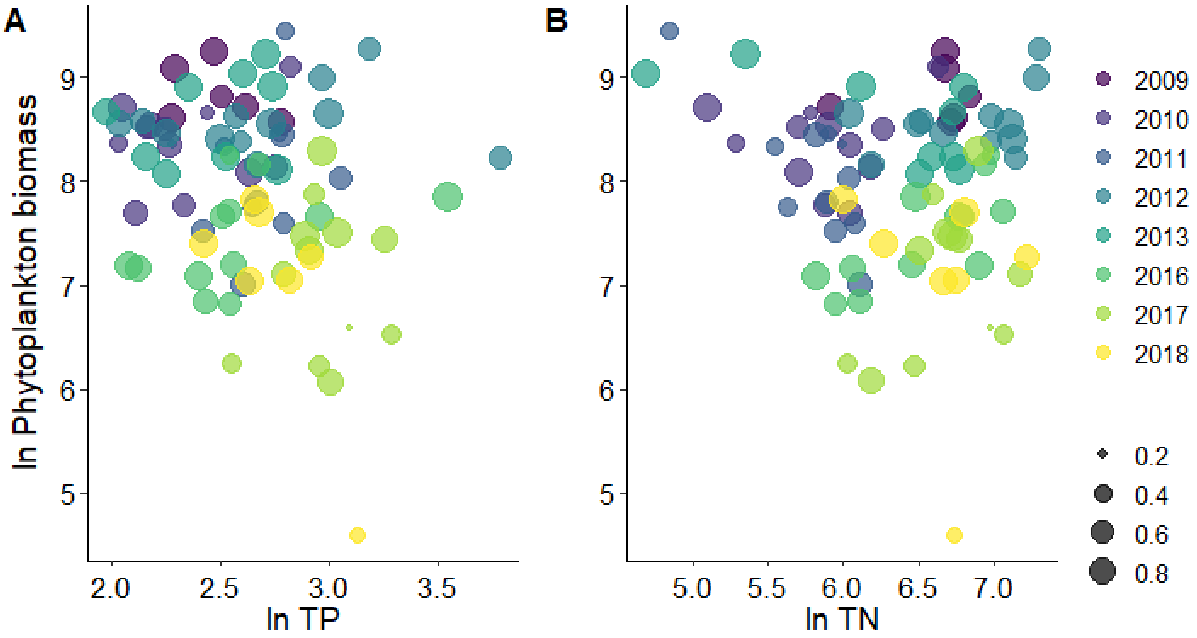


Figure S4 Scatter plots illustrating the relationship between total phytoplankton biomass and **A**) total phosphorus (log-transformed; lnTP, µg L^{-1}) and **B**) total nitrogen (log-transformed; lnTN, µg L-1) in Peri Lake from July 2009 to July 2018. The size of dots reflects the proportion of Cyanobacteria calculated as total biomass of Cyanobacteria to total phytoplankton biomass.

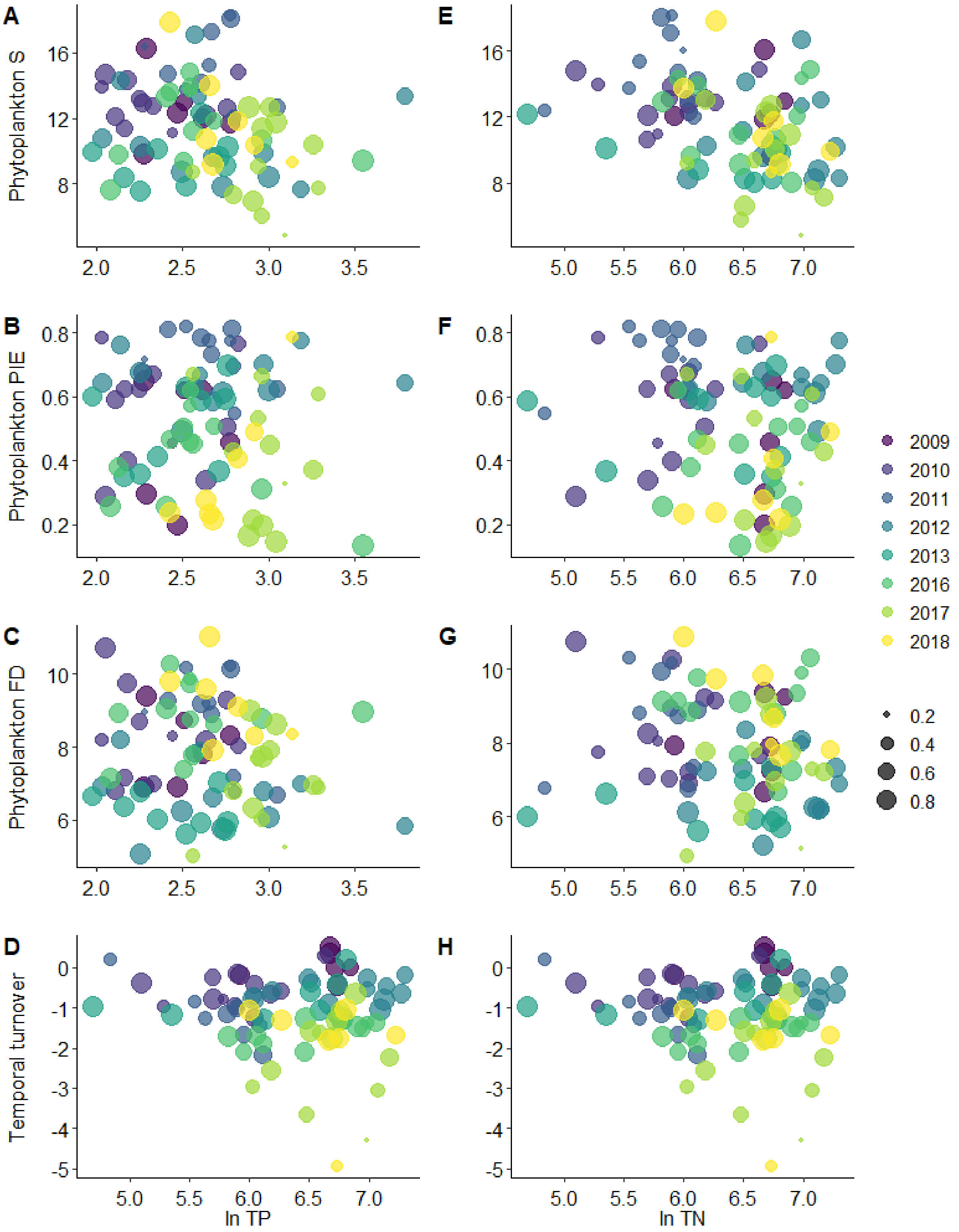


Figure S5 Relationships among total phosphorus (log-transformed; lnTP, µg L^{-1}; left panels) and total nitrogen (log-transformed; lnTN, µg L^{-1}; right panels) with **A**) phytoplankton richness (S), **B**) phytoplankton evenness (PIE) **C**) phytoplankton functional diversity, and **D**) temporal turnover of Reynolds functional groups in Peri Lake from July 2009 to July 2018. The proportion of Cyanobacteria was calculated as total biomass of Cyanobacteria to total phytoplankton biomass.

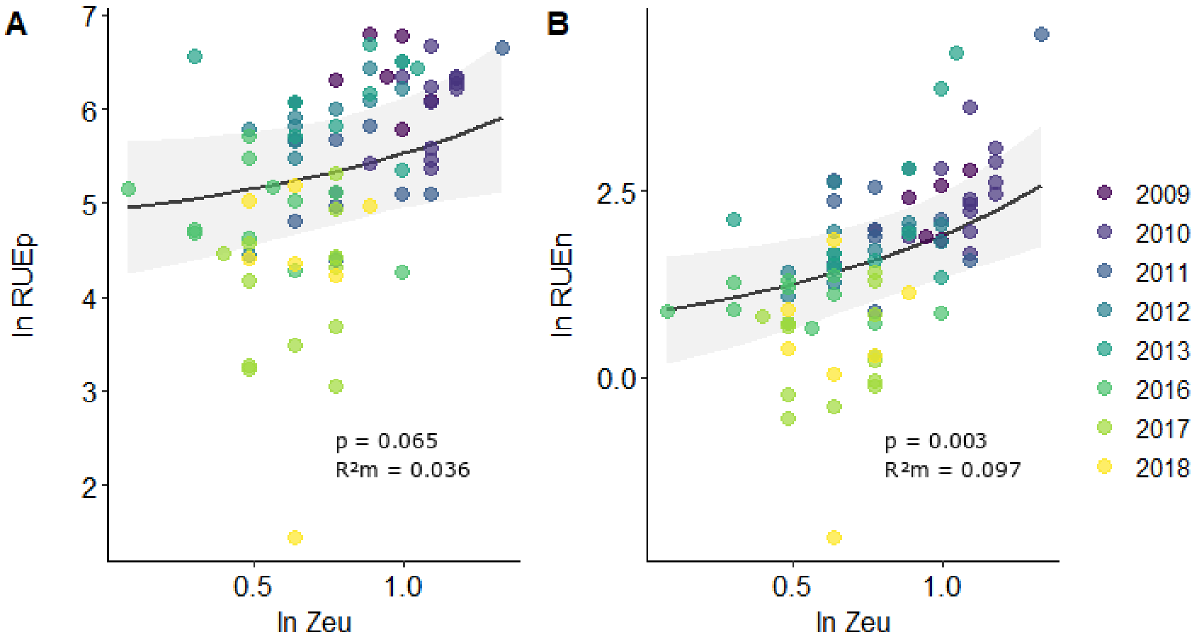


Figure S6 Euphotic zone depth (log-transformed; ln Z_{EU}, m) explaining phytoplankton resource use efficiency for **A**) phosphorus (RUE_P) and **B**) nitrogen (RUE_N) in Peri Lake from July 2009 to July 2018. The solid line represents the fitted values of the overall model, and it is based on linear mixed-effect model (random intercept and fixed slope). The confidence interval of 95%, p-value and marginal adjusted-R^2 (R^2m) of the overall model are provided.

Table S1 Phytoplankton Reynolds functional group (RFG) and all taxa included in each group in Peri Lake from July 2009 to July 2018.

RFG	Taxa	RFG	Taxa	RFG	Taxa
A	*Urosolenia* sp.	**K**	*Aphanocapsa holsatica*	**P**	*Closterium* sp1
C	*Aulacoseira ambigua* (Grun.) Sim. var. *ambigua*		*Cyanodyction* cf. *imperfectum* Cronberg e Weib.		*Melosira varians* Agard.
	Aulacoseira distans (Ehr.) Sim.		*Cyanogranis ferruginea* (Wawrik) Hindák		*Staurodesmus cuspidatus* (Breb.) Teil.
	Discostella stelligera (Cl. & Grun.) Houk & Klee		*Aphanocapsa* sp.	**S1**	*Limnothrix redekei* (Goor) Meffert
D	*Encyonema* sp.		*Aphanotece* sp1		*Planktolyngbya circumcreta* (G.S.West) Anagnostidis & Komárek
F	*Botryococcus braunii* Kütz.		*Chroococales* sp.		*Planktolyngbya limnetica* (Lemm.) Kom.-Legn. & Cronb.
	Dictyosphaerium ehrenbergianum Näg.	**$\mathrm{L_O}$**	*Parvodinium* cf. *umbonatum* (Stein) S.Carty		*Pseudanabaena catenata* Lauterborn
	Oocystis borgei Snow		*Peridiniopsis* sp.		*Pseudanabaena limnetica* (Lemm.) Kom.
	Oocystis lacustris Chod.		*Peridinium* sp.		*Planktolyngbya* sp.
	Nephrochlamys sp.		*Peridinium* sp1		*Pseudoanabaena* sp.
	Chlorophyceae colonial		*Peridinium* sp2	**S2**	*Romeria gracilis* Koczw.
H1	*Anabaena* sp.		*Peridinium* sp3	**$\mathrm{S_N}$**	*Raphidiopsis raciborskii* (Woloszynska) Aguilera, B. G., Kastovsky, E. & Salerno
J	*Desmodesmus opoliensis* (P. Richt.) Hegew.		Dino sem teca	**W2**	*Trachelomonas oblonga* Lemm.
	*Golenkinia pauscispina*West & G.S.West	**MP**	*Fragilaria capucina* Desm.		*Trachelomonas volvocinopsis* Swir.
	Golenkinia radiata Chod.		*Nitzschia palea* (Kütz.) W. Sm.		*Trachelomonas volvocina* (Ehr.) Ehr.
	Monactinus simplex (Meyen) Corda		*Ulnaria ulna* (Nitzch.) Comp.		*Trachelomonas* sp.
	Monoraphidium arcuatum (Kors.) Hind.		*Fragilaria* sp.		*Trachelomonas* sp1
	Monoraphidium contortum (Thur.) Kom. - Legn.		*Fragillaria* sp1	**X1**	*Actinastrum aciculare* Playf.
	Monoraphidium griffithii (Berk.) Kom.-Legn.		*Navicula* sp.		*Desmodesmus armatus* (Chod.) Hegew.
	Monoraphidium irregulare (G. M. Smith) Kom.-Legn.		*Pinnularia* sp.		*Desmodesmus communis (* Hegew.) Hegew
	Monoraphidium komarkovae Nyg.		*Eunotia* sp.		*Desmodesmus denticulatus* (Lag.) Am., Friedl & Hegew.
	Scenedesmus acuminatus (Lagerh.) Chod.	**N**	*Cosmarium porteanum* W.Archer		*Desmodesmus perforatus* (Lemmerm.) E. Hegew.
	Scenedesmus cf. *oahuensis* (Lemm.) G.M.Smith		*Cosmarium regnesi* Reins.		*Desmodesmus spinosus* (Chodat) E. Hegewald
	Scenedesmus ecornis var. *ecornis* (Ehr. ex Ralfs) Chod.		*Cosmarium* sp.		*Tetraedriella jovetti*
	Scenedesmus javanensis Chod.		*Cosmarium* sp1		*Tetraedron caudatum*
	Scenedesmus spinosus Chod.		*Cosmarium* sp2		*Chlorella* sp.
	Stauridium tetras (Ehrenberg) E.Hegewald		*Cosmarium* sp3		*Desmodesmus* sp1
	Tetraplektron acutum (Pasch.) Fott		*Staurastrum boergesenii* W.B.Turner	**X2**	*Cryptomonas marssonii* Skuja
	Ankistrodesmus sp.		*Staurastrum margaritaceum* (Ehr.) ex Ralfs		*Chlamydomonas* sp.
	Pediastrum sp.		*Staurastrum rotula* Nordst.		*Chroomonas* sp.
	Scenedesmus sp.		*Staurastrum tetracerum* (Kütz.) Ralfs ex Ralfs		Phytoflagellate 1
	Scenedesmus sp1		*Staurastrum* sp.		Phytoflagellate 2
	Scenedesmus sp2	**P**	*Aulacoseira granulata* (Ehr.) Sim. var. *angustissima* (O. Müller) Sim.		Phytoflagellate 3
K	*Aphanocapsa conferta*		*Aulacoseira granulata* (Ehr.) Sim. var. *granulata*		

CAPÍTULO II

Hydrobiologia (2020) 847: 2307–2320

Grazing efficiency asymmetry drives zooplankton top-down control on phytoplankton in a subtropical lake dominated by non-toxic cyanobacteria

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ABSTRACT

Body size is considered a powerful trait that impacts ecosystem processes and mediates species responses to environmental change. Diversity metrics informed by body size could thus predict ecosystem functions better than taxonomic diversity. However, despite its overwhelming power, the mechanisms by which size drives functions in freshwater ecosystems remain poorly known. Two mechanisms are often hypothesized to explain the relationship between diversity and ecosystem functioning: selection effects and complementarity. Here we evaluate the relative importance of size-based and taxon-based approaches in explaining the strength of top-down control on phytoplankton, and also aimed at disentangling the mechanism by which size operates. We found that size significantly explained the variation in top-down control, but size together with taxonomic diversity provided better predictions. The latter result differs somewhat from those reported in temperate regions and potentially reflects the limited size range that is typical of warmer waters. Our results also reveal the importance of selection effects relative to complementarity as a driver of top-down control. We highlight the importance of considering multiple aspects of biodiversity and recommend that metrics based on body size should complement, rather than replace, metrics of taxonomic diversity to predict ecosystem functions.

Keywords: body size, complementarity, biodiversity-ecosystem functioning, selection effect, trophic interactions

INTRODUCTION

Only recently, the gap between community structure and ecosystem ecology has been bridged, especially due to the growing need for a unified approach to predict ecosystem changes in response to increasing threats to biodiversity (e.g., climate change, habitat conversion and species invasion) (Van Der Plas, 2019). In the past two decades, hundreds of studies attempted to explain the relationship between biodiversity and ecosystem functioning (B-EF) (Hooper et al., 2005; Cardinale et al., 2012; Meyer et al., 2016). The traditional taxon-based approach extensively used in B-EF studies on both terrestrial and aquatic systems (Hooper et al., 2005; Cardinale et al., 2012) suggest that taxonomic diversity (e.g., number of species; TD) enhances ecosystem functioning (e.g., plant biomass production; Loreau & Hector, 2001; Hooper et al., 2005) and that this effect strengthens over time (Meyer et al., 2016). Yet, more recent studies clearly indicate that ecosystem functions can vary significantly among communities with the same number of species (Cardinale et al., 2006; 2012) and that part of such variance can be explained by differences in functional traits among species (e.g., Gianuca et al., 2016b).

The ecological role of organisms in ecosystems depend on their traits rather than on their taxonomy (Hillebrand & Matthiessen, 2009; Abonyi et al., 2018). The use of functional traits, therefore, offers a more direct mechanistic link between community structure responses to environmental change and ecosystem-level consequences (Hillebrand & Matthiessen, 2009). Moreover, it reduces the complexity of trophic interactions while retaining accurate predictions of biodiversity (Litchman et al., 2013). Hence, trait-based diversity metrics can potentially outperform taxonomic diversity indices in predicting ecosystem functions (e.g., Abonyi et al., 2018). Recently, a significant advance in B-EF research has been made with the growing emphasis on trait-based approaches and their power to predict biodiversity impacts on ecosystem functioning (Litchman et al., 2013; Hébert et al., 2015; 2016; García-Comas et al., 2016; Cadotte et al., 2017). Functional traits are defined as morphological, physiological and/or phenological attributes of an organism that influence its individual performance (Violle et al., 2007). Some traits can be overwhelmingly important because they simultaneously respond to environmental change (i.e., *response trait*) an also impact ecosystem processes (i.e., *effect trait*) (Lavorel & Garnier, 2002; Suding et al., 2008). In such cases, using a single and powerful trait has the potential to outperform multi-trait analysis (Butterfield & Suding, 2013; Gianuca et al., 2016a).

For most aquatic organisms, body size is correlated with several life-history traits and can be considered a key trait given its well-known influence in many biological processes, ranging from individual-level metabolic rates to the provision of ecosystem services to humans (e.g., water quality, food production) (Brown et al., 2004; Woodward et al., 2005; 2011). In the specific case of zooplankton, body size is correlated with traits such as generation time, growth rate, metabolism, dispersal, feeding rate and others (Litchman et al., 2013) that determine species responses to gradients of urbanization (Gianuca et al., 2018), temperature fluctuations (Havens et al., 2015), nutrient loading (Hart, 2011), cyanobacterial blooms (Ersoy et al., 2017), among other factors. Body size has also been shown to be a key trait determining zooplankton top-down control of algae, an important ecosystem function in aquatic systems (Jeppesen et al., 2003; Ye et al., 2013; Thompson et al., 2015; Gianuca et al., 2016b; Wong et al., 2016). However, most studies that assessed the role of body size on top-down control included large grazers that are typical of temperate systems (Jeppesen et al., 2003; Thompson et al., 2015; Gianuca et al., 2016b) and it is still unclear whether a more limited size range in subtropical systems would have a similar impact on species interactions and ecosystem processes.

In general, there are two main mechanisms that link biodiversity to ecosystem processes: selection effects and complementarity (Loreau & Hector, 2001; Petchey & Gaston, 2006; Cardinale, 2011; Barry et al., 2018). In the case of selection effects (aka sampling effect), a dominant species plays an overwhelming role on ecosystem function because of its functional traits. This means that, even in monoculture, such species can maintain high levels of ecosystem processes. In addition, species richer communities have an increased likelihood to include such a dominant species (Hector et al., 2002). On the other hand, complementarity happens when different species partition resources or when they have contrasting responses to environmental fluctuations. The relationship between body size and the strength of top-down control by zooplankton can be linked to the mechanisms of selection effects and complementarity described above (Fig. 1). Size-based selection effects happen when larger zooplankton species are more efficient grazers over a broader range of phytoplankton cell sizes than smaller zooplankton (Fig. 1a). If so, it is expected that changes in body size mean (i.e., trait mean) will be the main mechanism that drives top-down control on algae (Gianuca et al., 2016b). Conversely, size-based complementarity happens when large-bodied zooplankton could graze more efficiently on large algae whereas small zooplankton would graze mainly on small algae, leading to size-based niche partitioning (Fig. 1b). If size-based complementarity prevails, then one would expect a larger influence of size variance on this ecosystem process than body size mean (Fig. 1c) (Ye et al., 2013; Gianuca et al. 2016b).

While experimental studies have considerably contributed to our knowledge on B-EF, they are potentially limited by the simplification of biotic interactions and environmental conditions (e.g., Gianuca et al., 2016b) which makes it difficult to transfer the results to more natural settings (Hillebrand & Matthiessen, 2009; Van Der Plas, 2019). Another limitation of some experimental studies is their short-term duration, although previous work has demonstrated that the importance of the complementarity effect increases through time (Cardinale et al., 2007), which may hamper the ability of short-term experiments to detect this mechanism. In addition, most of controlled freshwater experiments have mainly focused on large-bodied cladocerans and edible algae (e.g., Gianuca et al., 2016b). However, the proliferation of cyanobacterial blooms due to natural and anthropogenic activities is a worldwide problem in aquatic ecosystems with important ecological, societal and economic implications (Sukenik et al., 2015). In such systems, edible phytoplankton tends to be replaced by cyanobacteria, which are known to be nutritionally inadequate as food source for zooplankton, especially for large-bodied cladocerans (Gliwicz & Lampert, 1990). This often leads to habitat filtering against large zooplankton, favoring small-bodied species, which in turn reduces zooplankton community size diversity (Ersoy et al., 2017; Josué et al., 2019). Consequently, such modifications in zooplankton size structure may influence the ecological relevance of size-based trophic interactions in these systems and the mechanisms by which zooplankton body size influences top-down control on phytoplankton (e.g., Ye et al., 2013; Gianuca et al., 2016b).

Here, we studied a shallow lake dominated by non-toxic cyanobacteria along one year to test for the impact of zooplankton body size on top-down control of phytoplankton. Also, and more importantly, we aimed at disentangling the mechanism by which this functional trait drives the top-down control of algae (Fig. 1). We used the ratio of zooplankton to phytoplankton biomass as a proxy for the strength of zooplankton top-down control to test two hypotheses. First, we expected that size-based approaches would enhance our capacity to explain zooplankton top-down control compared to the traditional taxon-based approach in a cyanobacteria dominated-system. This first hypothesis was inspired by studies that demonstrated a strong power of body-size to explain variation in grazing rates among communities (Thompson et al., 2015; Gianuca et al., 2016b) and also by studies showing that functional-based metrics often outperform taxon-based indices when the goal is to explain ecosystem functioning (Cadotte et al., 2011). Second, we tested whether complementarity in resource use among species that vary in body size is the main mechanism linking body-size to top-down control on phytoplankton, as suggested by Ye et al. (2013). This second hypothesis is based on the idea that local scale resource partitioning and contrasting responses to environmental fluctuation among species of different body sizes prevail in (sub)tropical lakes compared to selection effects. The rationale is that selection effects should be more important than complementarity when considering short-term experiments (Cardinale et al., 2007) and that involve large Daphniids from temperate regions (Gianuca et al., 2016b), especially because such settings rule out environmental fluctuations and favor grazing efficiency asymmetry between small and large Daphniids. Yet, we acknowledge that both mechanisms are not mutually exclusive, varying only in relative importance (Ye et al., 2013).

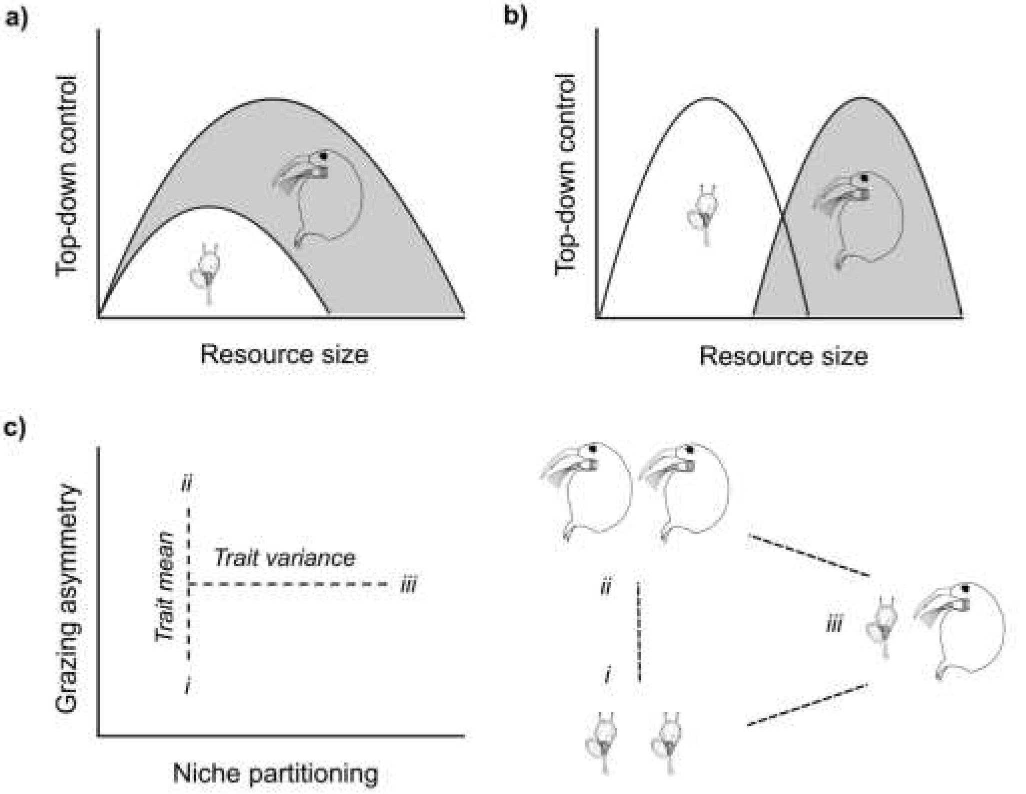

Fig. 1 Conceptual scheme showing hypothetical scenarios of alternative mechanisms by which zooplankton body size can impact ecosystem functioning via size-based selection effects and complementarity. **a)** Size-based selection effects would result from the fact that larger zooplankton species are more efficient grazers over a broader range of phytoplankton cell sizes than smaller zooplankton (Gianuca et al., 2016b). **b)** Alternatively, complementarity happens when small and large zooplankton species complement each other, for instance by foraging on different resource sizes (Ye et al., 2013) or by responding differently to environmental fluctuations

(e.g., temperature, fish predation) through time (Cardinale et al., 2007; Barry et al., 2018; Isbell et al., 2018). **c)** Three hypothetical communities are represented as *i*, *ii*, *iii*. If size-based selection effects are more important than complementarity, then it is expected that changes in body size mean (e.g., from scenario *i* to scenario *ii*) will be the main determinant of variation in grazing pressure (Gianuca et al., 2016b). However, if complementarity is more important, then it is expected that changes in body size variance (e.g., either from scenario *i* or scenario *ii* to scenario *iii*) will be the most important driver of top-down control (Ye et al., 2013). This conceptual scheme was adapted from Gianuca et al. (2016b).

MATERIAL AND METHODS

Field sampling and analytical methods

This study was conducted in Peri Lake (for details, see electronic supplementary material), a freshwater coastal lake in Southern Brazil (27° 44' S, 48° 31' W; Fig. S1). We sampled the lake monthly from April 2011 to March 2012 in pelagic and littoral zones (Fig. S1), recording *in situ* water temperature (WT; °C), dissolved oxygen (DO; mg l^{-1}), electrical conductivity (EC; µS cm^{-1}), and pH with multiparameter probe (model YSI-85), as well as water transparency using a Secchi disk. The euphotic zone (Z_{EU}; m) was estimated as 2.7 times the Secchi disk depth.

Total phytoplankton samples (100 ml) were taken from the subsurface of the water column and immediately preserved with formalin solution (final concentration 1.6%). The community abundance was analyzed in the laboratory using an inverted microscope following the Utermöhl method (1958) and settling time according to Lund et al. (1958). At least 400 individuals (cell, colony and filaments) of the most dominant species per sample were counted using a chamber, in which the fields were chosen randomly from each quadrat (Uehlinger, 1964). Phytoplankton was identified whenever possible to the lowest taxonomic level, and at least 30 individuals from each species were measured for biovolume calculations. The biovolume (mm^3 l^{-1}) of each species was estimated from the product of the population and the mean unit volume (Hillebrand et al., 1999). Carbon content (C) was obtained from the biovolume (V) using the following model $C = 0.1204V^{1.051}$ (Rocha & Duncan, 1985). Then, the mean carbon content of each species was multiplied by their density in order to obtain the carbon content of the populations ($B_{P;}$ µg C l^{-1}).

Zooplankton samples were obtained by filtering 50 l of water using a bucket (10 l capacity) and a plankton net (50 µm mesh size) from the subsurface of the water column. Carbonated water was added to decrease the contraction of individual's bodies and the samples were fixed *in situ* with formalin solution (final concentration 4 %). In the laboratory, the samples were counted using a Sedgewick-Rafter chamber under an optical microscope at 100x magnification (Zeiss®) for rotifers and copepods nauplii; and using an acrylic open chamber under a stereomicroscope at 50x magnification (Leica® MZ6 model) for cladocerans and copepods. Zooplankton was identified as the lowest taxonomic level possible. Immature copepods were separated in copepodits or nauplii and identified at the order level (i.e., Cyclopoida and Calanoida). For each month and sampling station, at least 30 individuals of each species were measured with a calibrated ocular micrometer, using appropriate allometric formulae. Biomass (B_{Z}; µg l^{-1}) for rotifers were estimated based on biovolume (Ruttner-Kolisko, 1977; Manca & Comoli, 1999), and for crustaceans (Cladocera and Copepoda) estimations were based on published allometric relationship between body length and dry weight (Bottrell et al., 1976; Azevedo et al., 2012). For copepods, individual lengths were measured for different life stages (adult, copepodite and nauplii). The carbon biomass (B_{Z}; µg C l^{-1}) was estimated assuming a conversion factor of 50% from the dry weight (Latja & Salomen, 1978).

Here we used the zooplankton (consumer) to phytoplankton (resource) biomass ratio (B_Z/B_P), log10 transformed, as a proxy for estimating the strength of zooplankton top-down control on phytoplankton as commonly used by other studies (e.g., Jeppesen et al., 2003; Hart, 2011; Ye et al., 2013).

Biodiversity metrics

To test the capacity of size-based approach to explain zooplankton top-down control (our H_1) and disentangle the mechanism by which body size affects grazing pressure (our H_2), we used two functional metrics: Community Weighted Mean body size (CWM) and the standardized effect size based on Mean Pairwise Distance ($_{\text{SES}}$MPD). CWM is expected to be positively associated with top-down control when dominance of larger zooplankton species enhance grazing rates via selection effect (Gianuca et al., 2016b). In contrast, $_{\text{SES}}$MPD is a measure of trait variance and it is expected to relate positively to top-down control when resource partitioning between large and small zooplankton species enhance grazing rates via niche complementarity effects (Gianuca et al., 2016b). For each sampling month, these metrics were calculated based on length measurements (mm) for zooplankton species.

To estimate CWM, we calculated the mean body size value of each species in the community weighted by their relative abundances (Laliberté et al., 2015). To estimate $_{\text{SES}}$MPD, we first calculated an Euclidean distance matrix based on body size. Then, based on a trait distance matrix, we calculated the standardized effect size of mean pairwise distance (SESMPD) between all species in the community (Kembel et al., 2010). Negative values of the index SESMPD indicate that zooplankton communities are composed of species that are more similar in size than expected by chance considering an appropriate null model (here, we used the model "taxa.label" from the picante package, which reduces the influence of richness on trait diversity values by shuffling the distance matrix labels across all taxa). This pattern of higher similarity than expected is called size "clustering". Conversely, positive values of this index (SESMPD) indicate that communities are composed of species that are more dissimilar in size than expected by chance, a pattern called size "overdispersion", indicating a scenario of high size diversity. Finally, values close to zero for this index indicate that the size difference among species within communities is not different from what would be expected by chance (Kembel et al., 2010). To represent zooplankton taxonomic diversity (taxon-based approach), we calculated the species richness (S) for each sampling month. Zooplankton community structure was analyzed in R 3.6.1 (R Core Team, 2019) using *FD* (Laliberté et al., 2015), and *picante* (Kembel et al., 2010) packages to generate all biodiversity metrics (SESMPD, CWM and S).

Statistical analysis

To test our hypotheses, we quantified the effects of biodiversity metrics on zooplankton top-down control using linear mixed-effect models (LMMs) (Laird & Ware, 1982). In all models, the biomass ratio log-10 transformed (B_Z/B_P) was the response variable and sampling sites was included as the random term. Additionally, a compound symmetry structure was included in LMMs to account for temporal autocorrelation (Zuur et al., 2009). Zooplankton size diversity (SESMPD; trait-based approach), community average size (CWM; trait-based approach) and taxonomic richness (S; taxon-based approach) were used as predictors. As explained in the introduction and also on our conceptual Fig. 1, each explanatory variable of the size structure (SESMPD and CWM) has the potential to reflect different mechanisms by which zooplankton body size influence the top-down control on phytoplankton (for details, please see Fig. 1 and also refer to Gianuca et al., 2016b). Although both mechanisms may only vary in relative importance (Ye et al., 2013), we expect a large contribution of CWM to explain variation in top-down control, which would indicate that selection effect is the main mechanism by which size operates. Conversely, if size-based complementarity prevails, then we would expect a larger contribution of $_{\mathrm{SES}}$MPD to explain variation in B_Z/B_P.

Spearman pairwise rank correlations (r_S) were performed to measure the strength and direction of associations among biodiversity metrics ($_{\mathrm{SES}}$MPD, CWM, S), and multicollinearity was checked in all multiple models by examining the variance inflation factor (VIF; Fox, 2008) using the *HH* package (Heiberger, 2018). We used Akaike's information criterion corrected for small sample size (AICc; Hurvich & Tsai, 1989) to select the "best possible" model. AICc differences (ΔAICc) were used to rank the models and we only considered models with $\Delta\mathrm{AICc} \leq 2$ from the top model ($\Delta\mathrm{AICc} = 0$) (Burnham & Anderson, 2002). The variance explained by LMMs was based on marginal and conditional adjusted R^2 (Nakagawa & Schielzeth, 2013). Marginal adjusted R^2 (R^2m) represents the variance explained by fixed parameters and conditional R^2 (R^2c) represents the variance explained by both fixed and random parameters. A visual examination of diagnostic plots (for details, see electronic supplementary material; Fig. S2) was applied to determine the model's goodness-of-fit (Zuur et al., 2009). In order to check possible temporal structure left in the residuals, we performed a visual inspection (Fig. S3) using "acf" function from *stats* package (R Core Team, 2019). All models were implemented using the *nlme* package (Pinheiro et al., 2015) and all analyses were run in R 3.6.1 (R Core Team, 2019).

RESULTS

Environmental conditions were similar among all sampling sites (see electronic supplementary material, Table S1). Water temperature followed a seasonal pattern that is typical of subtropical regions, with high values in the summer and low values during the winter (Table 1). The euphotic zone varied, on average, between 1.60 m and 2.40 m. Water pH values were near to neutral and electrical conductivity was homogeneous, with low values throughout the study period. Dissolved oxygen concentrations revealed that Peri Lake is well oxygenated, with high values registered during the winter and low values (> 5.0 mg l^{-1}) in the summer.

Phytoplankton was composed of 53 taxa belonging to 4 major algal groups (Cyanobacteria, Chlorophyceae, diatoms and mixotrophic flagellates). The highest phytoplankton biomass was registered during summer (Table 2), with larger relative biomass contribution of the Cyanobacteria group (mean ranged from 60.3 to 97.9%) over the entire study period (Fig. S4), followed by Chlorophyceae (mean ranged from 1.1 to 38.9%), and diatoms (mean ranged from 0.2 to 25%). By contrast, mixotrophic flagellates had the lowest contribution (< 2%) in terms of biomass along the sampling period. Nine species of cyanobacteria were registered, with the main contribution of two filamentous species, *Cylindrospermopsis raciborskii* and *Pseudanabaena catenata* Lauterborn (1915) during the sampling months.

Table 1 Statistical summary (mean values ± standard deviation) of the temporal variation of limnological variables in Peri Lake from April 2011 to March 2012. WT = water temperature; DO = dissolved oxygen; EC = electrical conductivity; Z_{EU} = euphotic zone depth.

	WT (°C)	**DO (mg l^{-1})**	**EC (µS cm^{-1})**	**pH**	**Z_{EU} (m)**
11-Apr	24.6 ± 0.3	9.0 ± 0.3	63.5 ± 5.5	6.0 ± 0.2	2.2 ± 0.4
11-May	21.8 ± 0.3	8.8 ± 0.2	61.5 ± 5.6	6.4 ± 0.3	2.4 ± 0.3
11-Jun	18.5 ± 0.4	8.5 ± 0.1	65.2 ± 4.3	8.3 ± 0.9	2.1 ± 0.3
11-Jul	14.6 ± 0.2	9.1 ± 0.4	67.4 ± 5.1	6.0 ± 0.5	1.8 ± 0.3
11-Aug	16.2 ± 0.1	8.3 ± 0.4	60.3 ± 5.1	7.8 ± 0.1	2.1 ± 0.3
11-Sep	19.5 ± 0.4	8.6 ± 0.4	58.6 ± 5.1	6.9 ± 0.1	2.2 ± 0.3
11-Oct	23.4 ± 0.2	6.1 ± 0.1	70.5 ± 5.1	8.1 ± 0.5	1.9 ± 0.3
11-Nov	23.5 ± 0.2	8.4 ± 0.4	61.6 ± 5.1	7.1 ± 0.3	2.2 ± 0.3
11-Dec	24.7 ± 0.2	8.1 ± 0.6	63.8 ± 5.1	7.3 ± 0.1	2.3 ± 0.3
12-Jan	27.5 ± 1.1	7.4 ± 1.4	74.5 ± 5.1	7.7 ± 0.7	1.6 ± 0.3
12-Feb	28.9 ± 0.2	7.1 ± 0.2	67.1 ± 5.1	6.4 ± 0.2	1.7 ± 0.3
12-Mar	28.2 ± 0.1	5.7 ± 1.1	63.1 ± 5.1	7.2 ± 0.3	1.8 ± 0.3

Table 2 Mean values (± SD) of the temporal variation of phytoplankton total carbon biomass, zooplankton carbon biomass per taxonomic group (Rotifera, Cladocera, Copepoda), zooplankton to phytoplankton biomass ratio (B_Z/B_P), zooplankton standardized effect size ($_{SES}$MPD), community weighed mean (CWM) and taxonomic richness (S) at four sampling stations (P1-P4) in Peri Lake from April 2011 to March 2012. SD represents the standard deviation.

	Carbon biomass (µg C l^{-1})				**B_Z/B_P**	**$_{SES}$MPD**	**CWM**	**S**
	phytoplankton	**Rotifera**	**Cladocera**	**Copepoda**				
11-Apr	2499.50 ± 581.53	88.75 ± 52.61	26.50 ± 23.39	30.75 ± 58.85	0.61 ± 0.10	- 0.86 ± 0.30	0.14 ± 0.02	6 ± 2
11-May	1917.75 ± 391.72	148.5 ± 73.30	2446.00 ± 1387.36	174.25 ± 107.34	1.04 ± 0.05	- 0.77 ± 0.21	0.19 ± 0.02	8 ± 1
11-Jun	1605.75 ± 226.64	643.50 ± 489.97	1105.25 ± 605.59	54.50 ± 40.45	1.00 ± 0.08	- 1.19 ± 0.21	0.14 ± 0.01	7 ± 1
11-Jul	1272.25 ± 115.21	377.50 ± 85.570	600.75 ± 541.99	63.25 ± 43.03	0.95 ± 0.09	- 0.97 ± 0.15	0.15 ± 0.01	8 ± 2
11-Aug	2001.25 ± 1030.41	135.75 ± 33.410	620.50 ± 252.03	15.00 ± 12.19	0.89 ± 0.07	- 0.90 ± 0.11	0.16 ± 0.01	7 ± 1
11-Sep	1305.25 ± 543.92	394.75 ± 158.72	1349.00 ± 773.31	4.50 ± 5.20	1.05 ± 0.03	- 0.89 ± 0.23	0.15 ± 0.02	6 ± 1
11-Oct	2092.75 ± 1048.18	314.75 ± 92.380	1936.00 ± 1651.53	30.25 ± 35.41	1.00 ± 0.12	- 0.87 ± 0.25	0.16 ± 0.02	7 ± 1
11-Nov	2566.75 ± 436.73	826.0 ± 53.63	447.50 ± 442.80	31.25 ± 36.51	0.91 ± 0.02	- 1.34 ± 0.27	0.12 ± 0.01	8 ± 1
11-Dec	2172.00 ± 571.05	2388.5 ± 428.24	1515.25 ± 564.60	40.00 ± 16.71	1.08 ± 0.03	- 1.20 ± 0.24	0.13 ± 0.01	9 ± 1
12-Jan	3208.00 ± 426.26	5253.75 ± 5297.69	79.25 ± 105.42	20.50 ± 19.33	1.03 ± 0.10	- 1.00 ± 0.54	0.15 ± 0.02	8 ± 2
12-Feb	3419.50 ± 679.08	2933.25 ± 3494.53	978.50 ± 1058.83	126.75 ± 125.81	1.00 ± 0.11	- 1.21 ± 0.24	0.13 ± 0.01	9 ± 1
12-Mar	5811.75 ± 1196.87	2087.0 ± 317.25	191.25 ± 112.79	319.00 ± 125.14	0.91 ± 0.03	- 0.33 ± 0.27	0.14 ± 0.01	6 ± 1

Zooplankton composition was similar in all sampling sites (Table S2). The community was composed of 16 taxa belonging to three major groups (Rotifera, Cladocera and Copepoda). Zooplankton biomass showed high temporal variability along the period sampled (Table 2). The community was dominated mainly by rotifers (mean ranging from 61.1 to 95.2%) between November 2011 and April 2012, while cladocerans (mean ranged from 48.6 to 85.1%) were dominant between May 2011 and October 2011 (Fig. S5), with the main contribution of *Ptygura libera* Myers (1934), *Filinia longiseta* Ehrenberg (1834), *Bosmina hagmanni* Stingelin (1904) and *Bosmina freyi* De Melo & Hebert (1994). Copepods contributed mainly with larval stages (nauplii and copepodits) and rarely with adult stage. Negative values of zooplankton $_{\text{SES}}$MPD indicated a clustered pattern in size distribution (Table 2), and according to zooplankton CWM values (Table 2), the community was composed mainly by small-bodied species (mean size ranged from 0.07 to 0.74 mm; Table S3). Zooplankton taxonomic richness (S) was very low during the entire study period (Table 2).

Results of LMMs reveal that both CWM and species richness accounted for approximately 25% of the explained variation in the strength of zooplankton top-down control (Table 3). The model with CWM and S exhibited the best goodness of fit (AICc = -48.1) compared to other models (ΔAICc $\geq$ 3.3). In addition, the lack of correlation between both variables (r_S = -0.24; p = 0.102; Fig. S6) reveals that the positive effect of both predictors on zooplankton top-down control (Fig. 2) were independent to each other. Nevertheless, we cannot rule out the contribution of $_{\text{SES}}$MPD because of its significant correlation with S (rs = -0.61; p < 0.001; Fig. S6) and CWM (rs = 0.65; p < 0.001; Fig. S6). CWM alone accounted for approximately 9% of the explained variance (Table 3) and was significantly superior to the model that considered only the effect of species richness (ΔAICc = 5.5) or $_{\text{SES}}$MPD (ΔAICc = 9.8).

Table 3 Linear mixed-effect models (LMMs) of relationships among zooplankton top-down control (log10-scale; B_Z/B_P), standardized effect size ($_{\text{SES}}$MPD), community weighed mean (CWM) and taxonomic richness (S). In all models, sampling sites are considered as a random-effect variable. d.f. refers to degrees of freedom; SE refers to standard error; R^2m and R^2c refer to marginal (only fixed terms) and conditional (fixed and random terms) adjusted R^2, respectively.

				Coefficients (SE)				
Models	**d.f.**	**AICc**	**Δ AICc**	**CWM**	**S**	$_{\text{SES}}$**MPD**	R^2**m**	R^2**c**
CWM + S	6	-48.1	0	2.568 (0.625)	0.036 (0.008)	-	0.253	0.254
CWM	5	-44.8	3.3	1.829 (0.836)	-	-	0.082	0.084
CWM + $_{\text{SES}}$MPD + S	7	-44.1	4.0	1.371 (0.888)	0.046 (0.009)	0.101 (0.055)	0.239	0.239
$_{\text{SES}}$MPD + S	6	-43.6	4.5	-	0.054 (0.003)	0.185 (0.010)	0.242	0.242
CWM + $_{\text{SES}}$MPD	6	-40.1	8.0	-0.079 (0.063)	-	2.681 (1.068)	0.118	0.120
S	5	-39.3	8.8	-	0.033 (0.011)	-	0.127	0.129
$_{\text{SES}}$MPD	5	-35.0	13.1	-	-	0.015 (0.054)	0.001	0.004

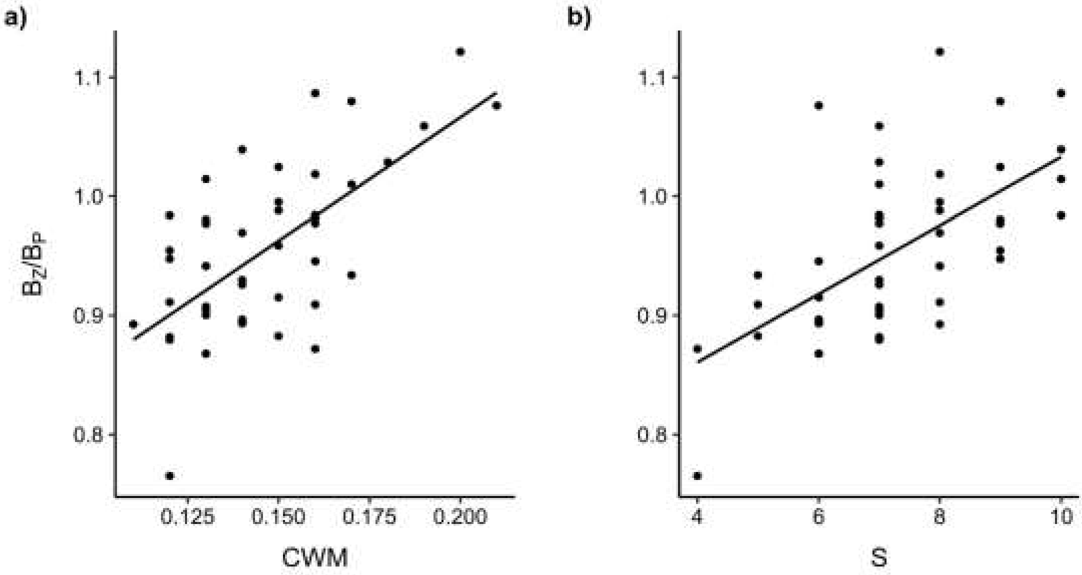

Fig. 2 Scatter plots describing the relationship between the biomass ratio (B_Z/B_P) and its predictors: a) community weighed mean based on body size (CWM) and b) taxonomic richness (S). The solid line represents the fitted values for all sampling sites, , and it is based on the selected linear mixed-effect model ($B_Z/B_P = 3.15 + 2.568*CWM + 0.036*S$).

DISCUSSION

In this study, we focused on whether zooplankton body size (i.e., average size and size variation) in a lake dominated by non-toxic cyanobacteria could better explain variation in grazing pressure than more traditional approaches based only on species identities. Our results show that considering body size adds significant power to explain zooplankton top-down control, largely in line with previous experimental studies. However, we also demonstrated that it is important to account for taxonomic diversity along with size structure, which partially rejects our first hypothesis. Furthermore, community average size was the most important variable linking community size structure to top-down control, which rejects our second hypothesis on the importance of size-based complementarity in warmer waters dominated by cyanobacteria. This result adds support to the idea that size-mediated selection effects via grazing efficiency asymmetry is the main mechanism influencing top-down control in our system, which is in accordance with a previous experimental study that focused on relatively large zooplankton species (i.e., Gianuca et al., 2016b). Below we discuss in detail the implications of these findings.

There is an ongoing debate on the relative power of taxonomic diversity measures, namely species richness, and functionally informed measures, such as those based on functional traits to predict ecosystem functions (Cadotte et al., 2011; Abonyi et al., 2018). One of the main critiques to traditional taxon-based approaches in ecosystem functioning research is that they are silent about species ecological similarities and differences (Cadotte, 2011). Therefore, some have argued that directly accounting for functional traits would provide stronger predictions of ecosystem functions than taxonomic-based diversity metrics (Thompson et al., 2015; Gianuca et al., 2018). We tested this hypothesis by comparing the power of zooplankton body size-diversity and composition as well as species richness to explain differences in resource use efficiency, a proxy of top-down control on algae, in a subtropical lake dominated by non-toxic cyanobacteria. Our results clearly indicate that body size explains a substantial and independent part of the variance in top-down control, but species richness also plays a role. Therefore, accounting for body size information along with species richness can significantly increase the total amount of explained variance in zooplankton resource use efficiency, as illustrated by our results.

Contrary to our results, some studies have shown a stronger power of functional traits, especially body size, to predict zooplankton top-down control compared with taxonomic diversity (Ye et al., 2013; Thompson et al., 2015; Gianuca et al., 2018). A potential explanation for this discrepancy is the lack of large grazers in our subtropical system, which is dominated by non-toxic cyanobacteria. In addition, a recent study in a tropical hypereutrophic lake demonstrated that cyanobacteria dominance can reduce zooplankton trait diversity, potentially limiting the functional role that zooplankton play on ecosystems (Josué et al., 2019). Our results also suggest that this redundancy in body size or other traits due to environmental filtering might influence the ecological relevance of body size on ecosystem functioning. This claim is supported by the fact that communities are strongly size clustered in our system (i.e., more similar in size than expected by chance; negative values of sesMPD), with a dominance of small zooplankton species. Therefore, this limited size range likely reduces the potential for size, compared to species richness, to explain top-down control on algae. However, despite of the limited size range, our results show that body size explains a unique and significant amount of variation in top down-control, which is in agreement with several studies demonstrating the role of zooplankton body size to control phytoplankton biomass (Jeppesen et al., 2003; Ye et al., 2013; Thompson et al., 2015; Gianuca et al., 2016b; Wong et al., 2016).

An important question that arises from our study then is whether there is a minimum size range to be able to assess the effect of size on ecosystem functions. For instance, one can expect that the smaller the size range within a region, the weaker the relationship between body size and ecosystem processes. Answering this question, however, would demand a large comparison across systems that vary considerably in the size range to establish whether this threshold exists. Although this is beyond the scope of our study, it is an interesting topic for a future meta-analysis. However, it is possible that multiple thresholds exist, instead of a universal one, depending on the interaction between body size with other factors, such as the quality (Ahlgren et al., 1990), diversity (DeMott et al., 2001) and the size structure of the phytoplankton (Wong et al., 2016). Secondly, evolutionary processes that influence the ability of zooplankton to graze as well as the resistance of phytoplankton to grazing (Schaffner et al., 2019) might continuously change the relation between zooplankton size and resource use efficiency. Finally, temporal fluctuation in environmental conditions may alter the relationship between body size and top-down control (Rosa et al., 2016).

In addition to the effect of body size, our results also demonstrate an important role of species richness in explaining variation in zooplankton resource use efficiency. These findings suggest that taxonomic richness adds information on community structure that cannot be solely represented by body size (see also Flynn et al., 2011). Species richness seem to capture information about other traits that were not quantified in our study (Flynn et al., 2011). Thus, directly accounting for functional traits other than size may increase even more the power to predict ecosystem functioning, especially in subtropical systems that have a limited size range. Indeed, a recent study has demonstrated that traits related to grazing mode can be more important than size to determine top-down control, especially when there is poor resource quality, like cyanobacteria (Ger et al., 2018). It is paramount that future studies in tropical waters include multiple traits in their analysis to compare their explanatory power with that attained only by body size or only by species richness. In the absence of information of several traits for multiple species, one could also use phylogenetic distances to synthetically represent functional diversity (Srivastava et al., 2012; Cadotte et al., 2015). The latter has been tested for zooplankton species of temperate systems with mixed supporting evidence (Thompson et al., 2015; Gianuca et al., 2016a).

In addition to evaluating the relative power of size-based and taxonomic approaches, we also aimed at testing the mechanism by which zooplankton controls algae, which may depend on environmental context and time span of different studies (Cardinale et al., 2007). Specifically, we rejected our second hypothesis that size complementarity would be more important than size-based selection effects in our system (for details, see also Fig. 1). Our findings, therefore, contrast with those reported by Ye et al. (2013), who suggested that zooplankton size diversity enhances top-down control on phytoplankton via niche partitioning and complementarity effects. These authors suggested that larger zooplankton would prey more efficiently on large algae whereas small zooplankton would feed mainly on small algae. In a more controlled experiment, Gianuca et al. (2016b) found that large cladocerans were more efficient grazers on both small and large green algae, indicating that selection effects (i.e., size-based grazing efficiency asymmetry) were more important than complementarity (i.e., size-based niche partitioning). Our results concur with those reported by Gianuca et al. (2016b) as we demonstrate that community average size (CWM) was more important than size diversity ($_{\text{SES}}$MPD) to explain variation in resource use efficiency, a proxy of top-down control on phytoplankton. This adds support to the idea that it is not the co-occurrence of small and large species that increase grazing pressure via niche partitioning but rather the replacement of small species by others that are relatively larger. We acknowledge the limited range size of species in our system compared to temperate regions, but our results clearly indicate that even a slight increase in CWM is enough to detect selection effects via grazing efficiency asymmetry.

The small cladoceran species of the Bosminidae family represent some of the larger species in our system, especially when compared with the tiny rotifers. The grazing pressure of Bosminidae species on cyanobacteria biomass have been previously reported by other studies (e.g., Fulton, 1988; Leonard & Paerl, 2005). Their ability to feed selectively (e.g., highly edible flagellates) and efficiently at low food concentrations (DeMott, 1982), switching their preference over time (DeMott & Kerfoot, 1982) and their ecological tolerance to cyanobacteria blooms (Leonard & Paerl, 2005) may have led to asymmetries in grazing efficiency (DeMott & Kerfoot, 1982), favouring the importance of selection effect in Peri Lake. Since size spectrum is very sensitive to any small change in zooplankton feeding preferences (Fuchs & Frank, 1988), the feeding behavior of *Bosmina* spp. (i.e., dual-option feeding mechanism) (DeMott, 1982; DeMott & Kerfoot, 1982) might also have influenced the strength of top-down forces. However, despite the observed importance of *B. hagmanni* and *B. freyi* to the strength of top-down control, an enough number of species may still be needed at larger scales to buffer their temporal variability (Isbell et al., 2018). Cladocera species might not be able to maintain stable populations in cyanobacteria-dominated systems throughout the year (Gliwicz & Lampert, 1990). Consequently, a number of small-bodied species, such as rotifers, might be important to buffer top-down control despite their relatively inefficient grazing rates on cyanobacteria. This makes even more sense when we consider that small zooplankton, such as rotifers can increase their biomass by feeding on alternative resources (e.g., bacteria, flagellates and organic detritus) and apply some grazing pressure, cutting filaments and making edible size of algae available for other zooplankton species to later consumption, especially smaller cladocerans (Kâ et al., 2012).

The effect of biodiversity on zooplankton top-down control in our system seems to depend mainly on the increasing dominance of larger zooplankton species (such as Bosminidae species) that are also more efficient in resource use (McKane et al., 2002; Isbell et al., 2018). However, such changes in dominance between more and less efficient species is only possible because of their complementarity responses through time. Hence, the interchanging temporal pattern of dominance between Bosminidae and Rotifera species in Peri Lake influences zooplankton size structure via complementarity, which in turn has an effect on the strength of top-down control on phytoplankton via size-based grazing efficiency asymmetry. This observation is in agreement with other studies that report simultaneous selection effects and complementarity, with changes only in the relative importance of each mechanism (Ye et al., 2013; Gianuca et al., 2016b). Moreover, the positive correlation that we found between CWM and $_{\text{SES}}$MPD indicates that the increased zooplankton size diversity reflects the addition of larger species in the zooplankton community (Ye et al., 2013). In our system, we find evidence that selection effects prevail, but cannot rule out complementarity, especially due to variations in zooplankton community structure, which are linked to size differences.

CONCLUSION

Our results demonstrate that approaches based on body size and taxonomic richness complement each other in explaining variation in zooplankton top-down control on phytoplankton. This is an important outcome when considering that in warmer waters zooplankton average size is smaller and less diverse compared to temperate systems. Therefore, we recommend the simultaneous use of multiple biodiversity metrics (e.g., taxonomic, functional and phylogenetic diversity) to improve our understanding of zooplankton-phytoplankton trophic interactions and ecosystem functioning. We also found evidence of size-based selection effects via grazing efficiency asymmetry as the main mechanism influencing zooplankton top-down control on algae. These findings indicate that the strength of zooplankton top-down control on phytoplankton results mainly from dominance of more efficient grazers on phytoplankton, which tend to be relatively larger than the less efficient species. Given the lack of large-bodied grazers in tropical and subtropical waters, and the evidence that cyanobacteria dominance will increase in freshwater ecosystems under the predicted future climate, the results of the present study highlight the concern about the energy flow in such cyanobacteria-dominated systems.

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ELECTRONIC SUPPLEMENTARY MATERIAL

Details on materials and methods

Study area

“Peri” is a coastal shallow lake (average and maximum depth of 4.2 m and 11.0 m, respectively), located within a legally protected area in Santa Catarina State, Southern Brazil (27° 44’ S, 48° 31’ W) (Fig. 2). The lake has a surface area of 5.07 km^2, a drainage basin of 20 km^2 approximately, and it is surrounded by mountains in its north, south, and west areas. It has no marine influences, a restricted human occupation, and it is the main freshwater source to local inhabitants. The climate of the region is wet subtropical with rainfall predominantly concentrated during the spring and summer (October to March), and a strong influence of winds along the year.

The water body is well-mixed and homogeneous in terms of abiotic variables (horizontal dimension) due mainly to wind action (Hennemann & Petrucio, 2010; Tonetta et al., 2013). The lake is classified as oligotrophic for nutrient concentrations (mean total nitrogen = 746 µg l^{-1} and mean total phosphorous = 14.8 746 µg l^{-1}; Tonetta et al., 2015) and meso-eutrophic for transparency (mean Secchi depth = 1.0 m; Tonetta et al., 2015) and chlorophyll-*a* (mean Chl-*a* = 17.7 µg l^{-1}; Tonetta et al., 2015) (Hennemann & Petrucio, 2011). This contrasting classifications is mainly due to high densities of *Cylindrospermopsis raciborskii* (Woloszynska) Seenayya et Subba Raju, 1972 observed during most of the year (Hennemann & Petrucio, 2010). This cyanobacterium has been recorded since 1994, and throughout the last 10 years, its dominance has been increasing (Tonetta et al., 2013). Despite the high densities of *C. raciborskii* (accounted for about 90% of phytoplankton total density; Tonetta et al., 2015), the concentration of the toxin saxitoxin produced by this blue-green algae remains low (mean STX = 0.31 µg l^{-1}; Brentano et al., 2016).

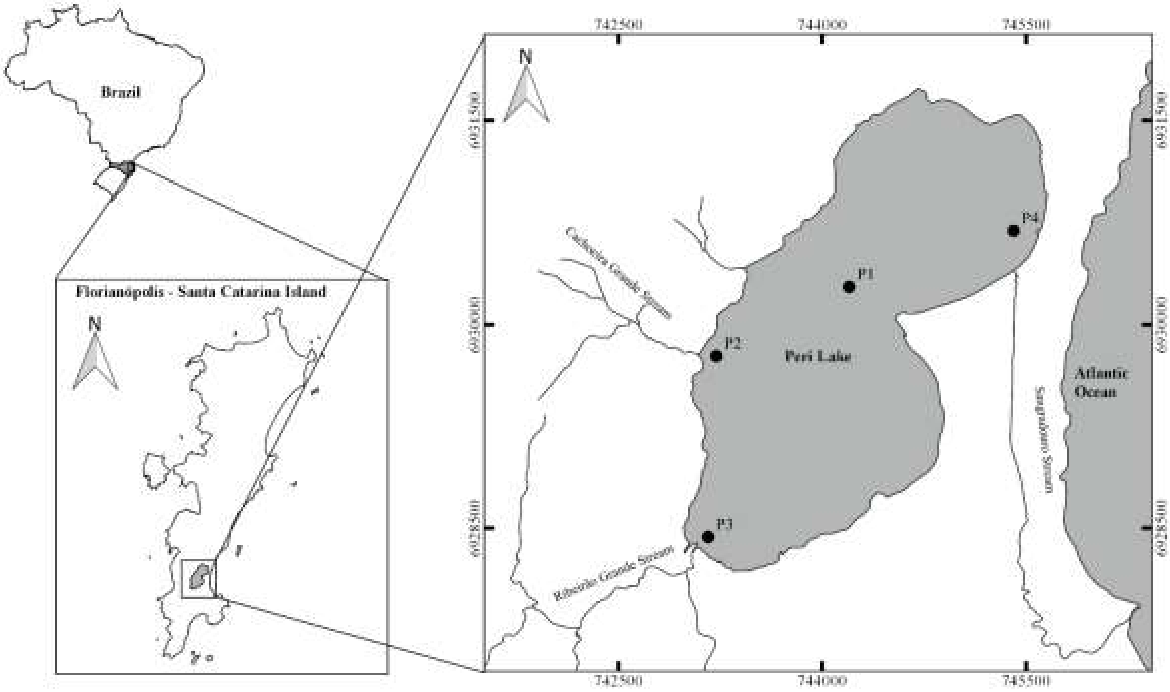

Fig. S1 Map of Peri Lake, Santa Catarina State, Brazil, showing the sampling sites (P1, P2, P3 and P4). Projection: Universal Transverse Mercator. DATUM: SIRGAS 2000. Shapefile Data: Secretariat of Sustainable Development of the State of Santa Catarina, 2012; National Water Agency, 2012 and Infrastructure and Urban Planning of Florianopolis, 2012.

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Supplementary results

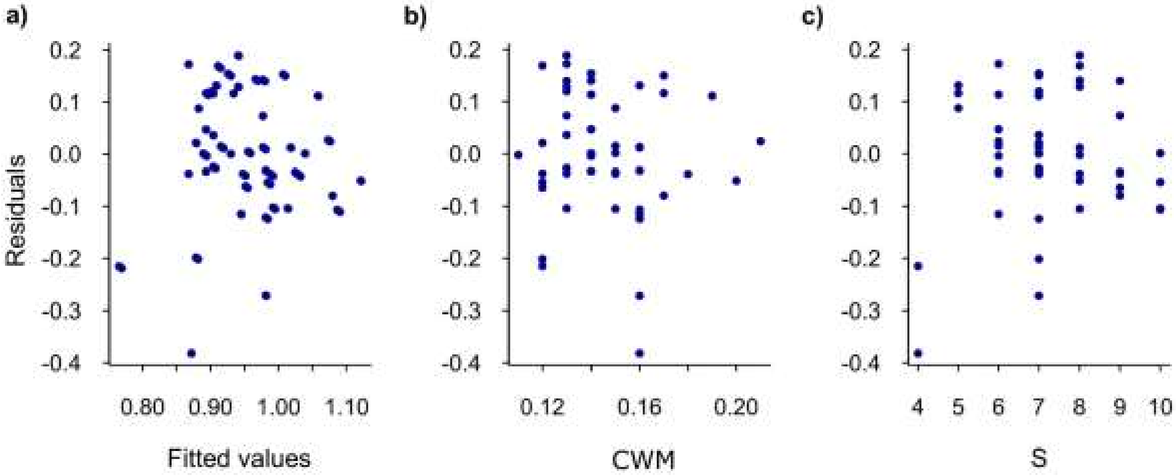

Fig. S2 Standard diagnostic plots used to determine whether model assumptions were met in the selected model (linear mixed-effect model; LMM). Scatter plots of the residuals against **a)** the fitted values and predictors: **b)** community weighed mean (CWM) and **c)** taxonomic richness (S). Note that the residuals do not show any pattern, which indicates that the variance of the residuals is constant. In the LMM, the biomass ratio between zooplankton and phytoplankton (log10-scale; B_Z/B_P) was the response variable and sampling sites were considered as a random-effect variable.

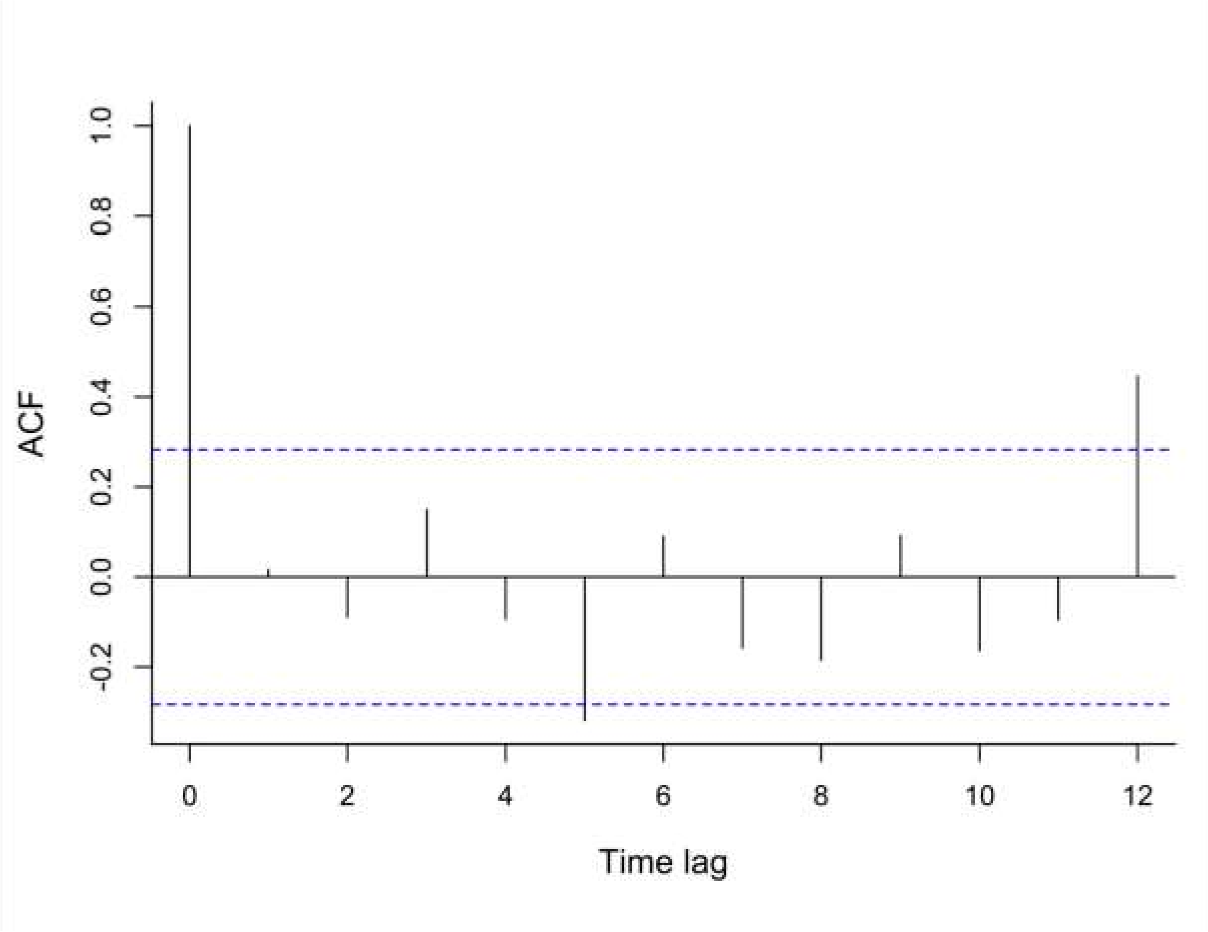

Fig. S3 Correlogram of the corrected residuals from the selected model (linear mixed-effect model; LMM) obtained through the autocorrelation function (ACF) using the "acf" function from stats package in R 3.6.1 (R Core Team, 2019). The horizontal red lines define the 95% confidence interval (CI). Note that most of the spikes are within CI, which indicates the lack of significant temporal autocorrelation in the residuals.

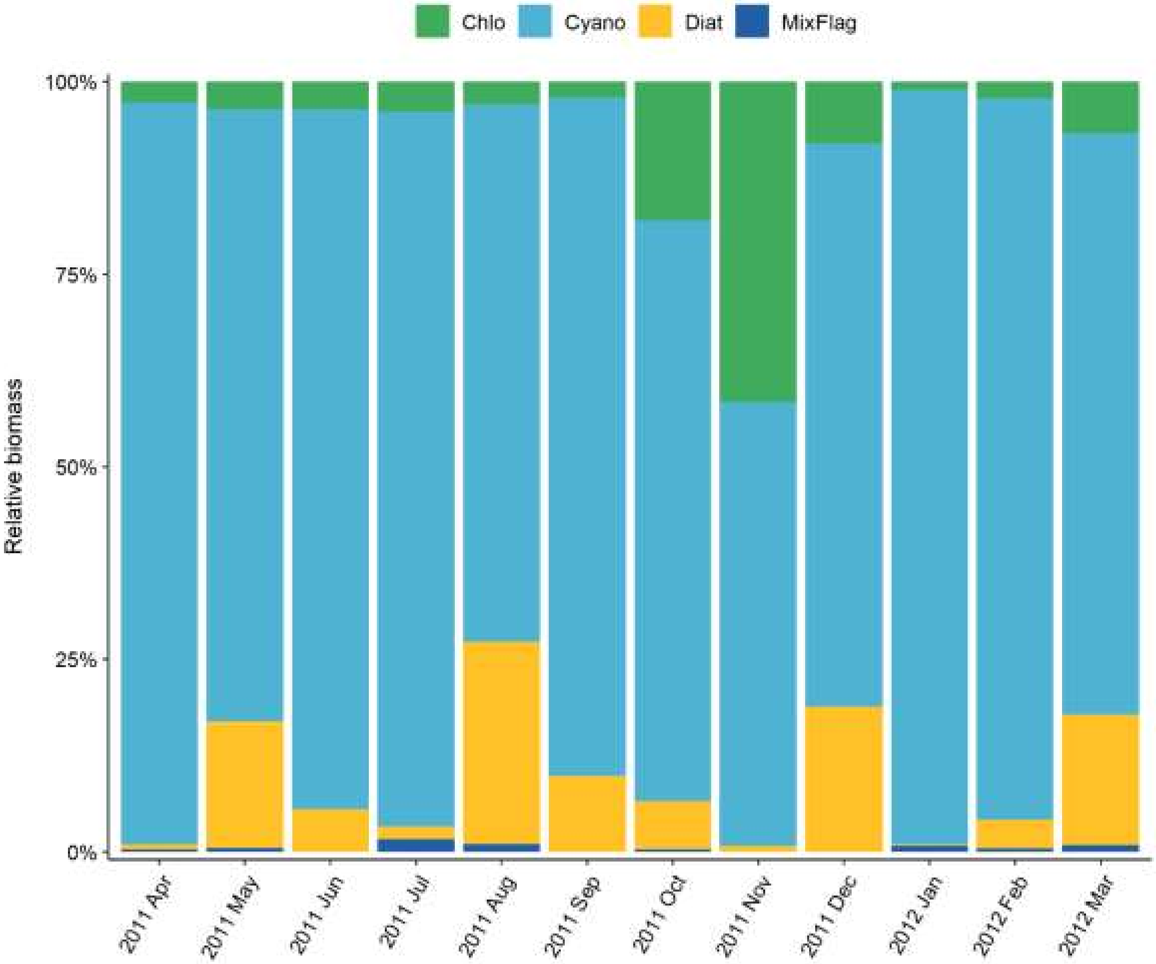

Fig. S4 Temporal variation of the relative contribution of phytoplankton biomass per major taxonomic group in Peri Lake from April 2011 to March 2012. Diat = diatoms; chlo = Chlorophyceae (green algae); MixFlag = mixotrophic flagellates; Cyano = Cyanobacteria.

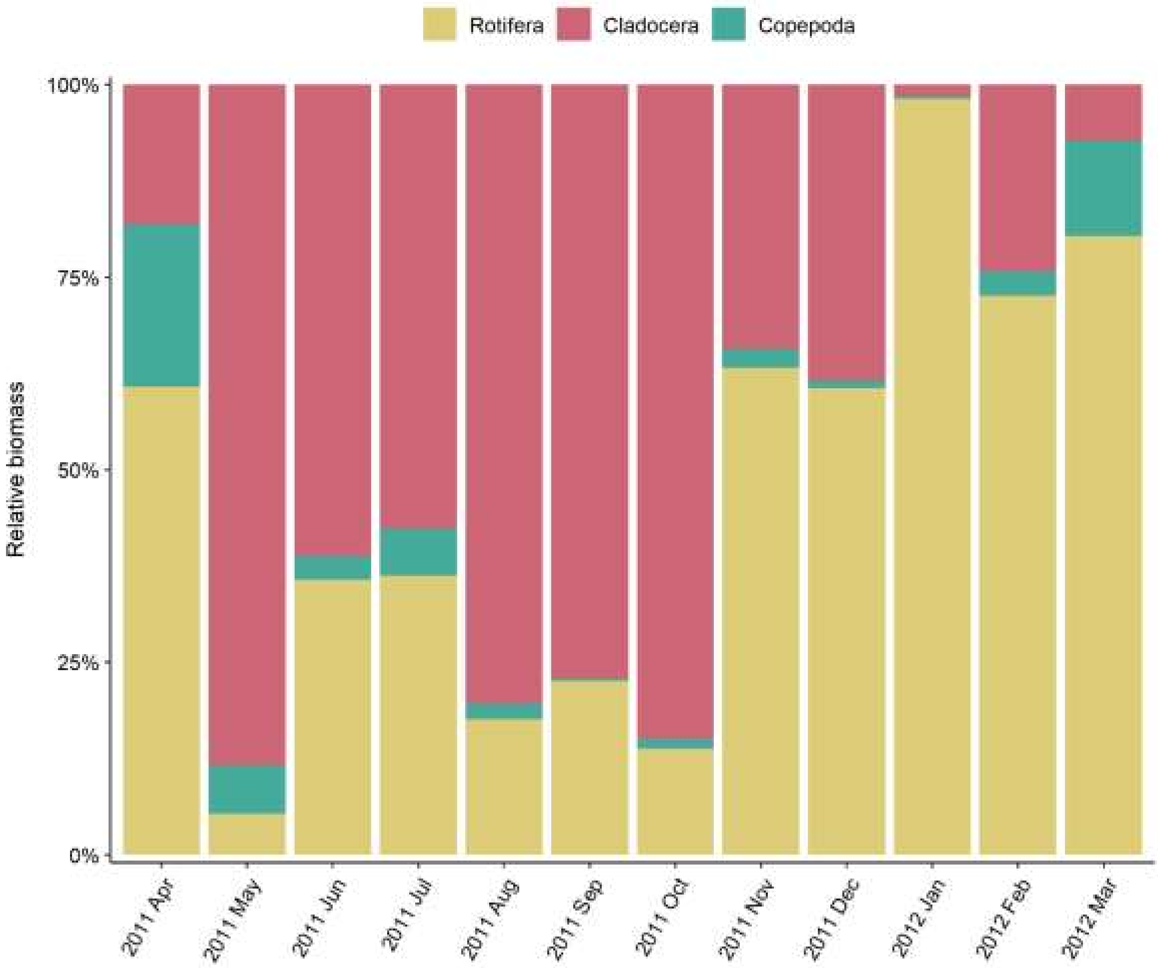

Fig. S5 Temporal variation of the relative contribution of zooplankton biomass per major taxonomic group (Rotifera, Cladocera and Copepoda) in Peri Lake from April 2011 to March 2012.

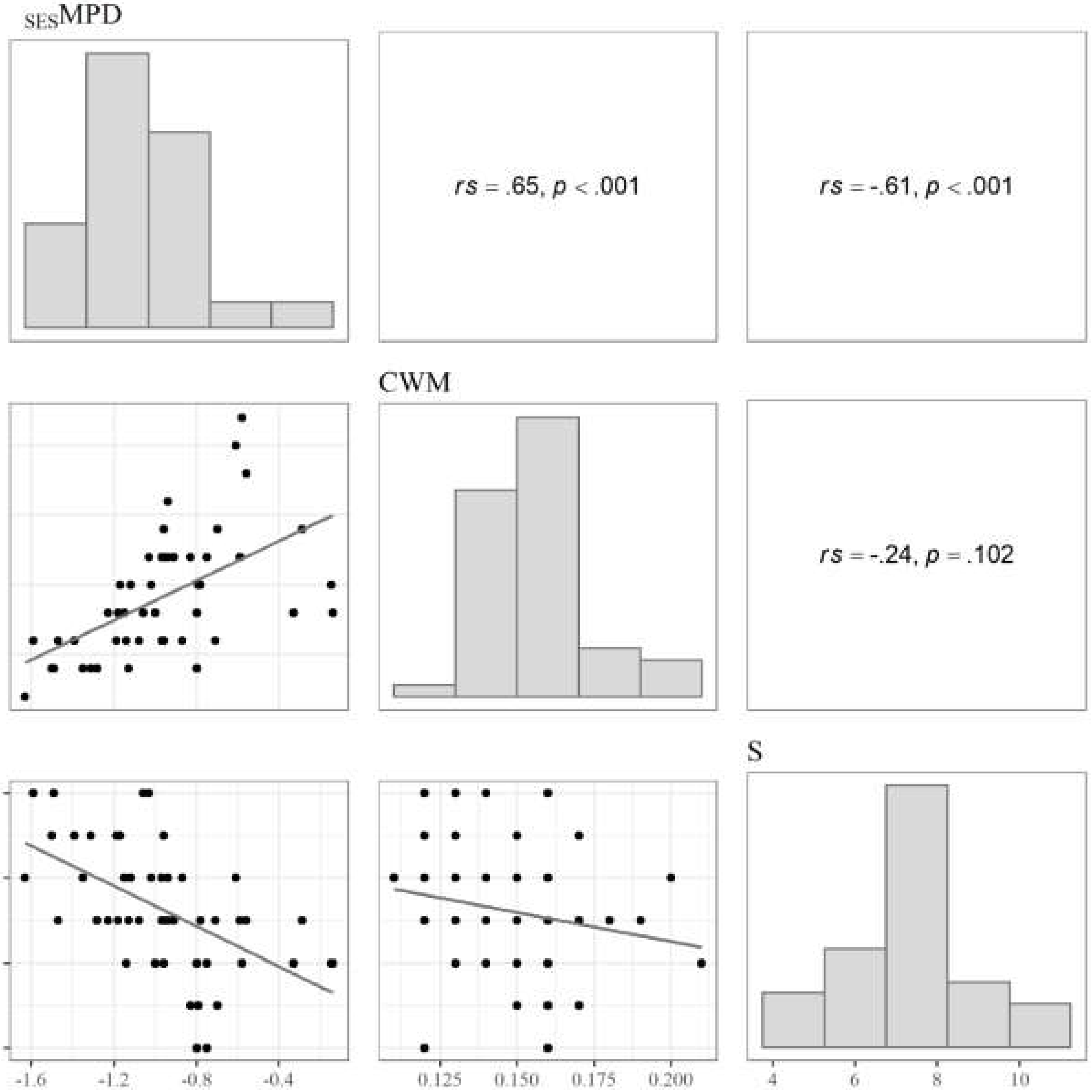

Fig. S6 Relationship between zooplankton standardized effect size ($_{\text{SES}}$MPD), zooplankton community weighed mean (CWM) and zooplankton taxonomic richness (S). In the orthogonal line, histograms in the middle panels show the distribution of each variable; scatter plots with trend lines in the lower panels show pairwise relationships; and the summary of the correlation analysis (*rs* = correlation coefficient, and *p* = probability value) are shown in the upper panels. Axes for scatter plots are in units of diversity for each metric.

Table S1 Statistical summary (mean values ± standard deviation) of the spatial variation of limnological variables at the four sampling sites (P1-P4) in Peri Lake from April 2011 to March 2012. WT = water temperature; DO = dissolved oxygen; EC = electrical conductivity; Z_{EU} = euphotic zone depth.

	WT (°C)	**DO (mg l^{-1})**	**EC (μS cm^{-1})**	**pH**	**Z_{EU} (m)**
P1	22.4 ± 4.6	8.0 ± 1.3	65.3 ± 5.5	7.1 ± 1.1	2.1 ± 0.4
P2	22.8 ± 4.7	8.1 ± 1.0	65.1 ± 5.6	7.0 ± 0.7	2.0 ± 0.3
P3	22.7 ± 4.7	7.8 ± 1.2	63.7 ± 4.3	6.9 ± 0.7	2.0 ± 0.3
P4	22.5 ± 4.5	7.8 ± 1.3	64.9 ± 5.1	7.0 ± 0.8	2.0 ± 0.3

CAPÍTULO III

Manuscrito a ser submetido ao periódico *Ecology*

Trait-based zooplankton community assembly and the functioning of aquatic ecosystems along a productivity gradient

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ABSTRACT

Hundreds of experiments conducted over the last decades demonstrate a positive relationship between species diversity and ecosystem functioning. Most of these studies have manipulated species richness artificially by assembling communities randomly. Natural communities along ecological gradients, however, often show niche-based responses to selection gradients and species extinction order is not a random process. Such responses are commonly trait-mediated and the effects of communities on ecosystem functioning also depend on species traits. Here we revisited a community assembly mesocosm experiment that simulated typical gradients of productivity and plant structural complexity to test how body size diversity and composition of zooplankton responded to such gradients and whether and how such trait responses impacted top-down control of unicellular algae, a key ecosystem function in aquatic systems. We find a positive effect of nutrient addition on both zooplankton size diversity (SESMPD) and community average size (CWM). In addition, we demonstrate a strong positive influence of both SESMPD and CWM on zooplankton resource use efficiency, but with a higher contribution of SESMPD. Our findings clearly indicate that limited productivity filters out larger zooplankton species whereas high productivity seems to increase competition, leading to higher size diversity than expected by chance, potentially due to limiting similarity in size. The presence of large zooplankton and the complementary responses of small and large species through time in more productive systems allow for enhanced top-down control via both selection effects and size-based compensatory dynamics. Although we focused here on the effects of productivity and structural complexity, our findings are likely representative to any selection gradient that influences SESMPD and CWM in zooplankton, given the importance of size as both response and functional effect trait. Our study illustrates the potential for trait-based community assembly experiments to reveal biodiversity responses to environmental change and their generalizable effects on ecosystems.

Keywords: Ecosystem functioning; resource use efficiency, metacommunity ecology

INTRODUCTION

Multiple anthropogenic drivers of global change, such as habitat degradation and fragmentation, eutrophication, and climate change, are leading to unprecedented rates of species extinctions worldwide (Brook et al. 2008, Pimm et al. 2014). These enhanced extinction rates have prompted researchers to conduct hundreds of experiments over the last two decades to understand how biodiversity loss or changes in abundances may impact the functioning of ecosystems and the provisioning of ecosystem services to humanity (Cardinale et al. 2012, Naeem et al. 2012). Nowadays, there is consensus that biodiversity positively influences ecosystem functioning (Cardinale et al. 2012, Lefcheck et al. 2015) and that species extinctions can hamper the provision of ecosystem services. However, most of those experiments relied on artificially assembled communities to infer losses in ecosystem functions, and there is increasing concern about the effectiveness of this approach in representing species extinctions in natural communities (Zavaleta et al. 2009, Leibold et al. 2017). In nature, species gains or losses are generally not random but strongly linked to changes in environmental conditions and species response traits; further the extinction order matter when communities are disassembled and reorganized (Larsen et al. 2005, Díaz et al. 2013). In addition, ecosystem functioning often can vary considerably when richness is held constant in experiments and part of such variance likely results from differences in species composition independently of species richness (Hector et al. 2002, Winfree et al. 2015) or from changes in species relative abundances in the absence of local populations extinctions. In response, recent studies propose tracking community assembly under more natural settings to disentangle the influence of species richness and composition on ecosystem functioning [i.e., the CAFE approach (Leibold et al. 2017, Bannar-Martin et al. 2018)].

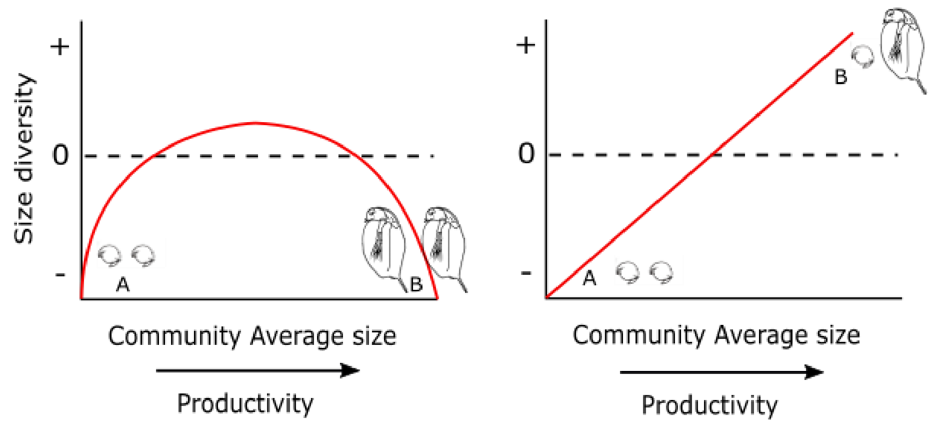
Even when considering more natural settings of community assembly, however, we argue that a strict focus on species richness and taxonomy may hinder identification of underlying traits shared by species that contribute the most, or the least, to functioning (Díaz et al. 2004, Cadotte et al. 2011, Abonyi et al. 2018). Indeed, differences in ecosystem functions can be mediated by species niches either via resource partitioning (i.e., complementarity) or via efficiency in resource use (i.e., selection effects) (Gianuca et al. 2016, Cadotte 2017). Because of that, taxonomic approaches that focus on species identities and treat all species as ecologically equivalent often have weaker power to predict ecosystem functions than trait- and phylogeny-based approaches, which have the potential to better approximate species niches

(Flynn et al. 2011, Srivastava et al. 2012, Cadotte 2013). Therefore, it is of paramount importance to understand how different trait combinations are assembled along selection gradients and how such trait combinations scale up to influence ecosystem functioning. For instance, trait combinations that maximize ecosystem functioning in artificial experiments of community assembly may not assemble under different environmental conditions in the field (Van Der Plas 2019). In addition, short-term and small-scale experiments that favor traits related to dominance and selection effects may overshadow the importance of other traits that are more related to niche partitioning through time in natural systems (Cardinale et al. 2007). Consequently, we argue that an important step forward is to use a trait-based metacommunity assembly approach, in which species are sorted from a regional species pool based on their traits along realistic selection gradients, and then the effects of trait diversity and trait composition on ecosystem functioning is quantified.

Previous studies with zooplankton have demonstrated the key role of body size in determining top-down control of algae, which is a key ecosystem function in aquatic systems (Mourelatos and Lacroix 1990, Ye et al. 2013). However, it remains unclear whether size-based selection effects or complementarity prevails in determining the capacity of top-down control by zooplankton (Ye et al. 2013, Gianuca et al. 2016). A recent conceptual framework proposed separating these two mechanisms based on the relative importance of community average size and size diversity (Gianuca et al. 2016). In an experimental setting, size-based selection effect was a dominant mechanism since larger cladoceran species were superior grazers on both small and large algae cells (Gianuca et al. 2016). By contrast, some field studies suggested size-based niche partitioning as the main mechanism influencing zooplankton top-down control of algae (Hansen et al. 1994, Ye et al. 2013). The rationale is that, when exposed to a broader range of resources in the field, larger zooplankton species, especially large-bodied cladocerans such *Daphnia magna*, would be superior grazers on larger phytoplankton, whereas smaller zooplankton species, such as small-bodied cladocerans, would graze more efficiently on smaller phytoplankton, leading to size complementarity (Ye et al. 2013, Thompson et al. 2015). It should be highlighted that field-based studies represent more realistic scenarios but are typically pestered by lower explanatory power than small-scale experimental studies; the latter, while providing proof of principles about underlying mechanisms, are limited by the lack of realism, especially when biodiversity is artificially manipulated and environmental conditions are held constant (Bannar-Martin et al. 2018). Finally, some studies with primary producers indicate that selection effects predominate at early experimental stages, whereas the relative importance of niche partitioning increases through time (Cardinale et al. 2007). Therefore, it remain to be understood how realistic gradients of selection, such as increasing eutrophication or habitat structural complexity, influence the size structure of zooplankton communities and how this modulates the top-down control of the primary producers. In the absence of predators (fish and invertebrates), it is relevant to focus on resource-use efficiency because it reflects the consumers' abilities to covert food in biomass and to graze it down to low levels.

Regarding community assembly rules, larger cladoceran zooplankton species may not withstand oligotrophic conditions associated with low phosphorus concentrations (Hessen and Andersen 1990, Andersen and Hessen 1991, Sommer 1992, Urabe et al. 1997, DeMott et al. 1998, Schulz and Sterner 1999, Guo et al. 2019, Hartnett 2019). Such phosphorus limitation often leads to habitat filtering against larger species, thereby reducing size diversity and community average size in oligotrophic ponds (i.e., dominance of small species) (Dodson et al. 2000, Gianuca et al. 2017). Increasing nutrient concentrations, therefore, is expected to increase cladoceran zooplankton community average size in fishless systems (Dodson et al. 2000), except when there is dominance of cyanobacteria, which also filters out large zooplankton (Walls et al. 1997, DeMott et al. 2001, Pinheiro-Silva et al., 2020). However, it is not clear whether this effect of increasing nutrients simultaneously enhances size diversity and community average size or whether it leads only to a dominance of larger species and the competitive exclusion of smaller ones. A positive correlation between community average size and size diversity may or may not emerge, depending on the relative importance of abiotic filtering and species interactions (Box 1). For instance, it is often assumed that larger zooplankton species outcompete smaller zooplankton in eutrophic, fishless systems (Jeppesen et al. 2000). In such a case of strong competitive asymmetry, it is expected that larger species will tend to dominate the community at the expense of smaller species, therefore increasing community average size and decreasing size diversity (i.e., dominance of larger species only; Box 1). Conversely, if small and large species co-occur in eutrophic systems—for instance due to high energy availability or niche complementarity—then community average size and size diversity will both increase (Box 1), potentially due to limiting similarity in body size (Hutchinson 1959, MacArthur and Levins 1967). This mechanistic theory (i.e., limiting similarity) implies that competitive exclusion should occur when two or more competing consumer species are ecologically similar (i.e., similar ecological requirements, such as resource use). In the case of zooplankton, there is evidence that niche partitioning increases size diversity whereas niche overlap tends to result in competitive exclusion (Ye et al. 2013). However, this is less clear for generalist filter feeders, such as Cladocera, and more studies are needed to address the importance of limiting similarity on community assembly. Also, eutrophication often reduces zooplankton species richness (Dodson et al. 2000).

Therefore, important questions remain unanswered: can increasing zooplankton community average size, and potentially size diversity, buffer ecosystem functioning despite of an expected decrease in richness in eutrophic systems? And how important such community effects mediated by size structure are compared to other eutrophication-related effects? For instance, eutrophication may also affect zooplankton top-down control through its effects on phytoplankton, such as by influencing its edibility to zooplankton (Vanni and Temte 1990, Schulhof et al. 2019), size structure (Irwin et al. 2006, Wong et al. 2016; Schulhof et al. 2019) and the relative dominance of cyanobacteria (Taipale et al. 2019). Another important driver of community structure is habitat heterogeneity (Tews et al. 2004). Higher structural complexity provides more opportunities for niche partitioning and for exploiting different resources, thus it often increases species diversity compared to more homogeneous habitats (Tews et al. 2004). Yet, it is poorly known if and to what extent this increased habitat complexity translates into average size and size diversity, and how these changes of community trait structure will be affected by interactions between habitat structure and nutrient loading.



Box 1: The scheme depicts likely patterns of size structure shifts along productivity gradients, which are based on previous studies and mechanisms proposed in literature. On the vertical axis, a metric of size diversity is represented, with zero representing random size structure compared to a regional pool, negative values indicating size clustering and positive values indicating size overdispersion. On the horizontal axis, the common pattern of increasing zooplankton average size along productivity gradients is represented. On the left panel, the two communities (A and B) are size clustered despite contrasting differences in community average size (CWM). This pattern can result either from competitive exclusion of smaller species by larger ones (size-based competitive asymmetry; size efficiency hypothesis, Brooks and Dodson 1965) in more productive systems or by habitat filtering related to inedible phytoplankton to small zooplankton (Dodson 2000). Indeed, Dodson (2000) suggested that highly productive systems become dominated by larger phytoplankton, which cannot be handled by small zooplankton, leading to habitat filtering against smaller zooplankton, except in cyanobacteria-dominated systems (DeMott et al. 2001). This would result in high size turnover along the productivity gradient, despite of no differences in size diversity. On the right panel, there is both an increase in size diversity ($_{\mathrm{SES}}$MPD) and CAS along the productivity gradient. This is expected to occur when small and large zooplankton species partition resources or microhabitats, leading to exclusion of species with similar size and therefore to overdispersion due to limiting similarity (MacArthur and Levins 1967, Bowers and Brown 1982, Abrams 1983, Davies 2006, Gianuca et al. 2017). Note that these two mechanisms of community assembly (competitive asymmetry / niche partitioning) are directly linked to mechanisms of ecosystem functioning (selection effects / complementarity) that we aim at investigating in this study.

Here, we use a trait-based metacommunity assembly experiment to address the following key questions: (Q1) How do zooplankton body size diversity and composition respond to a gradient of nutrient addition? (Q2) Is the response of body size diversity and composition to the nutrient gradient modified by the presence of artificial macrophytes? (Q3) What is the relative importance of community average size and size diversity in determining trait-mediated variation in top-down control of algae? and (Q4) What is the relative importance of trait changes in response to nutrient addition compared with the effect of nutrient addition per se in determining top-down control of algae?

METHODS

Experimental design

We subset the data from a metacommunity assembly experiment performed by Declerck et al. (2007), where a multifactorial combination of nutrient concentrations and habitat complexity levels was performed using cattle tanks (200-L) under semistandardized outdoor conditions for 66 days (ARENA outdoor experimental area, Heverlee, Belgium). Here, we focus on the non-macrophytes (NPL) and artificial macrophytes (APL) treatments, to rule out the potential effect of competition of real plants with phytoplankton and to test only the effect of habitat structural complexity on zooplankton size structure and top-down control along a P-addition gradient.

A nutrient gradient (phosphorus and nitrogen) was created on Day 4 by addition of KH2PO4 in different concentrations (0, 10, 100, and 1000 μg L^{-1}). N was added under the form of $NaNO_3$. Additions of N were such that the molar N:P ratios equaled 16 in all nutrient addition treatments. In the experimental design, for each level of habitat complexity (i.e., with and without artificial macrophytes) by nutrient concentration (i.e., 0, 10, 100, and 1000 μg L^{-1}), five replicates were used, totalizing 40 cattle tanks. Phytoplankton and zooplankton of natural assemblages were collected from different water bodies in the region of Leuven (Belgium) and added to the tanks on Day 7 and Day 34, respectively, while artificial macrophytes were added on Day 18. For further details about the experiment design, see Declerck et al. (2007).

Sampling and analytical methods

Sampling for nutrients was performed at Day 7 and sampling for chlorophyll *a* was performed on Day 34, and at the end of the experiment (Days 64-66). Phytoplankton and zooplankton communities (crustacean zooplankton) were sampled at the end of the experiment and preserved with acid Lugol's solution (details in Declerck et al. 2007).

Species identification was performed to the species level with a stereomicroscope for cladocerans and to the genus level with an inverted microscope upon sedimentation in Utermöhl sedimentation chambers for phytoplankton. A list of all zooplankton taxa is provided in electronic supplementary material (Table S1). Total phosphorus was analyzed with a Technicon autoanalyzer II (Technicon, Tarrytown, New York, USA) after persulfate digestion. Chlorophyll *a* was spectrophotometrically determined. We obtained the body length of different

Cladoceran species from the literature (Brans et al. 2016). Then, we estimated biomass dry weight ($B_{Z;}$ µg L^{-1}) from allometric relationships between weight and the average body length (Bottrell et al. 1976). Additionally, to explore possible changes in the relative contribution of small and large species to total zooplankton density, the species were arbitrarily separated in two size classes, small for all species with body size < 2 mm, and large for all species with body size ≥ 2 mm (see details in Table S1).

Community average size, size diversity and species richness

We assessed zooplankton body size diversity using community average size (CAS) and size diversity (SD). To estimate CAS, we calculated the mean body size value of each species in the community weighted by their relative abundances using the function "dbFD" from the R package 'FD' (Laliberté et al. 2015). High values indicate a greater relative contribution of large-bodied individuals to the total biomass, whereas low values indicate a larger contribution of small-bodied individuals (Gianuca et al. 2016). The degree of change in CWM over P-addition gradient was calculated based on paired differences between tanks with and tanks without phosphorus addition (P_0) for each P-addition level (10 µg L^{-1}, 100 µg L^{-1}, and 1000 µg L^{-1}). To estimate SD, we first calculated Euclidean distances among species based on body size (Oksanen et al. 2019). Then, based on this trait distance, we calculated the mean pairwise distance among all species in the community using the function "ses.mpd" from the R package 'picante' (Kembel et al. 2010) taking species abundances into account. Negative indices indicate that communities are composed of species that are more similar in size than expected by chance (i.e., clustering), while positive values indicate that communities are composed of species that are more dissimilar in size than expected by chance (i.e., overdispersion) — therefore, negative or positive indices indicate scenarios of low and high size diversity, respectively. Values close to zero indicate that any difference in size among species within communities are not different from what would be expected by chance (Kembel et al. 2010). We also calculated species richness (S) for each replicate. We calculated all diversity metrics using the statistical environment R, version 3.6.1 (The R Development Core Team, 2019).

Resource use Efficiency calculations

We used resource use efficiency as a proxy for the ability of zooplankton to control phytoplankton (Tian et al. 2017, Verbeek et al. 2018). Here, we calculated resource use efficiency (RUE_{ZP}) as the observed zooplankton biomass (µg L^{-1}) per unit phytoplankton chlorophyll *a* (µg L^{-1}). Assuming that primary zooplankton consumers have reached carrying capacity (e.g., in the absence of predators, disease or disturbances), resource use efficiency is a function of the ability of the consumers to convert their food resource into own biomass and graze down resources to low levels.

Data analysis

We tested the effect of habitat heterogeneity (i.e., structural complexity) and P-addition on zooplankton body size diversity (CWM and $_{SES}$MPD) and species richness (S) using two-way analysis of variance (ANOVA) with permutation tests, as implemented in the 'lmPerm' package in R (Wheeler 2016). Here, habitat heterogeneity (two levels) and P-addition gradient (four levels) were used as independent variables in each model. Permutation analysis randomizes the data set while retaining the data structure to generate all possible permutations of the values obtained in the experiment. Then, *p*-value is obtained comparing each permuted data set to the raw data set to assess whether the treatment effects are the same or greater. We chose permutational methods since they do not make assumptions about underlying distributions and are suitable when sample sizes are small.

To quantify the relative importance of CWM and $_{SES}$MPD, as well as the effect of nutrient addition *per se* in determining top-down control of algae, we applied variation partitioning analyses based on partial regressions (Whittaker 1984, Bocard et al. 1992, Legendre and Legendre 2012) using the R package 'vegan' (Oksanen et al. 2019). In all models, zooplankton resource use efficiency (RUE_{ZP}) was used as a response variable. The proportion of explained variation for each independent variable is given by the adjusted R^2 to avoid type I error. The significance was determined by *p*-values at 0.05 level, calculated using Monte Carlo permutation test (999 permutations). We performed all analyses using the statistical environment R, version 3.6.1 (The R Development Core Team, 2019).

RESULTS

Influence of P-addition and habitat heterogeneity on zooplankton community structure

Zooplankton community descriptors ($_{SES}$MPD, CWM, S) were significantly correlated (electronic supplementary material, Fig. S1). $_{SES}$MPD was positively correlated to CWM (rs = 0.90, p < 0.001) but $_{SES}$MPD and S were not, indicating that both descriptors are independent to each other. S was moderately positively related to CWM (rs = 0.41, p = 0.02). The relative contribution of small (< 2 mm) and large species (≥ 2mm) to total zooplankton density were compared among P-addition levels for both levels of habitat complexity (i.e., with and without artificial macrophytes) (see electronic supplementary material, Fig. S2). We found a larger contribution of small cladocerans in low-P tanks (P_0, P_{10}, P_{100}) than in the highest-P tanks (P_{1000}) in treatments with and without artificial macrophytes. In contrast, we found a greater contribution of large cladocerans in the highest-P tanks (P_{1000}) than in the other tanks, representing more than 50% of total average density for both levels of habitat complexity.

We found a significant effect of P-addition on both size diversity ($_{SES}$MPD; Fig. 1a; Table 1; p-value = 0.001) and community average size (CWM; Fig. 1b; Table 1; p-value < 0.001), mainly resulting in considerably higher CWM and $_{SES}$MPD values in high-P tanks (P_{10}, P_{100} and P_{1000}) compared with low-P tanks (P_0) (Table S2). Yet, there were no differences between addition levels at high P concentrations. Moreover, the percentage change (i.e., degree of change) in CWM over the P-addition gradient (see electronic supplementary material, Fig. S3) revealed a pronounced difference between the highest and lowest-P tanks. Specifically, cladoceran body size showed a large increase in the highest-P tanks (P_{1000}) compared with tanks without P-addition (P_0) (Fig. S3), being higher in APL treatment (mean ± standard deviation = 76.2% ± 39.8) than in NPL treatment (mean ± standard deviation = 47.3% ± 46.3). We did not find any significant effect of habitat heterogeneity on $_{SES}$MPD (Table 1), but we found a significant effect on CWM (Table 1; p-value = 0.003) and species richness (S; Table 1; p-value < 0.001), with both response variables (CWM and S) being higher in APL treatment than in NPL treatment (Figs. 1b and 1c, respectively). We found a significant interaction effect between habitat heterogeneity and P-addition on S (Table 1; p-value = 0.003), mainly resulting in low S values in high P-levels (100, and 1000 $\mu g\ L^{-1}$) in the treatments with no artificial plants (Table S3).

Table 1 Two-way permutation ANOVA results, testing for the effect of P-addition (P) and habitat heterogeneity (HH) on zooplankton size diversity ($_{SES}$MPD), community average size (CWM) and species richness (S). d.f.: degrees of freedom; SS: sum of squares.

	d.f.	***SS***	***p*-value**
Response variable: $_{SES}$MPD			
P-addition (P)	3	2.80	**0.001**
Habitat Heterogeneity (HH)	1	0.54	0.097
P x HH	3	0.81	0.129
Response variable: CWM			
P-addition (P)	3	2.44	**<0.001**
Habitat Heterogeneity (HH)	1	0.86	**0.003**
P x HH	3	0.31	0.202
Response variable: S			
P-addition (P)	3	13.84	0.198
Habitat Heterogeneity (HH)	1	140.28	**<0.001**
P x HH	3	43.34	**0.003**

Bold values represent significant relationships obtained from permutation tests.

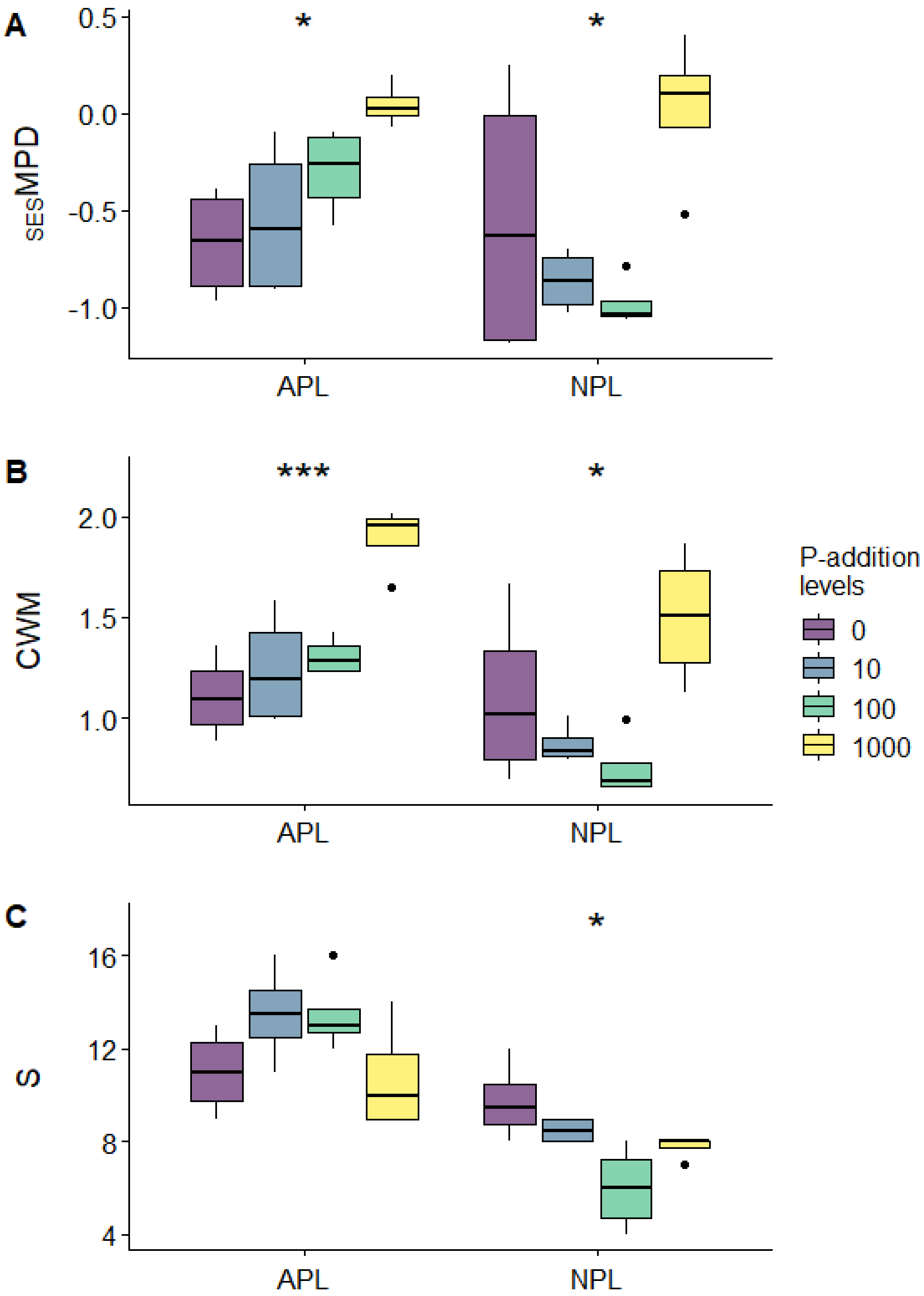


Fig. 1 Effects of P-addition (0, 10, 100, and 1000 μg L^{-1}) and macrophyte presence (APL refers to artificial plants and NPL refers to no artificial plants) on zooplankton **A**) size diversity index ($_{SES}$MPD), **B**) community average size (CWM), and **C**) species richness (S). In **A**), negative values of $_{SES}$MPD indicate that communities are less diverse than expected by chance (size clustering), whereas positive values indicate that communities are size over

dispersed. One asterisks (*) means p-value ≤ 0.05; two asterisks (***) means p-value ≤ 0.001. Note that non-significant (i.e., p-value > 0.05) are not shown.

Drivers of zooplankton top-down control on phytoplankton biomass

Taken together, body size diversity ($_{\text{SES}}$MPD), community average size (CWM) and species richness (S) explained near 70% of variation in zooplankton resource use efficiency (RUE$_{ZP}$; df = 5; F-statistic = 8.69; p-value = 0.001; Fig. 2a). Each of these variables showed a strong and positive relationship with RUE$_{ZP}$ (Fig. 3). Considering pure and shared effects together, $_{\text{SES}}$MPD accounted for 57% of the total amount of explained variation, while CWM and S accounted for 54% and 27%, respectively. The shared fraction of explanation provided by all community descriptors ($_{\text{SES}}$MPD, CWM and S) was 17% (Fig. 2a), and there was an overlap of 53% in the explained variation offered by $_{\text{SES}}$MPD and CWM (Fig. 2a). As unique effects, species richness explained 9% of variance in RUE$_{ZP}$ (F-statistic = 9.25; p-value = 0.005; Fig. 2a), whereas $_{\text{SES}}$MPD was only marginally significant (adjusted-R^2 = 4%; F-statistic = 4.26; p-value = 0.048) and CWM was non-significant.

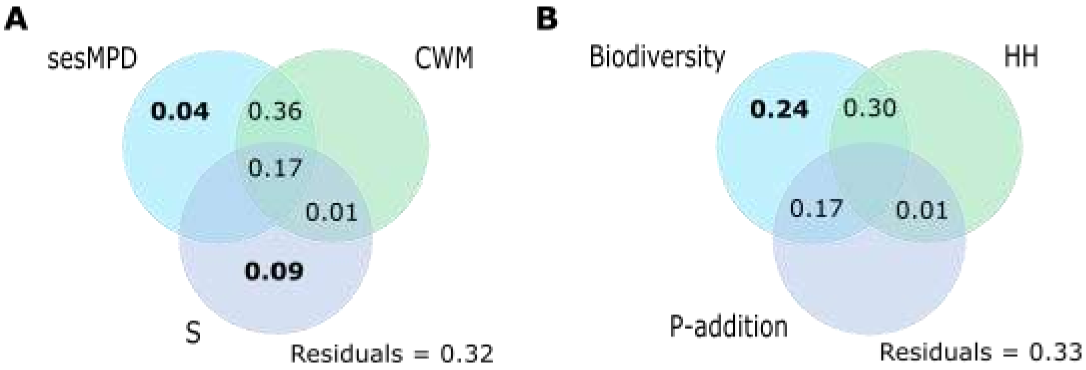


Fig. 2 Venn diagram showing the fraction of variation in zooplankton resource use efficiency (RUE$_{ZP}$; log-transformed) that can be explained by two different sets of explanatory variables (**A**, B): size diversity ($_{\text{SES}}$MPD), community average size (CWM), species richness (S), nutrient addition (P-addition) and habitat heterogeneity (HH). Biodiversity correspond to all zooplankton community descriptors together ($_{\text{SES}}$MPD, CWM and S). The values in the circles represent the unique contribution (based on adjusted R2) for each explanatory variable, and the intersections represent their shared contribution. The residuals represent the unexplained variation and only non-negative values ≥ 1% are shown. Statistically significant contributions are depicted in bold. Note that it is not possible calculate p-values for intersections. Graphs **A**-**B** are results from distinct variation partitioning analyses.

Variation partitioning showed that zooplankton community descriptors ($_{\mathrm{SES}}$MPD, CWM and S) had a large unique effect (adjusted-R^2 = 24 %) on RUE$_{ZP}$ in contrast to P-addition and HH treatments which were not found to have any unique explanatory power (Fig. 2b). Nevertheless, 17% of this variation was shared with the P-addition treatments whereas 30% was shared with the habitat heterogeneity treatments (Fig. 2b). More detailed variation partitioning analyzes (see electronic supplementary material, Fig. S4) revealed that P-addition treatments affected RUE$_{ZP}$ mainly through their effect on $_{\mathrm{SES}}$MPD (19%) and CWM (19%), whereas HH treatments affected RUE$_{ZP}$ mainly through their effect on S (31%) and CWM (26%) and to a lesser extent through their effect on $_{\mathrm{SES}}$MPD (15%).

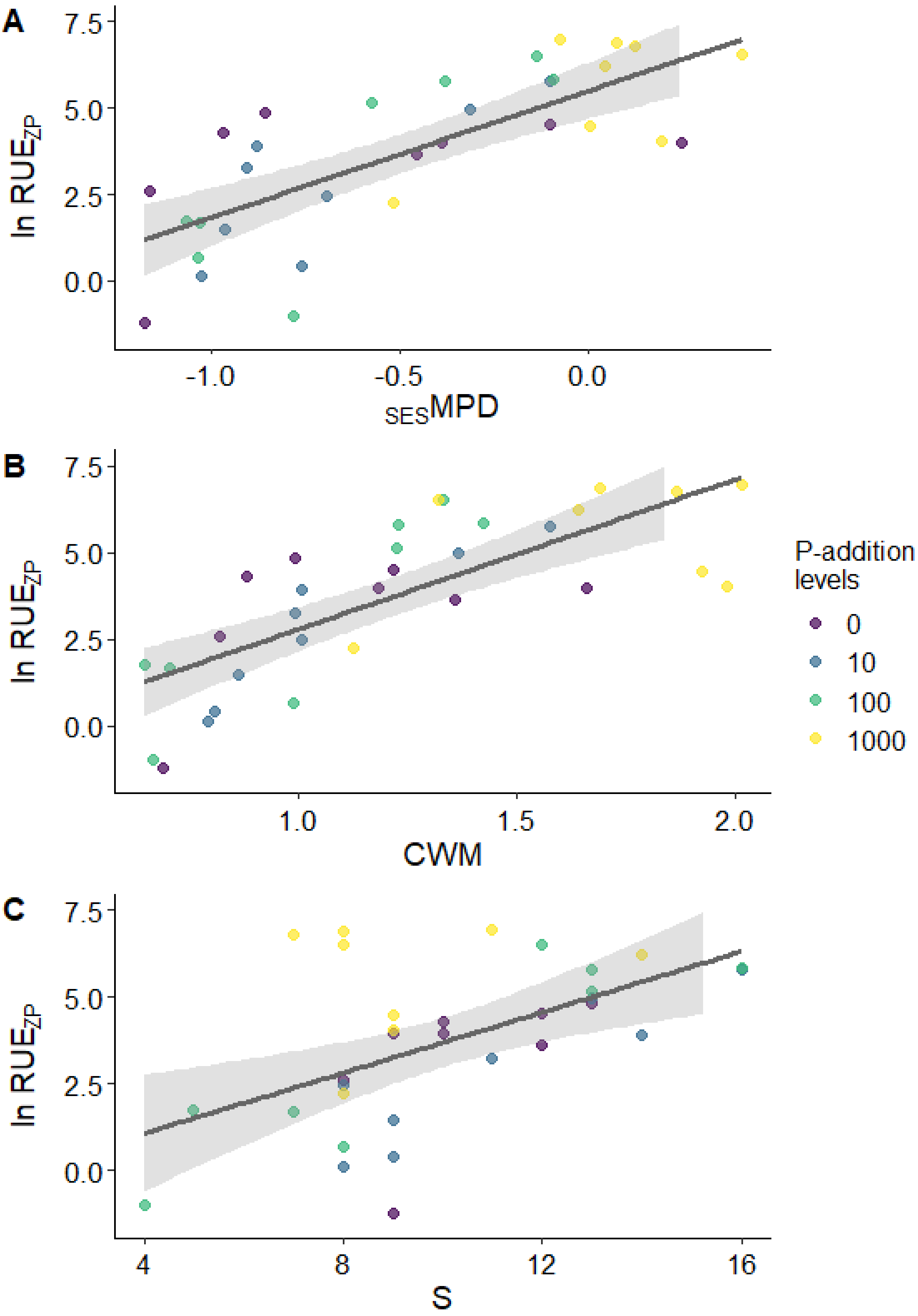


Fig. 3 Linear relationship between mean values of zooplankton resource use efficiency (RUE$_{ZP}$; log-transformed) and **A**) size diversity ($_{SES}$MPD), **B**) community average size (CWM), **C**) species richness (S). The confidence interval of 95% is provided.

DISCUSSION

Our tests of the impacts of community trait changes on the functioning of aquatic systems revealed a positive effect of nutrient addition on both zooplankton size diversity ($_{SES}$MPD) and community average size (CWM). By using a mesocosm experimental approach designed to investigate how environmental changes in productivity and habitat structural complexity influence community assembly (Declerck et al. 2007), we show that both CWM and $_{SES}$MPD increased simultaneously with high levels of nutrients added. In contrast, species richness is negatively affected by nutrient enrichment, particularly in treatments with simplified structural complexity. In addition, metrics informed by body size are more powerful in explaining variations in zooplankton resource use efficiency than species richness, and nutrient addition treatments affect RUE_{ZP} mainly through their effect on zooplankton body size diversity and composition (CWM and $_{SES}$MPD) and at less extent through their direct effect on ecosystem functioning. Although this stronger power of trait metrics has been previously recognized, early evidence of this hypothesis was mainly based on simplified conditions of manipulative experiments that artificially assembled communities based on trait distributions or phylogenetic distances (Díaz et al. 2004, Cadotte et al. 2011, 2013, Gianuca et al. 2016, Abonyi et al. 2018). Our results are based on a more ecologically realistic approach, in which selection gradients of nutrient concentrations and habitat complexity filtered species based on their traits, and then the influence of community average size (CWM), size diversity ($_{SES}$MPD) and species richness (S) on resource use efficiency were quantified.

Community assembly mechanisms

We observed a clear reduction in both body size diversity and community average size in the lowest phosphorus level (P_0) compared to other P-addition treatments (P_{10}, P_{100} and P_{1000}). This is largely in line with our conceptual scheme (see Box 1) and with previous studies that indicate that large zooplankton species demand high phosphorus concentrations to maintain viable populations (Hessen and Andersen 1990, Andersen and Hessen 1991, Sommer 1992, Urabe et al. 1997, DeMott et al. 1998, Schulz and Sterner 1999, Guo et al. 2019, Hartnett 2019) (see also conceptual panel 1). Therefore, nutrient limitation results in abiotic environmental filtering against larger Cladocera , particularly large *Daphnia* species. At the other extreme of the nutrient concentration, we observed a pattern of size overdispersion, which is in line with our conceptual scheme depicted in the right panel of Box 1 and indicates that species are less similar in size than expected by chance based on the species pool. Although Cladocera is considered a group of generalist filter feeders in respect to size particles, variation in body size or in other traits that correlate with size may be important to reduce competitive interactions whereas similarity in size may have the potential to drive competitive exclusion of species that are ecologically too similar (Hutchinson 1959, MacArthur and Levins 1967, Ye et al. 2013). For instance, large species of the genus *Daphnia* may compete fiercer with each other for resources when compared with the interaction between a large *Daphnia* and a small *Chidorid.* In this example, body size also relates with diet niche partitioning because small *Chidorids* tend to be scrapers whereas large *Daphnia* are pelagic filter feeders. Thus, being too similar in size also means to be too similar in resource use and can result in fiercer competition in our experiment. Such limiting similarity mechanism has been first discussed by Hutchinson (1959) and introduced by MacArthur and Levins (1967) trough competition models (i.e., Lotka-Volterra competition model) that become the basis for the research in the following decades. The relationship between body size and mechanisms of coexistence has been well described by Bowers and Brown (1982), who observed that rodent communities in deserts of California had regular intervals in body size, potentially allowing co-occurring species to partition niche space and to avoid competition for limiting resources. Such pattern was also observed in a field-based study of freshwater zooplankton along gradients of land-use, in which there was both an increase in community average size and size diversity with increasing nutrient concentrations and productivity (Gianuca et al. 2017). Taken together, these observational and experimental results indicate that such pattern of increasing size overdispersion with increasing productivity might be more common than usually assumed and that the most plausible underlying mechanism is the fiercer competition among similar sized species.

The simultaneous increase in SESMPD and CWM clearly indicates that large species do not replace smaller species through competition, which is at odds with the idea of the “size efficiency hypothesis” (Brooks and Dodson 1965). On the contrary, the increase in community average size (CWM) in mesocosms with high nutrient concentrations coincided with the addition of large species to these communities but without the removal of small species. Contrary to our results, some experimental studies reported either no effect of nutrient addition on zooplankton size variance (Tavşanoğlu et al. 2017) or a negative effect on both average size and size diversity in high-nutrient mesocosms (Šorf et al. 2015). These contrasting results could potentially be explained by the limited nutrient range used in these experiments (35 to 103 µg

L^{-1} and 13.3 to 285 μg L^{-1}, respectively) and by fish predation pressure on zooplankton community—a factor not considered in our study. Our results demonstrated that significant differences in zooplankton trait diversity and composition are observed only between the lowest and highest phosphorus levels. In our study, the large range in phosphorous concentration (i.e., 0, 10, 100, and 1000 μg L^{-1}) allowed us to adequately capture significant trait changes in response to nutrient addition. However, a strong phosphorus decreased through time were observed by Declerck et al (2007), who found that differences in phosphorus concentrations between addition levels were smaller at high than at low P concentrations, potentially explaining the lack of differences in community traits between our high P-level treatments.

We found a significant interaction between P-addition and habitat heterogeneity on species richness, but not on SESMPD or CWM. There was a significant decrease in species richness with increasing phosphorus addition in the absence of plant structures, whereas SESMPD and CWM mainly increased at the highest P-level for both plant treatments. Although species richness was not the main focus of our study, it is interesting that a larger number of species, most of them small, could tolerate low nutrient conditions in this experiment. The richness pattern reported here is consistent with that of Declerck et al. (2007) with the same database. Yet, by also investigating the size structure of communities, our study provides additional insights: the decrease in richness and the increase in SESMPD with productivity suggests that competition and limiting similarity were important mechanisms of species loss in mesocosms with high nutrient input.

Linking community assembly to ecosystem functioning mechanisms

In our study P-addition and structural complexity treatments had no unique effects on zooplankton resource use efficiency. However, they explained a considerable fraction of RUE_{ZP} mediated by CWM, SESMPD and S. This result suggests that their effects play completely through these zooplankton community descriptors. We found that all community descriptors (i.e., SESMPD, CWM, and species richness) were important drivers of zooplankton resource-use efficiency. In addition to effects of species richness, we observed particularly strong effects of CWM and SESMPD. The main advantage of our experiment was to increase ecological realism by allowing relevant environmental pressures to influence community assembly and ecosystem functioning through trait filtering. Nevertheless, strong co-variation between SESMPD and CWM hampered our ability to disentangle the contribution of size-based complementarity and selection effects in determining resource use efficiency. To separate such effects, Gianuca et al. (2016) artificially assembled communities in which CWM and ${}_{\text{SES}}$MPD were only weakly correlated and demonstrated that CWM and thus selection effects were dominant compared to size-based niche partitioning, but the latter also played a role. Our findings align with field studies that report simultaneous effects of body size on complementarity and selection, with changes only in the relative importance of these mechanisms through time (Ye et al. 2013, Pinheiro-Silva et al. 2020). Taken all these results together, it seems clear that simultaneous increases in size diversity and CWM along a productivity gradient enhances RUE_{ZP} through both complementarity and selection effects.

The rather limited pure effect of ${}_{\text{SES}}$MPD on RUE_{ZP} likely represents a relatively larger, albeit small, contribution of species complementary responses to environmental fluctuations through time. In Canadian lakes, higher zooplankton ${}_{\text{SES}}$MPD was also important for zooplankton biomass production, which is another ecosystem process with important impacts on the aquatic food webs (Thompson et al. 2015). For instance, large zooplankton feed mainly on large algae whereas small zooplankton feed more efficiently on small algae, leading to size-based complementarity in communities with higher ${}_{\text{SES}}$MPD (Ye et al. 2013). However, we argue that such complementarity in resource use alone might be a fragile explanation when we consider cladocerans, which are non-selective filter-feeders that can feed on a broad algae size spectrum (Gianuca et al. 2016). Functional traits other than body size (e.g., feeding type, grazing selectivity) can determine the response of species to disturbances (e.g., nutrient addition, fish predation) and influence the structure of ecological communities (Bowers and Brown 1982). Part of the variation in such traits may have been captured by species richness (see also Flynn et al. 2011). Thus, species richness may adequately represent some unmeasured traits that also influence ecosystem functioning (see for instance Flynn et al. 2011). Such unmeasured traits that were potentially captured by species richness may also have influenced diet partitioning or complementary responses of species to environmental fluctuations through time, as previously reported for terrestrial plants (Cardinale et al. 2007).

In addition to zooplankton community trait effects on RUE_{ZP}, nutrient addition can affect the size structure and edibility of phytoplankton as well as phytoplankton stoichiometry (Klausmeier et al. 2004, Meunier et al. 2017), with potential direct impacts on grazing efficiency of herbivores. For instance, high nutrient input in freshwater systems, which were not considered here, select for large and potentially toxic phytoplankton species, such as cyanobacteria (Reynolds, 1987; Downing et al., 2001). The interaction between nutrient enrichment (eutrophication) and cyanobacteria dominance can lead to biodiversity loss (Josué et al. 2019), including the local extinction of large zooplankton species (Hansson et al. 2007, Rangel et al. 2016) with potential detrimental effects on top-down control of algae (Pinheiro-Silva et al. 2020). However, in our study we did not find any direct effect of P-addition per se on RUE_{ZP}. Rather, we found that any measurable effect of P-addition could also be attributed to $_{\text{SES}}$MPD and CWM through their shared effects. This suggests that changes in zooplankton size structure, beyond changes in species richness alone, mediate the long-term effects of nutrient enrichment on RUE_{ZP}. Therefore, we suggest that to maintain high levels of ecosystem functioning, such as top-down control of algae and secondary biomass production, it is important to maintain high body size diversity along with community average size in addition to the high number of species.

CONCLUSION

We have demonstrated that increasing nutrients had a strong and positive effect on species diversity and community average size and that both parameters of zooplankton size structure were very important in determining zooplankton resource use efficiency. Although we have focused here on nutrients and structural complexity as drivers of zooplankton size structure, we argue that our results are likely representative of any other determinants of size structure, such as gradients of fish predation pressure, urbanization, and pollutants, which have also been shown to strongly determine zooplankton community size, with potentially strong consequences for ecosystem functioning, as illustrated by our study. This approach can be extrapolated to other systems that are characterized by different species compositions but share similar traits along environmental gradients (e.g., body size, specific leaf area, or any other functionally relevant traits).

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CONFLICT OF INTEREST

We declare that there is no conflict of interest.

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ELECTRONIC SUPPLEMENTARY MATERIAL

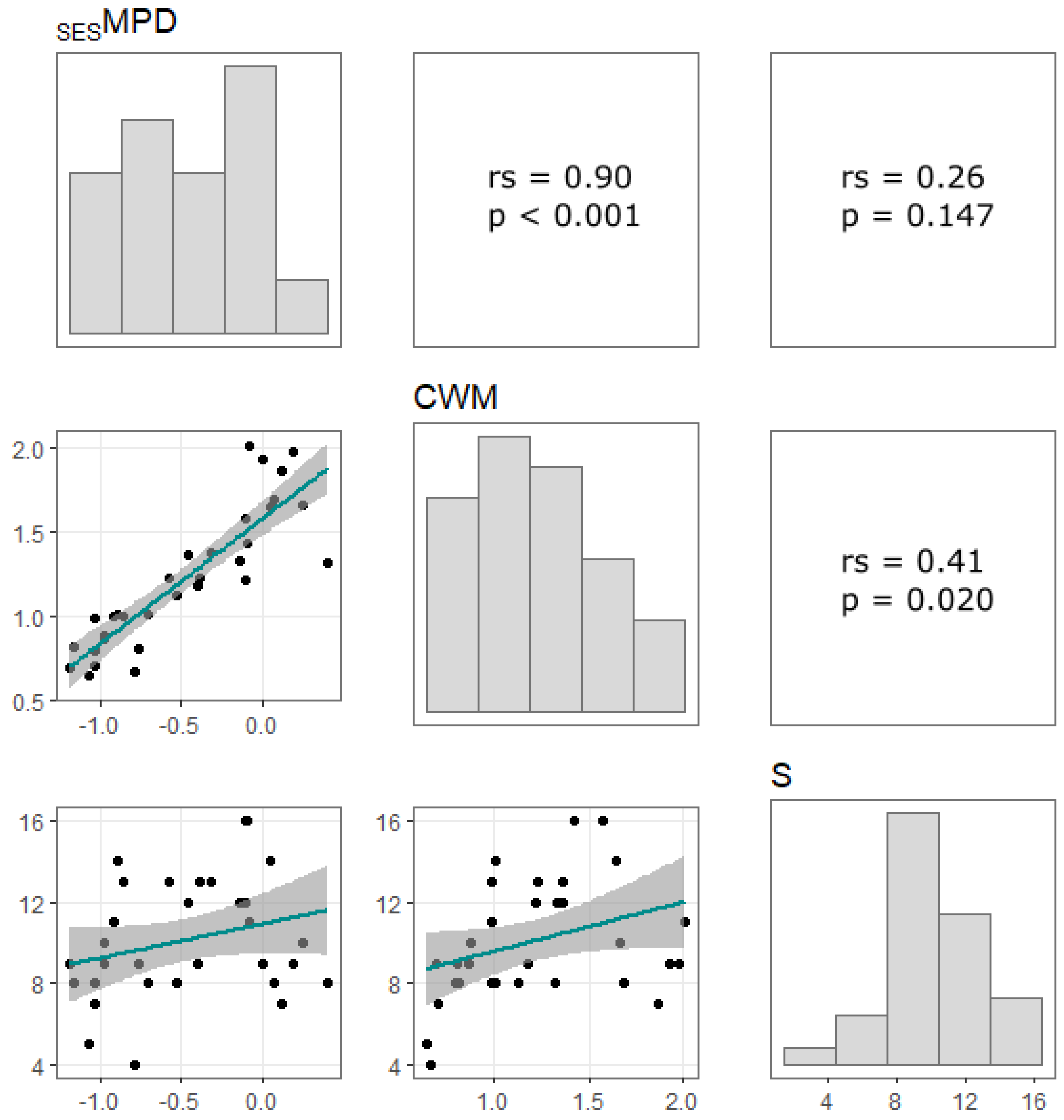

Fig. S1 Relationship between zooplankton size diversity ($_{SES}$MPD), zooplankton community average size (CWM) and zooplankton species richness (S). In the orthogonal line, histograms in the middle panels show the distribution of each variable; scatter plots with trend lines in the lower panels show pairwise relationships; and the summary of the correlation analysis (rs = correlation coefficient, and p = probability value) are shown in the upper panels. Axes for scatter plots are in units of diversity for each metric.

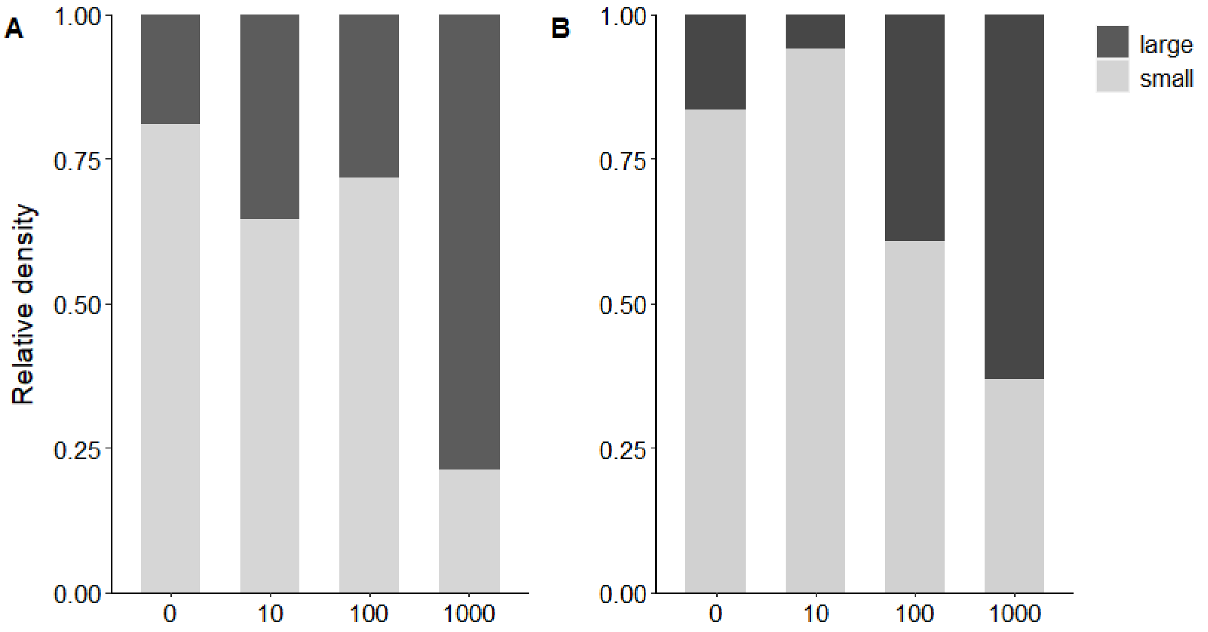

Fig. S2 Relative contribution of large and small cladocerans to total zooplankton density in different phosphorus addition levels (P1 = 0 µg L^{-1}, P2 = 10 µg L^{-1}, P3 = 100 µg L^{-1}, and P4 = 1000 µg L^{-1}) for each level of habitat complexity, **A**) with and **B**) without artificial macrophytes.

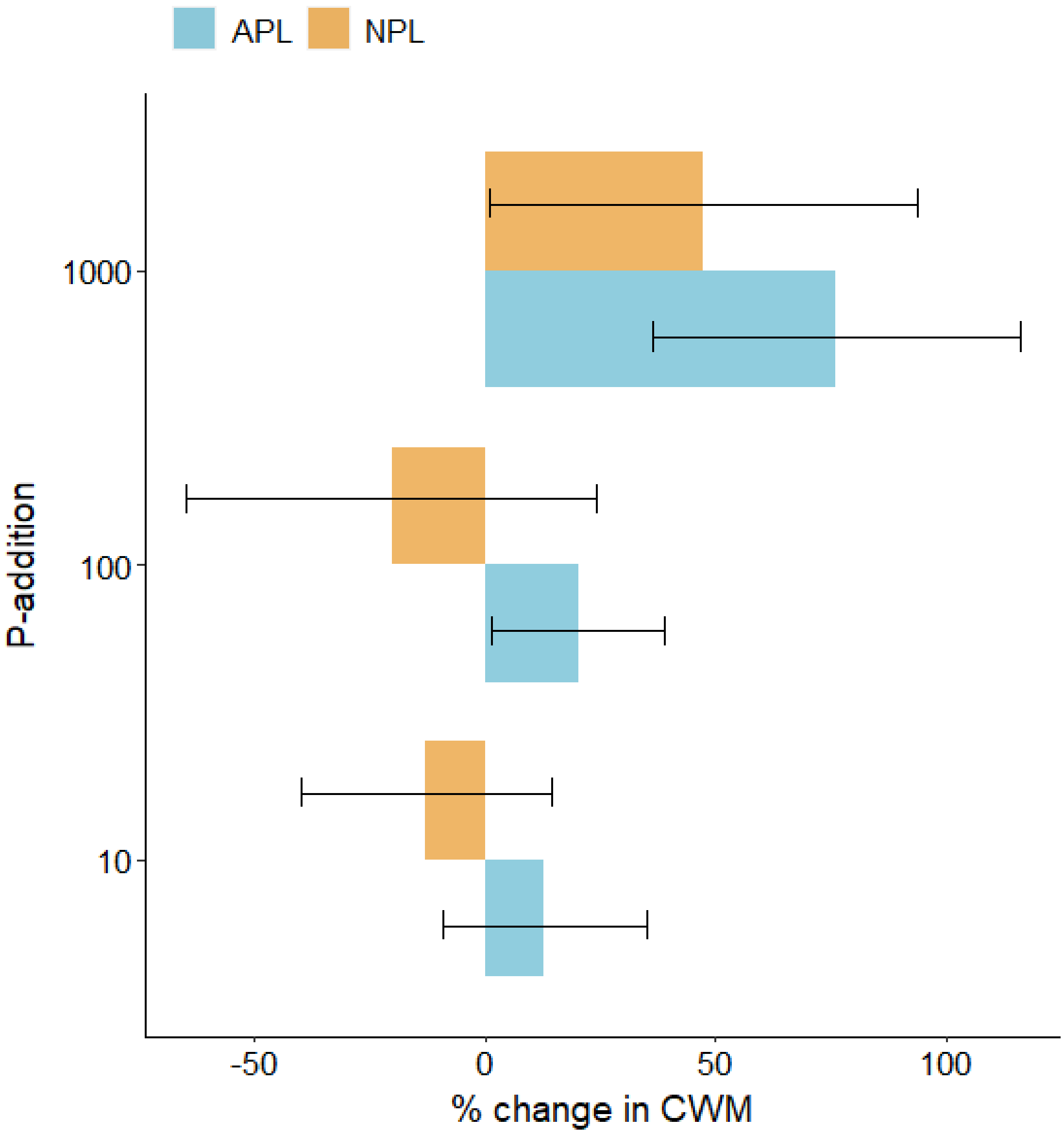

Fig. S3 Percentage change (% change) in community average size (CWM) over phosphorus (P) addition gradient (10 µg L^{-1}, 100 µg L^{-1}, and 1000 µg L^{-1}) for each level of habitat complexity, **A**) with (APL) and **B**) without artificial macrophytes (NPL). Percentage change in CWM was calculated based on paired differences between tanks with and tanks without phosphorus addition (P_0) for each P-addition level (10 µg L^{-1}, 100 µg L^{-1}, and 1000 µg L^{-1}). Error bars represent standard deviation (sd).

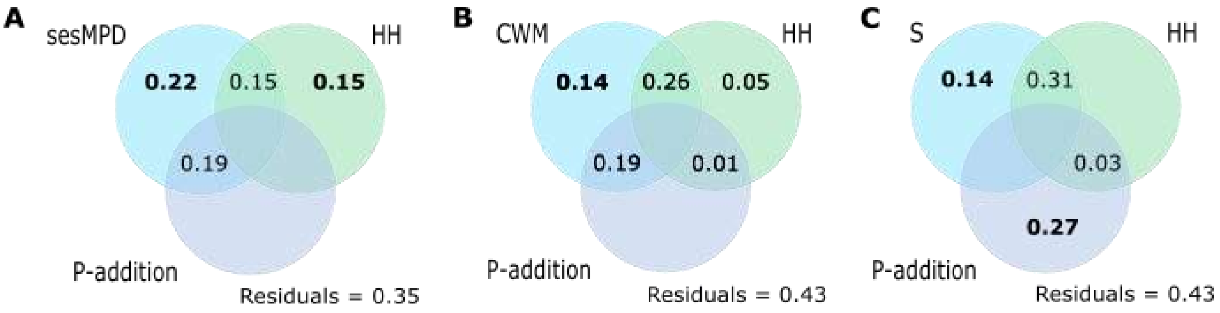

Fig. S4 Venn diagram showing the fraction of variation in zooplankton resource use efficiency (RUE$_{ZP}$; log-transformed) that can be explained by three different sets of explanatory variables (**a**, **b**, **c**): size diversity (sesMPD), community average size (CWM), species richness (S), nutrient addition (P-addition) and habitat heterogeneity (HH). The values in the circles represent the unique contribution (based on adjusted R^2) for each explanatory variable, and the intersections represent their shared contribution. The residuals represent the unexplained variation and only non-negative values $\geq$ 1% are shown. Statistically significant contributions are depicted in bold. Note that it is not possible calculate p-values for intersections. Graphs **a**-**c** are results from distinct variation partitioning analyses.

Table S1 List of cladocerans species found in the mesocosm experiment and mean body size (length; mm) used for zooplankton size diversity ($_{SES}$MPD) and community average size (CWM) calculations. All species with length < 2 mm are considered small size and all species with length > 2 are considered large size.

Species	**Length (mm)**	**Description**
Acroperus harpae	0.80	small
Alona elongatus	0.80	small
Alona excisa	0.40	small
Alona exigua	0.35	small
Alona guttata	0.40	small
Alona quadrata	0.55	small
Alona rectangula	0.26	small
Bosmina longirostris	0.60	small
Ceriodaphnia sp.	1.10	small
Chydorus sphaericus	0.50	small
Daphnia galeata	2.00	large
Daphnia magna	4.00	large
Diaphanosoma brachyurum	1.30	small
Eurycercus lamellata	3.30	large
Graptoleberus testudinaria	0.60	small
Pleurocus truncatus	0.65	small
Pleuroxus aduncus	0.65	small
Pleuroxus denticulata	0.60	small
Polyphemus pediculus	0.64	small
Scapholeberis mucronata	1.20	small
Sida crystallina	3.50	large
Simocephalus vetulus	2.70	large

Table S2 Multiple comparisons of the zooplankton size diversity ($_{SES}$MPD), community average size (CWM) and species richness (S) among P-addition levels (P_0, P_{10}, P_{100}, and P_{1000}; µg L^{-1}). The groups were based on P values obtained using Tukey's test adjusted for multiple comparisons, and significance level defined at *p*-value < 0.05.

	Difference	lower	upper	*p*-value
Response variable: $_{SES}$MPD				
P_{10} - P_0	-0.704	-1.216	-0.192	**0.005**
P_{100} - P_0	-0.737	-1.249	-0.225	**0.003**
P_{1000} - P_0	-0.412	-0.924	0.100	0.147
P_{100} - P_{10}	-0.032	-0.544	0.479	0.998
P_{1000} - P_{10}	0.292	-0.220	0.804	0.411
P_{1000} - P_{100}	0.325	-0.187	0.837	0.321
Response variable: CWM				
P_{10} - P_0	-0.593	-0.939	-0.248	**<0.001**
P_{100} - P_0	-0.732	-1.078	-0.387	**<0.001**
P_{1000} - P_0	-0.391	-0.737	-0.045	**0.022**
P_{100} - P_{10}	-0.139	-0.485	0.206	0.686
P_{1000} - P_{10}	0.202	-0.144	0.548	0.390
P_{1000} - P_{100}	0.341	-0.004	0.687	0.054
Response variable: S				
P_{10} - P_0	1.852	-0.491	4.195	0.157
P_{100} - P_0	0.810	-1.533	3.153	0.776
P_{1000} - P_0	0.795	-1.547	3.138	0.786
P_{100} - P_{10}	-1.042	-3.385	1.301	0.617
P_{1000} - P_{10}	-1.057	-3.400	1.286	0.606
P_{1000} - P_{100}	-0.015	-2.358	2.328	1.000

Bold values represent significant relationships obtained from permutation tests.

Table S3 Multiple comparisons of the zooplankton species richness (S) among P-addition levels (P_0, P_{10}, P_{100}, and P_{1000}; µg L^{-1})and habitat heterogeneity (APL and NPL). The groups were based on P values obtained using Tukey's test adjusted for multiple comparisons, and significance level defined at *p*-value < 0.05. APL refers to artificial plants and NPL refers to no artificial plants.

	Difference	lower	upper	*p*-value
P_0:NPL - P_0:APL	7.125	3.147	11.103	**<0.001**
P_{10}:NPL - P_0:APL	7.102	3.124	11.080	**<0.001**
P_{100}:NPL - P_0:APL	4.810	0.832	8.788	**0.010**
P_{1000}:NPL - P_0:APL	7.045	3.067	11.024	**<0.001**
P_0:NPL - P_{10}:APL	3.398	-0.580	7.376	0.134
P_{10}:NPL - P_{10}:APL	3.375	-0.603	7.353	0.139
P_{100}:NPL - P_{10}:APL	1.083	-2.895	5.061	0.983
P_{1000}:NPL - P_{10}:APL	3.318	-0.660	7.296	0.152
P_0:NPL - P_{100}:APL	3.190	-0.788	7.168	0.185
P_{10}:NPL - P_{100}:APL	3.167	-0.811	7.145	0.191
P_{100}:NPL - P_{100}:APL	0.875	-3.103	4.853	0.995
P_{1000}:NPL - P_{100}:APL	3.110	-0.868	7.088	0.208
P_0:NPL - P_{1000}:APL	5.455	1.476	9.433	**0.003**
P_{10}:NPL - P_{1000}:APL	5.432	1.454	9.410	**0.003**
P_{100}:NPL - P_{1000}:APL	3.140	-0.838	7.118	0.199
P_{1000}:NPL - P_{1000}:APL	5.375	1.397	9.353	**0.003**

Bold values represent significant relationships obtained from permutation tests.

3 CONSIDERAÇÕES FINAIS E CONCLUSÃO

No primeiro capítulo, eu e meus coautores avaliamos a relação entre múltiplos aspectos da diversidade biológica e a eficiência no uso de recursos limitantes (nitrogênio e fósforo) em uma lagoa subtropical que está passando por um processo de eutrofização. Nesse capítulo observamos que a diversidade e a composição do fitoplâncton não são afetadas diretamente pelo aumento das concentrações de nutrientes na lagoa (**pergunta i**). No entanto, a eficiência no uso de N e P pelo fitoplâncton se mostrou negativamente afetada pelo aumento de nutrientes ao longo do tempo (**pergunta iv**). Apesar da importância da riqueza de espécies (relação diversidade-RUE positiva), da uniformidade (relação diversidade-RUE negativa) e da diversidade funcional (relação diversidade-RUE positiva) para o funcionamento do ecossistema (**pergunta ii**), nossos resultados demonstram que variações na biomassa do fitoplâncton é o principal direcionador da relação positiva observada entre a diversidade e eficiência no uso de N e P pelo fitoplâncton (**pergunta iii**). Apesar de não termos encontrado relação entre a biomassa do fitoplâncton e as concentrações de nutrientes na lagoa, essa diminuição no uso eficiente de N e P pelo fitoplâncton, pode vir a contribuir significativamente para o aumento da concentração de nutrientes nos próximos anos.

No segundo capítulo, eu e meus coautores demonstramos o importante papel da diversidade de espécies e do tamanho do corpo de organismos aquáticos (zooplâncton) sobre o funcionamento do ecossistema (**pergunta i**). Especificamente, comunidades ecológicas com maior tamanho do corpo (CWM) e número de espécies (S) tem maior capacidade filtradora (efeito de seleção; **pergunta ii**), potencialmente diminuindo os impactos nocivos das cianobactérias em ambientes aquáticos. No terceiro capítulo, utilizando uma abordagem experimental (para maiores detalhes, ver Declerck et al. 2007) foi possível testar os impactos das mudanças nas características da comunidade zooplanctônica no funcionamento dos ecossistemas aquáticos em resposta ao aumento de nutrientes (fósforo). Os resultados obtidos demonstraram que na ausência de fatores como dominância de cianobactérias e predação por peixes, o aumento de nutrientes tem um efeito positivo na diversidade de tamanho do zooplâncton ($_{SES}$MPD) e no tamanho médio da comunidade (CWM) (**pergunta i**), independente da complexidade estrutural do habitat, aqui medida através do efeito (presença vs. ausência) de macrófitas artificiais (**pergunta ii**). Especificamente, nossas descobertas indicam que espécies zooplanctônicas de maior tamanho corporal não aguentam condições oligotróficas e são excluídas do ambiente, enquanto em ambientes eutróficos, a elevada disponibilidade de recursos promove maior competição interespecífica, levando a uma maior diversidade de tamanhos do que o esperado ao acaso. Além disso, demonstramos o importante papel do tamanho do corpo para eficiência do uso de recursos (RUE$_Z$) pelo zooplâncton, corroborando com os resultados encontrados no segundo capítulo, porém abrangendo um amplo gradiente de adição de nutrientes. No entanto, a diversidade de tamanho (sesMPD) se mostrou mais importante que o tamanho médio da comunidade (CWM) para o controle *top-down* das algas (**pergunta iii**), o que difere do resultado encontrado no segundo capítulo, onde o efeito de seleção foi o principal mecanismo subjacente a relação entre a diversidade e o funcionamento do ecossistema. Por fim, demonstramos que a adição de nutrientes afeta o funcionamento do ecossistema principalmente através de seu efeito na diversidade e composição do tamanho do corpo do zooplâncton (**pergunta iv**).

Com os resultados obtidos nos três capítulos, demonstramos que perturbações ecológicas, como a disponibilidade de nutrientes e a dominância de cianobactérias, afetam a biodiversidade e alteram as taxas de diferentes processos ecossistêmicos (controle *top-down* e eficiência no uso de recursos), principalmente através de seus efeitos sobre a estrutura e composição das comunidades planctônicas. Também demonstramos que diferentes dimensões da biodiversidade (e.g., taxonômica e funcional) podem ter respostas e efeitos divergentes no funcionamento do ecossistema dependendo da perturbação ecológica, e que os mecanismos — efeito de seleção e complementaridade — subjacentes a essas relações atuam de forma complementar nos ambientes aquáticos, onde a importância relativa de cada mecanismo varia não só de acordo com a escala de tempo, mas também com o gradiente de seleção considerado (e.g., disponibilidade de nutrientes, dominância de cianobactérias). Além disso, demonstramos que as abordagens funcional e taxonômica se complementam na explicação da variação do controle *top-down* das algas, o que destaca a importância de se considerar múltiplas dimensões da biodiversidade nas pesquisas B-EF. Nossos resultados indicam claramente que o tamanho do corpo do zooplâncton explica uma parte substancial e independente da variação do controle *top-down*, o que está de acordo com diversos estudos que demonstram a importância do papel do tamanho do corpo do zooplâncton no controle da biomassa do fitoplâncton. No entanto, ao contrário do esperado, a riqueza de espécies também desempenhou um importante papel, indicando que a diversidade taxonômica pode representar adequadamente alguns atributos (e.g., modo de alimentação) não avaliados que também influenciam o funcionamento do ecossistema.

No geral, os resultados obtidos nesta tese de doutorado ilustraram o potencial do efeito combinado de múltiplas abordagens para revelar as respostas da biodiversidade às mudanças ambientais e seus efeitos nos processos e serviços ecossistêmicos, e também enfatizam a preocupação com o fluxo de energia em ambientes aquáticos que apresentam prolongados períodos de dominância de cianobactérias, principalmente em regiões tropicais e subtropicais. A maioria dos estudos que buscam compreender as relações entre a dinâmica de nutrientes e a dominância de cianobactérias são desenvolvidos em ambientes que apresentam altas concentrações de nutrientes (eutróficos e hipereutróficos) e nem sempre gradientes são considerados. No entanto, prolongados períodos de dominância de cianobactérias em ambientes oligotróficos tem sido cada vez mais reportada ao redor do mundo nos últimos anos (Sukenik et al., 2015), e a expansão do conhecimento dessa relação (i.e., nutrientes-cianobactérias) para esses ambientes pode levar a uma melhor compreensão sobre a estrutura das comunidades e suas respostas funcionais a pressões e mudanças nos ecossistemas aquáticos.

Por fim, devido a severa a redução do volume de água na lagoa do Peri e a forte influência da disponibilidade de nutrientes e luz sobre a estrutura e dinâmica do plâncton na lagoa, o presente estudo objetiva contribuir para despertar, na administração pública municipal, a necessidade de um adequado planejamento e gestão dessa bacia hidrográfica que leve em consideração o monitoramento das características hidrológicas (e.g., nível da água) associada a estrutura das comunidades aquáticas ali presentes, principlamente o fitoplâncton. Tal monitoramento deverá ocorrer de forma a permitir a caracterização, análise de tendências e prospecções de cenários futuros de acordo com variações climáticas (e.g., regime de precipitação) na bacia hidrográfica em questão.

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