PRIMARY RESEARCH PAPER

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.

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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 depends 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, 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), and 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., 2019). 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-
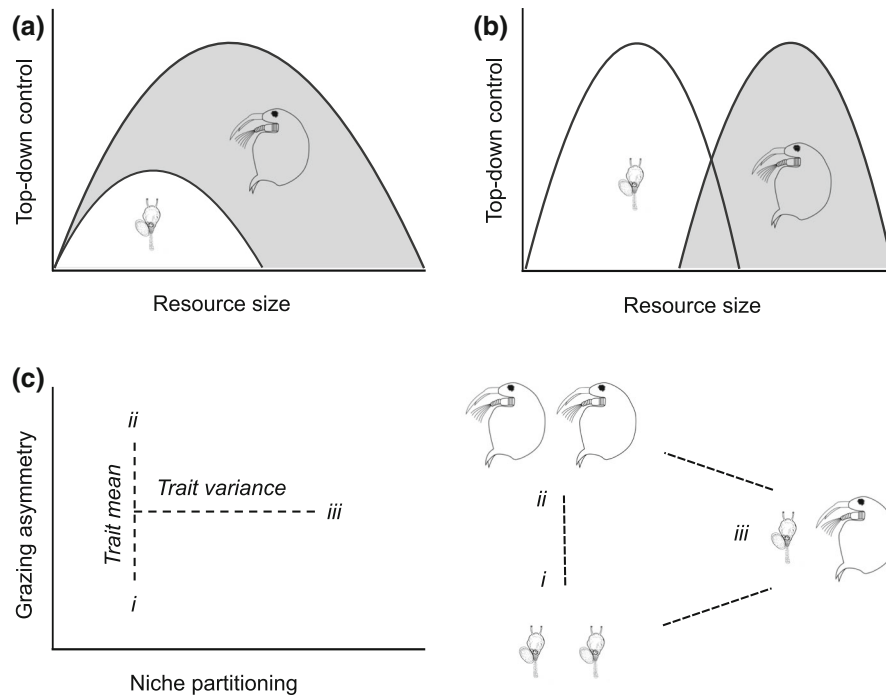
Fig. 1 Conceptual scheme showing hypothetical scenarios of alternative mechanisms by which zooplankton body size can impact ecosystem functioning via size-based selection effects and complementarity. **a** Size-based selection effects would result from the fact that larger zooplankton species are more 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., 2019; Isbell et al., 2018). **c** Three hypothetical communities are represented as i, ii, and 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)

down control on algae (Fig. 1c) (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 nontoxic cyanobacteria along 1 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).

Materials 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 $C = 0.1204\ V^{1.051}$ (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 $\times 100$ magnification (Zeiss®) for rotifers and copepods nauplii, using an acrylic open chamber under a stereomicroscope at $\times 50$ 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 & Dias, 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 & Salonen, 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 (CWM) body size and the standardized effect size based on mean pairwise distance ($_{SES}$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, $_{SES}$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 $_{SES}$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 ($_{SES}$MPD) between all species in the community (Kembel et al., 2010). Negative values of the index $_{SES}$MPD 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 ($_{SES}$MPD) 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 ($_{SES}$MPD, 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 ($_{SES}$MPD; trait-based approach), community average size (CWM; trait-based approach), and taxonomic richness (S; taxon-based approach) were used as

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 (°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

WT: water temperature, DO: dissolved oxygen, EC: electrical conductivity, Z$_{EU}$: euphotic zone depth

predictors. As explained in the introduction and also on our conceptual Fig. 1, each explanatory variable of the size structure ($_{SES}$MPD 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 $_{SES}$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 ($_{SES}$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 ΔAICc ≤ 2 from the top model (ΔAICc = 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 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* (Woloszynska 1912) Seenayya and SubbaRaju (1972) and *Pseudanabaena catenata* Lauterborn (1915) during the sampling months.

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 $_{SES}$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) was independent to each other. Nevertheless, we cannot rule out the contribution of $_{SES}$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 $_{SES}$MPD (ΔAICc = 9.8).

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 et al., 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

Table 2 Mean values ($\pm$ SD) of the temporal variation of phytoplankton total carbon biomass, zooplankton 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

|	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

SD represents the standard deviation

Table 3 Linear mixed-effect models (LMMs) of relationships among zooplankton top-down control (response variable; log10-scale B_Z/B_P), standardized effect size (predictor; $_{SES}$MPD), community weighed mean (predictor; CWM), and taxonomic richness (predictor; S)

Models	d.f.	AICc	Δ AICc	CWM	Coefficients (SE)			
					S	$_{SES}$MPD	R^2m	R^2c
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 + $_{SES}$MPD + S	7	− 44.1	4.0	1.371 (0.888)	0.046 (0.009)	0.101 (0.055)	0.239	0.239
$_{SES}$MPD + S	6	− 43.6	4.5	–	0.054 (0.003)	0.185 (0.010)	0.242	0.242
CWM + $_{SES}$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
$_{SES}$MPD	5	− 35.0	13.1	–	–	0.015 (0.054)	0.001	0.004

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
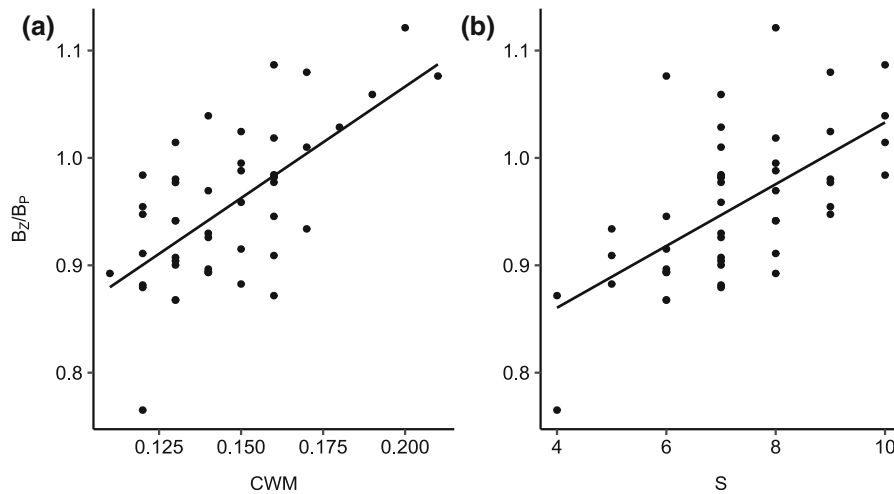
Fig. 2 Scatter plots describing the relationship between the biomass ratio (B_Z/B_P) and its predictors: **a** community weighed mean (CWM) based on body size and **b** taxonomic richness (S).

The solid line represents the fitted values for all sampling sites, and it is based on the selected linear mixed-effect model ($B_Z/B_P = 3.15 + 2.568 \times \text{CWM} + 0.036 \times \text{S}$)

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 $_{SES}$MPD), 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 (Da 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 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 ($_{SES}$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), favoring the importance of selection effect in Peri Lake. Since size spectrum is very sensitive to any small change in zooplankton feeding preferences (Fuchs & Franks, 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 $_{SES}$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 tends 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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