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Research article

Quantifying the contribution of community trait mean and diversity to ecosystem functioning

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Hundreds of experiments conducted over the last decades demonstrate a positive relationship between species diversity and ecosystem functions. Following good experimental practice, most of these studies have manipulated species richness artificially by assembling communities randomly. Yet, natural communities along ecological gradients often show niche-based responses to selection gradients and species extinction order is generally not a random process. Such responses are commonly trait-mediated and the effects of communities on ecosystems' functions also depend on species traits. In an effort to disentangle the relationship of trait mean value and diversity with ecosystem functioning, we revisited a community assembly mesocosm experiment that simulated habitat heterogeneity and a typical gradient of productivity to test how body size diversity and composition of cladocerans 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. Nutrient addition lead to an increase in average body size (CWM_{BS}), which ultimately resulted in an increased zooplankton resource use efficiency (RUE_{ZP}). This increase in CWM_{BS} acted as a buffer for ecosystems functions despite the decline in species richness under high phosphorus levels. Habitat heterogeneity modified the response of both richness and size diversity (SD) along the nutrient gradient, suggesting that habitat structure provided by aquatic plants can modify zooplankton diversity under eutrophic conditions. We also show that CWM_{BS} and SD are both important and largely independent determinants of variation in RUE_{ZP}, whereas the explanatory power of species richness was mostly shared with SD. Overall, our findings illustrate the potential for a key trait, such as body size, to predict top–down control of algae through selection effect mediated by differences in trait mean, as well as complementarity associated with trait diversity among coexisting species.

Keywords: body size, ecosystem functioning, metacommunity ecology, resource use efficiency

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Introduction

Multiple anthropogenic drivers of global change are leading to biodiversity loss, with negative impacts on ecosystem functions (Cardinale et al. 2012, Lefcheck et al. 2015). Early evidence of a positive biodiversity–ecosystem functioning (B–EF) relationship initially comes mainly from studies that focused on the impact of species richness on ecosystem processes using artificially constructed communities (Hector et al. 1999, Engelhardt and Ritchie 2001, Cardinale et al. 2007, Cardinale 2011). Such positive B–EF relationship has been similarly supported by a number of studies conducted mostly in natural terrestrial ecosystems (Maestre et al. 2012, Duffy et al. 2017, van der Plas 2019). More recently, trait-based experimental approaches have also artificially manipulated functional and/or phylogenetic diversity to gain new insights into B–EF (Gianuca et al. 2016, Huang et al. 2020, Setubal et al. 2020) and revealed that ecosystem functions may vary considerably even when richness is held constant (Cadotte et al. 2009, 2011, Gianuca et al. 2016). However, in nature, species gains or losses are generally not random but strongly linked to changes in environmental conditions, species interactions and response traits (Tanaka 2012, Bestion et al. 2018) and the order in which species appear or disappear from a community can strongly determine its functioning (Larsen et al. 2005, Díaz et al. 2013). Studying community assembly trajectories under more natural settings may thus help to disentangle the influence of species richness and composition on ecosystems functions (Leibold et al. 2017, Bannar-Martin et al. 2018).

Despite the advances that can be gained by considering more natural community assembly conditions, an exclusive focus on species richness and taxonomic composition ignores the role that traits play on ecosystems functions (Cadotte et al. 2011, Godoy et al. 2020). Functional traits influence the response of species to environmental change and also determine how species contribute to specific ecosystems functions (Litchman et al. 2013, Zwart et al. 2015, Hébert et al. 2016). Communities with similar richness but contrasting trait distributions may therefore perform very differently (Cadotte 2013, Gianuca et al. 2016). Given that, it is essential to better understand how trait distributions are shaped along environmental gradients and how they influence ecosystems functions.

Zooplankton are key grazers of phytoplankton in many ponds and lakes (Brooks and Dodson 1965, Lampert et al. 1986, Scheffer et al. 1997). Phytoplankton abundances in lakes and ponds are a function of both nutrient concentrations and top–down control by zooplankton (McQueen et al. 1986, Li et al. 2020). Top–down control is an important ecosystem function with added societal value (Declerck and de Senerpont Domis 2022), as it can prevent (Sarnelle 1993, Matveev et al. 1994) or facilitate (Ger et al. 2019) (harmful) algal blooms. Previous studies have demonstrated the importance of zooplankton body size in determining top–down control of algae (Ye et al. 2013, Gianuca et al. 2016, Pinheiro-Silva et al. 2020). There is evidence that average body size of zooplankton populations and communities is the main driver of top–down control, especially because larger individuals are more efficient grazers (i.e. selection effect; Gianuca et al. 2016, Pinheiro-Silva et al. 2020). However, body size diversity and complementarity among species that vary in size may also be important, particularly when small and large zooplankton feed on alternative resources, such as small and large unicellular algae (Ye et al. 2013). In this scenario, the diversity of body sizes, rather than the average size, would be the main determinant of top–down control.

Eutrophication can either increase only average body size or both average body size and body size diversity. In the absence of fish predation, high nutrient concentrations have been reported to favor large daphnids (Dodson et al. 2000). In addition, the effect of eutrophication on size structure will depend on whether eutrophication leads to the competitive exclusion of small zooplankton species by competitively superior larger species (Gliwicz 1990, Jeppesen et al. 2000) or leads to an increased diversity of food resources allowing small and large species to coexist (Ye et al. 2013). This pattern may be further influenced by habitat heterogeneity (Stein et al. 2014), for instance caused by the presence of macrophytes (Lucena-Moya and Duggan 2011). Habitat heterogeneity may lead to an increase in niche availability in zooplankton and therefore promote a higher trait and species diversity (Declerck et al. 2007). In this context, habitat heterogeneity may indirectly influence the capacity of zooplankton for top–down control of phytoplankton.

In this study, we used a mesocosm experiment in which nutrient concentrations and habitat heterogeneity (presence or absence of artificial macrophytes) were manipulated to quantify: 1) how zooplankton average body size, size diversity, and species richness respond to a gradient of nutrient addition; 2) how this response is mediated by habitat heterogeneity; 3) the relative importance of average body size, size diversity and species richness in determining top–down control of algae; and 4) trait-mediated impacts of zooplankton on top–down control in comparison to the direct effects of nutrient addition and habitat heterogeneity. First, we hypothesize that increasing nutrient concentrations would reduce species richness and size diversity but increase average body size due to the selection of a subset of larger species. This is expected because larger species have a higher demand for nutrients but can outcompete smaller species under high nutrient conditions (Dodson et al. 2000). Second, we expected that habitat heterogeneity would increase species richness and size diversity by creating niche opportunities and thus reducing competition (Declerck et al. 2007). Third, we expected a higher relative contribution of average body-size on top–down control compared to size diversity and species richness because previous studies have demonstrated that larger species are more efficient grazers than smaller species (Gianuca et al. 2016, Pinheiro-Silva et al. 2020). Finally, we hypothesize that trait-mediated impacts of zooplankton on top–down control would be relatively more important than the pure effects of nutrients additions through bottom–up control in the presence of macrophytes, due to increased niche

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availability within zooplankton community (Declerck et al. 2007). The rationale is that in fishless systems, increased grazing pressure on phytoplankton by zooplankton would lead to stronger top–down control and weaker bottom–up effects compared to food web structures under relatively high fish densities (Lemmens et al. 2018).

Material and methods

Experimental design

We used a subset of the data from a metacommunity assembly experiment performed by Declerck et al. (2007). In this study, a multifactorial combination of nutrient concentrations and habitat complexity levels was performed using cattle tanks (200 litres) under semi-standardized outdoor conditions at the ARENA outdoor experimental area in Heverlee, Belgium. The experiment lasted 32 days following a 34-day inoculation/acclimatation period. Of the habitat complexity levels, we here only consider the treatments without macrophytes (NPL) and those with artificial macrophytes (APL). We deliberately chose not to include treatments with real plants because we wanted to only test the effect of habitat heterogeneity on zooplankton size structure and RUE_{ZP}. As such, we ruled out the nutrient competition effects of macrophytes on phytoplankton, the latter being the major resource base of the zooplankton used in the experiment.

A nutrient gradient (phosphorus and nitrogen) was created on day 4 by addition of KH_2PO_4 in different concentrations (0, 10, 100 and 1000 µg l^{-1}). Nitrogen 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 heterogeneity (i.e. without and with artificial macrophytes) by nutrient concentration (i.e. 0, 10, 100 and 1000 µg l^{-1}), five replicates were used, resulting in a total of 40 cattle tanks. Natural assemblages of phytoplankton and zooplankton were collected from different water bodies in the region of Leuven (Belgium), mixed, 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 experimental design, see Declerck et al. (2007).

Sampling and analytical methods

Sampling for nutrients was performed on day 7 and sampling for chlorophyll a was performed on day 34. At the end of the experiment (day 64–66), samples were collected for nutrients, chlorophyll a, and zooplankton community. Nutrients were sampled with a 250-ml bottle from the middle of each tank, while crustacean zooplankton was sampled using a tube sampler after thoroughly mixing the tanks. To avoid sampling bias due to zooplankton patchiness, 12 litres of water were collected from six locations per tank (Declerck et al. 2007). Zooplankton samples were then preserved with acid Lugol's solution.

Total phosphorus was analyzed with a Technicon autoanalyzer II after persulfate digestion. Chlorophyll a was spectrophotometrically determined. A minimum of 300 cladocerans from each zooplankton sample were identified to the species level using a stereomicroscope. Calanoids and cyclopoid copepods were not further identified due to feasibility constraints (Declerck et al. 2007). For this reason, only cladocerans were considered in our analysis. A list of all identified Cladocera species is provided in the Supporting Information. Body size information was compiled from previous studies (Brans et al. 2017), based on measurements of 15 individuals per species collected from Belgian ponds along a rural-to-urban gradient. When species-level data was not available, we used genus-specific averages (Fig. 1, Supporting information). Additional body size information was supplemented from Alonso (1996) for *Acroperus harpae*. Average body length values were then used to estimated individual biomasses (B_Z; µg l^{-1}) using existing allometric relationships between weight and the average body length from the literature (Bottrell et al. 1976).

Average body size (CWM_{BS}), size diversity (SD) and species richness (S)

We assessed the body size distribution of the cladoceran communities by a combination of average body size (CWM_{BS}) and size diversity (SD). To estimate CWM_{BS}, we used species-specific average body sizes (mm; Supporting information) weighted by species' relative abundances. We calculated interspecific SD from the average body size data following the nonparametric method proposed by Quintana et al. (2008), which is an analogue to the Shannon diversity index adapted for continuous variables, such as body size, described by the following equation:

$$\mu = -\int_0^{+\infty} p_x\left(x\right)\log_2 p_x\left(X\right)dx$$

where $p_x(x)$ represents the probability density function of the average length of each species. Length data were standardized beforehand by division by the sample geometric mean value.

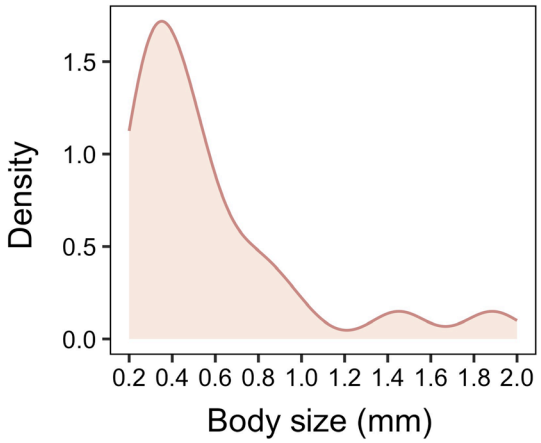

Figure 1. Histogram of cladoceran body size distribution used to calculate average body size (CWM_{BS}) and size diversity (SD).

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Since this approach employs a continuous probability density function for the estimation of the SD of size distributions, negative values may occur, which in that case indicate an extremely low SD. Given that we have no individual-based size measurements, we were unable to account for the effects of intraspecific size variation in our analyzes.

We also calculated species richness (S) for each replicate. We calculated CWM_{BS} and SD using the statistical environment R. ver. 4.2.2 (www.r-project.org). The functions and libraries used for each calculation are shown in the Supporting information.

Resource use efficiency calculations (RUE_{ZP})

We used resource use efficiency (RUE_{ZP}) as a proxy for the ability of zooplankton to control phytoplankton. Here, we calculated RUE_{ZP} as the ratio between zooplankton biomass (μg l^{-1}) and chlorophyll a (μg l^{-1}) (Verbeek et al. 2018). Assuming that primary zooplankton consumers have reached carrying capacity (e.g. in the absence of predators, disease or disturbances), RUE_{ZP} can be considered indicative for the ability of the consumers to convert their food resource into own biomass and graze down resources to low, limiting levels.

Data analysis

We tested the effect of the factors P-addition (four levels; 0, 10, 100 and 1000 μg l^{-1}) and habitat heterogeneity (two levels; presence and absence of artificial macrophytes) and their interaction on zooplankton CWM_{BS}, SD and S using a two-way analysis of variance (ANOVA) with permutation tests. We chose permutational methods since they do not make assumptions about underlying distributions and are suitable when sample sizes are small. When significant main or interaction effects were detected after ANOVA, we applied multiple Conover–Iman tests with Benjamini–Hochberg-adjusted p-values for multiple comparisons.

We applied variation partitioning analysis to reveal the main drivers of RUE_{ZP} and to be able to disentangle the pure effects of treatments and community features from their shared effects. First, to assess the overall degree to which the experimental factors were linked with community features in determining RUE_{ZP}, we partitioned variation in RUE_{ZP} between phosphorus addition (P), habitat heterogeneity (HH) and a set of three community variables CWM_{BS}, SD and S as a whole. Second, we assessed the relative importance of each of the community variables irrespective of the experimental factors by applying a variation partitioning analysis with only CWM_{BS}, SD and S as explanatory variables. The third and fourth variation partitioning analysis focused on the impact of the size related community variables, respectively CWM_{BS} and SD, and the degree to which their impact on RUE_{ZP} was shared with both experimental factors. Variation partitioning allows one to separate the unique (conditional) and shared (marginal) contributions of predictors to the variation in a response variable (Borcard et al. 1992). Conditional effects represent the contribution of an explanatory variable or set of variables to the total variation assessed while accounting/controlling for the effect of other variables in the model. On the other hand, marginal effects represent the contribution of a particular explanatory variable or set of variables to the total variation, but this contribution is assessed without accounting/controlling for the effect of any other variables in the model. The proportion of explained variation is given by the adjusted R^2 (R^2_{adj}) to avoid type I error. These variance components were assumed to be significant when p-values were 0.05 or smaller, based on Monte Carlo permutation testing (999 permutations). Prior to variation partitioning analyses, Spearman pairwise rank correlations were performed for each habitat heterogeneity scenario (APL and NPL) to assess the strength and direction of associations between CWM_{BS}, SD and S along the phosphorus gradient.

We performed all analyses and produced all figures using R ver. 4.2.2 (www.r-project.org). The functions and libraries used for each analysis are shown in the Supporting information.

Results

Influences of P-addition and habitat heterogeneity on zooplankton diversity and body size structure

We found a strong effect of P-addition on CWM_{BS} (Fig. 2a, Table 1) that was independent of the presence of artificial macrophytes (interaction term not significant). CWM_{BS} was found to be especially high in the highest nutrient (1000 μg l^{-1}) treatment compared to low P concentration (0 μg l^{-1}) treatment (Fig. 2a). The main effects of P-addition on both SD and S were not significant, but there was a macrophyte-dependent effect of P-addition (marginally significant and significant interaction terms, respectively; Table 1). More specifically, SD values at high P concentrations (1000 μg l^{-1}) were lower than at low concentrations (10 μg l^{-1}) in the treatments with artificial plants (Fig. 2b, Supporting information). Similarly, S values were higher at intermediate P levels (10 and 100 μg l^{-1}) compared to both the lowest (0 μg l^{-1}) and highest (1000 μg l^{-1}) P levels in treatments with artificial macrophytes (APL; Fig. 2c). In contrast, S values at low P concentrations (0 and 10 μg l^{-1}) were higher than at intermediate concentrations (100 μg l^{-1}) in the NPL treatment.

Spearman rank correlation analysis (Supporting information) revealed distinct correlation patterns between CWM_{BS} and SD across treatments. In the APL treatment, CWM_{BS} and SD were negatively correlated ($r = -0.51$, $p = 0.045$), whereas no correlation was found in the NPL treatment. Additionally, no correlation was found between S and body size metrics (CWM_{BS} and SD) in either of the macrophyte treatments.

Drivers of zooplankton top–down control on phytoplankton biomass (RUE_{ZP})

We found a significant effect of P-addition, habitat heterogeneity and their interaction on RUE_{ZP} (Fig. 2d, Table 1). RUE_{ZP} was lower at intermediate nutrient concentrations (10 and 100 μg l^{-1}) than at high concentrations (1000 μg l^{-1}) in the NPL treatment and showed no significant response to nutrient additions in the APL treatment.

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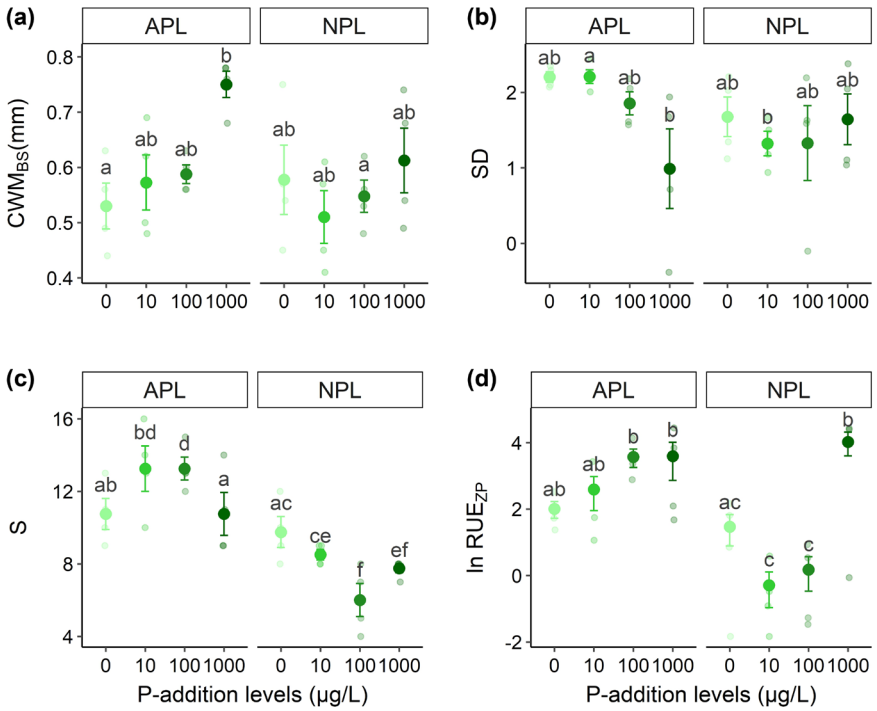

Figure 2. Response of (a) cladoceran average body size, (b) cladoceran size diversity index, (c) cladoceran species richness, and (d) resource use efficiency (RUE_{ZP}; ln-transformed) to phosphorus addition (P-addition; 0, 10, 100 and 1000 µg l^{-1}) and habitat heterogeneity (with artificial plants and without plants; APL and NPL, respectively) treatments. All means and standard error of replicates. Dots represent the raw data. Different letters represent the significant differences (p-values ≤ 0.05) caused by P-addition, habitat heterogeneity and the interaction between the two treatments.

Variation partitioning showed that community size structure and diversity (i.e. CWM_{BS}, SD and S together) explained a total of 69% of the variation in RUE_{ZP} (Fig. 3a; $F_{3,24}=7.54$, $p=0.001$). Remarkably, a large proportion of this explained variation (R^2_{adj}= 26%) was unique to the cladoceran community features and independent of the experimental treatments of nutrient addition and habitat heterogeneity (Fig. 3a). P-addition explained 32% of the variation in RUE_{ZP} (Fig. 3a; $F_{3,24}=4.52$, $p=0.015$) and a significant part of this variation was independent of community features (significant conditional effect). On the other hand, habitat heterogeneity explained 27% of the variation in RUE_{ZP} (Fig. 3a; $F_{1,24}=1.13$, $p=0.32$) and all this variation was shared with community size structure and diversity (Fig. 3a; no significant conditional effect).

CWM_{BS} explained 38% of the variation in RUE_{ZP}, while SD and S explained 29 and 30%, respectively (Fig. 3b). CWM_{BS} uniquely explained 27% of the variation in RUE_{ZP} (Fig. 3b; $F_{1,24}=16.37$, $p=0.001$). In contrast, SD uniquely explained 12% of the variation in RUE_{ZP} (Fig. 3b; $F_{1,24}=7.65$, $p = 0.009$) whereas no significant conditional effect of S could be observed (Fig. 3b; $R^2_{adj}=2\%$, $F_{1,24}=1.88$, $p=0.19$). There was no variation shared by all community features simultaneously (Fig. 3b). The amount of variation jointly explained by each of the possible pairs of community features was low for CWM_{BS} and S (11%), but for SD and S, it equaled 17% (Fig. 3b). No shared explained variation was observed between CWM_{BS} and SD. All cladoceran community descriptors studied (CWM_{BS}, SD and S) showed a positive relationship with RUE_{ZP} (Fig. 4).

Two more detailed variation partitioning analyses (Fig. 3c–d) combining each of the experimental treatments with both size features (CWM_{BS} and SD) revealed that P-addition affected RUE_{ZP} mainly through its effect on variation in CWM_{BS} (23%). Habitat heterogeneity affected RUE_{ZP} mainly through its effect on both variation in CWM_{BS} (12%) and SD (10%).

Discussion

There is growing concern about anthropogenic impacts on biodiversity and on how this may impair ecosystem functions and services. Here we used a dataset from a mesocosm experiment to assess how environmental pressures related to eutrophication and loss of habitat heterogeneity influence a key ecosystem function through its impacts on cladoceran community features. Experimental manipulations of nutrient concentrations and habitat heterogeneity had a profound impact on the size structure and species richness of the cladoceran communities, and these changes significantly influenced resource use efficiency of the zooplankton. More specifically, high phosphorus concentrations increased CWM_{BS}, which was an important determinant of RUE_{ZP}. In addition, there

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Table 1. Two-way permutation ANOVA results, testing for the effect of phosphorus addition (P), habitat heterogeneity (HH) and their interaction (P × HH) on zooplankton average body size (CWM_{BS}), size diversity (SD), species richness (S) and resource use efficiency (RUE_{ZP}; ln-transformed). df: degrees of freedom; SS: sum of squares. Bold values represent $p < 0.05$.

Response by factor	df	SS	pseudo-F	p
Response variable: CWM_{BS}				
P-addition (P)	3	0.100	4.269	**0.013**
Habitat heterogeneity (HH)	1	0.019	2.381	0.151
P × HH	3	0.035	1.491	0.313
Residuals	24	0.187		
Response variable: SD				
P-addition (P)	3	1.701	1.474	0.269
Habitat heterogeneity (HH)	1	0.823	2.138	0.111
P × HH	3	2.709	2.346	0.087
Residuals	24	9.239		
Response variable: S				
P-addition (P)	3	12.25	1.410	0.226
Habitat heterogeneity (HH)	1	128.00	44.201	**0.000**
P × HH	3	46.25	4.863	**0.010**
Residuals	24	69.50		
Response variable: RUE_{ZP}				
P-addition (P)	3	23.87	4.574	**0.011**
Habitat heterogeneity (HH)	1	29.15	16.755	**0.000**
P × HH	3	18.82	3.606	**0.028**
Residuals	24	41.75		

was a marginally significant interaction between phosphorus addition and habitat heterogeneity on SD as well as a significant interaction between these two treatments on species richness. Although species richness could be considered an important determinant of RUE_{ZP}, our variation partitioning analysis revealed that most of the explanatory power provided by richness was shared with SD. Furthermore, SD also contributed a strong and unique fraction of explanation to variation in RUE_{ZP}. Our analyses thus clearly show that average body size and size diversity are both important and largely independent determinants of variation in resource use efficiency of zooplankton than species richness of the community. Although such higher explanatory power of trait-based as opposed to taxonomy-based metrics has previously been recognized, evidence has mainly been generated by manipulative experiments that artificially assembled communities based on trait distributions or phylogenetic distances (Cadotte et al. 2011, Cadotte 2013, Gianuca et al. 2016). In contrast, our approach was to allow experimentally manipulated environmental gradients to structure the community, permitting us to evaluate the influence of different community descriptors on ecosystem functioning in a more natural setting where these community descriptors are not manipulated artificially but result from species sorting and competitive interactions in the community.

Community assembly mechanisms

In line with our expectations, we observed that CWM_{BS} was considerably higher in the highest P-addition treatment (P_{1000}), compared with treatments with low phosphorus level. This increased dominance of large cladocerans at high nutrient concentrations can be related with two main perspectives of size-based zooplankton community assembly. First, the dominance of large zooplankton agrees with the size efficiency hypothesis (Brooks and Dodson 1965) as well as with some laboratory studies that showed that competitive exclusion of small zooplankton species by large species is more likely to occur under high than low food concentrations (Romanovsky and Feniova 1985, Vanni 1986). The rationale is that large zooplankton have the ability to exploit food sources to levels that are too low for small zooplankton to maintain positive population growth. The second perspective to explain the dominance of large species under high P is ecological stoichiometry. Indeed, large cladocerans, such as daphnids, are P-rich consumers that can grow faster than smaller cladocerans under conditions of high-quality food (Urabe and Watanabe 1992, Main et al. 1997). However, the high phosphorus demand for such large species constrains their growth under oligotrophic condition (Sommer 1992, DeMott et al. 1998, Guo et al. 2019). Under low P-concentration, large daphnids such as *Daphnia magna* do not dominate because they suffer P limitation and are therefore competitively inferior to smaller species, which have the capacity to grow relatively faster as a result of their low food requirements (Wilson 1975, Persson 1985). In combination, these two perspectives can explain why smaller species tended to dominate mesocosms with low to moderate nutrient concentrations whereas large zooplankton species dominate under high nutrient conditions.

We observed an interaction between P addition and habitat heterogeneity on species richness. Particularly, the relation between species richness and P addition was hump-shaped in treatments with artificial plants, whereas richness decreased monotonically with nutrients in the absence of artificial plants. These findings suggest that nutrient addition likely enhance species coexistence and niche partitioning in heterogenous habitats (Leibold and Tessier 1997) up until a point in which nutrient concentrations are too high that favor only a subset of species, such as large daphnids that prevail under high quality food (Dodson et al. 2000). Notable is the difference in resource use by small chydorids that attach to plants and scrape algae compared to large daphniids that are pelagic filter feeders (Vijverberg and Boersma 1997, Agasild et al. 2012, Tõnno et al. 2016). Our results align with those of Leibold (1999) who found that zooplankton diversity exhibits a unimodal relationship with nutrient levels. In contrast, in homogeneous settings, nutrient addition seems to quickly result in competitive exclusion, which reduces species richness. The latter is similar to what has been reported for grasslands, in which nutrient addition quickly leads to competitive exclusion as well as high dominance by a few strong competitors (Muehleisen et al. 2023), suggesting that this might be a common species diversity response to nutrients in homogeneous environments. However, our results also hint that heterogenous habitat structure provided by plants in aquatic systems can modify zooplankton diversity response to nutrient addition. We also observed a marginally significant

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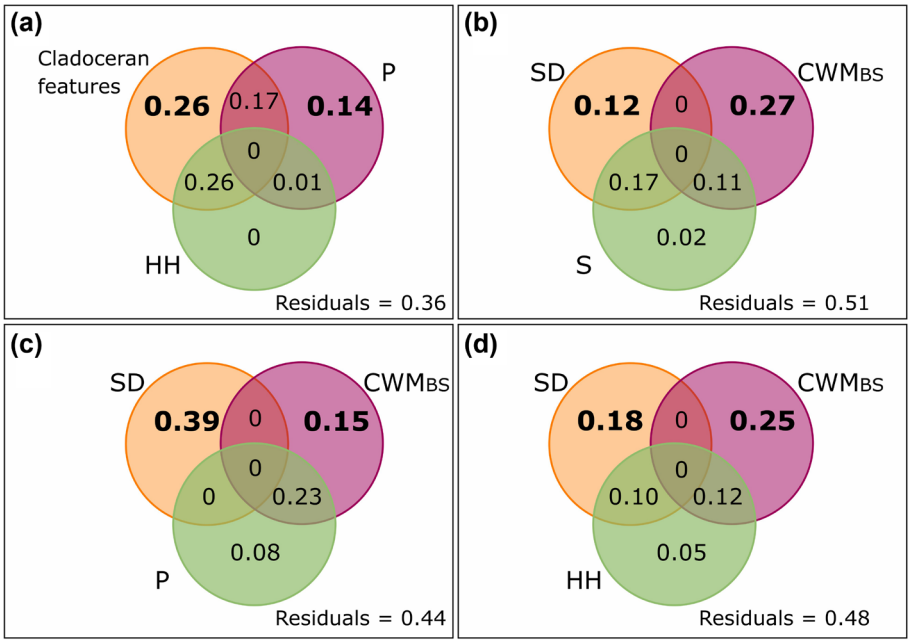

Figure 3. Venn diagram showing the fraction of variation in zooplankton resource use efficiency (RUE_{ZP}; ln-transformed) that can be explained by four different sets of explanatory variables (a–d) – SD: size diversity, CWM_{BS}: average body size, S: species richness, P: phosphorus addition, HH: habitat heterogeneity. Cladoceran features combines all three cladoceran community variables (SD, CWM_{BS} and S). 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 ≥ 1% are shown, which may cause discrepancy in variation explained by each component between distinct variation partitioning analysis. Statistically significant contributions are depicted in bold. Note that it is not possible to calculate p-values for intersections. l (a–d) are results from distinct variation partitioning analysis.

interaction between P-addition and habitat heterogeneity on SD. The weaker and somewhat divergent response of SD to nutrients and heterogeneity compared to richness indicates that competitive exclusion is likely not entirely mediated by size differences, and other traits associated with resource acquisition are likely involved in such dynamics (Ger et al. 2016, 2019). An important avenue for future research is to better understand how other traits and different aspects of functional diversity respond to nutrients and habitat heterogeneity.

Linking community assembly to ecosystem functioning mechanisms

In our study, P-addition and habitat heterogeneity treatments had significant effects on resource use efficiency of zooplankton (RUE_{ZP}). However, variation partitioning analyses revealed that these effects could to a large extent also be explained by cladoceran community features via their shared effects with P-addition and heterogeneity. For instance, we observed that CWM_{BS} was a stronger predictor of RUE_{ZP} compared to diversity in body size and species richness. In agreement with this observation, previous studies have reported that large zooplankton species tend to be more efficient grazers than smaller ones, so that communities composed by larger species can more effectively control algal blooms (Gianuca et al. 2016, Pinheiro-Silva et al. 2020). Despite of that, our study also clearly shows that zooplankton SD was also a significant predictor of variation in RUE_{ZP} and that an important fraction of explanation provided by SD could also be attained by species richness. These results indicate that zooplankton top–down control of algae is related to both a positive selection effect mediated by differences in CWM_{BS} (Loreau 2000) and also complementarity between coexisting species that vary in size (Loreau et al. 1998). Our results contrast with those obtained by Gianuca et al. (2016), who artificially assembled zooplankton communities and demonstrated that differences in grazing efficiency between small and large zooplankton species were more important than size-based niche differences in mediating trophic interactions. A plausible explanation to these divergent results could be the more natural settings of community assembly in our mesocosm experiments and the influence of habitat heterogeneity in driving such patterns. Indeed, whereas P-addition and CWM_{BS} jointly explained variation in RUE_{ZP} in our study, habitat heterogeneity explained variation in RUE_{ZP} through its shared effect with both SD and CWM_{BS}. Therefore, it seems that habitat heterogeneity enhances coexistence and complementarity in resource use in a way that influences RUE_{ZP}.

It is important to acknowledge that within our experimental framework, we focused on a single type of artificial microhabitat structure as a representation of habitat heterogeneity. However, macrophytes exhibit many different shapes and structures, resulting in a variety of microhabitats. Such diverse

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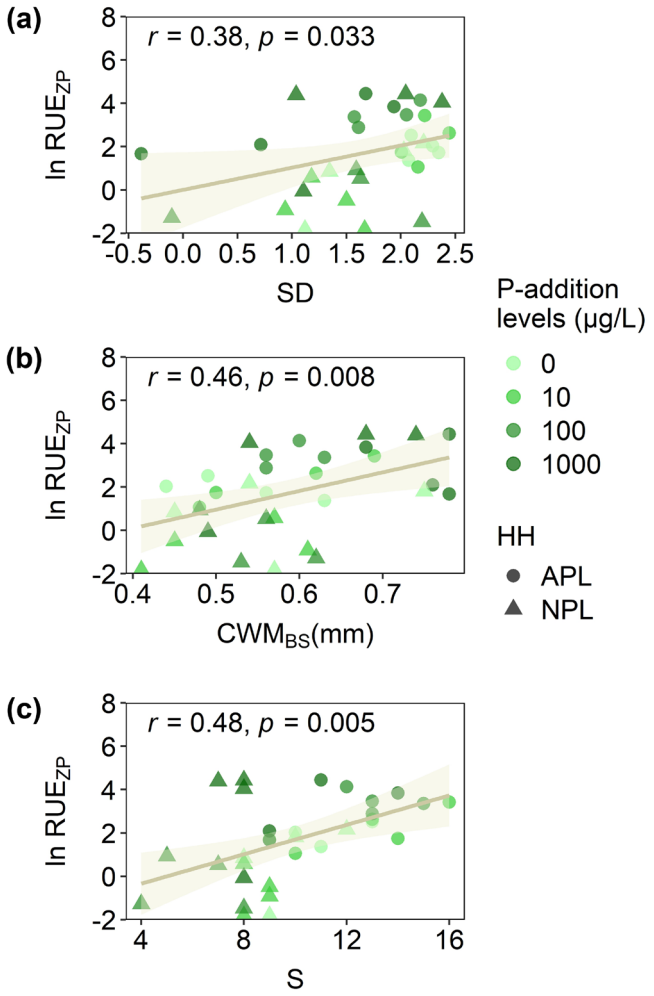

Figure 4. Linear relationship between zooplankton resource use efficiency (RUE_{ZP}; ln-transformed) and (a) size diversity (SD), (b) average body size (CWM_{BS}), and (c) species richness in phosphorus addition (P-addition; 0, 10, 100, and 1000 µg l^{-1}) and habitat heterogeneity (HH; with artificial plants and without plants; APL and NPL, respectively) treatments. The confidence interval of 95% is provided, as well as Spearman correlation coefficients (*r*) and p-values (p).

array of microhabitats can be an important determinant of the diversity (Meutter et al. 2008) and body size distribution (McAbendroth et al. 2005) of associated communities. One potential avenue for refining our experiment could involve investigating the combined effect of different vegetation types (e.g. emergent, free-floating, floating-leaved and submerged), levels of productivity and their potential interactions on zooplankton resource use efficiency. Furthermore, it is possible that by measuring RUE_{ZP} while considering not only pelagic but both pelagic and epiphytic algae could have led to an even higher contribution of complementarity relative to size-based selection effect.

Although we have demonstrated here the influence of nutrient addition and habitat heterogeneity on cladoceran community features that influence RUE_{ZP}, it is noteworthy that a large fraction of variation in RUE_{ZP} associated with community structure was unrelated to the experimental treatments. This suggests that other processes, such as drift in community assembly, may have influenced variation in community structure independently from nutrients and habitat structure. For instance, the lack of dispersal among mesocosms during the experiment suggests that local stochastic extinctions were not compensated by immigration, potentially resulting in a mismatch between species distributions and their suitable ecological requirements (Gianuca et al. 2017b). Whereas our analysis provides important new information on the influence of size-based complementarity and selection effects on RUE_{ZP} along a gradient of nutrients in homogeneous and heterogeneous environments, we acknowledge some limitations of the experimental dataset used here, which should ideally be improved in future studies. First, we lacked intraspecific body size information and thus relied on body size data from previous studies conducted in the same region. Ideally, we should have used data for each species in each mesocosm if this information was available, potentially increasing the amount of explained variance in RUE_{ZP}. However, the same approach used here has been used in many zooplankton community ecology studies (Brun et al. 2016, Gianuca et al. 2016, 2017a, Rizo et al. 2017, 2019, Diniz et al. 2021, Ribeiro et al. 2022) and we are confident that our results are representative of the mechanisms driving RUE_{ZP}, especially because it has been demonstrated that inter-specific size differences respond much stronger to environmental gradients compared to intra-specific differences (Brans et al. 2017). Secondly, the revisited experimental data did not include copepods. However, cladocerans are generally considered more efficient grazers on small phytoplankton, whereas copepods are more selective consumers that can actively search for large phytoplankton (Sommer and Sommer 2006, Ger et al. 2019). It would be an interesting next step to evaluate whether size-based complementarity in RUE_{ZP} increases in relative importance compared with selection effects mediated by CWM_{BS} by simultaneously considering copepods and cladoceran zooplankton.

To summarize, we have demonstrated that productivity had a strong and positive effect on average body size of cladoceran communities, whereas habitat heterogeneity interactively modified the responses of species richness and size diversity to P-addition. We showed that both average body size and size diversity were important components in explaining variation in resource use efficiency of zooplankton. This illustrates the potential for body size to predict top-down control of algae through different mechanisms, namely selection effects and complementarity. Although we have focused here on nutrients and habitat heterogeneity as drivers of cladoceran size structure, we argue that our results are likely representative of any other determinants of the size structure, such as temperature (Bomfim et al. 2023), fish predation (das Candeias et al. 2022, Bomfim et al. 2023) and gradients of urbanization (Brans et al. 2017), which have also been shown to strongly determine zooplankton community size, with potentially strong consequences for ecosystem functioning.

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Author contributions

Lorena Pinheiro-Silva and **Andros T. Gianuca** share first authorship. **Lorena Pinheiro-Silva**: Conceptualization (lead); Formal analysis (lead); Investigation (equal); Writing – original draft (lead); Writing – review and editing (equal). **Andros T. Gianuca**: Conceptualization (lead); Formal analysis (supporting); Investigation (equal); Writing – original draft (lead); Writing – review and editing (equal). **Luc De Meester**: Conceptualization (supporting); Formal analysis (supporting); Writing – review and editing (equal). **Steven A. J. Declerck**: Conceptualization (supporting); Data curation (lead); Formal analysis (supporting); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.nzs7h4502 (Pinheiro-Silva et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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