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ARTICLE

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A size-based perspective on the decoupling between compositional and functional changes in planktonic communities

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Abstract

Recent studies have shown a decoupling in the way community composition and functions respond to environmental changes. A common pattern observed is that aggregated functions at the community level are more stable than community composition, which is likely the result of functional compensatory dynamics driven by interspecific differences in response to environmental change. However, the mechanisms by which these patterns emerge remain largely unexplored. Here we investigated in a mesocosm experiment for four weeks the compositional and functional responses of edible phytoplankton ($<64\ \mu m$) and cladoceran zooplankton communities to climate warming (a constant increase of $+3.5^\circ C$ plus heat wave) and eutrophication (nutrient additions) from a size-based perspective. Our results show that warming increases small-sized taxa and decreases large-sized taxa within both phytoplankton and zooplankton community composition. We found that such opposite responses of different-sized taxa contributed to the stability of planktonic community functions and thereby resulted in a decoupling between compositional and functional changes. We also found that nutrient additions increased the abundance of all-sized algal taxa, while phytoplankton community function remained stable. Nutrient additions did not alter the zooplankton community, neither compositionally nor functionally. Under the combined stress of warming and nutrient additions, the compositional and functional responses of planktonic communities were mainly driven by warming. In a broader perspective, our findings reveal a size-dependent compensation mechanism and suggest that functional stability relies on compensatory effects among different-sized taxa, and it is therefore important that communities host a large range of taxa differing in size to withstand an increasingly more variable environment in the future.

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KEYWORDS
body size, climate warming, community composition, compensatory effect, ecosystem functions, eutrophication, mesocosm experiment

INTRODUCTION

Human-induced environmental changes, such as climate warming and eutrophication, are some of the most important drivers of change in aquatic communities (Hughes, 2000; Scheffer et al., 2001; Smith, 2003). How these environmental changes will affect species composition or community functions is widely studied (Hughes, 2000; Walther, 2010; Walther et al., 2002), but studies on how these two types of responses link to each other and under which circumstances remain largely unexplored (but see Baert et al., 2016; Guelzow et al., 2017). A recent meta-analysis revealed an overarching positive correlation between compositional and functional stability across multiple ecosystem realms (i.e., communities with a stable composition were also more functionally stable as a whole) (Hillebrand & Kunze, 2020). However, it was also observed that compositional and functional changes can often be decoupled, with changes in community composition occurring in conjunction with stable community functions (Hillebrand & Kunze, 2020). Similar patterns have also been observed in a wide range of studies, in both terrestrial and aquatic realms (Hillebrand et al., 2018; Kreyling et al., 2017). These findings indicate that the linkages between composition and function vary among communities and highlight the need for further studies to disentangle what drives decoupled responses of composition and function to environmental changes.

Previous studies indicate that interspecific differential responses change community composition but allow maintaining an unchanged community function under fluctuating environmental conditions, thereby resulting in a decoupling between compositional and functional changes (Bai et al., 2004; Grman et al., 2010; Kreyling et al., 2017; Yachi & Loreau, 1999). However, existing studies rarely explain how the interspecific differential responses act, often solely attributing the effect to species richness (i.e., communities with more species are more likely to host compensatory dynamics that lead to more stable aggregated functions at the community level) (Kreyling et al., 2017; Pan et al., 2016). These studies attribute interspecific differential responses as a probabilistic event, whereas functional trait-based approaches allow for mechanistic predictions since species respond directionally to specific environmental drivers based on response traits (Green et al., 2022; Lavorel & Garnier, 2002; Martini et al., 2021). Thus, measuring community composition based on functional traits can further our understanding of which species will be favored or unfavored by environmental change, and how these differential responses in composition will subsequently impact community functions.

Body size is one of the most important functional traits because it accounts for a large variation in metabolism rates, energy use, production, and mortality (Brown et al., 2004; Dickie et al., 1987). Specifically for phytoplankton, cell size is associated with traits such as nutrient uptake, metabolic rates, and resistance to grazers (Chisholm, 1992; Finkel et al., 2009; Litchman & Klausmeier, 2008). For zooplankton, body size affects metabolism, food size range, and life history traits (Hébert et al., 2016; Litchman et al., 2013). Thus, plankton size can serve as a proxy for many other traits (Barton et al., 2013; Litchman et al., 2013), which is why it is also often used as an overarching indicator for how biological communities respond to multiple environmental changes (Hillebrand et al., 2022; Moore & Folt, 1993).

As global mean temperature has been rising over the last decades and is expected to increase between 2.4 and 4.8°C by the end of this century under the high-emissions scenario (IPCC, 2021), climate warming may continue to affect community composition and functions across multiple ecosystem realms (Hughes, 2000; Walther, 2010; Walther et al., 2002). For aquatic ecosystems, it has been reported that warming favors small-sized phytoplankton and zooplankton taxa rather than large-sized ones (Winder et al., 2009; Yvon-Durocher et al., 2011). Thus, the shifts involved in community composition may result from higher abundances of small-sized species in a climate change scenario (Ohlberger, 2013).

In parallel with future projected climate warming scenarios, other environmental drivers such as eutrophication will act in conjunction upon many aquatic ecosystems (Moss et al., 2003; Su et al., 2021). Since major parameters of nutrient uptake scale with algal cell size, small-celled algae tend to have higher nutrient uptake efficiency, whereas the large-celled may have larger internal nutrient storage capacity (Aksnes & Egge, 1991; Litchman & Klausmeier, 2008; Marañón, 2015). In addition to the direct effects of nutrients, the community composition of phytoplankton and zooplankton can interact with each other through trophic interactions (Sommer et al., 2012). Overall, eutrophication may promote the growth of larger celled algae with greater resistance to grazers (Litchman et al., 2007), which subsequently support the growth of larger sized zooplankton with wider food size ranges (Brooks & Dodson, 1965). Therefore, the composition of planktonic communities is likely to be dominated by larger species in eutrophic waters without high trophic-level predators such as fish and shrimp (Vanni, 1987).

Although warming and eutrophication may alter community composition through body size as a response trait, the resulting functional effects remain unclear, as species in the same functional group can still perform the same functions (e.g., primary production and secondary production) despite differences in size. Therefore, there is a knowledge gap in linking compositional and functional changes from a size-based perspective. To address this, we first presented the hypotheses on compositional changes that (H1) warming would lead to an increase in small-sized taxa and a decrease in large-sized ones; (H2) eutrophication would increase large-sized taxa and decrease small-sized ones. Secondly, based on H1 and H2, we hypothesized innovatively that (H3) such size-dependent compositional changes would cause functional compensatory effects, thereby resulting in a decoupling between compositional and functional changes (Figure 1). To test these hypotheses, we conducted a mesocosm experiment including warming and nutrient additions, where we focused on the responses of size composition and primary and secondary production (as proxies of community functions) of phytoplankton and zooplankton communities. We first aimed to examine compositional and functional changes in planktonic communities in response to warming and eutrophication. In addition, we aimed to provide a size-based perspective on the linkage of compositional and functional changes and seek mechanistic explanations.

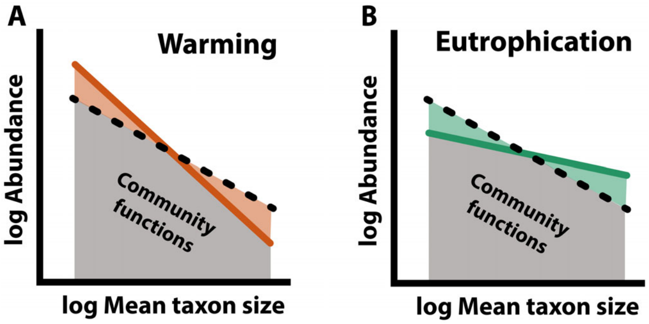

FIGURE 1 The hypothesis illustrating how the relationship between mean taxon size and abundance affects community functions under warming and eutrophication scenarios (community functions are calculated as the sum of all individual taxa performances). (A) Climate warming is expected to increase the abundance of small taxa and decrease the abundance of large ones, as indicated by a steeper slope compared with baseline conditions (dash line). (B) Eutrophication would increase large taxa and decrease small ones, as indicated by a flatter slope compared with baseline conditions (dash line). The different responses emerging across taxa will create a compensatory effect on community functions, as indicated by the total shaded area.

MATERIALS AND METHODS

Experimental setup

The mesocosm system consisted of 24 insulated cylindrical polyethylene containers with a total volume of approximately 2500 L (inner diameter = 1.5 m, depth = 1.45 m) located at Huazhong Agricultural University, Wuhan, China (30°29′ N, 113°12′ E). Before running the system, each of the containers was filled with a 100-mm thick layer of lake sediment at half of the bottom and with tap water to a depth of 1 m. Sediments (containing natural amounts of organism resting stages) were collected from Lake Liangzi (30°11′03″ N, 114°37′59″ E) and were homogenized and sieved through a 5 × 5 mm metal mesh to remove large blocks. Before the start of the experiment, all the mesocosms were left to acclimatize at ambient conditions for several weeks. In addition to phytoplankton, zooplankton, oligochaetes, and aquatic insects introduced through the sediment additions from Lake Liangzi, as well as through the addition of 10 L of lake water from the nearby Lake Nanhu (30°28′57″ N, 114°22′34″ E), we also introduced other biological components such as submerged macrophytes (*Potamogeton crispus* and *Hydrilla verticillata*), snails (*Bellamya aeruginosa* and *Radix swinhoei*), shrimp (five individuals of *Macrobrachium nipponense*), and fish (four individuals of *Rhodeus sinensis* and four individuals of *Carassius auratus*) to simulate a natural shallow lake ecosystem. In addition, aquatic insects with incomplete metamorphosis are introduced through the spawning of terrestrial adults. Although the taxa in the mesocosm community are diverse, here, in this study, we focus on phytoplankton and zooplankton, as well as their trophic interactions. Evaporation losses from mesocosms were replenished with distilled water additions, when not supplemented by natural rainfall.

We used a (two factors × two levels) fully factorial design and randomly divided the 24 mesocosms into four treatments with six replicates each. The control treatment (C) with ambient temperatures and no nutrient addition was used to mimic the current situation in most of the lakes in the middle and lower reaches of the Yangtze River in terms of temperature and nutrient concentrations. The warming treatment (W) experienced a constant increase of +3.5°C above ambient conditions plus simulated heat wave events. The nutrient addition treatment (E) experienced ambient temperatures with nutrient additions, and the fourth treatment (WE) consisted of a combination of the same warming and nutrient addition manipulations described above. The degrees of warming and the frequency and magnitude of the heat wave are based on model projections from historical meteorological data in the middle and lower reaches of the Yangtze River, which were predicted to occur in this area by the end of this century (IPCC, 2014). Nitrogen (N) and phosphorus (P) were added to the nutrient addition treatments (E and WE) at a mass ratio of 10:1 following González Sagrario et al. (2005), by dissolving $NaNO_3$ and KH_2PO_4 powder in demineralized water, respectively. Nutrient addition treatments were applied biweekly with the doses changing according to the agricultural activities and precipitation intensities in this area (Xu et al., 2020). The mesocosm system had been running since April 2021, but we were mainly interested in how the planktonic community responds to warming and nutrient additions during the peaks of the temperature and nutrient loading (between July 27 and August 23). Therefore, this study only discussed ecological processes during this period.

Each mesocosm contained zooplanktivorous shrimp and fish (five individuals of *M. nipponense*, four individuals of *R. sinensis*, and four individuals of *C. auratus*), which resulted in negligible zooplankton biomass levels in the water column. Hence, zooplankton captive devices were set up during this experiment period to prevent zooplankton from predation and thereby allow keeping track of the dynamics of zooplankton populations in the absence of top-down control. The captive device consisted of a 2-L Plexiglas cylinder (inner diameter = 10 cm, height = 25 cm) with 64-μm nylon mesh windows to allow circulation and exchange of phytoplankton but block the migration of zooplankton. The device was deployed 20 cm below the water surface for 4 weeks under natural day/night cycles. Populations of two cladoceran zooplankton taxa (*Daphnia sinensis* and *Moina* sp.) differing in size and commonly found in the middle and lower reaches of the Yangtze River were introduced in the devices. Both zooplankton taxa originated from lab cultures established from a single female collected from nearby lakes. At the beginning of the experiment, 20 individuals (10 adults without eggs and 10 juveniles of each of the two taxa) were randomly selected using a stereomicroscope and placed into each zooplankton captive device deployed in each mesocosm. The average size of *D. sinensis* was 1227 ± 170 μm for adults without eggs and 603 ± 121 μm for juveniles. The average size of *Moina* sp. was 790 ± 88 μm for adults without eggs and 392 ± 85 μm for juveniles. The body size was represented by body length and measured as the distance from the top of the head (above eye) to the start of the apical spine (if present) (Frances et al., 2021).

Sample collection and analyses

Environmental factors

Every two weeks water column samples were taken from the surface up to 0.2 m above the bottom of each enclosure using a Plexiglas tube (length = 1 m, diameter = 50 mm). For each sampling, a total of six water column samples collected across the diameter of each mesocosm were pooled and completely mixed in a bucket, thereby resulting in an integrated water column sample. Subsamples from the integrated samples were then collected for nutrient analyses. The concentrations of total nitrogen (TN), total phosphorus (TP), nitrate (NO_3^--N), and orthophosphate (PO_4^{3-}-P) were measured using a spectrophotometer (UV-2800, Unico, China). Turbidity was measured once on August 11 using a portable turbidity meter (WGZ-2B, Xinrui, Shanghai, China).

Phytoplankton enumeration and production

Samples for phytoplankton composition analyses were collected once in the middle of the experiment (August 9) when it is most representative of the experimental period. Since this study was mainly focused on edible small- and medium-sized algae (<64 μm) for zooplankton (i.e., the algae available to zooplankton grazing in the captive device) rather than inedible large-sized algae (>64 μm), the phytoplankton samples were filtered through a 64-μm nylon mesh when collected around the zooplankton captive devices (Ross & Munawar, 1981). Due to the same filtering process with a 64-μm nylon mesh, the phytoplankton samples can be considered the same as if they were exposed to zooplankton. The samples were preserved with Lugol's solution immediately after sampling. Subsequently, algae were identified to genus level and counted using a microscope at 400× magnification. Following Ross and Munawar (1981), the taxa enumeration was graded into three size classes according to cell lengths (maximum linear dimension), <5 μm, 5–20 μm, and 20–64 μm, such that algae belonging to the same genus but different size classes were recorded separately. The mean biovolume (in cubic micrometers) of each taxon was estimated using its approximate geometry volume formula (Hillebrand et al., 1999) based on our grading data combined with literature data (Zhao, 2005) and then converted to the average mass (in micrograms), referring to Zhao (2005).

The gross primary production (GPP) of the phytoplankton community was measured six times during the experiment using the classic dark and light bottle method (Talling, 1957). Both dark and light bottles (250 mL in volume) were filled with mesocosm water filtered through a 64-μm mesh. Both bottles were suspended in the mesocosms beside the zooplankton captive devices for 24 h and retrieved for dissolved oxygen (DO) measurements with portable oxygen meters (HQ40d, HACH). GPP was calculated as the DO difference between the light and dark bottles. Then, the oxygen mass was converted to carbon mass according to the carbon-to-oxygen ratio of the photosynthetic and respiratory reaction equations (Talling, 1957).

Zooplankton enumeration and production

The zooplankton community in the captive device was sampled weekly. The device was lifted to filter out three quarters (1500 mL) of the water first. After gently mixing, 10% (50 mL) of the leftover water (including all zooplankton) was carefully pipetted from the devices and preserved with Lugol's solution as a zooplankton sample. *D. sinensis* and *Moina* sp. were counted in the samples using a microscope at 40× magnification. In order to estimate the production of the cladocerans, adults and juveniles were distinguished according to the presence or absence of abdominal processes, and the eggs of adults were also counted (Stibor & Lampert, 1993).

We estimated the production of cladoceran using the method described by Mason and Abdul-Hussein (1991) (see Appendix S1 for details). To eliminate heterogeneity in taxa biomass because the zooplankton community was artificially set up, we used biomass-specific production rather than production. The biomass-specific production was calculated as the quotient of population carbon production and initial carbon biomass. Zooplankton productivity at the community level was calculated as the sum of biomass-specific production of two taxa.

Statistical analysis

We used linear mixed-effects models (LMMs) to evaluate the effects of warming, nutrient additions, and their interaction on TN, TP, NO_3^--N, and PO_4^{3-}-P concentrations by considering time and enclosures as random factors. We used the "lmer" function from the R software package "lme4" (Bates et al., 2015). The GPP and zooplankton abundance were analyzed in the same way but with time as a fixed factor to also include the effects of time in the analyses. The sequential decomposition of the contributions of fixed effects was calculated using the "Anova" function with Wald F tests from the R software package "car" (Fox & Weisberg, 2018).

The local size–density relationship (LSDR) is the relationship between the mean body size of a taxon and its local population abundance. The slope of this relationship can be used as an indicator of the size composition of communities (White et al., 2007), and the steeper the slope, the greater the dominance of small-sized species compared with large-sized species. To investigate the effects of warming and nutrient additions on the phytoplankton size composition, we conducted the statistical analysis for LSDR referring to Yvon-Durocher et al. (2011). We first constructed LSDR of the phytoplankton community for each mesocosm using regression analyses between the mean individual mass and abundance of each taxon after log transformation. Secondly, ANOVAs were used to test the effects of warming and nutrient additions on the slopes and intercepts after excluding insignificant linear regressions from the previous LSDR analyses. The effects of warming and nutrient additions on the biomass-specific production of *D. sinensis* and *Moina* sp. and their sums (i.e., zooplankton productivity), as well as on turbidity, were also analyzed using ANOVAs. All data analyses were performed in R-4.1.3 (R Core Team, 2022).

RESULTS

Environmental factors

The water temperature was, on average, 30.6 ± 2.1°C in the ambient temperature treatments (C and E) and 34.0 ± 2.7°C in the warming treatments (W and WE) during the experiment (from July 26 to August 23, 2021) (Figure 2A). Following our design, the heated mesocosms (W and WE) experienced a strong heat wave during the experiment, which coincided with a natural heat wave for all mesocosms. Thus, the mean water temperature during the peak of the heat wave (from August 3 to August 7) was 38.3 ± 0.7°C for the heated mesocosms (W and WE) and 32.8 ± 0.6°C for the ambient temperature mesocosms (C and E).

The concentrations of TN ($p < 0.001$), NO_3^--N ($p = 0.013$), and PO_4^{3-}-P ($p = 0.042$) were significantly higher in the nutrient addition treatments (E and WE) than in the ambient nutrition treatments (C and W) (Appendix S2: Table S1 and Figure S1). However, no significant difference was detected in TP ($p = 0.102$) between the nutrient addition treatments and the ambient nutrient treatment (Appendix S2: Table S1 and Figure S1). Nutrient additions had a marginally significant positive effect on turbidity ($p = 0.085$; Appendix S2: Table S2 and Figure S2). Experimental warming significantly increased the concentration of TN ($p = 0.029$; Appendix S2: Table S1), implying that the effects of warming treatment extended beyond elevated temperature alone, encompassing indirect effects mediated by

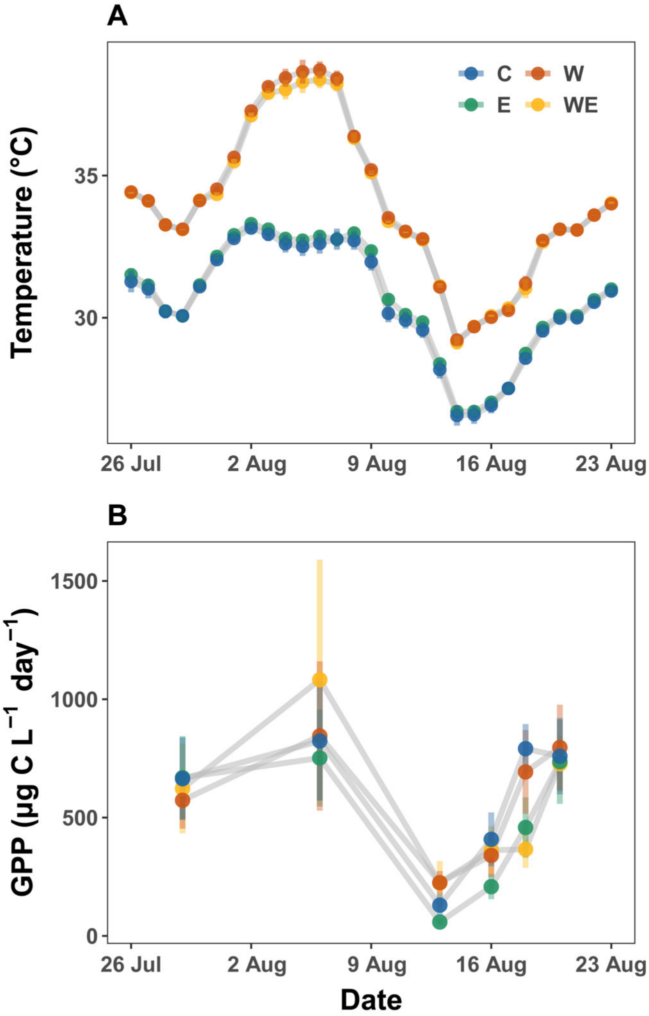

FIGURE 2 (A) Time series of water temperature during the experiment for each experimental treatment. (B) Time series of the gross primary production (GPP) of phytoplankton (<64 μm) community measured during the experiment. Error bars indicate ±1 SE. C, control treatment; E, nutrient additions; W, warming; WE, the combined warming and nutrient addition treatment.

warming, such as nutrient cycling. No significant interaction effect between warming and nutrient additions on the concentrations of TN, TP, $NO_3{}^{-}$-N, and $PO_4{}^{3-}$-P was observed (F test, $p > 0.1$; Appendix S2: Table S1).

Phytoplankton community responses

Regression analyses showed that the LSDRs for the phytoplankton (<64 μm) communities were significant in 21 out of the 24 mesocosms (Appendix S2: Table S3). Hence, the three insignificant mesocosms were excluded from the ANOVA tests performed to investigate the influence of the experimental treatments on the slopes and intercepts derived from the LSDRs (Figure 3). Warming induced steeper LSDR slopes, while the effect of nutrient additions was not statistically significant (Table 1; Figure 3). Warming significantly decreased the intercept of LSDRs, whereas nutrient additions increased the intercept (Table 1; Figure 3). No interaction effect between warming and nutrient additions on the LSDR slopes or intercepts was detected (Table 1). Thus, warming altered the phytoplankton (<64 μm) community composition by increasing the abundance of small-celled algal taxa and decreasing the abundance of large-celled algal taxa, whereas nutrient additions altered the phytoplankton (<64 μm) community by increasing the abundance of all different-sized algal taxa. Neither warming nor nutrient additions had a significant effect on the phytoplankton (<64 μm) community GPP (Table 2; Figure 2B), indicating that none of the experimental treatments altered the function of phytoplankton (<64 μm) community compared with the control treatment. Thus, both warming and nutrient additions induced a decoupling between compositional and functional responses in the phytoplankton community, but through different patterns of compositional changes.

Zooplankton community responses

Moina sp. and *D. sinensis* showed different population dynamics during the experiment (Figure 4). Warming induced opposite effects on these two cladoceran zooplankton taxa. Warming showed a marginally significant positive effect on the abundance of *Moina* sp., whereas it showed a strong negative effect on the abundance of *D. sinensis* (Table 2; Figure 4). We observed no significant effect of nutrient additions on any of the two zooplankton populations (Table 2; Figure 4). Similarly, warming marginally promoted the biomass-specific production of *Moina* sp., but significantly suppressed that of *D. sinensis* (Table 1; Figure 5). However, the zooplankton productivity (i.e., the sum of biomass-specific production of two taxa) was not significantly affected by either warming or nutrient additions (Table 1; Figure 5). Thus, warming induced a decoupling between compositional and functional responses in the cladoceran zooplankton community. In contrast, nutrient additions did not alter the cladoceran zooplankton community, neither compositionally nor functionally.

DISCUSSION

Recently, there is an increasing interest among ecologists and ecosystem managers to further our understanding of the relationship emerging between community compositional

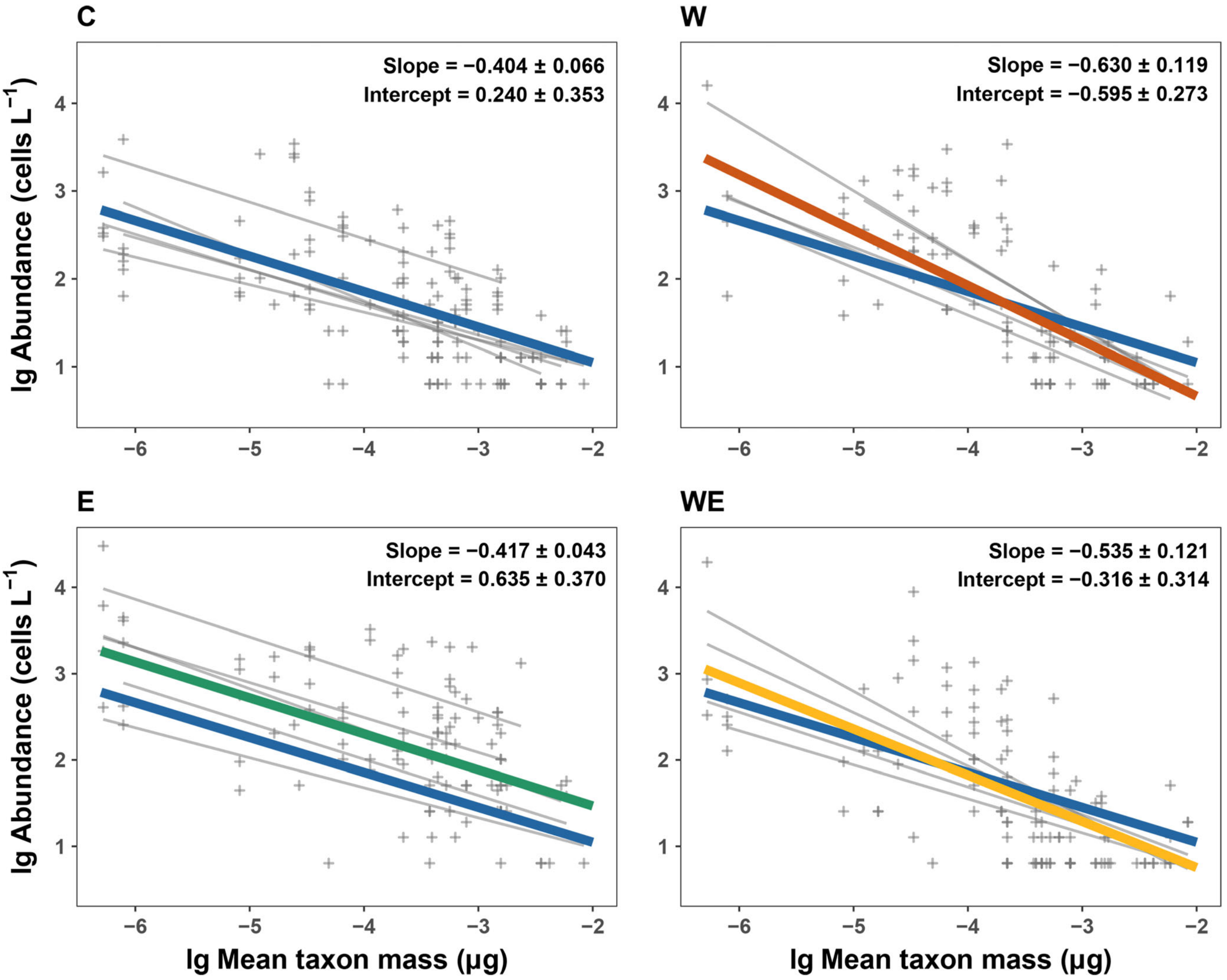

FIGURE 3 The local size–density relationship (LSDR) for the phytoplankton (<64 μm) community of each mesocosm: $\log_{10}(N_i) = b \times \log_{10}(M_i) + a$, where N_i is the abundance of the taxon i and M_i is the mean mass of the taxon i, and b and a are the slope and the intercept, respectively. The gray lines are the LSDRs for each mesocosm, while the colored lines are drawn from the mean slope and mean intercept calculated from all single relationships for each mesocosm. The slope and intercept for each treatment are shown as mean ± SD. C or blue stands for the control treatment, W or red refers to warming, E or green refers to nutrient additions, and WE or yellow refers to the combined warming and nutrient addition treatment.

and functional responses to environmental changes. Although a positive correlation between compositional and functional stability has been reported, it is also often the case that compositional and functional changes decoupled in response to environmental changes (Hillebrand & Kunze, 2020), a pattern that can also differ between biological communities across multiple trophic levels (Urrutia-Cordero et al., 2022). This decoupling is often thought to be the result of interspecific differences in response to environmental changes that contribute to functional stability, but previous studies rarely explain the mechanisms by which those differences act to stabilize aggregated functions at the community level. To address this gap, we examined the community composition and functions (primary production and secondary production) of phytoplankton (<64 μm) and cladoceran zooplankton communities from a size-based perspective in response to climate warming and eutrophication. First, our findings demonstrated that warming altered the phytoplankton and zooplankton community composition by increasing small-sized taxa and decreasing large-sized taxa, and that such opposite responses of different-sized taxa contributed to the stability of planktonic community functions. Second, our results showed that nutrient additions altered the phytoplankton community composition by increasing the abundance of all different-sized algal taxa, but these additions did not change the community function. Thus, warming and eutrophication induced a decoupling between

TABLE 1 Results from two-way ANOVA evaluating effects of warming (W) and nutrient additions (E), and their interaction on the phytoplankton (<64 μm) composition and cladoceran zooplankton function.

Response	Explanatory	SS	df	*F*	*p*
Phytoplankton (<64 μm) composition					
LSDR slope	W	0.159	1	15.031	**0.001**
	E	0.008	1	0.742	0.401
	W × E	0.015	1	1.458	0.244
	Residuals	0.179	17		
LSDR intercept	W	4.147	1	30.644	**<0.001**
	E	0.604	1	4.463	**0.050**
	W × E	0.018	1	0.131	0.722
	Residuals	2.301	17		
Cladoceran zooplankton function					
Moina sp. biomass-specific production	W	59,608	1	3.041	(**0.097**)
	E	7364	1	0.376	0.547
	W × E	5941	1	0.303	0.589
	Residuals	392,061	20		
Daphnia sinensis biomass-specific production	W	72,868	1	13.108	**0.002**
	E	2204	1	0.397	0.536
	W × E	443	1	0.080	0.781
	Residuals	111,181	20		
Zooplankton productivity	W	665	1	0.025	0.877
	E	17,626	1	0.653	0.429
	W × E	3139	1	0.116	0.737
	Residuals	540,057	20		

Note: LSDR means the local size–density relationship. Values in boldface and in parentheses indicate significant effects at α = 0.05 and α = 0.1, respectively.

compositional and functional changes in the planktonic community, but the underlying mechanisms may be different between treatments. Altogether, our results linked shifts in community size composition to functional compensatory effects and demonstrated that size-dependent compensation among taxa is a critical mechanism to maintain community functioning in response to future climate warming.

Responses to warming

An overwhelming body of scientific evidence from experiments, geographic comparisons, and fossil records shows that climate warming benefits the small (Daufresne et al., 2009; Millien et al., 2006; Reuman et al., 2014; Sheridan & Bickford, 2011). Shifts in body size can occur at three different levels (Ohlberger, 2013): (1) change in individual size (size-at-age shift); (2) change in juvenile versus adult proportion (population structure shift); and (3) change in species proportions (community composition shift). Our results support this view in terms of community composition. Warming increased the slope of the LSDRs of the phytoplankton community, indicating an increase in the abundance of small-celled algal taxa and a decrease in large-celled ones. This result is consistent with the shift in size structure of the phytoplankton community in previous studies (Winder et al., 2009; Yvon-Durocher et al., 2011). The zooplankton community showed a similar response with more abundance of the small-sized taxon *Monia* sp. and less abundance of the large-sized taxon *D. sinensis*. This result indicates that small-sized zooplankton taxa are also likely to increase their dominance in a climate warming scenario, a notion that is in accordance with previous experimental data (Rasconi et al., 2015; Yvon-Durocher et al., 2011). However, there is still a lack of fully targeted experimental examination on warming-induced changes in interspecific size structures of zooplankton communities with high species and taxon diversity. Recently, a study reviewed 123 experimental or observational studies on this (Uszko et al., 2022), and a majority of them (91) observed a shift from larger to smaller species, and

TABLE 2 Results from linear mixed-effects model analyses evaluating the effects of warming (W), nutrient additions (E), time (T), and their interactions on phytoplankton (<64 μm) function and cladoceran zooplankton composition.

Response	Explanatory	df	df residual	*F*	*p*
Phytoplankton (<64 μm) function					
Gross primary production	W	1	20	0.112	0.741
	E	1	20	0.431	0.519
	T	5	100	10.302	**<0.001**
	W × E	1	20	0.260	0.616
	W × T	5	100	0.412	0.839
	E × T	5	100	0.739	0.596
	W × E × T	5	100	0.167	0.974
Cladoceran zooplankton composition					
Moina sp. abundance	W	1	20	3.077	**(0.095)**
	E	1	20	0.118	0.735
	T	4	80	3.956	**0.006**
	W × E	1	20	0.012	0.915
	W × T	4	80	0.344	0.847
	E × T	4	80	0.611	0.656
	W × E × T	4	80	1.057	0.383
Daphnia sinensis abundance	W	1	20	11.847	**0.003**
	E	1	20	0.654	0.428
	T	4	80	6.288	**<0.001**
	W × E	1	20	0.057	0.814
	W × T	4	80	4.706	0.002
	E × T	4	80	1.661	0.167
	W × E × T	4	80	2.043	0.096

Note: Values in boldface and in parentheses indicate significant levels at $\alpha = 0.05$ and $\alpha = 0.1$, respectively.

only 14 reported the opposite effect. Besides, that study reproduced the expected warming effect at the community composition level by modeling. Thus, combined with our results and other studies, H1 (warming would increase small-sized taxa and decrease large-sized ones) is well supported for both phytoplankton and zooplankton communities.

Our results also showed that warming did not affect the phytoplankton community GPP or zooplankton community productivity despite compositional shifts, indicating a decoupling between compositional and functional changes in planktonic communities. Decoupled changes are likely to be caused by differential responses among taxa within communities, where the decrease in sensitive taxa to environmental change can be compensated by increases in other functionally redundant taxa (Gonzalez & Loreau, 2009). This mechanism has been widely accepted and is especially relevant in diverse communities where there is more room for compensatory dynamics that help maintain the functional stability of ecosystems (Yachi & Loreau, 1999). However, the differential response of taxa relies heavily on response traits (e.g., body size), which has often been ignored in previous studies. We linked shifts in community size composition to functional compensatory effects and revealed this size-dependent mechanism in planktonic communities, where the decrease in large-sized taxa can be functionally compensated by the increase in small-sized taxa under a warming scenario, thereby contributing to maintaining the integral stability of community functions. Here, our results supported H1 (warming-induced shifts in interspecific size structure) and H3 (size-dependent compensation) and revealed a decoupling between compositional and functional responses of plankton communities to climate warming whereby differences in response susceptibility by taxa with different sizes can compensate for the potential loss of community functions, thereby increasing functional stability.

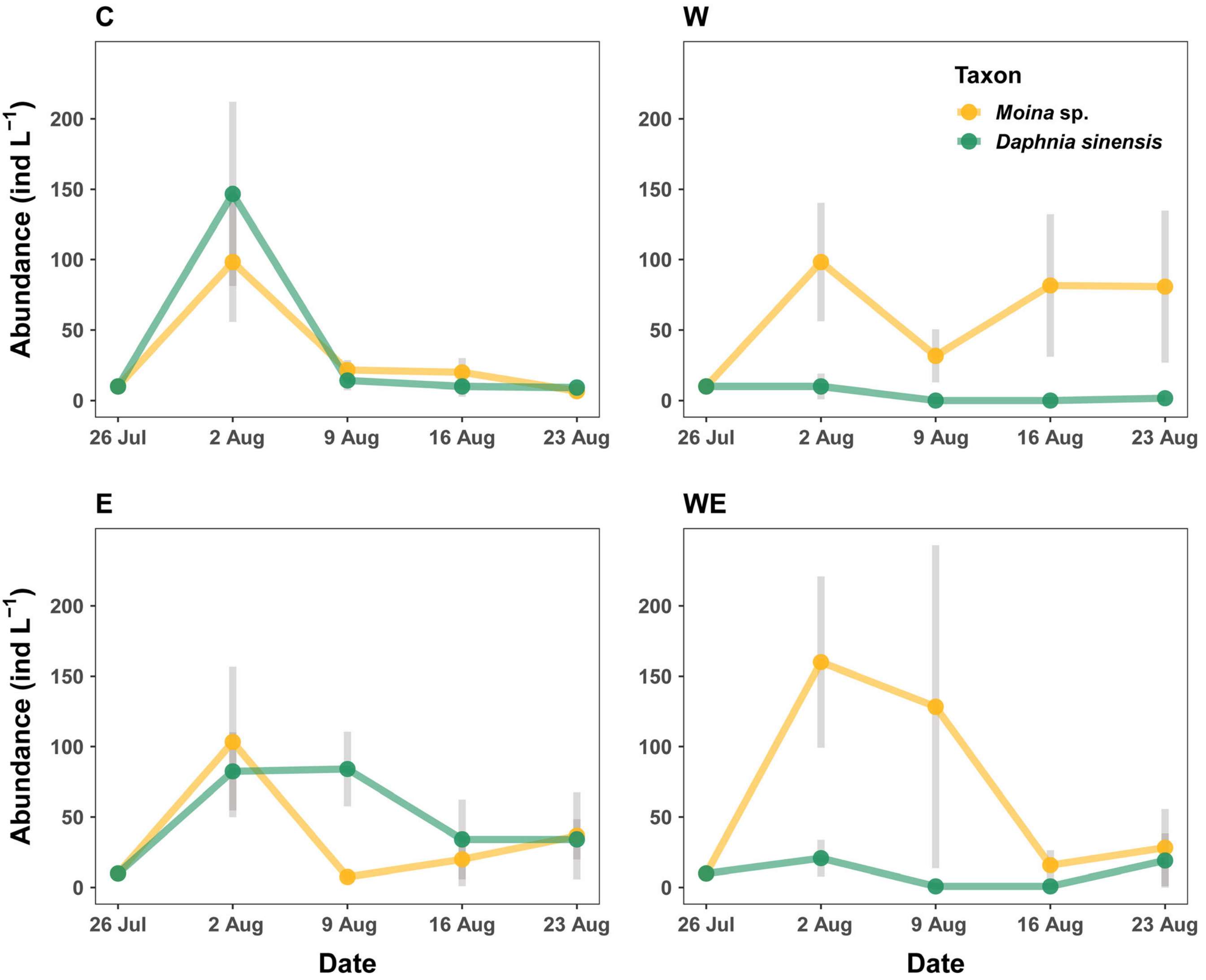

FIGURE 4 Population dynamics of *Moina* sp. (yellow line) and *Daphnia sinensis* (green line) during the experiment. Error bars indicate ±1 SE. C, control treatment; E, nutrient additions; W, warming; WE, the combined warming and nutrient addition treatment.

Responses to nutrient additions

Field observations (Cavender-Bares et al., 2001; Li, 2002), experiments (Schulhof et al., 2019, 2022), and meta-analyses (Marañón et al., 2012) have shown that the small-celled algae tend to dominate phytoplankton communities in nutrient-poor waters due to high nutrient uptake and use efficiency (Litchman et al., 2010). In contrast, aquatic systems generally display a shift toward the dominance of large-celled algae in nutrient-rich waters due to increased resistance to grazers (Litchman et al., 2010) as well as a competitive advantage under a high and fluctuating nutrient supply (Litchman et al., 2007). Consumer–prey interactions between phytoplankton and zooplankton may also affect the size structure of zooplankton communities. According to the size-efficiency hypothesis (Brooks & Dodson, 1965) and size-dependent predation (Barnes et al., 2010; Brose et al., 2006), large-celled algae are generally better able to support large-sized zooplankton compared with small-sized zooplankton. Thus, large-sized zooplankton may dominate in nutrient-rich waters due to the high abundance of large-celled algae.

In our experiment, we did not find that nutrient additions increased the dominance of either large-celled algal taxa or large-sized zooplankton taxa. Specifically for phytoplankton, nutrient additions increased the abundance not only of large-celled algal taxa but also of small-celled ones. For the zooplankton community, there was no sign that the population dynamics of the small-sized *Moina* sp. and the large-sized *D. sinensis* under nutrition additions differed from the control treatment with no nutrient additions. One possible explanation for the absence of response of zooplankton abundance to the nutrient additions might be that the strong heat wave masked the effect of the nutrient additions, which often cause strong changes in population dynamics through increased

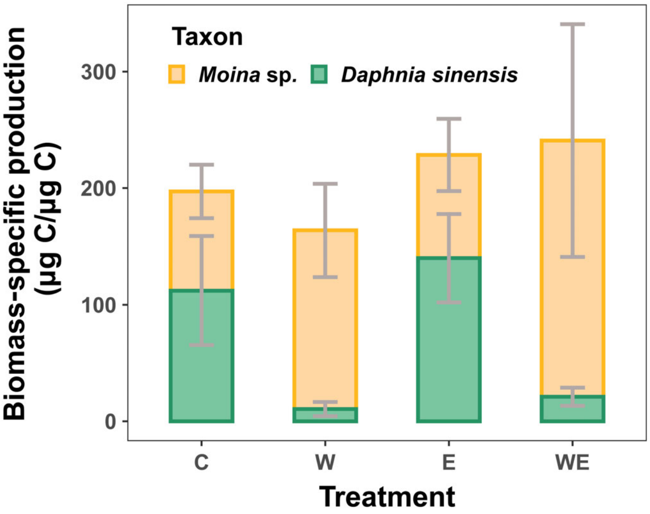

FIGURE 5 The biomass-specific production of *Moina* sp. (yellow bars) and *Daphnia sinensis* (green bars). Zooplankton productivity was calculated as the total sum of each biomass-specific production. Error bars indicate ±1 SE. C, control treatment; E, nutrient additions; W, warming; WE, the combined warming and nutrient addition treatment.

mortality or decreased reproduction (Gaston, 2003; Zhang et al., 2018). The potential disappearance of zooplankton individuals may have removed selective grazing on algae, which could explain why the abundance of both large-celled and small-celled algae increased.

Interestingly, nutrition additions did not significantly increase the phytoplankton community GPP, despite the increase in the abundance of all-sized taxa. These results suggest that the phytoplankton community GPP was not entirely driven by the overall phytoplankton standing stock. It might be that changes in light availability limited GPP since nutrient additions also increased the turbidity levels, thereby reducing light availability for phytoplankton photosynthesis (Dittmar & Kattner, 2003). For zooplankton, nutrition additions did not affect secondary production, neither at the population level nor at the community level. Inconsistent with our original hypothesis (H2: eutrophication would increase large-sized taxa and decrease small-sized ones), nutrient additions increased the abundance of all-sized algal taxa, but the phytoplankton maintained their original function in terms of primary production. Nutrient additions did not alter the zooplankton community, neither compositionally nor functionally.

Responses to the combined effects of warming and nutrient additions

The responses of phytoplankton size structure to temperature and nutrient changes have long been explored (Agawin et al., 2000). However, whether temperature or nutrients explain more of the variability in the size structure of phytoplankton communities remains controversial (López-Urrutia & Morán, 2015; Marañón et al., 2012, 2015). Our results showed that despite suffering from the stress from both warming and nutrient additions, phytoplankton and zooplankton showed strong responses to warming but minor responses to nutrient additions. While previous observations indicated that the response of phytoplankton size structure to climate warming is simultaneously mediated by the effects of high temperature and nutrient limitation in most marine areas (Agawin et al., 2000), our results revealed that the sole effect of high temperature remains strong under nutrient-rich conditions. On the other hand, our results also provided further insights into our understanding of how the body size of plankton trades off under the combined stress of multiple environmental disturbances, given the opposite response patterns induced by warming and eutrophication.

CONCLUSIONS

This study furthers our understanding of (1) the linkage between compositional and functional responses in plankton communities under different climate warming and eutrophication scenarios, as well as (2) a size-dependent compensatory mechanism contributing to stabilizing community functioning. Meanwhile, our conclusions still need to be developed in communities with higher species and size diversity. Furthermore, previous studies have attributed the compensatory effect in composition to species richness, while generally overlooking the role of biological traits. Here we suggest that this is a trait-dependent process, and therefore, trait measures rather than just species richness should be incorporated into tools for studying and predicting compositional and functional responses to environmental changes. Consequently, these results also shed light on the importance of trait variation for maintaining the functional stability of ecosystems to withstand a more variable environment in the future.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Zhu et al., 2023) are available from Dryad: https://doi.org/10.5061/dryad.ffbg79d0s.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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