# Energy transfer efficiency rather than productivity determines trophic cascades

Libin Zhou<sup>1</sup>, Mingyu Luo<sup>1</sup>, Pubin Hong<sup>1</sup>, Shawn Leroux<sup>2</sup>, Feizhou Chen<sup>3</sup>, and Shaopeng Wang<sup>1</sup>

<sup>1</sup>Peking University <sup>2</sup>Memorial University <sup>3</sup>Nanjing Institute of Geography and Limnology Chinese Academy of Sciences

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## Abstract

Trophic cascades are important determinants of food web dynamics and functioning, yet mechanisms explaining variations in trophic cascade strength remain elusive. Here we combine a mesocosm experiment (phytoplankton-zooplankton-shrimp) and theoretical models to disentangle the relative importance of two processes driving trophic cascade: primary productivity (productivity hypothesis) and energy transfer efficiency (energy transfer hypothesis). Our experimental systems showed consistently positive effects of trophic cascade across mesocosms with different nutrient inputs and zooplankton communities. Moreover, the strength of trophic cascade increased with the energy transfer efficiency between herbivores and predators, but did not change with the primary productivity. These findings are further corroborated by our analyses of food chain models in more general settings. Combined, our results support the energy transfer hypothesis but falsify the productivity hypothesis. Our study contributes an integrative perspective to reconcile energetic and population dynamics in food webs, which has useful implications for ecosystem management.

# Introduction

Trophic cascades characterize the top-down effects of predators propagating down trophic levels, which represent one of the most classic paradigms in community ecology and have stimulated tremendous amount of experimental and theoretical studies (Carpenter & Kitchell 1988; Polis*et al.* 2000; Carpenter 2010; Ripple *et al.* 2016). Mounting evidence have demonstrated the prevalence of trophic cascades in nature (Pace *et al.* 1999; Shurin & Seabloom 2005) and their far-reaching impacts on ecosystem functioning and services (Estes *et al.* 2011; Strickland*et al.* 2013; Walsh *et al.* 2016; Stock *et al.* 2017). Despite many previous studies to reveal various biotic and abiotic factors that potentially influence the strength of trophic cascades (Schmitz *et al.* 2004; Borer *et al.* 2005; Bruno & O'Connor 2005; Otto *et al.* 2008), the inconsistent outcomes, for example the idiosyncratic effects of predator diversity (Bruno & O'Connor 2005; Otto *et al.* 2008), suggest a continued uncertainty of its ultimate mechanisms.

One long recognized potential explanation is the productivity hypothesis, which predicts that the strength of trophic cascades increases with primary productivity (Fig. 1a). Primary productivity provides the essential energy and elements for upper trophic levels within a food web. Such bottom-up processes determine not only the trophic position of the apex predator, i.e., food chain length (Post 2002), but also the accumulation of its biomass (Moore & De Ruiter 2012; Barbier & Loreau 2019). By supporting higher biomass of apex predators, a higher primary productivity can potentially trigger a stronger trophic cascade. This hypothesis, historically illustrated as the ecosystem exploitation hypothesis (EEH) (Oksanen et al. 1981), has been supported by positive relationships between primary productivity and trophic cascade strength found across

various studies (Wootton & Power 1993; Su *et al.* 2021). However, evidence that does not support the relationship between primary productivity and the strength of trophic cascades was also reported in other studies (Borer *et al.* 2005). These contrasting findings are striking as they have been found even within the same realm, e.g., freshwaters (Borer *et al.* 2005; Su *et al.* 2021).

An implicit assumption underlying the productivity hypothesis is unimpeded vertical energy fluxes, where energy fixed by primary producers can reach higher trophic levels efficiently. This assumption, nevertheless, rarely holds in nature (Lindeman 1942; DeBruyn et al. 2007). In natural ecosystems, only a small proportion of energy from low trophic levels can be converted into biomass of high trophic levels, due to inefficiencies in food ingestion, assimilation, and biomass production (Barneche & Allen 2018; Eddy et al. 2021). For instance, food webs often involve many less edible plants (Oksanen & Oksanen 2000) or anti-predative herbivores (Degerman et al. 2018), which can significantly hamper vertical energy flow to apex predators (Stiboret al. 2004). Inefficiency in energy transfer can significantly influence the biomass distribution of food webs (de Ruiter et al. 1995; McCauley et al. 2018; Barbier & Loreau 2019) and thereby alter the strength of trophic cascades (Heath et al. 2014; Galiana et al. 2021). In particular, too low energy transfer may decouple biomass production at higher trophic levels from primary production, violating assumptions underlying the productivity hypothesis (Brett & Goldman 1997; Davis et al. 2010). In such cases, the strength of trophic cascade depends mainly on the efficiency of energy transfer (energy transfer hypothesis; Fig. 1b), rather than the amount of energy supply characterized by the primary productivity. While the transfer efficiency hypothesis has been formulated in mathematical models (DeBruyn et al. 2007), it has not been tested explicitly.

In this study, we conduct a field mesocosm experiment, combined with mathematical models, to test the aforementioned two hypotheses underlying trophic cascades (i.e., the productivity hypothesis and energy transfer hypothesis; Figure 1). We constructed mesocosms hosting a three-level food chain and quantified the strength of trophic cascade by simulating loss of top predator. We simultaneously manipulated nutrient supply and zooplankton community composition to generate variation in primary productivity and energy transfer efficiencies, respectively. Because both primary productivity and energy transfer processes are necessary for maintaining higher biomass of apex predators, we expected a weakened relationship between primary productivity (resp. energy transfer efficiency) and trophic cascade strength when energy transfer efficiency (resp. primary productivity) is impeded (Fig. 1). We end our discussion with scientific and practical implications of our results.

# Methods

## Mesocosm experiment

The mesocosm experiment was conducted to simulate three-level food chains (algae-zooplankton-shrimp) at the Taihu Laboratory for Lake Ecosystem Research, located at the eastern side of Taihu Lake (31[?]03'N. 120[?]42'E). Lake seston was used as basal resources to allow a regional assortment of phytoplankton species representative of local water bodies. We implemented a factorial design by crossing three levels of nutrient supply (HP, total phosphorus at 0.08 mg L<sup>-1</sup>; MP, total phosphorus at 0.058 mg L<sup>-1</sup>; LP, total phosphorus at  $0.028 \text{ mg L}^{-1}$ , Fig. S1) with three types of zooplankton communities (Daphnia magna + Daphnia brachyurum , Sinocalarus dorrii + D. brachyurum, and D. magna +S. dorrii + D. brachyurum). Nutrient manipulation was achieved by adding  $K_2$ HPO<sub>4</sub> solutions (0.5 mol L<sup>-1</sup>) to 150 L tanks that contained mixtures of lake water and aerated tap water (at the proportion of 1:1). Tanks receiving no P additions represents the LP treatments with total phosphorus concentration at  $0.028 \text{ mg L}^{-1}$  (Fig. S1c). In addition, KNO<sub>3</sub> solutions were added to all tanks to compensate for the dilution effects of tap water (Fig. S1d-f). Zooplankton communities were manipulated by manually adding pre-cultured zooplankton species (see details in SI Appendix 1) to each tank at a total density of around 30 ind.  $L^{-1}$ . Among these species, D. magna possesses larger body size, slower locomotion (thus lower anti-predation ability), and higher nutrient concentrations than the other two species (Sterner et al. 1992). We therefore expected D. magna to be higher-quality food for predators. The inclusion of D. brachyurum in all treatments was to prevent the extinction of zooplankton communities due to predator exploitation. Before filling the tanks, animals originally contained in lake water were eliminated

via repeatedly screening through a 15  $\mu$ m mesh. For each of the nine treatments (3 nutrient levels×3 zooplankton communities), we created six mesocosms, half with and the other half without predators (i.e., two individuals of juvenile shrimp *Exopalaemon Modestus*) in order to quantify the strength of trophic cascades (He *et al.*2021). Therefore, a total of 54 experimental units (i.e., 3 nutrient levels × 3 zooplankton community compositions × 2 predator treatments × 3 replicates) were created. All the mesocosms were fixed in a pond to ensure a relatively constant ambient temperature and checked three times a day to remove unexpected allochthonous materials. The experiment lasted for 6 weeks from 14 July to 25 August, 2021.

#### Measurement

During the course of the experiment, phytoplankton biomass (measured as Chl-a concentration) was quantified at a weekly basis to track phytoplankton response and calculate the trophic cascade strength. We also measured the net production at each trophic level for estimating energy transfer efficiencies. Specifically, primary production ( $P_{\rm phy}$ ) was measured via the light-dark bottles method at the end of the experiment (Devlin *et al.* 2016). Zooplankton production ( $P_{\rm zoo}$ ) was estimated based on changes in the body size and egg production for each taxon from the third week onwards. Predator production ( $P_{\rm shr}$ ) was estimated as the increase rate of shrimp biomass throughout the experiment (Dickman *et al.*2008). Production at all trophic levels were measured in the unit of C L<sup>-1</sup> day <sup>-1</sup> (*see details in SI Appendix 1*).

Total nitrogen (TN) and total phosphorus (TP) concentrations in waters were monitored weekly, and elemental composition of each trophic level were also measured at the end of the experiment to assess the stochiometric responses of food webs. Due to practical reasons, however, for zooplankton species we only measured elemental composition of species D. magna and S. dorrii (see details in SI Appendix 1).

Quantification of energy transfer efficiency and trophic cascade

The energy transfer efficiency between phytoplankton and zooplankton communities ( $E_{\rm her}$ , herbivore efficiency for short) was defined as the ratio of zooplankton production to phytoplankton production, i.e.,  $E_{\rm her} = P_{\rm zoo}/P_{\rm shr}$ , and that between zooplankton and top predator ( $E_{\rm pre}$ , predator efficiency for short) was defined as the ratio of predator production and zooplankton production, i.e.,  $E_{\rm pre} = P_{\rm shr}/P_{\rm zoo}$  (Dickman*et al.* 2008). Food chain efficiency (FCE) was calculated as the geometric average of herbivore efficiency and predator efficiency: FCE =  $\sqrt{E_{\rm her}} \bullet E_{\rm pre} = \sqrt{P_{\rm shr}/P_{\rm phy}}$  (Heymans *et al.* 2014).

The strength of trophic cascade was measured as the natural log ratios of phytoplankton biomass between treatments with  $(R_3)$  and without  $(R_2)$  predators (Borer *et al.* 2005):

$$STC = \ln \frac{R_3}{R_2}$$

Similarly, the strength of top-down control on zooplankton biomass was measured as the natural log ratio of zooplankton biomass between treatments with and without predators.

# Statistical analysis

We used ANOVAs to assess the responses of biomass, production, and energy transfer efficiencies to experimental manipulations. Specifically, we used three-way ANOVAs to test the responses of biomass and production of phytoplankton and zooplankton, as well as the energy transfer efficiency between these two trophic levels (i.e.,  $E_{her}$ ), to manipulations in nutrient supply, zooplankton community composition, and the presence of predators. Similarly, two-way ANOVAs were applied to test the responses of predator biomass and production, and energy transfer efficiency between zooplankton and predator (i.e.,  $E_{pre}$ ) and food chain efficiency (i.e., FCE), to manipulations in nutrient supply and zooplankton community composition. We also applied two-way ANOVAs to explore how nutrient supply and zooplankton community composition influence strengths of top-down control and trophic cascades. In addition, we also explored responses of TP and TN, as well as elemental composition at each trophic level to experimental manipulations using a three-way ANOVA. For all these analyses, Tukey post hoc tests were performed for pairwise comparisons.

To further test the productivity hypothesis (hypothesis I in Fig. 1a) and energy transfer hypothesis (hypothesis II in Fig. 1b), we applied stepwise regression models with trophic cascade strength as response variable and energy transfer efficiencies ( $E_{her}$ ,  $E_{pre}$ , and FCE), primary productivity, and their interactions as explanatory variables. We performed bidirectional model selection by iteratively adding variables to an intercept model and reducing variables from a full model, and selected models with the lowest Akaike Information Criterion (AIC) values. Similarly, we also performed stepwise regression models to test the effects of primary productivity and energy transfer efficiencies on the strength of top-down control on zooplankton biomass. Multivariate regression was performed to assess the contributions of selected variables. All the statistics were performed in R (R Core Team, 2019).

#### Theoretical models

To better understand the mechanisms underlying trophic cascades in our experiment and extend them to more general settings, we also used food chain models to investigate the relationship between trophic cascade, predator efficiency and primary production. The model is described as follows:

$$\begin{cases} \frac{\mathrm{dC}}{\mathrm{dt}} = e_C F_C - d_C C\\ \frac{\mathrm{dH}}{\mathrm{dt}} = e_H F_H - F_C - d_H H\\ \frac{\mathrm{dR}}{\mathrm{dt}} = rR\left(1 - \frac{R}{K}\right) - F_H \end{cases}$$

where R, H, and C are the biomasses of the basal, herbivore, and predator species, respectively (as in Fig. 1), r and K are the intrinsic growth rate and carrying capacity of the basal species, respectively.  $F_H$  and  $F_C$  are the foraging rates of the herbivore and predator species, respectively, for which we consider three types of functional responses. For the type I functional response,  $F_H = a_H RH$  and  $F_C = a_C HC$ . For the type II functional response,  $F_H = \frac{a_H RH}{1+a_H h_H R}$  and  $F_C = \frac{a_C HC}{1+a_C h_C H}$ . For the type III functional response,  $F_H = \frac{a_H RH}{1+a_H h_H R^2}$  and  $F_C = \frac{a_C H^2 C}{1+a_C h_C H^2}$ . In these formulas,  $a_H$  and  $a_C$  are attack rates,  $h_H$  and  $h_C$  are handling times,  $e_H$  and  $e_C$  are assimilation efficiencies, and  $d_H$  and  $d_C$  are mortality rates of the herbivore and predator species, respectively.

Let  $(R_3^*, H_3^*, C_3^*)$  denote the equilibrium biomasses of the three species in the presence of the top predator and  $(R_2^*, H_2^*)$  the equilibrium biomasses of the basal and herbivore species in the absence of top predator. Similar to our empirical analyses, we quantified the strength of trophic cascade as:

$$STC = \ln\left(R_3^*/R_2^*\right)$$

and the predator efficiency as:

$$E_{\rm pre} = \frac{e_C F_{3C}^*}{e_H F_{3H}^*}$$

where  $F_{3C}^*$  and  $F_{3H}^*$  represent the equilibrium foraging rates of the predator and herbivore, respectively, in three-species food chain models. In addition, primary productivity is given by (Loreau 2010):

$$P_{\rm pro} = rR_3^*$$

We then performed analytical investigations and simulations to understand the relationships between STC,  $E_{\rm pre}$  and  $P_{\rm pro}$ . For the type I functional response model, we derived analytic solutions for the relationship between trophic cascade strength STC and predator efficiency  $E_{\rm pre}$  (see SI Appendix 2). For all types of functional responses, we also performed numerical simulations to investigate the relationships between STC,  $E_{\rm pre}$ , and  $P_{\rm pro}$ . In our simulations, we fixed two intrinsic parameters for the plant or predator (both fixed in our experiment), i.e., r = 0.8 and  $d_C = 0.5$ , but changed other parameters to capture variation in the

herbivore species H and the nutrient supply level, as in our experiment. Specifically, we randomly draw parameters  $K \sim U[2,5], a_H, a_C \sim U[0.2, 0.8], h_H, h_C \sim U[0.01, 0.3], d_H \sim U[0.1, 0.5]$ , where U[x, y] denotes the uniform distribution over the interval [a, b]. For assimilation efficiencies, we used both fixed values (Yodzis & Innes 1992), i.e.,  $e_H = 0.45$  and  $e_C = 0.85$ , and varying values, i.e.,  $e_H \sim U[0.3, 0.6]$  and  $e_C \sim U[0.5, 0.9]$ . For each type of functional response, we retained 1000 replicates of simulated food chains where all three species can stably persist, for which we recorded the strength of trophic cascades, predator efficiency and primary productivity (see details in SI Appendix 2).

To test the robustness of our results to model complexity, we further considered a four-species model that includes one plant, two herbivores, and one predator (McCann 2011). Because our simulations of three-species food chains showed highly consistent results across different types of functional responses, we considered only the type II functional response for the four-species model (*see details in SI Appendix 2*). Overall, all models (with different functional responses or herbivore richness) showed similar patterns, so in the main text we presented only results based on the three-species food chain model with type II functional response. Results from other models were presented in *SI Appendix 2*.

# Results

The standing biomasses at all trophic levels were strongly affected by experimental treatments (Fig. 2). The biomass of the predator E. modestus was significantly lower in the LP (i.e., low phosphorous concentration) treatment compared with those in HP (i.e., high phosphorous) and MP (i.e., medium phosphorous) treatments, and lower in mesocosms consisting of S. dorrii and D. brachyurum than those consisting of D. magna and D. brachyurum (Fig. 2a, Table S2). Zooplankton biomass was influenced by the presence of predators  $(F_{1.36} = 114.36; P < 0.001)$ , nutrient supply  $(F_{2.36} = 235.87; P < 0.001)$ , zooplankton community composition ( $F_{2,36} = 40.3; P < 0.001$ ), as well as their interactions (Fig. 2b-c and Table S1). Specifically, zooplankton biomass was significantly suppressed by the presence of predators, while strongly promoted by nutrient enrichment (Fig. 2b-c). In the presence of predators, zooplankton communities consisting of all three species had the highest biomass across all nutrient treatments (Fig. 2b). In the absence of predators, zooplankton communities consisting of *D. magna* and *D. brachyurum* had higher biomass than those consisting of all three species in HP and MP treatments (Fig. 2d), due to higher biomass of D. magna in the former case (Fig. S2e-f). In the LP treatment, however, the inverse pattern was observed (Figs. 2c, S3a-b). Throughout the experiment, phytoplankton communities were dominated by green algae (Fig. S4). Nutrient enrichment and the presence of predators strongly boost phytoplankton biomass (P < 0.001 for both factors; Fig. 2d-e and Table S1). Our analyses also showed significant interactive effects between predators and zooplankton community composition on phytoplankton biomass ( $F_{2,36} = 3.9$ , P = 0.03) and nutrient supply ( $F_{2,36} =$ 10.8, P < 0.001). At all trophic levels, the responses of biomass production rates to experimental treatments were similar to those of standing biomass (Fig. S2, Table S1).

Nutrient supply not only altered the standing biomass and production rates at different trophic levels, but also their stoichiometric characteristics. Phytoplankton molar C:P ratios decreased with increased ambient P concentrations ( $F_{2,36} = 253.7$ ; P < 0.001; Fig. S4c; Table S1) and were higher in the presence of predators ( $F_{1,36} = 5.4$ , P = 0.026). By altering the stoichiometry of phytoplankton, nutrient supply also had carry-over effects on the stoichiometry of higher trophic levels. Specifically, an increase in ambient P concentration decreased the molar C:P ratios of zooplankton D. magna and S. dorrii (Fig. S4a-b), leading further to a lower body molar C:P ratios of predator E. modestus (Fig. S4d).

The energy transfer efficiency between producers and herbivores (hereafter herbivore efficiency) was strongly modulated by the presence of predators ( $F_{1,36} = 16.4$ , P < 0.001) and zooplankton community composition ( $F_{2,36} = 8.4$ , P = 0.001, Table S1). The presence of predators significantly decreased herbivore efficiency, especially in mesocosms with zooplankton communities of *D. magna* and *D. brachyurum* (Fig. 3a). Similarly, the energy transfer efficiency between herbivores and predators (hereafter predator efficiency) was higher in mesocosms with zooplankton community *D. magna and D. brachyurum*, compared with those containing other zooplankton communities (Fig. 3c). While nutrient supply had no significant effects on herbivore efficiency and only marginally significant effects on predator efficiency (Fig. 3b-c, Table S1-2), it significantly affected the overall energy transfer efficiency from producers to predators (hereafter food chain efficiency). That is, the food chain efficiency was significantly higher in MP treatments compared with those in HP and LP treatments ( $F_{2.18} = 7.68$ ; P = 0.001; Table S2; Fig. 3d).

The top-down effects of predators on zooplankton biomass and their cascading effects on phytoplankton biomass both differed significantly among mesocosms with different zooplankton community compositions  $(F_{2.18} = 49.51, P < 0.001$  for zooplankton biomass;  $F_{2.18} = 75, P < 0.001$  for phytoplankton biomass), but not with nutrient conditions (F<sub>2,18</sub> = 0.23, P = 0.796 for zooplankton biomass; F<sub>2,18</sub> = 0.084, P = 0.920for phytoplankton biomass) (Figs. 4, S6, Table S2). Mesocosms with zooplankton communities of D. magna and D. brachyurum showed the strongest cascading effects (on average 107.8% increase in phytoplankton biomass in the presence of predators across three nutrient levels), followed by those consisting of all three zooplankton species (57.3%) and those consisting of S. dorrii and D. brachyurum (41.5%) (Fig. 4). To further disentangle the drivers of trophic cascades, we conducted stepwise regression analyses and found that the strength of trophic cascades was best explained by variation in predator efficiency (Fig. 5b; Table S3-4). In food chains with higher predator efficiencies, the strengths of trophic cascade were stronger (Fig. 5b). In comparison, neither primary productivity nor its interaction with energy transfer efficiencies had significant impacts on the cascading effects (Fig. 5a, Table S1).

Using food chain models with the type I functional response, we derived analytical relationships between trophic cascade strength (STC) and energy transfer efficiencies, i.e.,

$$STC = \frac{e_C}{e_C - E_{\rm pre}}$$

and between trophic cascade strength and primary productivity  $P_{\rm pro}$ :

$$STC = \frac{e_1 a_1}{r d_1} P_{\rm pro}$$

These solutions suggest that the relationship between STC and  $E_{\rm pre}$  involves only one covariate, while that between STC and  $P_{\rm pro}$  involves multiple covariates and thus may be more variable. This expectation was confirmed by numerical simulation in general settings. Across simulated food chains with varying parameters, the trophic cascade strength is strongly related with predation efficiency, but relatively weakly related with primary production and herbivore efficiency (Figs. 5c-d, S7-12). Similar results were found in more complex food web models with two herbivore species (Figs. S13, S14). Overall, our mathematical models support the mechanistic link between energy transfer efficiency and the strength of trophic cascades observed in our mesocosm experiment.

# Discussion

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Despite long-standing interest in food web energetics (after Lindeman 1942) and trophic cascades (after Hairston et al. 1960), research on these two processes have been largely disconnected in the literature. Energy transfer was considered mainly by ecosystem ecologists as a diagram to understand ecosystem energetics and functioning (Chassot *et al.* 2010; Eddy *et al.* 2021), whereas trophic cascades were widely adopted by community ecologists to understand population dynamics (Layman et al. 2015; Jonsson 2017; Barbier & Loreau 2019). These two paradigms, however, address highly related processes of the same ecosystem, so a unified framework has increasingly been advocated by theoretical studies (DeBruyn et al. 2007; Barbier & Loreau 2019). In line with these theoretical advances, our study proposes to understand trophic cascades from an energetic perspective and combines mesocosm experiments and food chain models to disentangle two energetically relevant hypotheses. Our results showed strong associations between trophic cascade strength and predator efficiency but not with primary productivity (Fig. 5; Table S3, S4), supporting the energy transfer hypothesis rather than the productivity hypothesis. Thus, although primary productivity plays vital roles in food webs by providing ultimate energy for all trophic species (Oksanen & Oksanen 2000; Post 2002), an impeded energy transfer could limit the biomass of top predators and weaken their cascading effects (Mooney *et al.*2010; Kersch-Becker & Thaler 2015). These findings corroborate a recent study on grassland experiments, where a decreased energy flow to predatory beetles led to stronger suppressing effects of arthropod herbivores on plants, i.e., weaker cascading effects (Barnes *et al.* 2020).

In our experiment, the predator efficiency varies significantly among mesocosms with different zooplankton community compositions. Mesocosms dominated by D. magna (e.g., those initialized with D. magna and D. brachyurum) showed the highest predator efficiency (Fig. 3c) and strongest trophic cascades. In comparison, mesocosms dominated by other zooplankton species (e.g., those initialized with S. dorrii and D. brachyurum , or with all three zooplankton species) showed lower predator efficiency and weaker trophic cascades in spite of higher total zooplankton biomass (Fig. 2b). This may be explained by the physical and chemical characteristics of *D. maqna*, making them better food sources for predators (Vincent *et al.* 2020). Specifically, the lower motility of *D. magna* can increase the attack rate of predators (Rall *et al.* 2012), and its high body nutrient concentration can increase the assimilation efficiency (DeMott et al. 1998). Therefore, the lower predator efficiency may be attributed to the lack of high-quality resources in mesocosms without D. magna, or low amount of high-quality resources (i.e., lower biomass of D. magna) in mesocosms with all three zooplankton species (Fig. S3). These results highlight the roles of species identity (O'Connor & Crowe 2005), rather than species richness per se (Duffy 2002), in mediating the strength of trophic cascades. Similar patterns have been reported for plant-herbivore interactions, where a higher primary productivity driven by plant diversity does not propagate to higher trophic levels due to the presence of inedible or anti-herbivory plant species (Brett & Goldman 1997; Davis et al. 2010).

While nutrient supply had no significant impacts on trophic cascades, it nevertheless imposed strong regulation on other processes of food webs. In line with previous studies (Teurlincx *et al.* 2017; Zhou & Declerck 2019), nutrient manipulations strongly shape the relative abundance of zooplankton species (Fig. S3) as well as their biomass and stoichiometry (Figs. 2a, S4). Moreover, the impaired performance of the predator under LP treatments, e.g., low biomass, production, and body P content, indicates a carryover effect of phytoplankton P limitation on top trophic levels (Boersma *et al.* 2008). Interestingly, we found that food chain efficiency (FCE) exhibited a unimodal pattern along the gradient of nutrient supply (Fig. 3d). The lower FCE in LP than MP treatments agrees with previous findings on the negative effects of nutrient limitation (Dickman *et al.* 2008; Atkinson *et al.*2021). But with further P enrichment, FCE started to decline, due to the relatively lower herbivore and predator efficiencies. This result may suggest a disadvantages of high nutrients for food web efficiency (Karpowicz *et al.* 2021), due to for example, differences in responding magnitudes between primary producers and apex consumers to nutrient enrichment (Fig. S2).

Our results may have useful implications for natural resource management. In particular, the classic biomanipulation approach for lake restoration is rooted in the theory of trophic cascades, which assumed that addition of piscivorous fish suppresses the biomass of planktivorous fish and releases the herbivorous zooplankton, thus controlling algal biomass via grazing (Carpenter *et al.* 1995). The importance of predator efficiency in determining trophic cascades revealed in the present study suggests that the biomanipulation approaches are most effective in systems with a higher efficiency of energy flow into apex predators, whereas eutrophic systems with low energy transfer efficiency may benefit weakly from the manipulating practices of piscivores (Langeland 1990; Brett & Goldman 1996). In addition, our results also highlight the importance of trophic interactions as drivers of ecosystem energy budgets, e.g., carbon related functions (Strickland *et al.* 2013; Schmitz *et al.*2018; Wyatt et al. 2021). For example, elevated efficiencies of energy transfer allowed increased biomass accumulation in apex consumers (McCauley *et al.* 2018) and therefore stronger trophic cascades, which may turn an ecosystem from carbon source into carbon sink (Schmitz & Leroux 2020).

# Conclusion

By bridging the bottom-up energetic processes and top-down cascading effects, our study contributes to reconciling food web studies using different currencies, e.g., energy and population size. Our findings advocate an energetic perspective in ecosystem management based on trophic cascade theory, where strategies should be designed according to the energetic dynamics of the focal system (Barnes *et al.* 2018). Our study serves as a benchmark for future research on more complex ecosystems over larger scales. In particular, in diverse food

webs, energy transfer efficiencies between trophic levels are jointly determined by herbivore diversity and composition (e.g., in our experiment), plant (Behl *et al.* 2012; Buzhdygan *et al.*2020) or predator diversity (Griffin *et al.* 2008), as well as abiotic factors (Barneche *et al.* 2021; Eddy *et al.* 2021). Disentangling the influences of these processes is challenging but key to understanding the feedback between energetic processes and trophic interactions in natural ecosystems. Moreover, over long timescales, eco-evolutionary dynamics may alter species properties, e.g., anti-predation trait (Vestheim & Kaartvedt 2006) and thus food web energetics. Empirical and theoretical studies with respect to these directions should further contribute to a mechanistic understanding of the responses of multitrophic communities to environmental changes.

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## **Competing interests**

The authors declare no competing interests.

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Fig. 1 Conceptual illustration of two hypotheses underlying trophic cascade strengths: the productivity hypothesis (a) and the energy transfer hypothesis (b). R (horizontal green bars), H (horizontal brown bars), and C (horizontal red bars) represent the biomass of plants, herbivores, and predators, respectively. The upper arrows between adjacent trophic levels represent energy transfer, where  $E_{her}$  (green arrows) and  $E_{pre}$ 

(brown bars) represent herbivore and predator efficiency, respectively, with the thickness of arrows representing the relative magnitude. The bottom dark-green upper arrows (P) refer to the primary productivity. The dashed arrows indicate the indirect effects of the apex predator on plant biomass (i.e., trophic cascades) with their thickness representing the relative strength. The productivity hypothesis posits that a higher productivity can increase the biomass of apex predators and thereby enhance trophic cascades (Fig. 1a, Hypothesis I). The energy transfer hypothesis posits that a higher efficiency of energy transfer promotes the biomass accumulation of apex predators and subsequently strengthens trophic cascades (Fig. 1b, Hypothesis II). The dashed line with a smaller slope in Fig 1a (resp. Fig. 1b) indicates weakened production effects (resp. weakened effects of energy transfer) under a lower energy transfer efficiency (resp. lower production).

Fig. 2 Responses of standing biomass at different trophic levels to experimental manipulations: (a) predator E.modestus, (b, d) zooplankton herbivores, (c, e) phytoplankton. Different capital characters indicate significant differences (P < 0.05) among treatments varying in zooplankton community composition, and different lowercases indicate significant differences among treatments varying in nutrient supply. The bars and error bars show the averages and standard errors across three replicates, respectively.

Fig. 3 Responses of energy transfer efficiencies across trophic levels to experimental manipulations: (a-b) Herbivore efficiency, (b) predator efficiency, (d) FCE. The red arrows in the illustration schemes represent the focal energy transfer processes. Different capital characters indicate significant differences (P < 0.05) among treatments varying in zooplankton community composition, and different lowercases indicate significant differences among treatments varying in nutrient supply. The bars and error bars show the averages and standard errors across three replicates, respectively.

Fig. 4Responses of trophic cascade strength to experimental manipulations. Different capital characters indicate significant differences (P < 0.05) among treatments varying in zooplankton community composition, and different lowercases indicate significant differences among treatments varying in nutrient supply. The bars and error bars show the averages and standard errors across three replicates, respectively. The horizontal grey lines correspond to no cascading effect, i.e., no change in phytoplankton biomass following the removal of the top predator.

Fig. 5 Relationships between trophic cascade strength with primary production  $(\mathbf{a}, \mathbf{c})$  and predator efficiency  $(\mathbf{b}, \mathbf{d})$ , derived from experimental data  $(\mathbf{a}, \mathbf{b})$  and theoretical models  $(\mathbf{c}, \mathbf{d})$ . In  $\mathbf{a}$  and  $\mathbf{b}$ , each symbol represents one mesocosm, where circles (SD) represent zooplankton communities consisting of *S. dorrii* and *D. brachyurum*,triangles (DD) represent zooplankton communities consisting of *D. magna* and *D. brachyurum*; and squares (SDD) represent zooplankton communities containing all the three species. The dashed black line in  $(\mathbf{a})$  represents a non-significant relationship (P > 0.05), whereas the solid black line in  $(\mathbf{b})$  indicates a significant relationship (P < 0.05). Shaded areas are the error bands and denote 95% confidence intervals. Inc and d, each point represents one simulated food webs with randomized assimilation efficiencies, i.e.,  $e_H \sim U$  [0.3, 0.6] and  $e_C \sim U$  [0.5, 0.9], where trophic interactions follow the type II functional response. Other parameters are specified in Methods. The horizontal grey lines correspond to no cascading effect.



Figure 1



Figure 2



Figure 3



Figure 4



Figure 5