Can biomass distribution across trophic levels predict trophic cascades?

Núria Galiana[1*], Jean-François Arnoldi[2], Matthieu Barbier[1], Amandine Acloque[1], Claire de Mazancourt[1] and Michel Loreau[1]

[1] *Theoretical and Experimental Ecology Station, CNRS and Paul Sabatier University, 09200 Moulis, France.*
[2] *Zoology department, School of Natural Sciences, Trinity College Dublin, The University of Dublin, Ireland.*
[*] *nuria.galianaibanez@sete.cnrs.fr*

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Abstract

Food chains present an interconnected set of structural, functional and dynamical properties. Their most conspicuous feature is the static distribution of biomass across trophic levels. But decades of ecological research have affirmed the importance of another, harder to measure, feature: the dynamical propagation of perturbations up and down these chains, creating trophic cascades. These two features are shaped by the same physiological and environmental variables, and seem intuitively related: for instance, more abundant predators should indicate the potential for stronger downward cascades. We interrogate this intuition, combining theory and data from 31 pelagic experiments. We find that basic expectations do not necessarily hold: while for bottom-up perturbations trophic levels respond proportionally to their biomass, for top-down perturbations more top-heavy communities show stronger amplifications. Our framework points at self-regulation (e.g. intra-guild competition) as a major determinant of dynamical-structural relationships. Our approach provides a comprehensive understanding of the link that binds structural and dynamical properties of food chains, and its possible determinants.

1 Introduction

Food chains are a central concept of ecology. They provide intuitions and predictions for basic static properties of food webs, such as the distribution of biomass across the trophic hierarchy (Lindeman, 1942; Elton, 1927). They also predict dynamical behaviour, such as cascading perturbation effects known as trophic cascades (Shurin *et al.*, 2002; Borer *et al.*, 2005; Carpenter *et al.*, 1985; Polis *et al.*, 2000). Yet, studies devoted to understanding each of these properties have historically developed in isolation, generating different lines of investigation, which have seldom been connected (but see Jonsson (2017); McCauley *et al.* (2018); Barbier & Loreau (2019); Rossberg *et al.* (2019)). Recent research, however, has shown that a few key physiological and environmental synthetic variables play a major role in characterizing both the structure and the dynamics of a food chain (Barbier & Loreau, 2019), suggesting that an intrinsic relationship between structure and dynamics should exist.

This proposition is at the core of the present study. We specifically ask whether the static shape of the food chain, i.e. the biomass distribution across trophic levels, can be a good predictor of its dynamical responses, i.e. the propagation of a perturbation downward from the top of the food chain, or upward from the bottom (Figure 1).

The simplest expectation is that the response of each level to a perturbation should be proportional to its biomass. Deviations from this proportionality can be interpreted as an amplification or attenuation of perturbations as they propagate along the chain, and this is how many empirical studies have defined whether a cascade is strong or weak (Shurin & Seabloom, 2005). We can take this expectation as our baseline:

H0 (Proportional response):
The response of any trophic level to any perturbation is proportional to its biomass.

While this expectation appears intuitive, many classical food chain models do *not*, in fact, support proportional response for either upward or downward cascades (and especially not for both at the same time). Two perspectives are commonly used to understand food chain structure and dynamics. The resource-based perspective posits that resources regulate the biomass of higher trophic levels (Elton, 1927; Lindeman, 1942), and thus determine the shape of the biomass pyramid. In this perspective we do expect proportional response at all levels when changing the amount of energy at the bottom; however, perturbations at higher levels should have limited impact below, suggesting highly attenuated downward cascades. In contrast, the consumer-based perspective emphasizes the role of consumers in regulating the biomass of lower trophic levels (Hairston *et al.*, 1960; Gruner *et al.*, 2008). This would suggest strong downward cascades. However, in a consumer-controlled system, adding nutrients at the bottom of the food chain might not increase the abundance of lowest trophic level, but only lead to a boom in consumers, suggesting highly amplified upward cascades.

Although empirical studies recognize that both resources and consumers interact to structure ecological communities (Gruner *et al.*, 2008; Sinistro, 2010; Whalen *et al.*, 2013), understanding whether ecosystems are "limited from below" or "controlled from above" remains an open question that has fascinated ecologists for decades (White, 1978). We saw that these two perspectives suggest different degrees of cascade amplification or attenuation. They are also traditionally associated with different biomass distributions. For example, in many resource-control models, inefficient energy transfer and metabolic costs cause biomass to decrease with trophic height, or at most stay constant (Elton, 1927; Lindeman, 1942; Jennings *et al.*, 2008; Trebilco *et al.*, 2013). Conversely, consumer-control models often have high rates of resource depletion (MacArthur, 1970; Tilman, 1982), leading to strongly top-heavy distributions.

Therefore, we can propose a second hypothesis: the biomass distribution of a food chain could signal resource or consumer control, and therefore predict deviations from proportional response (amplification or attenuation). Contrary to H0, this hypothesis makes different predictions for upward and downward perturbations.

H1 (Classic food chain expectations):
a) Bottom-heavy chains signal resource control while top-heavy chains signal consumer control.
b) In resource control, responses to perturbations at the bottom of the chain are proportional while responses to perturbations at the top are attenuated.
c) In consumer control, responses to perturbations at both the bottom and the top of the chain are amplified.

In fact, the three-way relationship between control type, biomass distribution, and cascades is more subtle than suggested by these simple arguments, so that H1 could be invalidated in various ways. In particular, while trophic cascades are prevalent in nature, their strength has been shown to be highly variable across systems (Polis *et al.*, 2000; Shurin *et al.*, 2002; Frank *et al.*, 2006), prompting the widespread emergence of studies exploring the mechanisms behind their existence and magnitude (Halaj & Wise, 2001; Shurin & Seabloom, 2005; Borer *et al.*, 2005; Heath *et al.*, 2014; Ripple *et al.*, 2016). Several hypotheses have been proposed to explain the variability in the strength of cascades in empirical systems, ranging from environmental variables, such as temperature or spatial complexity (Frank *et al.*, 2006, 2005), to characteristics of the organisms in the system, such as their metabolic type (i.e., endotherms or ectotherms), their size or edibility (Shurin *et al.*, 2002; Shurin & Seabloom, 2005; Borer *et al.*, 2005), or their intraspecific trait variation (Sentis *et al.*, 2020). Thus, several factors may prevent this relationship from being apparent in nature. In addition, different mechanisms, such as omnivory or energetic subsidies, have been proposed to explain the emergence of top-heavy communities (Trebilco *et al.*, 2016; McCauley *et al.*, 2018; Woodson *et al.*, 2018), so that a direct link between the shape of the biomass pyramid and the strength of consumer control has yet to be established.

Thus there may be a complex reality going beyond H0 and H1, which we intend to explore both empirically and theoretically. The theoretical part of this inquiry requires a model which permits both resource and consumer control, and allows us to identify which parameters may control or confound the expected relationships between biomass distribution and dynamical response.

Here we provide a theoretical framework linking the structural and dynamical food chain features and use empirical data from 31 mesocosm experiments of pelagic food webs, including both top-down and bottom-up perturbations, to test our theoretical expectations. We find in experimental data that H0 appears to hold for bottom-up perturbations: biomass ratios are roughly proportional to response ratios to nutrient enrichment. On the other hand, H1 is upheld for top-

down perturbations only: More top-heavy communities show stronger amplification in response to fish addition. These apparently contradictory empirical observations are reconciled in our theory.

We identify one main confounding parameter, ρ, which critically depends on intra-level interactions (e.g. self-regulation). We explain how this non dimensional parameter can shape the biomass distribution without any relationship to either upward and downward perturbations,thereby invalidating both H0 and H1. Furthermore, we show that whether we observe a signature of downward trophic cascades in the biomass distribution depends on the relative strength of the intra-level (i.e., consumer's self-regulation) and inter-level (i.e., attack rate) interactions. Thus, intra-level interactions (self-regulation) stand out as a fundamental factor in shaping the relationship between structure, dynamics and function in food chains. The framework presented here allows us to draw a direct link between the static and dynamic properties of trophic communities, and provides a comprehensive understanding of the mechanisms controlling this relationship. This is essential to properly interpret the patterns observed in natural communities and enhance our capacity to predict the long-term effects of perturbations.

Box 1. Definition of main concepts.

- **Bottom-heavy biomass pyramid:** the biomass of organisms across trophic levels decreases with increasing trophic levels conforming a classic trophic pyramid of biomass.
- **Top-heavy biomass pyramid:** the biomass of organisms across trophic levels increases with increasing trophic levels conforming an inverted pyramid of biomass.
- **Resource control:** resources regulate the biomass of higher trophic levels by determining the flow of energy up the chain.
- **Consumer control:** consumers regulate the biomass of lower trophic levels through their consumption.
- **Upwards amplification:** stronger response of higher trophic levels relative to lower trophic levels to a perturbation at the bottom of the chain.
- **Downwards amplification:** stronger response of lower trophic levels relative to higher trophic levels to a perturbation at the top of the chain.
- **Self-regulation:** regulatory mechanisms that cause per capita growth rates to depend on the abundance of the species in question (e.g. intraspecific interference, cannibalism or effects from hidden compartments).
- **Dynamically consistent chains:** food chains where prey have long-term positive effects on predators, predators have negative long-term impacts on prey. Hidden compartments or species from outside the considered chain might impact the latter while maintaining the chain-like behaviour.

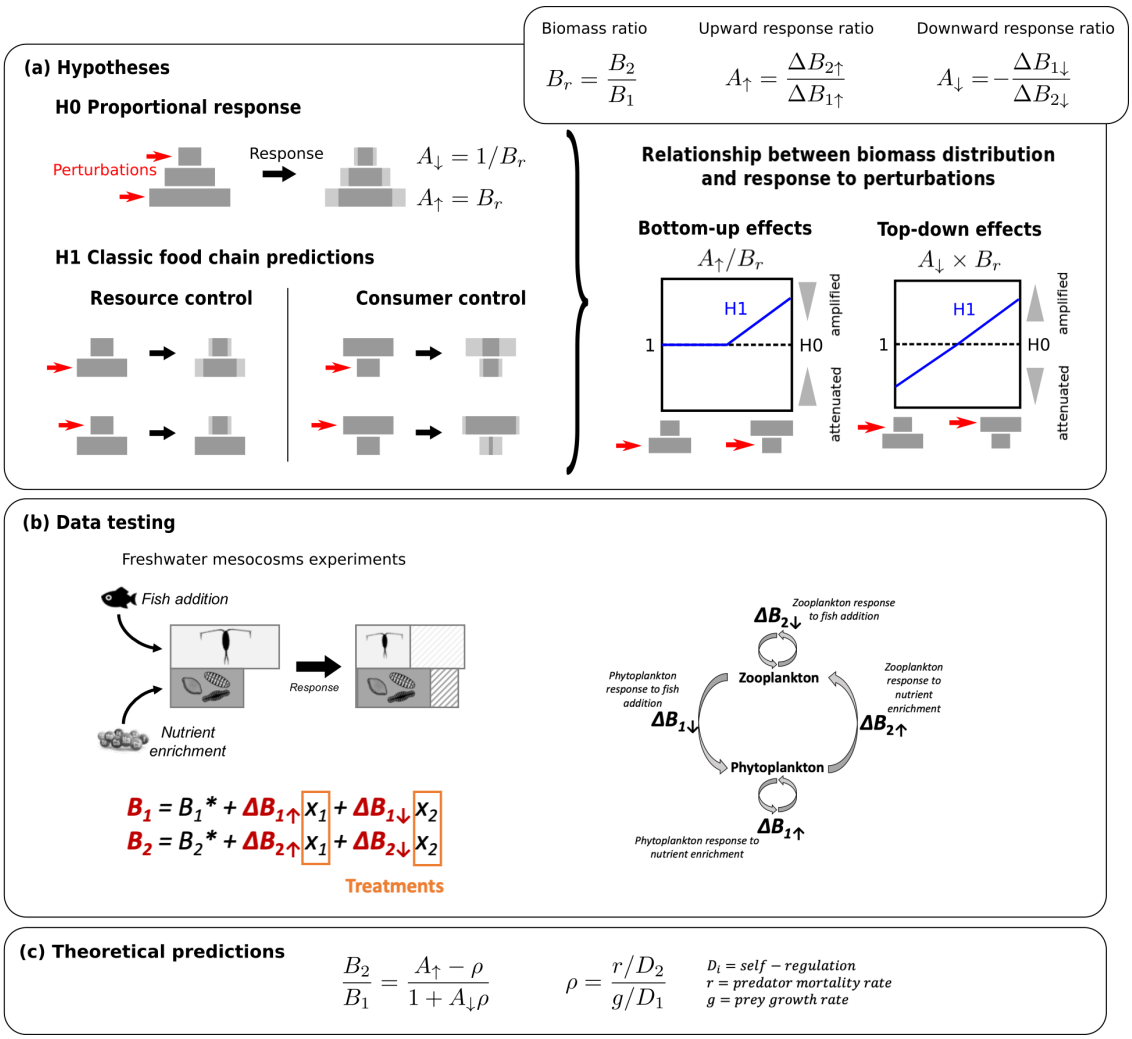

Figure 1: Conceptual framework used to study the relationship between static and dynamic properties in food chains. (a) We investigate the existence of a relationship between biomass distribution across trophic levels and the prevalence of trophic cascades. A simple expectation (H0), unrelated with trophic interactions, is that the response of a level to a perturbation is simply proportional to its biomass, and therefore, no relationship between biomass distribution and trophic cascades should be expected (dashed line). Deviations from this proportionality (H1) may indicate the effect of trophic interactions in amplifying or attenuating perturbations across trophic levels. For instance, a perturbation at the bottom of the chain can be amplified in a consumer-controlled system (blue line). Similarly, a perturbation at the top of the chain could be amplified or attenuated depending on whether the system is consumer-controlled or resource-controlled, resulting in a positive relationship between biomass ratio and trophic cascades. (b) We used data from 31 mesocosm experiments of pelagic food webs that monitored community responses to nutrient enrichment and fish addition, and estimated the biomass response of two trophic levels. (c) Following Barbier and Loreau (2019), we developed a theoretical framework linking biomass ratio with upward and downward amplification (see Theoretical predictions in Results) and we compared our data to the theoretical expectations.

2 Methods

2.1 Empirical testing

2.1.1 Data collection and formatting

We searched the literature for studies analysing bottom-up and top-down effects after press perturbations in food chains. We selected 21 independent studies reporting on 31 lake mesocosm experiments of pelagic food webs as they were all based on the same ecological system and performed the same experimental treatments (see Appendix S1; Hulot *et al.* (2014)). Specifically, all studies investigated community responses to nutrient enrichment and fish addition and they all reported the biomass of identified species (or determined trophic levels) before and after the perturbation, which is fundamental to test whether biomass distribution across trophic levels is related to the strength of trophic cascades. Detailed information about the studies used can be found in Appendix S1.

The pelagic communities considered contain different paths of energy transmission across trophic levels (Figure 2a). To properly study biomass distribution across trophic levels and, in particular, the dynamics of trophic cascades in the community, it is fundamental to identify paths of energy flux in the food web that adequately behave as food chains (Barbier & Loreau, 2019). We thus define as *dynamically consistent chains* those where prey have positive effects on predators and predators have negative impacts on prey (Box 1). We decomposed empirical food webs into all the possible chains and analysed them independently to identify which responded to perturbations the way an isolated chain would (Figure 2a). Not all the experiments considered had information for all the food web compartments. Thus, the decomposition of the complex food webs was based on the information available (Appendix S1).

2.1.2 Data analyses

The third trophic level (fish) was viewed as a perturbation treatment in the experiments considered (only presence/absence reported). Therefore, the biomass distribution considered was the pair of biomasses of the first two trophic levels (phytoplankton and zooplankton, respectively). We characterized biomass distribution as the ratio

$$B_r = \frac{B_2^*}{B_1^*} \tag{1}$$

where B_i^*, $i = 1, 2$ corresponds to the non-perturbed biomass of trophic level 1 (phytoplankton) and level 2 (zooplankton), respectively. B_r quantifies the bottom- or top-heaviness of the biomass pyramid. In particular, if $B_r > 1$, the pyramid is inverted.

We were interested in the response of food chains to bottom-up (i.e., nutrient enrichment) and top-down (i.e., fish addition) perturbations. To evaluate these specific responses we performed a multilinear fit based on equilibrium biomasses and responses of both trophic level to various combinations of treatments: nutrient enrichment (treatment binary variables $x_\uparrow = 1$ and $x_\downarrow = 0$), fish addition ($x_\uparrow = 0$ and $x_\downarrow = 1$) and both ($x_\uparrow = 1$ and $x_\downarrow = 1$). In other words, we estimated the unknown terms $\Delta B_{i\uparrow,\downarrow}$ in the right hand side of the following system of 4 linear equations (one system for each level):

$$B_i - B_i^* = x_\uparrow \Delta B_{i\uparrow} + x_\downarrow \Delta B_{i\downarrow}; x_\uparrow = 0, 1;\ x_\downarrow = 0, 1. \tag{2}$$

For each level $i = 1, 2$, the coefficients $\Delta B_{i\uparrow}$, correspond to the changes in biomass due to nutrient enrichment, while $\Delta B_{i\downarrow}$ correspond to the changes in biomass due to fish addition.

For each treatment, the estimation error in those fits informs us on the discrepancy between two responses. For instance, for nutrient enrichment, we have two instances, one with no fish addition and one with fish addition. The associated error is large when the two measurements are incompatible (Figure 2b and 2c).

We then selected the fitted coefficients that were estimated with low errors (i.e., estimated error $<$ coefficient value) and the appropriate sign (Figure 2b and 2c). That is, $\Delta B_{i\uparrow}$ had to be positive (or zero) for both trophic levels in the case of nutrient enrichment while for fish addition treatments, $\Delta B_{2\downarrow}$ had to be negative and $\Delta B_{1\downarrow}$ had to be positive (or zero) (i.e., cascade effect). Discarded coefficients can be interpreted as a sign of energy gain (or dissipation) across the chain from (or into) other compartments outside the chain, resulting in a dynamical behaviour that is not consistent with a food chain. Large errors could also be a sign of strong nonlinear behaviour, which we do not consider here.

From selected coefficients, we deduced upward and downward response ratios, defined respectively as

$$A_{\uparrow} = \frac{\Delta B_{2\uparrow}}{\Delta B_{1\uparrow}}, \text{ and } A_{\downarrow} = -\frac{\Delta B_{1\downarrow}}{\Delta B_{2\downarrow}} \tag{3}$$

$A_{\uparrow}$ measures the biomass change of level 2 relative to that of level 1 following nutrient enrichment, while $A_{\downarrow}$ represents the biomass change of level 1 relative to that of level 2 following fish addition. To see how these measurements deviate from the baseline expectation H0 of proportional response, we define amplifications

$$a_{\uparrow} = A_{\uparrow}/B_r = \frac{\Delta B_{2\uparrow}/B_2}{\Delta B_{1\uparrow}/B_1}, \text{ and } a_{\downarrow} = A_{\downarrow} \times B_r = -\frac{\Delta B_{1\downarrow}/B_1}{\Delta B_{2\downarrow}/B_2} \tag{4}$$

For either direction, we interpret $a = 1$ as a proportional response (following H0), $a > 1$ as an amplified response, which we call a strong cascade, and $a < 1$ as an attenuated response, which we call a weak cascade.

Finally, to analyse the empirical relationship between biomass distribution and trophic cascades, we performed linear mixed effects models including biomass ratios B_r as fixed effects, study system as random effects (given that we decomposed each study system in multiple chains) and response ratios $A_{\uparrow}$ and $A_{\downarrow}$, as response variables. For bottom-up response ($A_{\uparrow}$) we found that the variance explained by the study system was 0.19, therefore, we included study system as a random effect. However, we found no significant differences between the model including the study system as random effect (AIC=57.9) and the model including only biomass ratio as fixed effect (AIC=57.0). For the top-down response ($A_{\downarrow}$) the variance associated to the study system was 0.002, and the model including only biomass ratio as a fixed effect was significantly better (AIC=58.3; linear mixed model with study system as random effect AIC=60.3). Thus, the results presented below correspond to the analyses were only biomass ratio was included as a fixed effect in the model.

2.2 Lotka-Volterra model

We focus here on a simple two-level system to match the empirical analyses, and assume Lotka-Volterra interactions (i.e. type-I functional responses). However, the theoretical framework presented has no restrictions on the length of the food chain, and can be extended to different functional responses (see Appendix S2 for multi-level and nonlinear chain results).

Let B_i, $i = 1, 2$ be the biomass density of primary producers and consumers, respectively (e.g grams per unit of volume).

$$\begin{cases} \frac{1}{B_1}\frac{dB_1}{dt} = & g - D_1 B_1 - \alpha B_2 \\ \frac{1}{B_2}\frac{dB_2}{dt} = & \epsilon\alpha B_1 - D_2 B_2 - r \end{cases} \tag{5}$$

We denote by $g > 0$ the intrinsic growth rate of primary producers, and $r > 0$ the intrinsic death rate of consumers. The per-capita attack rate of consumers is denoted as $\alpha > 0$ (a rate per unit of biomass density). In the same units we denote by D_i $i = 1, 2$ the density-dependent mortality (or reduction of biomass productivity) of both trophic levels (i.e., self-regulation). Finally, we write $0 < \epsilon < 1$ the efficiency of productivity transfer from primary producers to consumers. There are two units: time and biomass density. Here we are interested only in non dimensional ratios, such as biomass ratio and response ratios. We therefore adimensionalized the model (See Appendix S2 for details), reducing the number of parameters to 4. These are: transfer efficiency ϵ (unchanged), relative attack rate $a = \frac{\alpha}{D_1}$; relative self-regulation $\psi = \frac{D_2}{D_1}$; and finally, relative intrinsic rates $\phi = \frac{r}{g}$.

2.3 Approximate Bayesian Computation (ABC)

We can identify parameter ranges in data using Approximate Bayesian Computation (Beaumont, 2010). The idea behind the use of ABC is to leverage empirical patterns to constrain the distribution of simulation parameters. Thus, we used the dynamical model above to find parameter values compatible with empirical results. We generated many predator-prey systems with different parameter values drawn from broad prior distributions, and computed their equilibrium biomass ratios B_r and top-down and bottom-up response ratios $A_{\uparrow}$ and $A_{\downarrow}$. We then retained only model realizations for which (i) the two species coexisted and (ii) the relationship between B_r and $A_{\uparrow}$ and between B_r and $A_{\downarrow}$ were consistent with those observed in our data analyses, so that we could capture the mechanisms underlying the patterns observed in our pelagic systems (see figure S3.1 in Appendix S3). Overall we retained 1500 model realizations, and used the corresponding parameter values to compute a joint posterior distribution for all model parameters. All parameters

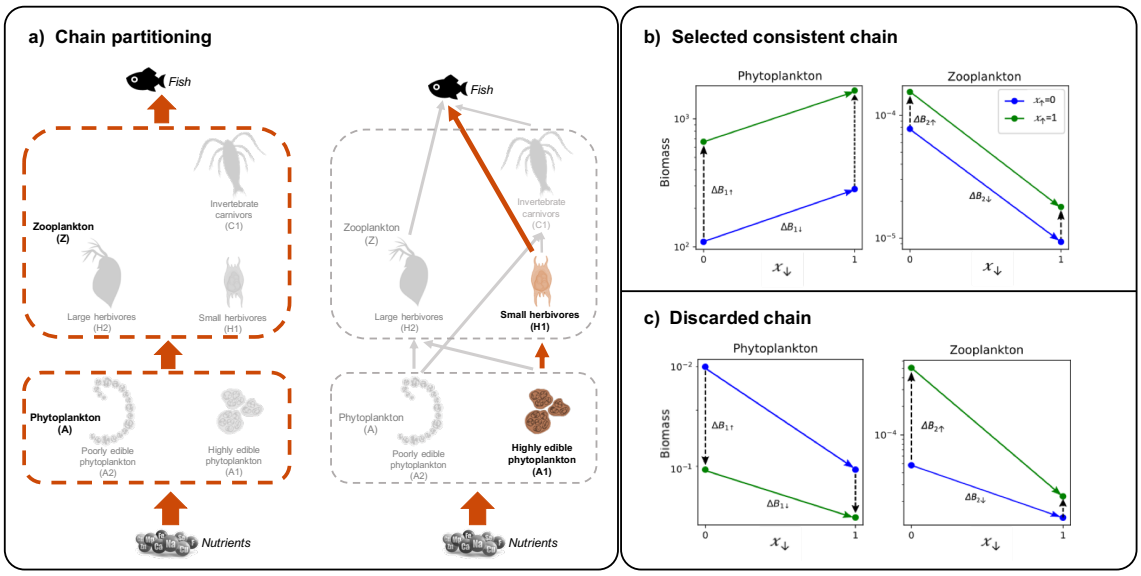

Figure 2: Data analyses illustration. (a) Conceptual representation of the structure of the experimental communities. Multiple chains can be identified in these communities. We analysed all possible chains to ensure we capture the dynamics of a *consistent chain* and discarded those chains that did not follow the expected dynamics. Two examples are provided. On the left, all zooplankton species are aggregated into trophic level 2 and all phytoplankton species are aggregated into trophic level 1 (chain: Z-A). On the right, the chain analysed is composed by small herbivores (trophic level 2) consuming highly edible phytoplankton (trophic level 1) (chain: H1-A1). All chains analysed are: Z-A (31), C1-A2 (17), C1-H1 (22), H1-A1 (21), H2-A2 (14), H2-A1 (14), where the numbers in brackets indicate the number of experiments that contained information for each chain type. (b and c) Examples of response evaluation to determine if the chains considered behave as *dynamically consistent chains*. The evaluation was based on the response to both perturbations (i.e., nutrient enrichment and fish addition) of each trophic level. In dynamically consistent chains, we expect both trophic levels to respond positively to nutrient enrichment and to have opposite responses to fish addition. In (b) we illustrate a case where the system behaved as a dynamically consistent chain. Both trophic levels respond positively to nutrient enrichment (dashed arrows point towards nutrient enrichment), shown by the increase in biomass from blue (no nutrient treatment, $x_{\uparrow} = 0$) to green lines (nutrient enrichment, $x_{\uparrow} = 1$), and they show opposite responses to fish addition (coloured arrows point towards fish addition). Phytoplankton biomass increases from $x_{\downarrow} = 0$ (no fish addition) to $x_{\downarrow} = 1$ (fish addition), while zooplankton biomass decreases with fish addition. In (c) we show a case where the system do not behave as a consistent chain. First, phytoplankton biomass decreases with nutrient enrichment while zooplankton biomass increases. Second, both trophic levels respond negatively to fish addition. Finally, we have a large error associated to the estimation of the responses, shown by the differences in the slope between green and blue lines.

were drawn uniformly on a log scale, over a span of several orders of magnitude: biomass conversion efficiency $\epsilon \in [10^{-2}, 10^{-1}]$; relative attack rate $a = \frac{\alpha}{D_1} \in [10^1, 10^4]$; relative self-regulation $\psi = \frac{D_2}{D_1} \in [10^{-5}, 10^5]$; and relative intrinsic rate $\phi = \frac{r}{g} \in [10^{-4}, 10^4]$. Posterior distributions of parameters are presented on log scales and compared to their prior distributions, constrained on coexistence.

3 Results

3.1 Empirical results

We analyzed 120 potential chains, defined by all the possible paths of energy flux across trophic levels in the experiments considered (i.e. Z-A (31), C1-A2 (17), C1-H1 (22), H1-A1 (21), H2-A2 (14), H2-A1 (14)). We found 68 responses to perturbations that were consistent with that of a dynamical food chain. That is, 33 of the considered paths showed a chain-like behaviour of significant positive correlation between predator and prey biomass for upward cascades, i.e. $A_\uparrow > 0$, while 35 chains showed significant negative correlation between predator and prey biomass for downwards cascades, i.e. $A_\downarrow > 0$ (Table S1.2 in Appendix S1).

Paths where all zooplankton species and all phytoplankton species were grouped together to form two trophic levels (chain Z-A in Figure 2a) showed the highest percentage of chain-like responses across all experiments, together with the chain composed by small herbivores (H1) consuming highly edible phytoplankton (A1). The estimated responses to perturbations had low fit significance or wrong signs in approximately 60% of the instances analysed (61% for $\Delta B_{1\uparrow}$, 68% for $\Delta B_{2\uparrow}$, 58% for $\Delta B_{1\downarrow}$ and 60% for $\Delta B_{2\downarrow}$), see Figure S1.1. For instance, we observed many cases of zooplankton biomass increasing after fish addition, or phytoplankton biomass decreasing due to nutrient enrichment[1].

The biomass distribution was bottom-heavy in most selected paths (Figure 3), corresponding to biomass ratios B_r smaller than 1. Nonetheless, the range of biomass ratios (and response ratios) across all systems covered several orders of magnitude, which allowed us to analyse the relationship between biomass distribution and trophic cascades. In the selected experimental systems, B_r was positively correlated with the upwards response ratio ($A_\uparrow$). That is, for a given response of the lower trophic level to nutrient addition, more top-heavy biomass pyramids were associated with stronger responses of the higher level (Figure 3a). However, the slope of this relationship was close to one in log scale, indicating that the responses to nutrient addition of each trophic level were proportional to their biomass, showing no further effect of trophic interactions in amplifying the upwards response. Consequently, when looking at the relative amplification $a_\uparrow$ (Figure 3c), we observed no relationship with biomass ratio. Thus, hypothesis H0 (proportional response) cannot be rejected for upward effects.

In contrast, B_r was negatively correlated with downwards response ratio $A_\downarrow$ with a slope of -0.5 in log scale (Figure 3b), indicating that the response to fish addition across trophic levels was not proportional to their biomass. Instead, we found that relative amplification $a_\downarrow$ was positively correlated with the biomass ratio (Figure 3d), indicating that downward cascades were relatively stronger (more amplified) for more top-heavy chains.

3.2 Theoretical predictions

We now show how these empirical results can be understood in a theoretical framework that allows both resource control and consumer control. We compute the predicted quantitative relationship between the equilibrium biomass ratio and the response ratios $A_\uparrow$ and $A_\downarrow$, allowing us to understand deviations from both hypotheses H0 and H1.

Solving for the equilibrium of a two-species Lotka-Volterra dynamical system (see Methods), we find that the biomass ratio should be

$$B_r = \frac{\epsilon\alpha g - D_1 r}{D_2 g + \alpha r} \tag{6}$$

If we apply a perturbation in the growth rate of primary producers Δg, such as a nutrient enrichment treatment, we get that the changes in the biomass of trophic level 1 and trophic level

[1]Note that even in such cases, we retained paths when they showed consistent chain-like dynamics, i.e. the expected correlation between predator and prey response. We interpret these as valid trophic cascades created by indirect, rather than direct, impacts of the experimental treatments.

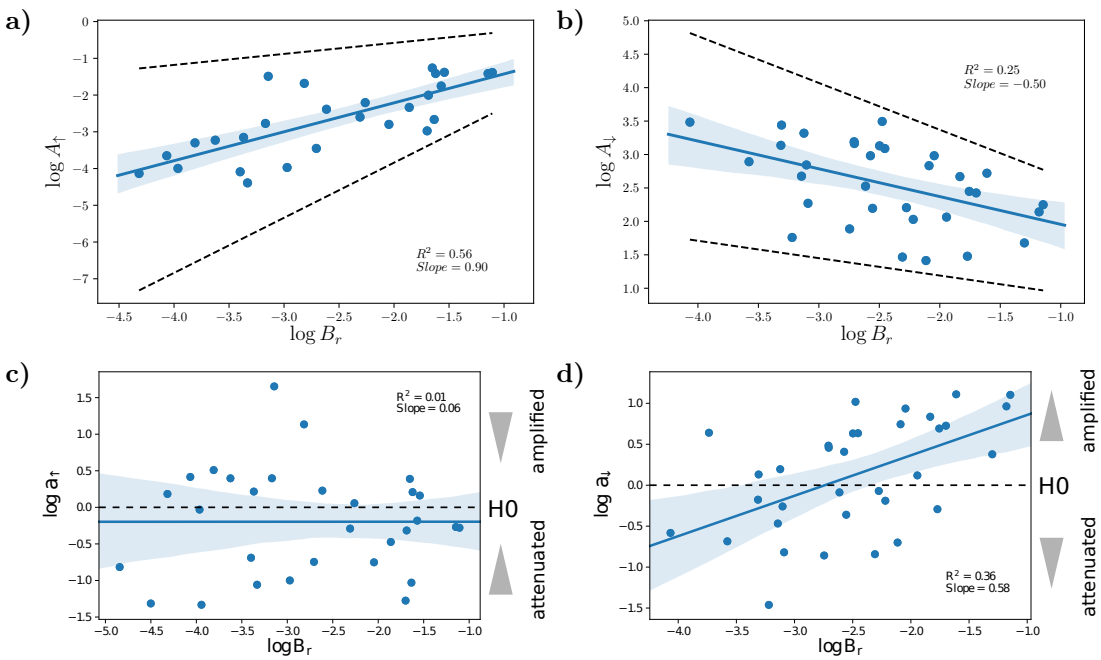

Figure 3: Empirical relationship between biomass ratio and response ratios and relative amplification. (a) Relationship between biomass ratio and bottom-up response ratio ($A_\uparrow = \frac{\Delta B_{2\uparrow}}{\Delta B_{1\uparrow}}$) due to nutrient enrichment. In (b) relationship between biomass ratio and top-down response ratio ($A_\downarrow = -\frac{\Delta B_{1\downarrow}}{\Delta B_{2\downarrow}}$) due to fish addition. Each point represents a food chain in our analyses. Blue lines represent the linear regression and shaded areas represent 95% confidence intervals. Dashed lines represent the limits of the empirical pattern used in the simulation analyses to filter the prior distribution of parameters. Notice that patterns shown in (a) and (b) are excluding the outliers, which results into an exclusion of the extremes of the biomass ratio distribution (See Figure S3.2 in Appendix S3 for results including the outliers). (c) Bottom-up amplification ($a_\uparrow = \frac{\Delta B2\uparrow/B_2}{\Delta B_{1\uparrow}/B_1}$) due to nutrient enrichment. (d) Top-down amplification ($a_\downarrow = -\frac{\Delta B_{1\downarrow}/B_1}{\Delta B_{2\downarrow}/B_2}$) due to fish addition.

2 will be respectively given by

$$\Delta B_{1\uparrow} = \frac{\Delta g}{b} D_2, \text{ and } \Delta B_{2\uparrow} = \frac{\Delta g}{b} \epsilon\alpha \tag{7}$$

where $b = D_1 D_2 + \epsilon\alpha^2$ (but b will play no role in what follows). Similarly, changes in biomass due to a perturbation in the mortality rate of consumers Δr, such as fish addition, read for both levels

$$\Delta B_{1\downarrow} = \frac{\Delta r}{b}\alpha \text{ and } \Delta B_{2\downarrow} = -\frac{\Delta r}{b} D_1 \tag{8}$$

Thus, defining response ratios as in the empirical analysis Eq. (3), bottom-up and top-down responses will respectively read

$$A_\uparrow = \frac{\epsilon\alpha}{D_2} \text{ and } A_\downarrow = \frac{\alpha}{D_1} \tag{9}$$

By combining eqs. (6-9), we deduce a relationship between biomass ratio and response ratios (see Appendix S2 for details)

$$B_r = \frac{A_\uparrow - \rho}{1 + A_\downarrow \rho}; \; \rho = \frac{\phi}{\psi} = \frac{r/g}{D_2/D_1} \tag{10}$$

In this expression $\rho \geq 0$ is the ratio of the two non-dimensional quantities, ϕ and ψ. Recall that the former is the ratio of intrinsic rates $\phi = r/g$, while the latter is the ratio of intra-level interactions $\psi = D_2/D_1$. ρ can also be interpreted as a ratio of characteristic densities $\rho = K_2'/K_1$, where $K_1 = g/D_1$ is the carrying capacity of the producer. $K_2' = r/D_2$ is not a carrying capacity, but the density of consumer population for which consumer competition affects growth as much as does linear mortality.

This expression makes it clear that three different factors determine the predator-prey biomass ratio: the interactions that shape the two dynamical response ratios $A_\uparrow$ and $A_\downarrow$, and the additional within-level effects of growth and mortality in ρ, which can act as a confounding factor.

We can now understand why the proportional response H0 can easily hold for bottom-up effects, as seen in Figure 3c. If $\rho \approx 0$ (for instance, low predator mortality and high prey growth, $r \ll g$), we see that $B_r \approx A_\uparrow$, meaning that the biomass distribution is strictly shaped by upward effects, and proportionality holds between the two. In contrast, we see that proportional response is never expected to hold exactly for downward cascades. In the limit $\rho \approx 0$, the biomass ratio contains no information about downward cascades $A_\downarrow$, no matter whether they are weak or strong (Figure 4a). In the opposite limit of large ρ, $A_\downarrow$ will be anticorrelated with B_r, but not with strict proportionality (Figure 4b). Finally, for intermediate values of ρ, we expect B_r to determine *the ratio* of upward and downward responses $A_\uparrow/A_\downarrow$ (illustrated in Fig. S3.3 on simulations and data).

To see how our framework informs hypothesis H1, we can manipulate equation (10) to relate the biomass ratio to the amplification factors, which signal whether cascades are weak or strong relative to the proportional baseline H0. We get that:

$$B_r = \rho \frac{a_\downarrow + 1}{a_\uparrow - 1} \tag{11}$$

This expression can be misleading, because the amplifications $a_\uparrow = A_\uparrow/B_r$ and $a_\downarrow = A_\downarrow \times B_r$, are not independent of the biomass ratio, which is in turn shaped by ρ: in particular, we know from (10) that, if $\rho = 0$, then $a_\uparrow = 1$. What this expression shows, however, is the confounding role of ρ. If this parameter varies across systems more than either amplification factor, no relationship between B_r and cascade strength will be found. If, however, ρ has low variance across ecosystems while $a_\downarrow$ varies significantly, then we can expect a relationship such as the one observed in Figure 3e. In particular, for intermediate values of ρ that vary less across systems than amplifications, we do expect a relationship between structure B_r and dynamics, in the form of the ratio of amplifications $a_\downarrow/a_\uparrow$ (illustrated in Fig. S3.3 on simulations and data).

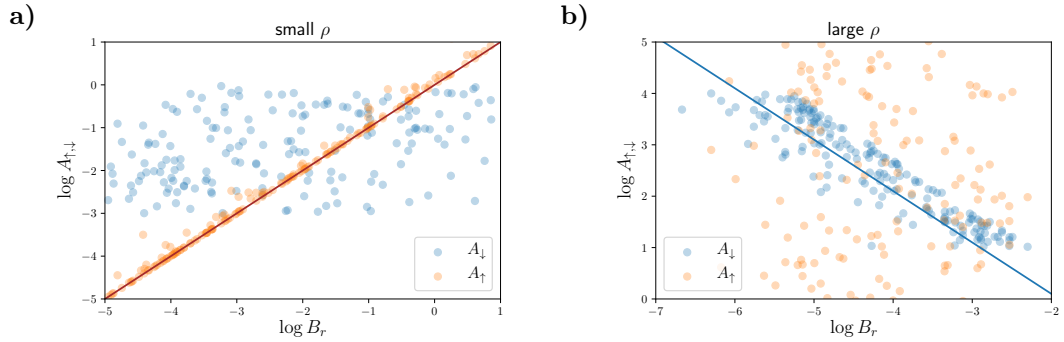

Figure 4: The relationship between biomass ratio and response ratios is driven by ρ. Simulations of the model (5) (for the range of parameters described in the main text) showing two limit cases of Eq. (10). a) For small ρ (here we selected realizations where $\rho < 10^{-3}$), upward response ratio $A_\uparrow$ shows a proportional relationship with biomass ratio (solid line has slope 1 on log-log scales) while there is no correlation between B_r and downward response ratio $A_\downarrow$. b) For large ρ (here $\rho > 0.95 \cdot A_\uparrow$ and $A_\uparrow > 10^{-1}$), we observe the opposite trend: downward response ratio $A_\downarrow$ is inversely proportional to biomass ratio (solid line has slope -1 on log-log scales) while there is no correlation with $A_\uparrow$.

3.3 Comparing theory and data

We can now use our theoretical results to explain empirical patterns and find out what they suggest about underlying mechanisms. In particular, we have seen theoretically that the existence of relationships between biomass distribution and cascade strength depends on which ecological parameters vary more or less between ecosystems.

By using Approximate Bayesian Computation we constrained the distribution of simulation parameters to match empirical patterns (Figure 5). As a test of the consistency of our approach, it is noteworthy that, although we did not constrain the model parameters to match the empirical biomass ratios (but only to follow the empirical relationships between response and biomass ratios), the selected simulated data points constituted a remarkably similar distribution of biomass ratios (Figure S3.1).

Once filtered to match empirical patterns, the distribution of ρ shifted towards small values (Figure 5a). Given that $\rho = \phi/\psi$, we analysed which parameter was driving this shift. The distribution of $\phi = r/g$ did not change after filtering by the empirical patterns (Figure 5b), indicating no constrains on intrinsic rates (only coexistence constrains them).

In contrast, the distribution of $\psi = D_2/D_1$ was strongly shifted towards higher values after filtering by the empirical patterns (Figure 5c). Remarkably, This indicates higher consumer self-regulation than resource self-regulation. We found no limit on how strong this relative self-regulation could be, only that it must be roughly larger than one.

On the other hand, we see in Eq. 10 that the signature of top-down cascades in the biomass distribution depends on the product $A_{\downarrow}\rho$. Note that $A_{\downarrow}\rho \propto \alpha/D_2$, the ratio between inter- and intra-level interactions. In other words, the distribution of α/D_2 drives the signature of top-down cascades in the biomass distribution. And indeed, this parameter is most constrained by the empirical patterns: its posterior distribution shows a unimodal distribution relatively tightly centered around one (Figure 5d). These findings thus highlight the importance of consumers' self-regulation for the empirical patterns observed, and furthermore suggest that attack rates and consumers' self-regulation are of similar magnitude in those pelagic systems.

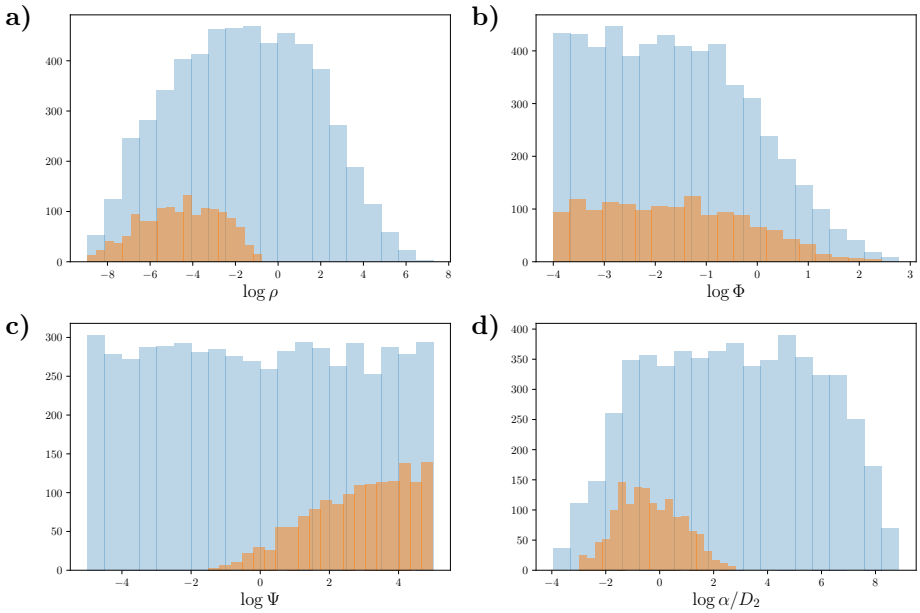

Figure 5: Prior and posterior distributions of model parameters. Blue histograms represent the prior distribution of the parameters introduced into the model (conditioned on coexistence). Orange histograms represent the distribution of the parameters after filtering them to match the empirical patterns. a) Distribution of the synthetic parameter $\rho = \phi/\psi$. b) Distribution of the ratio of predator mortality to prey growth $\phi = r/g$, c) distribution of the ratio self-regulations $\psi = D_2/D_1$. d) Distribution of the ratio α/D_2, which represents the relative strength of trophic interactions and predator self-regulation. We see that the posterior distribution is centered close to 0 in log scale, suggesting that self-regulation rates are comparable to predation rates.

4 Discussion

Trophic cascades are widespread in nature (Pace *et al.*, 1999; Shurin *et al.*, 2002; Estes *et al.*, 2011). Changes in the abundance of a given trophic level can have further consequences along the food chain through the effects of both direct and indirect interactions, ultimately altering ecosystem structure and functioning (Paine, 1969; Carpenter *et al.*, 1985; Polis *et al.*, 2000; Duffy, 2002; Estes *et al.*, 2011). Understanding the causes of variation in their prevalence and strength has dominated a big part of the food chain literature (Shurin & Seabloom, 2005; Borer *et al.*, 2005; Heath *et al.*, 2014; Barbier & Loreau, 2019; Sentis *et al.*, 2020). Multiple sources of empirical data have been used as indices of trophic cascades in natural systems (Baum & Worm, 2009; Heath *et al.*, 2014). Most of these indices are based on observations of dynamical behaviour, such as the correlations between time series of interacting pairs of trophic levels (Frank *et al.*, 2007), or the response of a given trophic level to a perturbation applied elsewhere in the ecosystem (Baum & Worm, 2009; Estes *et al.*, 2011; Hulot *et al.*, 2014).

Another salient feature of food chains is the static distribution of biomass across trophic levels. It has long been studied in the form of pyramids of abundance or biomass (Elton, 1927), or as a size spectrum when, instead of discrete trophic levels, communities are ordered by organism body size (Sheldon *et al.*, 1972; Cousins, 1985; Blanchard *et al.*, 2017).

Since biomass distributions are more easily measured than dynamical properties, some previous studies have discussed whether these static distributions can or cannot hint at the underlying dynamics (McCauley *et al.*, 2018; Barbier & Loreau, 2019). For instance, Rossberg *et al.* (2019) related size *domes* (i.e., high biomass density in some body-size range and depleted troughs in between) in pelagic systems to the existence of downwards trophic cascades. But a systematic and quantitative exploration of possible relations between downward and upward cascade strength and biomass distributions was still lacking.

4.1 Summary of results

Here, using both empirical data from pelagic food web experiments, and a simple model (studied analytically and related to data through Approximate Bayesian Computation), we explicitly investigated the relationship between structure and dynamics, asking under which conditions the strength of trophic cascades can have a signature in the biomass distribution across trophic levels (Figure 3).

We framed our analysis between two basic hypotheses drawn from the literature. Hypothesis H0 was proportional response, where each compartment responds in accordance to its size. Hypothesis H1 was a set of expectations from classical food chain theory. Bottom-heavy food-chains signal bottom-up control, with attenuated downward cascades (weak relative effects on lower levels). Top-heavy food chain signal top-down control, where both up- and downwards cascades are amplified: each trophic level responds more to perturbations that directly affect the other level.

We find in experimental data that H0 holds for bottom-up perturbations: biomass ratios are roughly proportional to response ratios to bottom-up perturbations (nutrient enrichment). On the other hand, H1 holds for top-down perturbations (fish addition) only: more top-heavy communities showed stronger amplification, i.e. an increasing prey-to-predator ratio of relative responses.

These apparently contradictory empirical observations reveal a complex reality beyond H0 and H1, which our theoretical investigation was able to explain synthetically. Indeed, if our theoretical framework predicts a relationship between biomass distribution across trophic levels and trophic cascades in both directions, bottom-up and top-down, it also highlights the importance of another parameter. This parameter can modify the biomass distribution independently of cascade strength; it is defined as the balance between intrinsic rates (i.e. growth and mortality) and self-regulation.

We demonstrated that whether we observe a signature of downward trophic cascades in the biomass distribution depends on the relative strength of the intra-level (i.e., consumer's self-regulation) and inter-level (i.e., attack rate) interactions. The stronger the attach rate relative to intra-level interactions, the stronger the signature of top-down cascades on the biomass ratio. Experimental data strongly suggests that intra- and inter-level interactions are of comparable strength. An important and novel take-away message of our analysis is that intra-level interactions (self-regulation) are a fundamental driver of the relationship between structure and dynamics in food chains, as shown in Eq. 10 and 11.

4.2 On the importance of self-regulation

Previous research has already pointed at the importance of self-regulatory processes, such as intra-guild predation, to stabilize community dynamics by preventing consumers from exhausting their resource's production (Barabás *et al.*, 2017), and more concretely, to modulate the strength of trophic cascades (McCann *et al.*, 1998; Herendeen, 2004; Heath *et al.*, 2014; Barbier & Loreau, 2019). McCann *et al.* (1998) showed how incorporating strong interference within the zooplankton level yielded trophic cascade patterns matching those found in aquatic pelagic communities. Similarly, Herendeen (2004) demonstrated that both top-down and bottom-up effects were found to depend strongly on consumers' mortality regulation, whilst bottom-up effects were additionally dependent on prey density (Heath *et al.*, 2014). Here we showed that both consumer and resource self-regulation are involved in the response to perturbations at all levels (Eq. 7 and 8). However, when synthesising the responses of both trophic levels in a single measure of amplification (i.e., bottom-up amplification or top-down amplification) by looking at the ratio of responses, we observe that consumers self-regulation is involved in bottom-up amplification patterns while resources self-regulation determines top-down amplification patterns (Eq. 9). Barbier & Loreau (2019) also demonstrated how self-regulation is fundamental to fully understand food chain dynamical patterns, but they further emphasized the need to incorporate self-regulation to bridge the gap between static and dynamical approaches in food chain studies. In line with their claim, we showed that self-regulation is indeed at the basis of a direct relationship between static and

dynamic properties, in the sense that it determines whether an observable relationship between biomass distribution and trophic cascades can emerge.

Effects from species or compartments outside of the considered chain could also impact the densities of trophic levels in a way that maintains chain-like behaviour but changes the effective self-regulation. Furthermore, we obtained the largest fraction of chain-like responses when considering all zooplankton species as a single trophic level and all phytoplankton species as another trophic level, suggesting that consistent chain dynamics can generically emerge as a complexity reduction of communities into few interacting levels composed by multiple species or groups of species (Ulanowicz, 1995). Thus, if self-regulation is a key determinant of trophic cascades and their signature in biomass patterns, in the two cases described above (food web with hidden connections and complex food webs reduced to a chain), self-regulation itself would be an emergent property, that would not be directly accessible from individual behaviour such as predator interference. Therefore, the framework presented here can give us a way to quantify the self-regulatory processes present in each system, even though their origin is unknown.

4.3 Limitations

Our theoretical predictions held across the data from multiple experimental pelagic communities. Unfortunately, we had very few instances of consistent responses to bottom-up and to top-down perturbations in the same chain. Had this been the case, we could have inferred the magnitude of self-regulation in each system by combining the measured responses with knowledge on, e.g. metabolic rates (to infer ϕ, the ratio of intrinsic rates). This would have been particularly valuable, as very few empirical studies provide reliable direct estimates of self-regulation (Skalski & Gilliam, 2001). Thus, as a proposal for future work, our theoretical framework would provide an alternative way of estimating the relative importance of self-regulation in empirical systems by only measuring the biomass distribution and the response to perturbations across trophic levels.

An important limitation of the empirical data that we used is the absence of quantitative information on the prevalence and strength of omnivorous links. The analyses performed to ensure the applicability of food-chain theory indicated that only around 50% of the energy pathways considered behaved as dynamically consistent food chains. Different mechanisms could explain this high rate of dynamical discrepancies, among which omnivory is a prominent one. The presence of omnivorous links in food webs has been well documented (Polis *et al.*, 1989; Polis, 1994; Emmerson & Yearsley, 2004; Neutel *et al.*, 2007), and several studies have shown that the presence of large omnivorous consumers is able to obviate cascading effects in food chains due to the creation of weak links in the system (Diehl, 1993; Pringle & Hamazaki, 1998; Polis, 1999; McCauley *et al.*, 2018). Indeed, many 'herbivorous' zooplankton species consume phytoplankton but also a substantial amount of microzooplankton, such as rotifers and ciliates (Sprules & Bowerman, 1988; Gilbert, 1988; Brett *et al.*, 1994; Hansson *et al.*, 2004), which can explain some of the non-chain-like responses observed in our systems. Similarly, the existence of compensation between species of different functional groups within trophic levels (Gonzalez & Loreau, 2009) could also prevent the propagation of perturbations to lower trophic levels (Leibold, 1989; Hunter & Price, 1992; Strong, 1992; McCann *et al.*, 1998), indicating the non-independence of the chain considered.

Conclusion

We established a direct link between structural and dynamical properties of food chains. We have shown, both theoretically and empirically, that biomass distribution across trophic levels and the strength of trophic cascades can be related, and that such relationship depends largely on the strength of consumers' self-regulation. The empirical analyses, together with the numerical simulations performed, provide circumstantial evidence for the prevalence of significant consumer self-regulation in pelagic aquatic ecosystems. Thus, the framework presented here might provide an indirect way of estimating the relative importance of self-regulation in empirical systems. Furthermore, it provides a comprehensive understanding of the mechanisms controlling the relationship between the biomass distribution across trophic levels and the prevalence of trophic cascades, which is the first step towards using measurements of structural properties of ecosystem as indicators to predict their dynamical response to perturbations.

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Author contributions

All authors contributed to the design of the study. NG and AA assembled the empirical data and, jointly with MB, performed the empirical analyses. JFA and MB developed the theoretical framework. NG and JFA performed the numerical simulations. NG wrote the manuscript with substantial contributions from MB and JFA, and feedback from all the authors.

References

Barabás, G., Michalska-Smith, M.J. & Allesina, S. (2017). Self-regulation and the stability of large ecological networks. *Nature ecology & evolution*, 1, 1870–1875.

Barbier, M. & Loreau, M. (2019). Pyramids and cascades: a synthesis of food chain functioning and stability. *Ecology letters*, 22, 405–419.

Baum, J.K. & Worm, B. (2009). Cascading top-down effects of changing oceanic predator abundances. *Journal of animal ecology*, 78, 699–714.

Beaumont, M.A. (2010). Approximate bayesian computation in evolution and ecology. *Annual review of ecology, evolution, and systematics*, 41, 379–406.

Blanchard, J.L., Heneghan, R.F., Everett, J.D., Trebilco, R. & Richardson, A.J. (2017). From bacteria to whales: using functional size spectra to model marine ecosystems. *Trends in ecology & evolution*, 32, 174–186.

Borer, E.T., Seabloom, E.W., Shurin, J.B., Anderson, K.E., Blanchette, C.A., Broitman, B., Cooper, S.D. & Halpern, B.S. (2005). What determines the strength of a trophic cascade? *Ecology*, 86, 528–537.

Brett, M.T., Wiackowski, K., Lubnow, F.S., Mueller-Solger, A., Elser, J.J. & Goldman, C.R. (1994). Species-dependent effects of zooplankton on planktonic ecosystem processes in Castle Lake, California. *Ecology*, 75, 2243–2254.

Carpenter, S.R., Kitchell, J.F. & Hodgson, J.R. (1985). Cascading trophic interactions and lake productivity. *BioScience*, 35, 634–639.

Cousins, S. (1985). Ecologists build pyramids again. *New Scientist*, 106, 50–54.

Diehl, S. (1993). Relative consumer sizes and the strengths of direct and indirect interactions in omnivorous feeding relationships. *Oikos*, pp. 151–157.

Duffy, J.E. (2002). Biodiversity and ecosystem function: the consumer connection. *Oikos*, 99, 201–219.

Elton, C.S. (1927). The animal community. *Animal ecology*, pp. 239–256.

Emmerson, M. & Yearsley, J.M. (2004). Weak interactions, omnivory and emergent food-web properties. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 271, 397–405.

Estes, J.a., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B.C., Marquis, R.J., Oksanen, L., Oksanen, T., Paine, R.T., Pikitch, E.K., Ripple, W.J., Sandin, S.a., Scheffer, M., Schoener, T.W., Shurin, J.B., Sinclair, A.R.E., Soulé, M.E., Virtanen, R. & Wardle, D.a. (2011). Trophic downgrading of planet Earth. *Science (New York, N.Y.)*, 333, 301–6.

Frank, K.T., Petrie, B., Choi, J.S. & Leggett, W.C. (2005). Trophic cascades in a formerly cod-dominated ecosystem. *Science*, 308, 1621–1623.

Frank, K.T., Petrie, B. & Shackell, N.L. (2007). The ups and downs of trophic control in continental shelf ecosystems. *Trends in Ecology & Evolution*, 22, 236–242.

Frank, K.T., Petrie, B., Shackell, N.L. & Choi, J.S. (2006). Reconciling differences in trophic control in mid-latitude marine ecosystems. *Ecology Letters*, 9, 1096–1105.

Gilbert, J.J. (1988). Suppression of rotifer populations by Daphnia: a review of the evidence, the mechanisms, and the effects on zooplankton community structure 1. *Limnology and Oceanography*, 33, 1286–1303.

Gonzalez, A. & Loreau, M. (2009). The causes and consequences of compensatory dynamics in ecological communities. *Annu. Rev. Ecol. Evol. Syst.*, 40, 393–414.

Gruner, D.S., Smith, J.E., Seabloom, E.W., Sandin, S.A., Ngai, J.T., Hillebrand, H., Harpole, W.S., Elser, J.J., Cleland, E.E. & Bracken, M.E.S. (2008). A cross-system synthesis of consumer and nutrient resource control on producer biomass. *Ecology letters*, 11, 740–755.

Hairston, N.G., Smith, F.E. & Slobodkin, L.B. (1960). Community structure, population control, and competition. *The american naturalist*, 94, 421–425.

Halaj, J. & Wise, D.H. (2001). Terrestrial trophic cascades: how much do they trickle? *The American Naturalist*, 157, 262–281.

Hansson, L., Gyllström, M., Ståhl-Delbanco, A. & Svensson, M. (2004). Responses to fish predation and nutrients by plankton at different levels of taxonomic resolution. *Freshwater Biology*, 49, 1538–1550.

Heath, M.R., Speirs, D.C. & Steele, J.H. (2014). Understanding patterns and processes in models of trophic cascades. *Ecology letters*, 17, 101–114.

Herendeen, R.A. (2004). Bottom-up and top-down effects in food chains depend on functional dependence: an explicit framework. *Ecological Modelling*, 171, 21–33.

Hulot, F.D., Lacroix, G. & Loreau, M. (2014). Differential responses of size-based functional groups to bottom–up and top–down perturbations in pelagic food webs: a meta-analysis. *Oikos*, 123, 1291–1300.

Hunter, M.D. & Price, P.W. (1992). Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology*, 73, 724–732.

Jennings, S., Mélin, F., Blanchard, J.L., Forster, R.M., Dulvy, N.K. & Wilson, R.W. (2008). Global-scale predictions of community and ecosystem properties from simple ecological theory. *Proceedings of the Royal Society B: Biological Sciences*, 275, 1375–1383.

Jonsson, T. (2017). Conditions for Eltonian pyramids in Lotka-Volterra food chains. *Scientific reports*, 7, 1–10.

Leibold, M.A. (1989). Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. *The American Naturalist*, 134, 922–949.

Lindeman, R.L. (1942). The trophic-dynamic aspect of ecology. *Ecology*, 23, 399–417.

MacArthur, R. (1970). Species packing and competitive equilibrium for many species. *Theoretical population biology*, 1, 1–11.

McCann, K.S., Hastings, A. & Strong, D.R. (1998). Trophic cascades and trophic trickles in pelagic food webs. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 265, 205–209.

McCauley, D.J., Gellner, G., Martinez, N.D., Williams, R.J., Sandin, S.A., Micheli, F., Mumby, P.J. & McCann, K.S. (2018). On the prevalence and dynamics of inverted trophic pyramids and otherwise top-heavy communities. *Ecology Letters*, 21, 439–454.

Neutel, A.M., Heesterbeek, J.a.P., van de Koppel, J., Hoenderboom, G., Vos, A., Kaldeway, C., Berendse, F. & de Ruiter, P.C. (2007). Reconciling complexity with stability in naturally assembling food webs. *Nature*, 449, 599–602.

Pace, M.L., Cole, J.J., Carpenter, S.R. & Kitchell, J.F. (1999). Trophic cascades revealed in diverse ecosystems. *Trends in ecology & evolution*, 14, 483–488.

Paine, R.T. (1969). A note on trophic complexity and community stability. *The American Naturalist*, 103, 91–93.

Polis, G.A. (1994). Food webs, trophic cascades and community structure. *Australian Journal of Ecology*, 19, 121–136.

Polis, G.A. (1999). Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. *Oikos*, pp. 3–15.

Polis, G.A., Myers, C.A. & Holt, R.D. (1989). The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annual review of ecology and systematics*, 20, 297–330.

Polis, G.A., Sears, A.L.W., Huxel, G.R., Strong, D.R. & Maron, J. (2000). When is a trophic cascade a trophic cascade? *Trends in Ecology & Evolution*, 15, 473–475.

Pringle, C.M. & Hamazaki, T. (1998). The role of omnivory in a neotropical stream: separating diurnal and nocturnal effects. *Ecology*, 79, 269–280.

Ripple, W.J., Estes, J.A., Schmitz, O.J., Constant, V., Kaylor, M.J., Lenz, A., Motley, J.L., Self, K.E., Taylor, D.S. & Wolf, C. (2016). What is a trophic cascade? *Trends in Ecology & Evolution*, 31, 842–849.

Rossberg, A.G., Gaedke, U. & Kratina, P. (2019). Dome patterns in pelagic size spectra reveal strong trophic cascades. *Nature communications*, 10, 1–11.

Sentis, A., Bertram, R., Dardenne, N., Simon, J.C., Magro, A., Pujol, B., Danchin, E. & Hemptinne, J.L. (2020). Intraspecific difference among herbivore lineages and their host-plant specialization drive the strength of trophic cascades. *bioRxiv*, p. 722140.

Sheldon, R.W., Prakash, A. & Sutcliffe Jr, W. (1972). THE SIZE DISTRIBUTION OF PARTICLES IN THE OCEAN 1. *Limnology and oceanography*, 17, 327–340.

Shurin, J.B., Borer, E.T., Seabloom, E.W., Anderson, K., Blanchette, C.A., Broitman, B., Cooper, S.D. & Halpern, B.S. (2002). A cross-ecosystem comparison of the strength of trophic cascades. *Ecology letters*, 5, 785–791.

Shurin, J.B. & Seabloom, E.W. (2005). The strength of trophic cascades across ecosystems: predictions from allometry and energetics. *Journal of animal Ecology*, 74, 1029–1038.

Sinistro, R. (2010). Top-down and bottom-up regulation of planktonic communities in a warm temperate wetland. *Journal of Plankton Research*, 32, 209–220.

Skalski, G.T. & Gilliam, J.F. (2001). Functional responses with predator interference: viable alternatives to the Holling type II model. *Ecology*, 82, 3083–3092.

Sprules, W.G. & Bowerman, J.E. (1988). Omnivory and food chain length in zooplankton food webs. *Ecology*, 69, 418–426.

Strong, D.R. (1992). Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. *Ecology*, 73, 747–754.

Tilman, D. (1982). *Resource competition and community structure*. Princeton university press.

Trebilco, R., Baum, J.K., Salomon, A.K. & Dulvy, N.K. (2013). Ecosystem ecology: size-based constraints on the pyramids of life. *Trends in Ecology and Evolution*, 28, 1–9.

Trebilco, R., Dulvy, N.K., Anderson, S.C. & Salomon, A.K. (2016). The paradox of inverted biomass pyramids in kelp forest fish communities. *Proceedings of the Royal Society B: Biological Sciences*, 283, 20160816.

Ulanowicz, R.E. (1995). Ecosystem trophic foundations: Lindeman exonerata. *Complex Ecology: the part-whole relation in ecosystems. Prentice Hall, Englewood Cliffs, NJ*, pp. 549–550.

Whalen, M.A., Duffy, J.E. & Grace, J.B. (2013). Temporal shifts in top-down vs. bottom-up control of epiphytic algae in a seagrass ecosystem. *Ecology*, 94, 510–520.

White, T.C.R. (1978). The importance of a relative shortage of food in animal ecology. *Oecologia*, 33, 71–86.

Woodson, C.B., Schramski, J.R. & Joye, S.B. (2018). A unifying theory for top-heavy ecosystem structure in the ocean. *Nature communications*, 9, 1–8.

Can biomass distribution across trophic levels predict trophic cascades?

Supporting Information

Núria Galiana, Jean-François Arnoldi, Matthieu Barbier, Amandine Acloque, Claire de Mazancourt and Michel Loreau

Appendix S1. Empirical data

Table S1.1: Experimental studies used in the analyses. We extracted 31 experimental studies analysing bottom-up and top-down effects in pelagic food chains after press perturbations. Detailed information about the studies used can be found in (Hulot *et al.*, 2014).

Article	N. of experiments
(Vanni, 1987a,b)	2
(Van De Bund & Van Donk, 2004)	2
(Lacroix & Lescher-Moutoue, 1991)	1
(Fernández-Aláez *et al.*, 2004)	2
(Stephen *et al.*, 2004)	2
(Lynch & Shapiro, 1981)	1
(Menezes *et al.*, 2010)	1
(Qin & Culver, 1995)	1
(Hansson *et al.*, 2004)	1
(Romo *et al.*, 2004)	2
(Dickman *et al.*, 2008)	1
(Acuña *et al.*, 2008)	1
(Beresford & Jones, 2010)	1
(Drenner *et al.*, 1990, 1989)	2
(Faafeng *et al.*, 1990)	2
(Hietala *et al.*, 2004)	2
(McQueen *et al.*, 1992)	1
(Proulx *et al.*, 1996)	2
(Sinistro, 2010)	1
(Riemann, 1985)	1
(Mazumder *et al.*, 1990)	1

Table S1.2: Total number of experiments analysed per chain type and number of chain-like responses for upwards amplification and downwards amplification for each chain type.

Chain type	Total number of experiments	Upwards amplification	Downwards amplification
Z-A	31	10	12
C1-A2	17	4	2
C1-H1	22	5	6
H1-A1	21	7	7
H2-A1	14	3	6
H2-A2	14	4	2

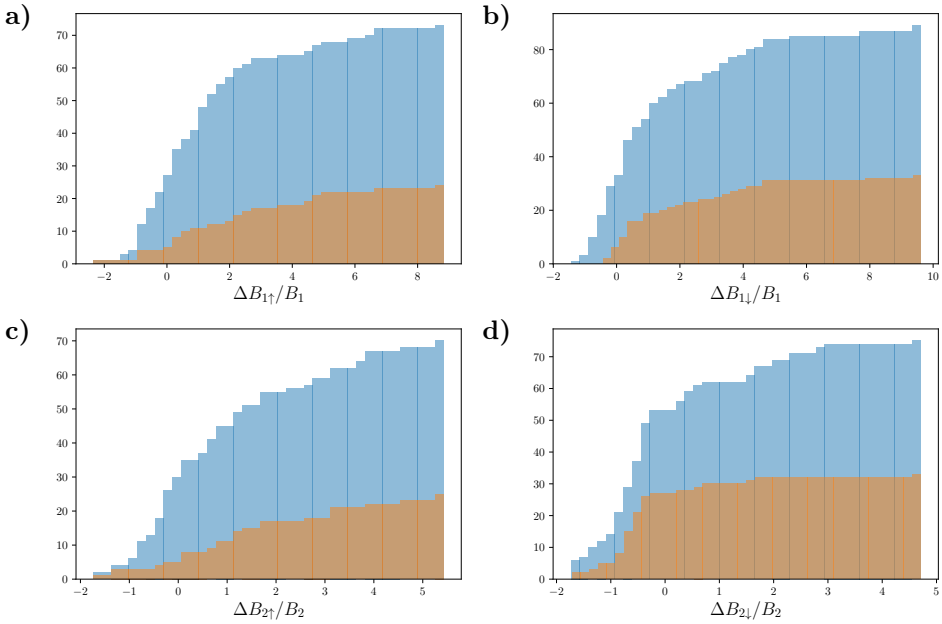

Figure S1.1: Cumulative distributions of the estimated responses to nutrient enrichment (↑) and fish addition (↓) treatments of each trophic level biomass (B_1 and B_2, for trophic level 1 and 2, respectively) relative to their original biomass in experimental mesocosms. Blue distributions represent the estimated responses of all possible chains analysed before filtering them to ensure they behave like dynamically consistent chain. Orange distributions show the estimated responses of the chains that were identified as dynamically consistent chains. In dynamically consistent chains, we expect responses of trophic level 1 to nutrient enrichment (a) and to fish addition (b) to be positive, together with the biomass responses of trophic level 2 to nutrient enrichment (c). Therefore, most of the chains selected are accumulated above 0, indicating that they presented a positive biomass response to the perturbation. In contrast, biomass responses of trophic level 2 to fish addition (d) are expected to be negative. Thus, we observe most of the accumulation before 0, indicating that very few chains are selected when trophic level 2 presents a positive response to fish addition.

Appensix S2. Theoretical framework

Two-level chain

Let $B_i,\ i = 1, 2$ be the biomass density of primary producers and consumers, respectively (e.g grams per unit of volume). We denote by $g > 0$ the intrinsic growth rate of primary producers, and $r > 0$ the intrinsic death rate of consumers. The per-capita attack rate of consumers is denoted as $\alpha > 0$ (a rate per unit of biomass density). In the same units we denote by $D_i\ i = 1, 2$ the density-dependent mortality (or reduction of biomass productivity) of both trophic levels (i.e., self-regulation). Finally, we write $0 < \epsilon < 1$ the (non dimensional) efficiency of productivity transfer from primary producers to consumers. This leads us to the following expression for the growth rates $W_i = \frac{1}{B_i}\frac{dB_i}{dt}$ of both populations

$$\begin{cases} W_2 = & \epsilon\alpha B_1 - D_2 B_2 - r \\ W_1 = & g - D_1 B_1 - \alpha B_2 \end{cases} \tag{12}$$

which define a Lotka-Volterra dynamical system (See Appendix S2 for the nonlinear chain approximation). In what follows we are interested only in non dimensional ratios, such as the biomass ratio of the two levels, and the amplification of a perturbation across the chain (i.e., effects of a perturbation on one trophic level relative to the effects on the other level in which the perturbation was directly applied). We therefore begin by adimensionalizing the problem. There are two units: time and biomass density. To remove the former we can express time relatively to the rate of growth g of primary producers. We write $\tau = gt$ (non dimensional time) and, since $\frac{d}{dt} = g\frac{d}{d\tau}$, expressing the dynamics in those units amounts to dividing by g all terms of the right hand side of (12). To remove the units of biomass, we can express all densities with respect to the carrying capacity $K_1 = g/D_1$ of primary producers. We thus define $b_i = B_i/K_1$ (non dimensional biomass). This lead us to the non dimensional system, denoting $w_i = \frac{1}{b_i}\frac{db_i}{d\tau}$ non dimensional rates, we get that

$$\begin{cases} w_2 = & \epsilon a b_1 - \psi b_2 - \phi \\ w_1 = & 1 - b_1 - a b_2 \end{cases};\ a = \frac{\alpha}{D_1};\ \psi = \frac{D_2}{D_1};\ \phi = \frac{r}{g} \tag{13}$$

At equilibrium $\frac{1}{b_i}\frac{db_i}{d\tau} = 0$ so that (if both species coexist), their respective densities satisfy

$$\begin{pmatrix} \psi & -\epsilon a \\ a & 1 \end{pmatrix}\begin{pmatrix} b_2^* \\ b_1^* \end{pmatrix} = \begin{pmatrix} -\phi \\ 1 \end{pmatrix} \Leftrightarrow \begin{pmatrix} b_2^* \\ b_1^* \end{pmatrix} = V\begin{pmatrix} -\phi \\ 1 \end{pmatrix}$$

where the matrix V is

$$V = \begin{pmatrix} \psi & -\epsilon a \\ a & 1 \end{pmatrix}^{-1} = \frac{1}{\psi + \epsilon a^2}\begin{pmatrix} 1 & \epsilon a \\ -a & \psi \end{pmatrix}$$

We deduce, in particular, the biomass ratio $B_r = b_2^*/b_1^* = B_2^*/B_1^*$ equal to

$$B_r = \frac{\epsilon a - \phi}{\psi + a\phi}$$

where we can observe that the coexistence condition is that ϵa (consumption) must be larger than ϕ (mortality). We can also recognize in this expression of B_r the amplification of perturbations. This is because the matrix V that gave us the equilibrium densities also gives us their sensitivity to changes in growth rates. Indeed, consider a perturbation of the primary producer in the form of a persistent change δg of growth rate. In the non dimensional formulation, this is a perturbation $\delta w_1 = \delta g/g$ and it leads to the shift of biomass:

$$\begin{pmatrix} \delta b_2 \\ \delta b_1 \end{pmatrix} = \begin{pmatrix} \psi & -\epsilon a \\ a & 1 \end{pmatrix}^{-1}\begin{pmatrix} 0 \\ \delta w_1 \end{pmatrix} = \frac{\delta w_1}{\psi + \epsilon a^2}\begin{pmatrix} \epsilon a \\ \psi \end{pmatrix}$$

where we recognize the second column of V, times δw_1. We can do the same for a perturbation δw_2 of the consumer's growth rate, which would give us the first column of V, times δw_2. Thus

$$V_{ij} = \frac{\partial b_i^*}{\partial w_j}$$

so that bottom-up amplification (i.e., perturbation applied on resources), defined as $A_\uparrow = \left|\frac{\partial b_2}{\partial w_1}/\frac{\partial b_1}{\partial w_1}\right| = |V_{21}/V_{11}|$ reads

$$A_\uparrow = \frac{\epsilon a}{\psi}$$

Similarly, if the perturbation is applied to the consumer we get that top-down amplification $A_\downarrow = \left|\frac{\partial b_1}{\partial w_2}/\frac{\partial b_2}{\partial w_2}\right| = |V_{12}/V_{22}|$ is in fact

$$A_\downarrow = a$$

From these notations yields the following expression for the relationship between biomass ratio and trophic cascades:

$$B_r = \frac{A_\uparrow - \rho}{1 + A_\downarrow \rho};\ \rho = \phi/\psi \tag{14}$$

Where $\rho = \frac{\phi}{\psi} = \frac{K_2'}{K_1}$ can be interpreted as the ratio of intraspecific characteristic densities: carrying capacity K_1 for the producer, and the characteristic density K_2' of consumer population where intraspecific competition affects the growth as much as linear mortality.

Multi-level chain

The above reasoning lends itself to a generalization to arbitrary number levels. If $\alpha_{i,i-1}$ is the attack rate of level i on the level below, D_i is the strength of intraspecific competition and r_i is mortality, as for the the two level system, removing dimensions leads to the system

$$\begin{cases} w_N = & \epsilon_N a_N b_{N-1} - \psi_N b_N - \phi_N \\ \vdots & \vdots \\ w_i = & \epsilon_i a_i B_{i-1} - \psi_i B_i - a_{i+1} b_{i+1} - \phi_i;\ a_i = \dfrac{\alpha_{i,i-1}}{D_1};\ \psi_i = \dfrac{D_i}{D_1};\ \phi_i = \dfrac{r_i}{g} \\ \vdots & \vdots \\ w_1 = & 1 - b_1 - a_2 b_2 \end{cases}$$

From these we could compute the sensitivity matrix $V = (V_{ij})$ as previously defined. It is the inverse of the interaction matrix $\alpha = (\alpha_{ij})$

$$V_{ij} = \frac{\partial b_i^*}{\partial w_j} = (\alpha^{-1})_{ij} \text{ where } \alpha_{ij} = \frac{\partial w_i}{\partial b_j}$$

which takes the more explicit form here

$$\alpha = \begin{pmatrix} \psi_N & \epsilon_N a_N & & & \\ -a_N & \psi_{N-1} & \epsilon_{N-1} a_{N-1} & & \\ & & \ddots & & \\ & & & \psi_1 & \epsilon_1 a_1 \\ & & & -a_1 & 1 \end{pmatrix}$$

The equilibrium densities (assuming coexistence) are then given by

$$b_i^* = V_{i1} - \sum_{j>1} V_{ij}\phi_j$$

Amplifications now read, if $j > i$ (upward amplification)

$$A_{ij}^\uparrow = \frac{V_{ji}}{V_{ii}}$$

and the same holds if $j < i$ (downward amplification $A_{ij}^\downarrow$). The biomass ratio between top and lowest level reads

$$B_r = \frac{b_N^*}{b_1^*} = \frac{B_N^*}{B_1^*} = \frac{\frac{V_{N1}}{V_{11}} - \sum_{j>1}\frac{V_{Nj}}{V_{11}}\phi_j}{1 - \sum_{j>1}\frac{V_{1j}}{V_{11}}\phi_j} = \frac{A_{1N}^\uparrow - \rho_N - \sum_{1<j<N} A_{jN}^\uparrow \rho_j}{1 + \sum_{j>1} A_{j1}^\downarrow \rho_j}$$

where we defined

$$\rho_i = \frac{V_{jj}}{V_{11}}\phi_j$$

thus showcasing the generality of our approach: top down amplifications may have signature in biomass ratios if $A_{j1}^\downarrow \rho_j$ is comparable (or larger) than 1.

Nonlinear chain

In fact, the above results are not specific to linear growth rates (i.e Lotka-Volterra). For any form of growth rate functions w_i we can still define the interaction matrix $\alpha_{ij} = \frac{\partial w_i}{\partial b_j}$ and the write the density independent part of those functions $-\phi_i$ for consumers (relative intrinsic mortality) and 1 for the primary producer (intrinsic growth rate, used to set a time scale). As before $V_{ij} = (\alpha^{-1})_{ij} = \frac{\partial b_i}{\partial w_j}$ and we can therefore write

$$\begin{aligned} b_i^* &= \int_0^1 \frac{\partial b_i^*}{\partial w_1} dw_1 + \sum_{j>1} \int_0^{-\phi_j} \frac{\partial b_i^*}{\partial w_j} dw_j \\ &= \int_0^1 V_{i1} dw_1 - \sum_{j>1} \int_0^{\phi_j} V_{ij} dw_j \\ &= \langle V_{i1} \rangle - \sum_{j>1} \langle V_{ij} \rangle \phi_j \end{aligned}$$

where $\langle V_{ij} \rangle$ is the average sensitivity of species i to a change in growth rate of species j, as relative mortality is varied from 0 to its actual value, ϕ_j. We now have

$$B_r = \frac{b_N^*}{b_1^*} = \frac{B_N^*}{B_1^*} = \frac{\frac{\langle V_{N1} \rangle}{\langle V_{11} \rangle} - \sum_{j>1} \frac{\langle V_{Nj} \rangle}{\langle V_{jj} \rangle} \frac{\langle V_{jj} \rangle}{\langle V_{11} \rangle} \phi_j}{1 - \sum_{j>1} \frac{\langle V_{1j} \rangle}{\langle V_{jj} \rangle} \frac{\langle V_{jj} \rangle}{\langle V_{11} \rangle} \phi_j}$$

The difference with the linear chain is that now the amplification of a weak perturbation will be (for instance)

$$A_{Nj}^{\downarrow} = \frac{V_{Nj}}{V_{jj}}$$

evaluated at the actual conditions defined by the relative intrinsic rates ϕ_i. The amplification is not exactly equal to the term $\frac{\langle V_{Nj} \rangle}{\langle V_{jj} \rangle}$ that appears in the above expression of biomass ratio. Nonetheless, unless the growth rates w_i are strongly nonlinear functions of b_i , $A_{Nj}^{\downarrow}$ and $\frac{\langle V_{Nj} \rangle}{\langle V_{jj} \rangle}$ can be expected to be roughly equivalent. Thus if

$$\rho_i = \frac{\langle V_{ii} \rangle}{\langle V_{11} \rangle} \phi_i$$

we may still write that

$$B_r \approx \frac{A_{1N}^{\uparrow} - \rho_N - \sum_{1<j<N} A_{jN}^{\uparrow} \rho_j}{1 + \sum_{j>1} A_{j1}^{\downarrow} \rho_j}$$

This extension is useful to understand why nonlinearities can allow for some patterns in the data that would be forbidden by a the linear chain model. Indeed, if we go back to the expression of B_r in two level chain (14) we see that $A_{\uparrow}$ must be strictly larger than B_r. In the data this is not always the case. Slight non-linearity will remove this strong constraint since it is now $\frac{\langle V_{21} \rangle}{\langle V_{11} \rangle}$ that must be larger than B_r and not $A_{\uparrow}$. As we show numerically, only slight non-linearity (in the form of handling time by the consumers) is enough to produce theoretical pattern consistent with the data, as shown in Fig. (S3.4).

Appendix S3. Supplementary results

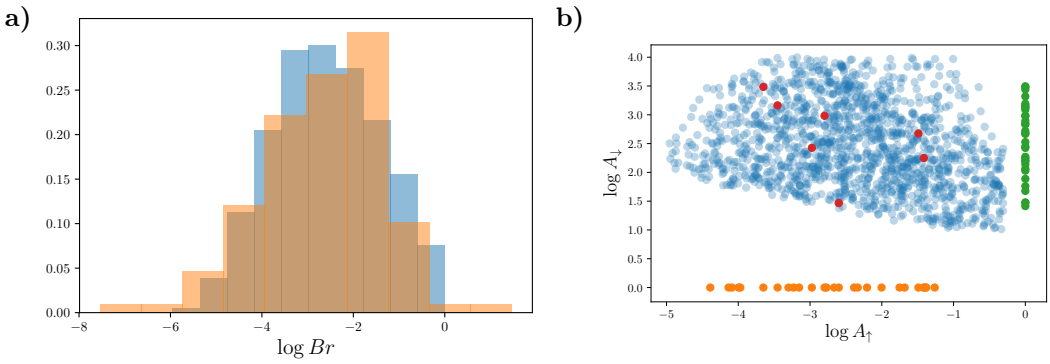

Figure S3.1: Experimental data versus simulated data. (a) Histograms of the biomass ratio in the experimental systems (orange) and in the simulated data (blue). Both distributions are normalised such that the area under the histogram sums to 1. (b) Relationship between bottom-up amplification ($A_\uparrow = \frac{\Delta B_{2\uparrow}}{\Delta B_{1\uparrow}}$) due to nutrient enrichment and top-down amplification ($A_\downarrow = -\frac{\Delta B_{1\downarrow}}{\Delta B_{2\downarrow}}$) due to fish addition. Red points represent all the $A_\uparrow$ values in the empirical data. Green points represent all the $A_\downarrow$ values in the empirical data. Orange points represent the empirical data for which both values of $A_\uparrow$ and $A_\downarrow$ were accessible. Blue points represent the simulated data.

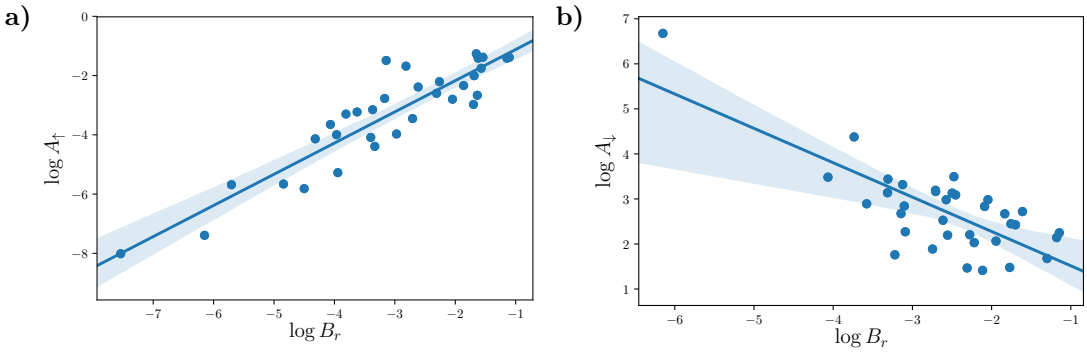

Figure S3.2: Empirical relationship between biomass distribution across trophic levels and response ratio without exclusion of the outliers. (a) Relationship between biomass ratio ($B_r = \frac{B_2}{B_1}$) and bottom-up response ratio ($A_\uparrow = \frac{\Delta B_{2\uparrow}}{\Delta B_{1\uparrow}}$) due to nutrient enrichment. (b) Relationship between biomass ratio and top-down response ratio ($A_\downarrow = -\frac{\Delta B_{1\downarrow}}{\Delta B_{2\downarrow}}$) due to fish addition. Each point represents a food chain in our analyses. Blue lines represent the linear regression and shaded areas represent 95% confidence intervals.

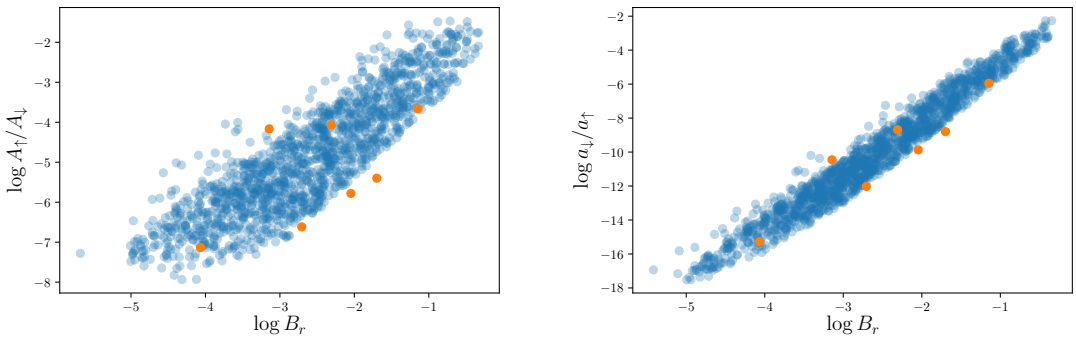

Figure S3.3: From our theoretical expression (6) at intermediate values of ρ, as in the case of the selected simulated data points, we expect a linear relationship between B_r and the ratio of upwards and downwards responses $A_\uparrow/A_\downarrow$ (left panel). Similarly, the variant (11) predicts a similar relationship relationship between B_r and the ratio of upwards and downwards amplifications $a_\downarrow/a_\uparrow$ (right panel, notice, however, difference in range of the two axis).

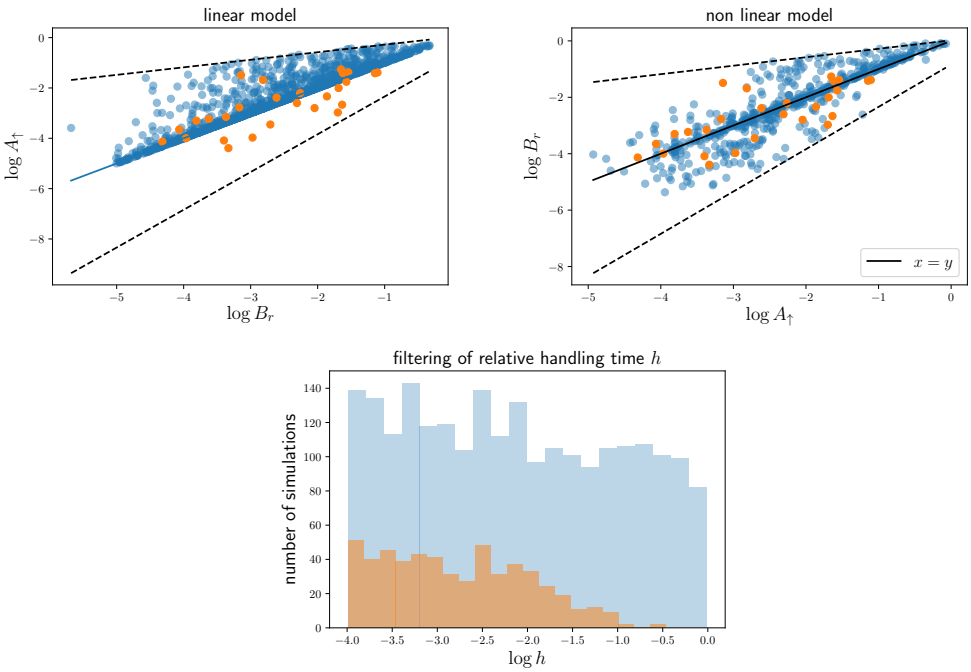

Figure S3.4: Comparison of simulations and data for linear and non-linear resource-consumer models. In the non-linear model, we use a Holling type II functional response $f(b_1) = \frac{ab_1}{1+hab_1}$ for consumption, with relative handling time h. All other parameters are the same, and drawn from the same distributions, as in the linear model described in the main text, and h is drawn uniformly on log scales in $[10^{-4}, 10^0]$. Upper row: $A_\uparrow$ vs B_r for empirical data points (orange) and simulated data points (blue). In the linear model (left), $A_\uparrow$ cannot be smaller than B_r, yet the data shows points that violate this condition. (right) slight non linearity can relax this constraint. Bottom row: distribution of handling time after filtering by the empirical patterns. We observe that only small values are selected (weak non linearity).

References

Acuña, P., Vila, I. & Marín, V.H. (2008). Short-term responses of phytoplankton to nutrient enrichment and planktivorous fish predation in a temperate South American mesotrophic reservoir. *Hydrobiologia*, 600, 131–138.

Beresford, A.L. & Jones, J.I. (2010). Weedbeds and big bugs: the importance of scale in detecting the influence of nutrients and predation on macroinvertebrates in plant-dominated shallow lakes. *Freshwater Biology*, 55, 514–530.

Dickman, E.M., Newell, J.M., González, M.J. & Vanni, M.J. (2008). Light, nutrients, and food-chain length constrain planktonic energy transfer efficiency across multiple trophic levels. *Proceedings of the National Academy of Sciences*, 105, 18408–18412.

Drenner, R.W., Smith, J.D., Mummert, J.R. & Lancaster, H.F. (1990). Responses of a eutrophic pond community to separate and combined effects of N: P supply and planktivorous fish: a mesocosm experiment. *Hydrobiologia*, 208, 161–167.

Drenner, R.W., Threlkeld, S.T., Smith, J.D., Mummert, J.R. & Cantrell, P.A. (1989). Interdependence of phosphorus, fish, and site effects on phytoplankton biomass and zooplankton. *Limnology and oceanography*, 34, 1315–1321.

Faafeng, B.A., Hessen, D.O., Brabrand, Å. & Nilssen, J.P. (1990). Biomanipulation and food-web dynamics—the importance of seasonal stability. In: *Biomanipulation Tool for Water Management*. Springer, pp. 119–128.

Fernández-Aláez, M., Fernández-Aláez, C., Bécares, E., Valentín, M., Goma, J. & Castrillo, P. (2004). A 2-year experimental study on nutrient and predator influences on food web constituents in a shallow lake of north-west Spain. *Freshwater Biology*, 49, 1574–1592.

Hansson, L., Gyllström, M., Ståhl-Delbanco, A. & Svensson, M. (2004). Responses to fish predation and nutrients by plankton at different levels of taxonomic resolution. *Freshwater Biology*, 49, 1538–1550.

Hietala, J., Vakkilainen, K. & Kairesalo, T. (2004). Community resistance and change to nutrient enrichment and fish manipulation in a vegetated lake littoral. *Freshwater Biology*, 49, 1525–1537.

Hulot, F.D., Lacroix, G. & Loreau, M. (2014). Differential responses of size-based functional groups to bottom–up and top–down perturbations in pelagic food webs: a meta-analysis. *Oikos*, 123, 1291–1300.

Lacroix, G. & Lescher-Moutoue, F. (1991). Interaction effects of nutrient loading and density of young-of-the-year cyprinids on eutrophication in a shallow lake: an experimental mesocosm study. *Mem. Ist. Ital. Idrobiol*, 48, 53–73.

Lynch, M. & Shapiro, J. (1981). Predation, enrichment, and phytoplankton community structure 1. *Limnology and oceanography*, 26, 86–102.

Mazumder, A., McQueen, D.J., Taylor, W.D., Lean, D.R.S. & Dickman, M.D. (1990). Micro-and mesozooplankton grazing on natural pico-and nanoplankton in contrasting plankton communities produced by planktivore manipulation and fertilization. *Archiv für Hydrobiologie*, 118, 257–282.

McQueen, D.J., France, R. & Kraft, C. (1992). Confounded impacts of planktivorous fish on freshwater biomanipulations. *Archiv für Hydrobiologie*, 125, 1–24.

Menezes, R.F., Attayde, J.L. & RIVERA VASCONCELOS, F. (2010). Effects of omnivorous filter-feeding fish and nutrient enrichment on the plankton community and water transparency of a tropical reservoir. *Freshwater Biology*, 55, 767–779.

Proulx, M., Pick, F.R., Mazumder, A., Hamilton, P.B. & Lean, D.R.S. (1996). Effects of nutrients and planktivorous fish on the phytoplankton of shallow and deep aquatic systems. *Ecology*, 77, 1556–1572.

Qin, J. & Culver, D.A. (1995). Separate and combined effects of larval walleye and fertilization on plankton community structure in enclosures. *Journal of Freshwater Ecology*, 10, 385–391.

Riemann, B. (1985). Potential importance of fish predation and zooplankton grazing on natural populations of freshwater bacteria. *Appl. Environ. Microbiol.*, 50, 187–193.

Romo, S., Miracle, M.R., Villena, M., Rueda, J., Ferriol, C. & Vicente, E. (2004). Mesocosm experiments on nutrient and fish effects on shallow lake food webs in a Mediterranean climate. *Freshwater Biology*, 49, 1593–1607.

Sinistro, R. (2010). Top-down and bottom-up regulation of planktonic communities in a warm temperate wetland. *Journal of Plankton Research*, 32, 209–220.

Stephen, D., Balayla, D.M., Collings, S.E. & Moss, B. (2004). Two mesocosm experiments investigating the control of summer phytoplankton growth in a small shallow lake. *Freshwater Biology*, 49, 1551–1564.

Van De Bund, W.J. & Van Donk, E. (2004). Effects of fish and nutrient additions on food-web stability in a charophyte-dominated lake. *Freshwater Biology*, 49, 1565–1573.

Vanni, M.J. (1987a). Effects of food availability and fish predation on a zooplankton community. *Ecological Monographs*, 57, 61–88.

Vanni, M.J. (1987b). Effects of nutrients and zooplankton size on the structure of a phytoplankton community. *Ecology*, 68, 624–635.