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LETTER

Can biomass distribution across trophic levels predict trophic cascades?

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Abstract

The biomass distribution across trophic levels (biomass pyramid) and cascading responses to perturbations (trophic cascades) are archetypal representatives of the interconnected set of static and dynamical properties of food chains. A vast literature has explored their respective ecological drivers, sometimes generating correlations between them. Here we instead reveal a fundamental connection: both pyramids and cascades reflect the dynamical sensitivity of the food chain to changes in species intrinsic rates. We deduce a direct relationship between cascades and pyramids, modulated by what we call trophic dissipation – a synthetic concept that encodes the contribution of top-down propagation of consumer losses in the biomass pyramid. Predictable across-ecosystem patterns emerge when systems are in similar regimes of trophic dissipation. Data from 31 aquatic mesocosm experiments demonstrate how our approach can reveal the causal mechanisms linking trophic cascades and biomass distributions, thus providing a road map to deduce reliable predictions from empirical patterns.

Keywords

Biomass ratio, consumer-resource dynamics, food chain, food web, perturbation, response amplification, self-regulation.

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INTRODUCTION

Food chains are a central concept of ecology, providing intuitions and predictions not only about basic static properties of food webs, such as the distribution of biomass across the trophic hierarchy, that is the trophic pyramid (Elton, 1927; Lindeman, 1942), but also about more complex dynamical processes, such as the propagation of a perturbation along the chain, that is trophic cascades (Carpenter *et al*., 1985; Polis *et al*., 2000; Shurin *et al*., 2002; Borer *et al*., 2005). Trophic cascades are prevalent in nature, yet of highly variable strength across systems (Polis *et al*., 2000; Shurin *et al*., 2002; Frank *et al*., 2006) and thus hard to predict, an observation that has prompted the proliferation of studies exploring the mechanisms behind their existence and magnitude (Halaj and Wise, 2001; Shurin and Seabloom, 2005; Borer *et al*., 2005; Heath *et al*., 2014; Ripple *et al*., 2016).

Studies of static and dynamical properties of food chains have historically developed in isolation, generating different lines of investigation, which have seldom been connected rigorously (but see Jonsson (2017); McCauley *et al.* (2018); Barbier and Loreau (2019); Rossberg *et al.* (2019)). A number of applied studies have proposed to predict an ecosystem's 'health' and dynamical response from its more accessible static biomass pyramid or size spectrum (Shin *et al*., 2005; Cury *et al*., 2005). Yet, others claim that such static features are not informative about the underlying food chain dynamics (Trebilco *et al*., 2016; McCauley *et al*., 2018; Woodson *et al*., 2018). Here, we propose that there are several ways in which cascades and biomass pyramids could be related (or not), leading to contrasting interpretations. They can correlate across ecosystems via dependency on common parameters, as suggested by recent theory (Heath *et al*., 2014; Barbier and Loreau, 2019; Fig. 1a). But, as we will argue in depth, they can also be more tightly connected, when the two phenomena arise from a single dynamical mechanism that acts as a common proximate cause (Fig. 1b). Importantly, a direct link is required to reliably predict dynamical behaviours from static snapshots alone, without additional knowledge of potential confounding factors.

This dichotomy is at the core of the present study. We specifically ask when the shape of the standing biomass pyramid is – or is not – *causally* related to the strength of trophic cascades. In other words, we investigate the nature and drivers of *the relationship* between cascade strength and the shape of the biomass pyramid, to then determine when and how the latter can be used to predict the former. This novel perspective complements previous studies: we do not ask why the cascades are weak or strong (Borer *et al*., 2005), but rather why their strength can or cannot be predicted from the observation of the biomass pyramid.

The simplest expectation, for any ecosystem with multiple compartments, is that the response of a compartment to a perturbation is proportional to its standing biomass. We take it as our baseline (Fig. 2a). This expectation may appear intuitive, yet many classical results on food chains do *not*, in fact, support it. On a quantitative level, deviations from strict proportionality occur in many theoretical and empirical studies, and have been used to define whether a cascade is strong or weak (Hedges *et al*., 1999; Shurin *et al*., 2002). These deviations are commonly interpreted as an amplification or attenuation of perturbations as they propagate along the chain (Box 1). The proportionality hypothesis implies that *both* upward and downward effects are directly related to the

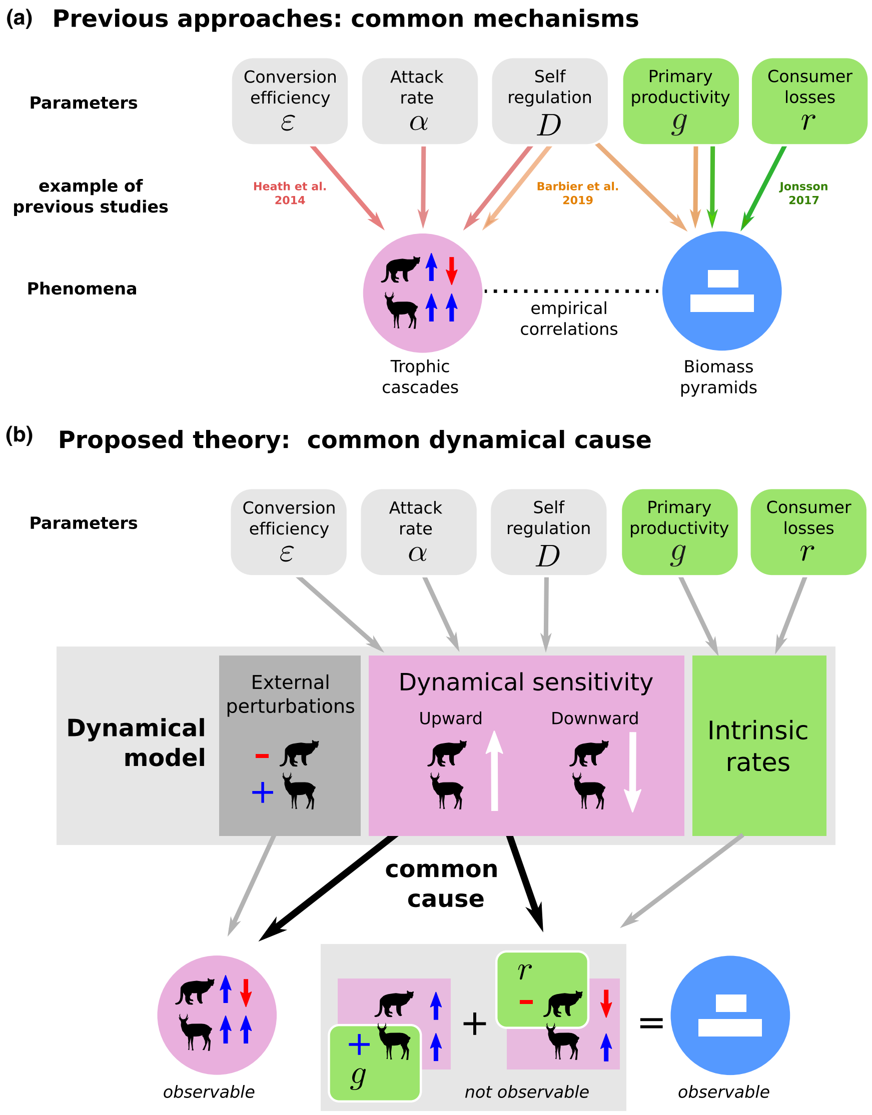

Figure 1 Relating biomass pyramids and trophic cascades. (a) Previous studies have investigated ecological parameters that affect the pyramidal distribution of biomass across trophic levels and the strength of trophic cascades (e.g. Heath *et al.*, 2014; Jonsson, 2017; Barbier and Loreau, 2019) (arrows are not exhaustive). These parameters may drive empirical correlations between the two phenomena. (b) Here we focus on a direct common cause: the dynamical sensitivity of the ecosystem to both upward and downward effects along the food chain. This dynamical sensitivity combines with external perturbations to create trophic cascades, and with the food chain's intrinsic rates of biomass gain and loss (g and r) to determine biomass pyramids. By factoring out perturbation intensity, trophic cascades readily provide an estimate of dynamical sensitivity. Biomass pyramids, however, are the result of a complex entanglement of upward and downward effects, which cannot be directly observed and separated. Across ecosystems, a one-to-one relationship between biomass pyramids and trophic cascades exists if the main source of variation is dynamical sensitivity (see Figure 2).

biomass distribution. Yet, it has long been noticed that the significance of these two types of effects can widely differ across systems. Each has been the focus of a classic perspective on food chain structure and dynamics. The resource-based perspective posits that producers determine the biomass of higher trophic levels (Elton, 1927; Lindeman, 1942), while the consumer-based perspective emphasises the role of predators in regulating the biomass of lower trophic levels (Hairston *et al.*, 1960; Leibold, 1996; Gruner *et al.*, 2008).

The key intuition that we explore here is that standing biomasses and trophic cascades both reflect some aspects of the dynamical sensitivity of the food chain. This is obviously true of trophic cascades, but we argue that standing biomasses can also reflect either (1) bottom-up responses of the food chain to primary productivity, (2) top-down response to consumer losses (e.g. mortality and metabolic costs) or both. Thus, if we can tease apart those contributions, we can then infer the chain's dynamical response to perturbations (Fig. 1b). What can and cannot be inferred will clearly be context dependent: for instance, when the rate of consumer intrinsic losses are negligible compared to primary productivity (as in Barbier and Loreau, 2019), the biomass distribution is entirely driven by bottom-up propagation of primary productivity, and cannot tell us whether response to a top-down perturbation (e.g. predator removal) would be weak or strong. Conversely, in some models such as 'exploitation ecosystems' (Oksanen *et al.*, 1981), standing biomasses are driven by top-down effects, with primary productivity only controlling the number of trophic levels allowed in the food chain.

We reveal a synthetic mechanism that controls the relative contribution of top-down and bottom-up dynamical effects in the biomass pyramid, and thus determines which causal relationships exist, in a given system, between cascades and biomass pyramids. We call this mechanism *trophic dissipation* as it encodes the net effects of consumer intrinsic losses on standing biomasses (Box 1). In particular, this means that primary productivity, trophic interactions or self-regulation (e.g. intraguild competition) affect the relationship between cascades and pyramids as much as they affect trophic dissipation (Box 1, Fig. 1).

Using data from 31 mesocosm experiments of pelagic food webs, which monitored standing biomass and long-term responses to top-down and bottom-up perturbations, we then

Box 1. Definition of main concepts.

Upward amplification/attenuation: stronger/weaker response of higher trophic levels relative to lower trophic levels after a perturbation at the bottom of the chain (e.g. nutrient enrichment).

Downward amplification/attenuation: stronger/weaker response of lower trophic levels relative to higher trophic levels after a perturbation at the top of the chain (e.g. fish addition).

Self-regulation: regulatory mechanisms that cause per capita growth rates to depend on the biomass of the species in question (e.g. intraspecific interference, cannibalism or effects from hidden compartments such as pathogens).

Trophic dissipation: general concept representing, at any trophic level, the relative importance of consumer intrinsic loss versus primary productivity (i.e. energy dissipation versus basal influx) in shaping the standing biomass. This concept can be defined formally for a given trophic level, becoming dissipative loss for the consumer, and dissipative release for the resource (eqn (3)). In every case (including longer and nonlinear food chains), it combines the base magnitude of productivity and consumer losses, and how they are transmitted and modulated by trophic interactions and by self-regulation.

–*Dissipative loss*: $\boldsymbol{\chi}$ in the consumer's standing biomass, reduction caused by consumer intrinsic loss (from metabolic costs and mortality), divided by gains from primary production.

–*Dissipative release*: $\boldsymbol{\xi}$ in the ressource's standing biomass, gains (by prey release) caused by consumer intrinsic loss, divided by gains from primary production.

Dynamically consistent chains: food chains where, in the long-term, the two levels respond in the same direction to nutrient enrichment, and in opposite directions to fish addition.

ask when causal relationships within one ecosystem can translate into statistical patterns across ecosystems (Fig. 2b). Combining theory and data, we find that the experimental systems demonstrate two types of relationships between biomass and cascades: correlations driven by common factors, and direct causation (Fig. 1). We conclude that understanding the entangled dependencies between biomass distribution and dynamical responses is essential to properly interpret the patterns observed in natural communities, and enhance our capacity to predict the long-term effects of perturbations.

THEORETICAL FRAMEWORK: WITHIN-SYSTEM RELATIONSHIPS

We build on the work presented in (Barbier and Loreau, 2019) to develop a theoretical framework spanning the various dynamical regimes previously studied in food chains (e.g. resource and consumer control). Our goal is to determine what dynamical signatures ought to be present, or not, in the standing biomass pyramid of a food chain, and how these signatures can be used to predict the strength of trophic cascades. We complement the framework of (Barbier and Loreau, 2019) by explicitly accounting for consumer intrinsic rate of biomass loss (e.g. due to mortality or metabolic costs). For simplicity, and to match the experimental systems analysed in the next section, we focus on a two-level system, and further 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 S1 for multilevel and nonlinear chain results). Here, long-term responses to perturbations are understood as shifts in equilibrium biomasses. Although empirical systems are never perfectly stationary, equilibrium analysis of such dynamical models have proven successful in quantifying species interactions and responses even in data with significant temporal variance (Maynard *et al.*, 2019; Barbier et al., 2020).

Let $B_i, i=1,2$ be the biomass density of primary producers and consumers respectively. We model the growth rate of species biomass as

$$\begin{pmatrix} \dfrac{1}{B_1}\dfrac{dB_1}{dt} = & g - D_1 B_1 - \alpha B_2 \\ \dfrac{1}{B_2}\dfrac{dB_2}{dt} = & \varepsilon\alpha B_1 - D_2 B_2 - r \end{pmatrix} \tag{1}$$

where $g>0$ denotes the intrinsic biomass production rate of primary producers, and $r>0$ the intrinsic biomass losses 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 rate of biomass loss at both trophic levels (i.e. self-regulation). Finally, $0<\varepsilon<1$ is the efficiency of productivity transfer from producers to consumers. There are two units: time and biomass density. Here we are interested only in non-dimensional quantities, such as biomass ratio $B_r = B_2/B_1$ and response ratios

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

where $A_{\uparrow}$ reflects the biomass change of level 2 relative to that of level 1 following a perturbation at the bottom of the chain, while $A_{\downarrow}$ represents the biomass change of level 1 relative to that of level 2 following a perturbation at the top. Regardless of the dynamical model considered, if perturbations are not severe enough to elicit significant nonlinear responses, the use of response ratios as measures of response to perturbations eliminates potential differences in the magnitude of the perturbations performed across systems.

Solving for the equilibrium of a two-species Lotka–Volterra system (see Appendix S2), we find that the biomass ratio B_r can be expressed as follows:

$$B_r = \left(\frac{\varepsilon\alpha}{D_2}\right)\frac{1-\chi}{1+\xi};\ \ \chi = \frac{D_1\, r}{\varepsilon\alpha\, g};\ \ \xi = \frac{\alpha\ r}{D_2\, g} \tag{3}$$

In this expression, we have isolated two terms, χ and ξ, that express the relative effect of consumer intrinsic losses r and

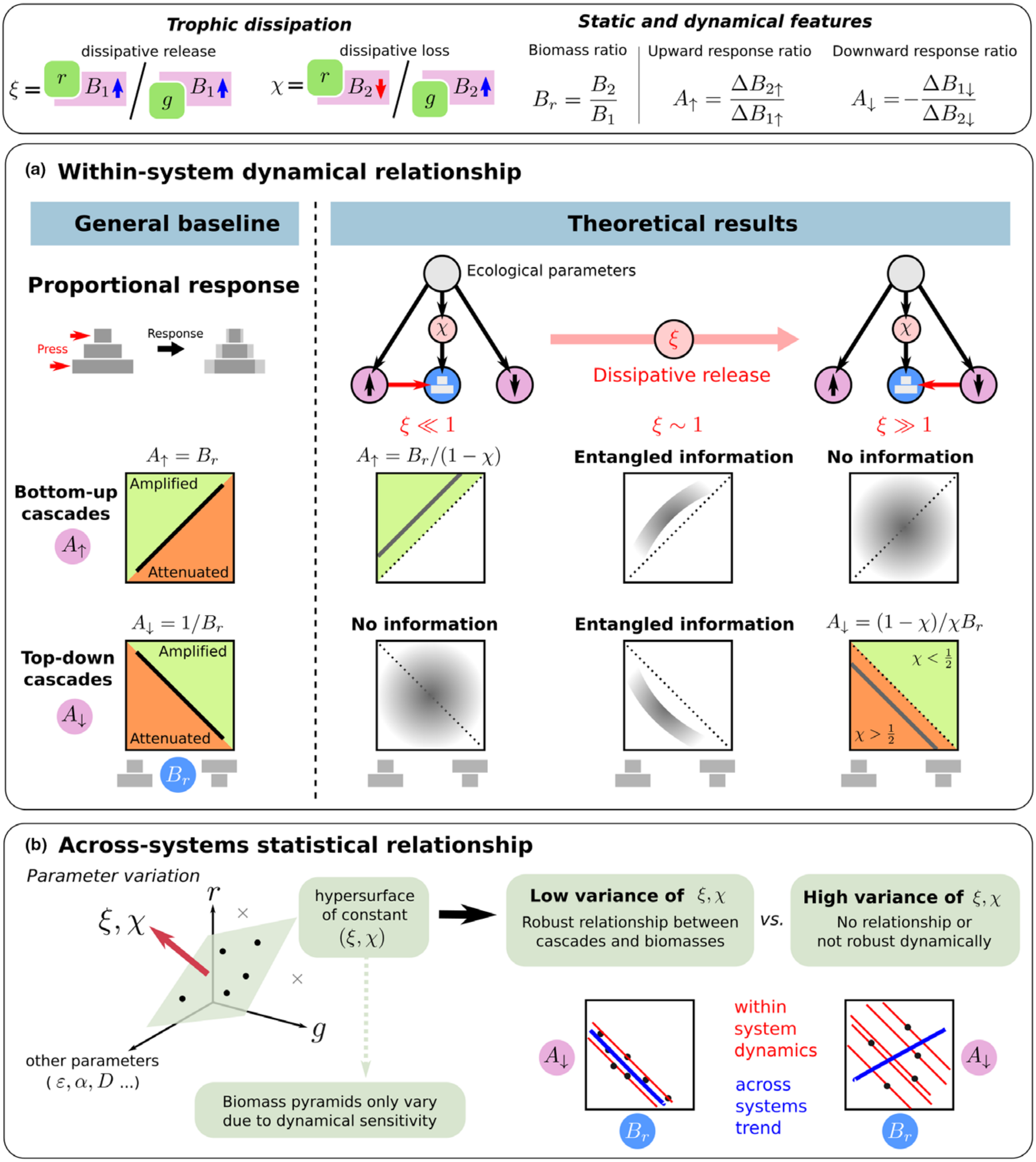

Figure 2 Relationship between static and dynamic properties in food chains. (a) Within one system, the simplest expectation is that a trophic level's response to a perturbation is proportional to its biomass. Deviations from this trend indicate the amplification or attenuation of perturbations between levels (Shurin *et al.*, 2002). Food chain theory instead suggests two limiting cases where equilibrium biomasses are related either to bottom-up effects only, or to top-down effects only. Our framework connects these two limits on a single axis of *trophic dissipation*. From the consumer perspective, we identify *dissipative loss* χ and from the resource perspective *dissipative release* ξ (see Box 1). When these two parameters are fixed, all other sources of variation affect biomasses only through the same dynamical effects that generate trophic cascades, so that a direct link can be established between these properties (Figure 1). Dissipative release ξ determines the qualitative nature of the dynamical-structural relationship, while dissipative loss χ governs its quantitative expression. When dissipative release is small, biomass ratio B_r is proportional to upward response ratio $A_\uparrow$ (red arrow), with amplification quantified as $1/(1-\chi)$. However, B_r says nothing of the downward response. Conversely, if dissipative release is large, then B_r predicts the downward response, amplified or attenuated by a factor $(1-\chi)/\chi$. Around the threshold $\xi \sim 1$, downward or upward dynamical effects are entangled in the biomass distribution, so that B_r is partially correlated with both cascade directions (see Figure 3). (b) A within-system relationship between biomass ratio and cascade strength translates into a statistical pattern across ecosystems if they are in similar regimes of *trophic dissipation*. More precisely, any hyperplane of constant ξ and χ in the larger ecological parameter space leads to a relationship between the shape of the biomass pyramid and trophic cascade strength.

primary productivity g on the standing biomasses of both levels. Similar terms appear in more complex models (e.g. longer food chains and nonlinear dynamics, Appendix S1).

χ is the ratio of predator biomass losses (at equilibrium) due to predators' intrinsic losses r, over gains from consumption of primary productivity g (Appendix S1). We call χ *dissipative loss*, as it represents a decrease from the maximum predator biomass allowed by primary productivity. In contrast, ξ is the ratio of biomass gains of the prey due to predators' intrinsic losses, over the contribution to standing biomass of productivity. We call ξ *dissipative release*, as it reflects the relative importance of prey release caused by consumer losses. Both notions – which are not independent from one another – relate to what we call *trophic dissipation*, seen from either the consumer's (χ) or the producer's (ξ) perspective (Box 1).

We now explain how static properties – B_r, the prefactor $\varepsilon\alpha/D_2$ in eqn (3), χ and ξ – can be associated with dynamical responses to bottom-up and top-down perturbations. To see this, consider a perturbation Δg of primary productivity, such as a nutrient enrichment treatment. The changes in biomass of trophic level 1 and trophic level 2 read, respectively, as follows:

$$\Delta B_{1\uparrow} = \frac{\Delta g}{b} D_2, \text{ and } \Delta B_{2\uparrow} = \frac{\Delta g}{b} \varepsilon\alpha \tag{4}$$

where $b = D_1 D_2 + \varepsilon\alpha^2$ (b plays no role in what follows). Similarly, changes in biomass due to a change in consumer mortality Δr (e.g. caused by fish addition), are as follows:

$$\Delta B_{1\downarrow} = \frac{\Delta r}{b}\alpha \text{ and } \Delta B_{2\downarrow} = -\frac{\Delta r}{b} D_1. \tag{5}$$

Thus, bottom-up and top-down responses read, respectively, as follows:

$$A_\uparrow = \frac{\varepsilon\alpha}{D_2} \text{ and } A_\downarrow = \frac{\alpha}{D_1}. \tag{6}$$

We recognise in $A_\uparrow$ the prefactor of the r.h.s of eqn (3). Furthermore, by comparing eqn (6) with the expressions of ξ and χ in eqn (3), we can deduce that

$$\xi = \chi A_\uparrow A_\downarrow \tag{7}$$

This expression is not just an algebraic manipulation. It reveals the dynamical mechanism that allows us to move from the predator to the prey's perspective of trophic dissipation. This mechanism is represented by the product $A_\uparrow A_\downarrow$ of upwards and downwards growth propagation, which measures the strength of the dynamical feedback loop in the food chain (denoted λ in Barbier and Loreau, 2019).

With eqns (3 and 7), we now have all the ingredients to propose a formal relationship between biomass ratio, response ratio and trophic dissipation (see Appendix S2 for details and generalisations).

$$B_r = \frac{A_\uparrow(1-\chi)}{1+\chi A_\uparrow A_\downarrow} \tag{8}$$

This expression makes it clear that three different factors determine the predator–prey biomass ratio: the two dynamical response ratios $A_\uparrow$ and $A_\downarrow$, and the additional effects of growth and losses that enter in the dissipative loss χ.

The value of dissipative release ξ (7) determines three main qualitative regimes of eqn (8), as shown in Figs 2 and 3. At the extremes, only upward or downward cascades are related to biomasses:

$$\begin{aligned} B_r &\approx A_\uparrow(1-\chi) \quad &&\text{if } \xi \ll 1, \\ B_r &\approx \frac{1-\chi}{\chi A_\downarrow} \quad &&\text{if } \xi \gg 1. \end{aligned} \tag{9}$$

For intermediate values $\xi \sim 1$, the contributions of upward and downward responses in the biomass ratio are entangled in eqn (8). They cannot be separated (and thus up- or downwards cascade strength cannot be predicted from B_r) without knowing the precise value of both ξ and χ.

We see that ξ determines the qualitative regime in which the system is in, while χ controls the slope of the relationship within each regime. If $\xi \ll 1$, then $A_\uparrow \approx B_r/(1-\chi)$, the biomass distribution is entirely shaped by upward effects. Upward perturbations either follow proportional response if $\chi \approx 0$, as in Barbier and Loreau (2019), or are amplified. In contrast, the biomass ratio contains no *a priori* information about downward responses $A_\downarrow$ (Fig. 3a). In the opposite limit of large ξ, $A_\downarrow$ will be inversely proportional to B_r, but with a prefactor $(1-\chi)/\chi$ that can lead to downward cascade amplification if $\chi < 1/2$ and attenuation if $\chi > 1/2$ (Fig. 3b). Proportional response is thus unlikely for top-down effects, as it requires exactly $\chi = \frac{1}{2}$. If consumer self-regulation is very weak or zero, we find $A_\uparrow, \xi \to \infty$ and only the top-down driven regime is observed, as in classical models (e.g. Oksanen *et al.*, 1981; Rossberg *et al.*, 2019) that have been used to display counterintuitive dynamical effects in food webs.

EMPIRICAL ANALYSES

Data collection and formatting

To analyse whether causal relationships within one ecosystem translate into statistical patterns across ecosystems, we selected from the literature 21 independent studies reporting on 31 mesocosm experiments of pelagic food webs that performed long-term bottom-up and top-down treatments (see Appendix S2; Hulot *et al.* (2014)). All studies investigated community responses to nutrient enrichment, fish addition, and both perturbations together. They reported species biomass before and after the perturbation. Detailed information about the studies can be found in Appendix S2. These studies allow us to illustrate how our framework can be used to interpret empirical patterns. Even though those patterns might be specific to the pelagic setting of the experiments, we stress that our framework has no restriction on the type of system considered (e.g. marine or terrestrial).

The pelagic communities considered contain different paths of energy transmission across trophic levels (Fig. 4a). To properly study biomass pyramids and trophic dynamics, it is fundamental to identify paths of energy that adequately behave as food chains (Barbier and Loreau, 2019). We define as *dynamically consistent chains* those where prey and predators respond in the same direction to bottom-up perturbations, and in opposite directions to top-down perturbations (Box 1). We thus decomposed empirical food webs into all the

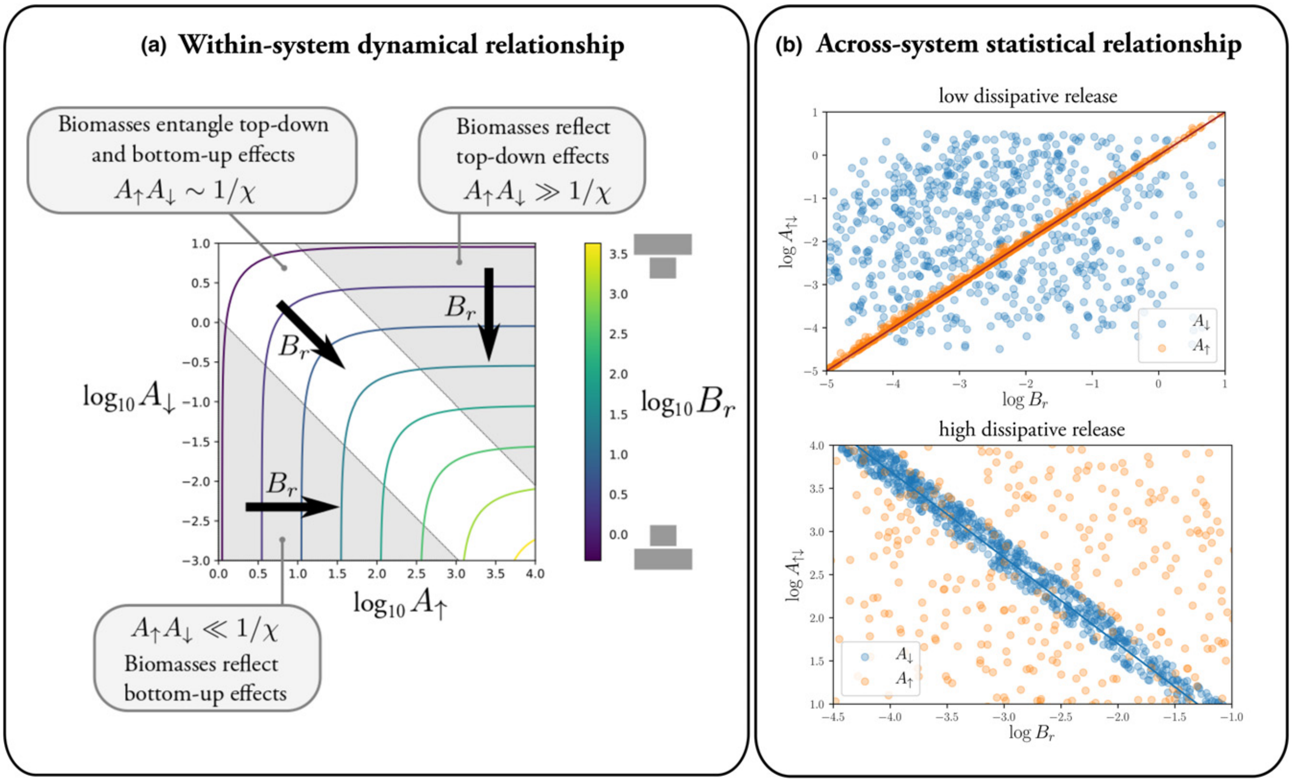

Figure 3 The relationship between biomass distribution across trophic levels and response to perturbations, given dissipative loss χ (Box 1). (a) Within a system, if we vary responses $A_\uparrow$ and $A_\downarrow$, the threshold $1/\chi$ determines the importance of bottom-up and top-down effects. When $A_\uparrow A_\downarrow \ll 1/\chi$ (corresponding to $\xi \ll 1$ in Figure 2), the biomass distribution only reflects bottom-up effects, as shown by the vertical isolines. Above that threshold, B_r only reflects top-down effects (horizontal isolines), and close to the threshold, it entangles information about both bottom-up and top-down effects. (b) An across-system statistical relationship emerges when there is small variation in χ. Simulations of the model (1) (for the range of parameters described in the main text) showing two limit cases of eqn (8). For low dissipation (here we selected realisations where $\xi < 10^{-1}$, and $\chi \in (0, 0.4)$), upward response ratio $A_\uparrow$ shows a proportional relationship with biomass ratio (the solid line has slope 1 in log-log scale) while there is no correlation between B_r and downward response ratio $A_\downarrow$. For large dissipation (here $\xi > 10$ and $\chi \in (0.6, 0.8)$), 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 $A_\uparrow$.

possible chains and analysed them independently (Fig. 4a; Appendix S2). To ensure that the decomposition of the food webs into multiple chains do not bias our analyses, we included a study system as a random effect in our statistical models (see below).

Data analyses

The third trophic level (fish) was viewed as a perturbation treatment in the experiments considered (only presence/absence reported). Therefore, we characterised the biomass distribution only for the first two trophic levels (phytoplankton and zooplankton), using the following ratio:

$$B_r = \frac{B_2^*}{B_1^*} \tag{10}$$

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.

The experiments were designed to observe long-term responses to bottom-up (i.e. nutrient enrichment) and top-down (i.e. fish addition) perturbations (6–12 months). Therefore, we considered the biomasses reported as stationary. To remove the dependency on (unknown) perturbation intensity, we further based our analysis on the expectation of a linear response of biomasses to the two treatments (perturbation intensity is removed by only considering response ratios).

For each level $i = 1, 2$, we estimated the bottom-up change in biomass $\Delta B_{i\uparrow}$ due to nutrient enrichment, and the top-down effect $\Delta B_{i\downarrow}$ due to fish addition. We measured these changes comparing the perturbed biomasses with the unperturbed value B_i^*. But since there was also a cross-treatment with both enrichment and fish, we fitted a multilinear model.

$$B_i = \tilde{B}_i + x_\uparrow \Delta B_{i\uparrow} + x_\downarrow \Delta B_{i\downarrow}; \;\; x_\uparrow = 0, 1; x_\downarrow = 0, 1. \tag{11}$$

where the binary treatment variable $x_\uparrow = 0$ or 1 represents the absence or presence of nutrient enrichment, and $x_\downarrow = 0$ or 1 represents the absence or presence of fish. We thus identified the coefficients $\Delta B_{i\uparrow}$ and $\Delta B_{i\downarrow}$ as the slopes of the multilinear response, with an intercept $\tilde{B}_i$.

The goodness-of-fit informed us of whether these estimates were robust: a large fitting error indicates significant interaction between the two treatments. For instance, nutrient

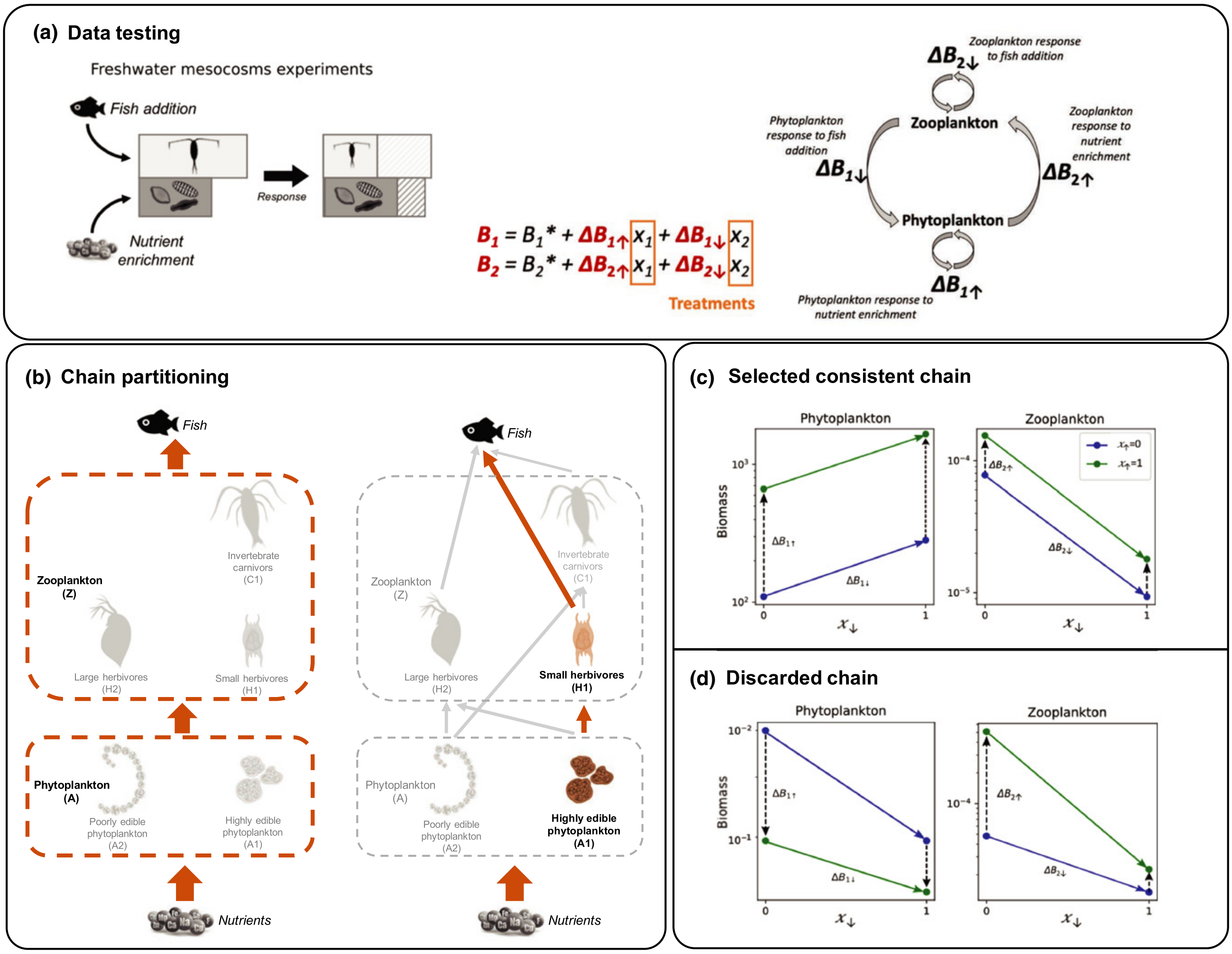

Figure 4 Data analyses illustration. (a) We used data from 31 mesocosm experiments of pelagic food webs that monitored both biomass distributions and long-term responses to nutrient enrichment and fish addition, and estimated the biomass response of two trophic levels to evaluate whether we could detect any of the possible patterns in a natural system. (b) 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. (c and d) 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 the two trophic levels to respond in the same direction to nutrient enrichment, and in opposite directions to fish addition. In (c), 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 (d), we show a case where the system does not behave as a consistent chain. First, phytoplankton biomass decreases with nutrient enrichment while zooplankton biomass increases. Second, both trophic level respond negatively to fish addition. Additionally, we can also observe the filtering of the responses based on the associated estimated error. While in (c) we observe similar slopes between the green and blue lines (i.e., low error) in (d) the error associated to the estimation of the responses is large, shown by the differences in the slope between green and blue lines.

enrichment is realised both without and with fish addition. The associated error on response $\Delta B_{i\uparrow}$ is large when the two measurements are incompatible (Fig. 4b and c). This can hint either to measurement error, non-stationary behaviour or strong nonlinearities, which we do not consider here.

We therefore selected the fitted coefficients estimated with low errors (i.e. estimated error < coefficient value, see Fig. 4b and c). From selected coefficients, we deduced as in eqn (2), upward ($A_\uparrow$) and downward ($A_\downarrow$) response ratios, where $A_\uparrow$ 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.

In addition to the filtering for coefficients estimated with low errors, we only selected the *dynamically consistent chains* (Box 1). Discarded response ratios can indicate other dynamical behaviours (such as competition) that are not consistent with a simple food chain. We verified using Kolmogorov–Smirnov tests that both filters (i.e. low error and expected response direction) did not bias the distribution of the responses considered (Appendix S2).

To analyse the across-system statistical relationship between biomass distribution and trophic cascades, we performed linear mixed effects models including B_r as a fixed effect, study system as a random effect, and $A_\uparrow$ and $A_\downarrow$ as response variables. For $A_\uparrow$, we found that the variance explained by the study system was 0.19; therefore, we included the study system as a random effect. However, we found no differences between the model including the study system as a random effect (AIC = 57.9) and the model including only B_r as a fixed effect (AIC = 57.0). For $A_\downarrow$, the variance associated to the study system was 0.002, and the model including only B_r as a fixed effect was better (AIC = 58.3; the linear mixed model with the study system as a random effect AIC = 60.3). Thus, the results presented below correspond to the analyses were only B_r was included as a fixed effect in the model.

ACROSS-SYSTEMS STATISTICAL RELATIONSHIP: EMPIRICAL RESULTS

We analysed 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) and 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 similar response direction between predator and prey biomass for upward cascades, that is $A_\uparrow > 0$, while 35 chains showed opposite response direction between predator and prey biomass for downwards cascades, that is $A_\downarrow > 0$ (Table S1.2 in Appendix S2).

Paths where all zooplankton species and all phytoplankton species were grouped together to form two trophic levels (chain Z-A in Fig. 4a) 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 (61% for $\Delta B_{1\uparrow}$, 68% for $\Delta B_{2\uparrow}$, 58% for $\Delta B_{1\downarrow}$ and 60% for $\Delta B_{2\downarrow}$, cf. Figs 3 and 4). For instance, we observed zooplankton biomass increasing after fish addition, or phytoplankton biomass decreasing due to nutrient enrichment.

The biomass distribution was bottom-heavy (i.e. $B_r < 1$) in most selected paths (Fig. 5). In the selected experimental systems, B_r was positively correlated with $A_\uparrow$. In log scale, the slope of this relationship was close to one with an intercept close to zero, 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.

In contrast, B_r was negatively correlated with $A_\downarrow$ with a slope of −0.5 in log scale (Fig. 5b). Yet, as we discuss below, this trend may be spurious, if top-down effects are not causally involved in shaping the biomass ratios.

COMPARING THEORY AND DATA: APPROXIMATE BAYESIAN COMPUTATION (ABC)

We can use our theoretical results to understand the empirical patterns and underlying mechanisms. We used ABC to identify parameter ranges consistent with the data (Beaumont, 2010). The idea of ABC is to leverage empirical patterns to constrain the distribution of simulation parameters. In this way, we can use across-system patterns to infer within-system dynamics. We generated predator–prey systems with different parameter values drawn from broad prior distributions, and computed their equilibrium biomass ratios B_r and top-down ($A_\downarrow$) and bottom-up response ratios ($A_\uparrow$). We then retained only model realisations for which (1) the two species coexisted and (2) the relationship between B_r and $A_\uparrow$ and between B_r and $A_\downarrow$ were consistent with those observed in our data analyses (Fig. S3.1). We retained 1500 model realisations, and used the corresponding parameter values to compute a joint posterior distribution for all model parameters. We thus simulated systems in which the theoretical within-system relationship holds exactly, and infer how the variation of key ecological parameters can explain the empirical relationship across systems. All parameters were drawn uniformly on a log scale, over a span of several orders of magnitude: biomass conversion efficiency $\varepsilon \in [10^{-2}, 10^{-1}]$; 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 $\phi = \frac{r}{g} \in [10^{-4}, 10^{4}]$.

We note that, although we did not constrain the model parameters to match the empirical biomass ratios (but only to follow the relationship of biomass and response ratios), the selected simulated data points displayed a remarkably similar distribution of biomass ratios (Fig. S3.1). Once filtered to match empirical patterns, the distribution of dissipative release ξ (i.e. prey release due to dissipation) shifted towards small values (*c.* 67% had $\xi < 0.1$ cf. Fig. 6a). This suggests that for two-thirds of systems (*c.* 67%), biomass ratios were shaped by bottom-up effects. The empirical trend between biomass ratio and top-down effects was allowed in our model and simulations, yet mainly driven by a weak anticorrelation between upward and downward responses (Fig. S3.1). Grouping simulations by dissipative release (low, intermediate and high), we found that the three classes presented qualitatively similar patterns with top-down responses (Fig. S3.2), with a slight steepening of the slope for systems with strongest dissipative release.

In terms of model parameters, dissipative release reads $r/g \times \alpha/D_2$. The distribution of $\phi = r/g$ remained broad after filtering by the empirical patterns (Fig. 6b). In contrast, the ratio of attack rate and consumer self-regulation α/D_2 was more constrained by the empirical patterns: its posterior distribution shows a unimodal distribution centered around 1 (Fig. 6c). Thus, the ratio r/g may be driving the across-system variation in dissipative release.

DISCUSSION

Trophic cascades are widespread in nature (Pace *et al.*, 1999; Shurin *et al.*, 2002; Estes *et al.*, 2011), where changes in the biomass of a given trophic level ripple along the food chain

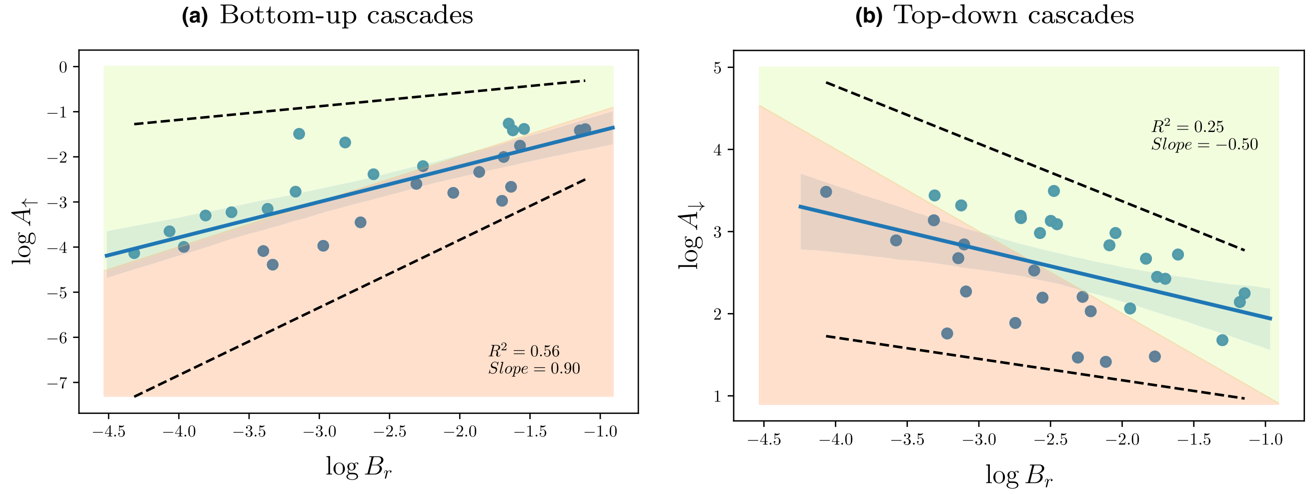

Figure 5 Empirical relationship between biomass ratio and response ratios. (a) Relationship between biomass ratio and bottom-up response ratio ($A_\uparrow = \frac{\Delta B_{2\uparrow}}{\Delta B_{1\uparrow}}$) due to nutrient enrichment. (b) Relationship between biomass ratio and top-down response ratio ($A_\downarrow = -\frac{\Delta B_{1\downarrow}}{\Delta B_{2\downarrow}}$) 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. Coloured regions represent the simple expectation scenario where a trophic level's response to a perturbation is proportional to its biomass. In the green region perturbations are amplified through the chain while in the orange perturbations are attenuated. Thus, the interface between the two regions represents the 1:1 line where the response of each trophic level is proportional to their biomass. 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 5 in Appendix S3 for results including the outliers).

through both direct and indirect biotic 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 prevalence and strength of trophic cascades has occupied a large part of the food chain literature (Shurin and Seabloom, 2005; Borer *et al.*, 2005; Heath *et al.*, 2014; Barbier and Loreau, 2019; Sentis et al., 2020). Here, rather than investigating the drivers of trophic cascades, we explored the nature and drivers of *the relationship* between cascade strength and the more empirically accessible notion of biomass pyramids (Elton, 1927) (Fig. 1). We do not ask why cascades are weak or strong, but rather why their strength can or cannot be predicted from the biomass pyramid.

Although previous studies have discussed whether the static properties of the food chain, such as its biomass pyramid or its size spectra (the distribution of organism body size) can hint at the underlying dynamics (McCauley *et al.*, 2018; Barbier and Loreau, 2019; Rossberg *et al.*, 2019), a systematic understanding of the link between static and dynamical properties of food chains is still lacking. Our contribution to bridge this gap is to provide a general and synthetic description of the relationship between the strength of trophic cascades and the shape of biomass pyramids.

Summary of results

Using both theory and data from pelagic experiments, we asked under which conditions the strength of trophic cascades can have a signature in the biomass pyramid.

Our results are based on the realisation that cascading responses to perturbations *and* the biomass pyramid, both reflect some aspect of the dynamical sensitivity of a food chain (Fig. 1b). Indeed, the standing biomass distribution is the product of a bottom-up dynamical response to primary productivity, as well as a top-down response to consumer intrinsic losses. Our approach was to determine the relative contributions of those bottom-up and top-down dynamical processes, to then predict the relationship (or lack thereof) between the shape of the biomass pyramid and either bottom-up, top-down cascades or a combination of both. We stress that this question is not equivalent to asking whether the system is bottom-up or top-down controlled (as in e.g. Kokkonen *et al.*, 2019), but whether bottom-up or top-down dynamical effects, relevant to predict trophic cascades, can be seen in the biomass distribution.

We showed that the contribution of bottom-up and top-down dynamical effects in the biomass pyramid is determined by *trophic dissipation*, which can be seen from either the consumer's or the resource's perspective (dissipative loss and release, respectively – see Box 1), and gives us the key combinations of primary productivity, predator losses, self-regulation and attack rates that determine the relationship between cascades and biomass pyramids. These perspectives are complementary: ξ determines three qualitative scenarios, while χ controls the slope of the relationship. Low dissipative release, $\xi \ll 1$ implies that standing biomasses only reflect bottom-up dynamical effects, which are the ones that determine the strength of bottom-up cascades. Conversely, $\xi \gg 1$ indicates that only top-down dynamical effects (which determine top-down cascades) shape the equilibrium state. For intermediate values, $\xi \sim 1$, bottom-up and top-down effects become entangled, so that the biomass pyramid does not provide precise information about the strength of either bottom-up or top-down cascades, but rather a combination of the two. We noted that, by construction, many classic food chain models

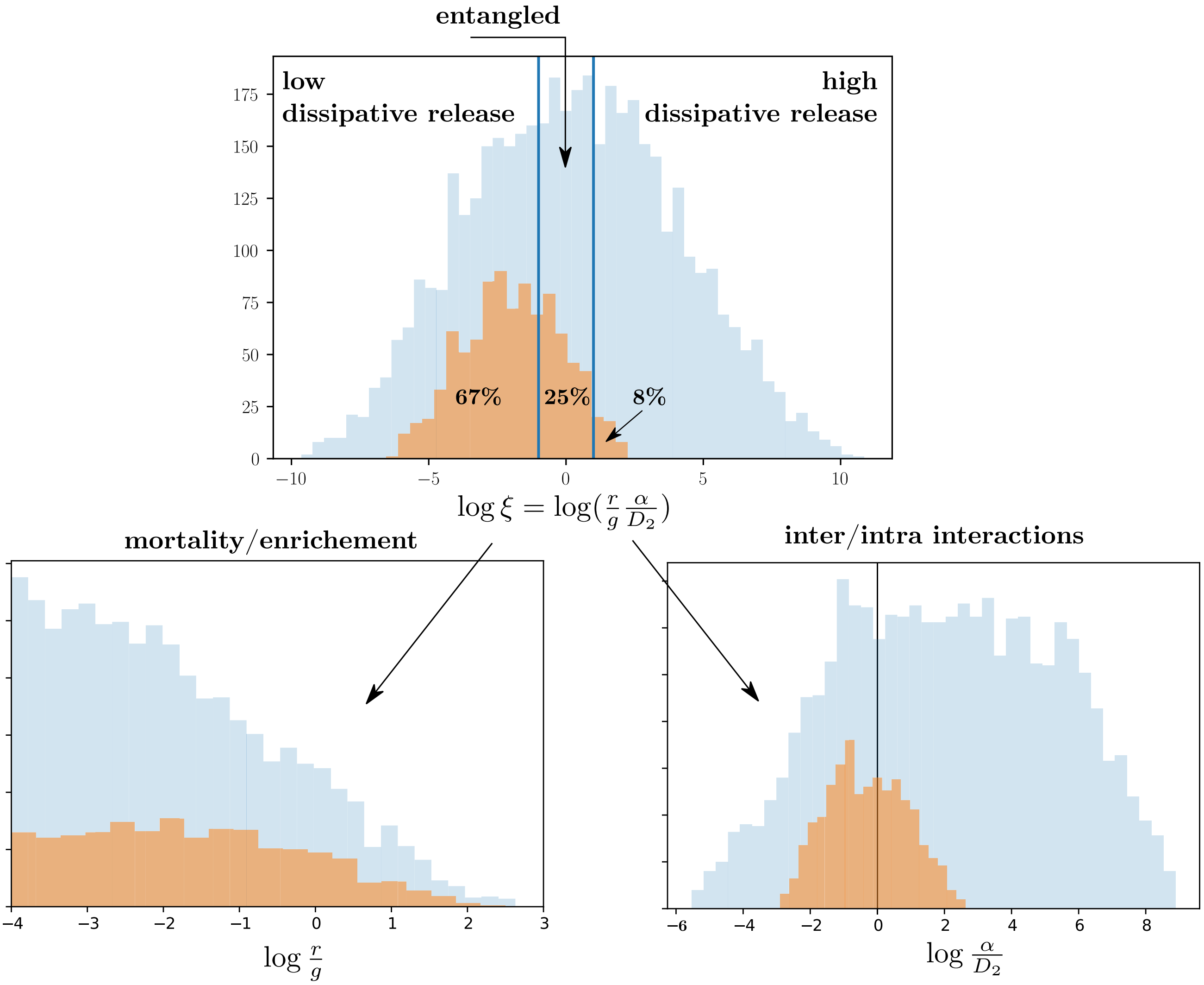

Figure 6 Prior and posterior distributions of model parameters. Blue histograms represent the prior distribution of the parameters introduced into the model (conditioned on coexistence). Orange histograms represent the distribution of the parameters after filtering them to match empirical patterns. Top: distribution of $\xi = (r/g)(\alpha/D_2)$ (dissipative release) which determines the nature of within-system relationship between biomass ratio and upwards and downwards response ratios. Dissipative release is the product of two non dimensional ratios. Lower left: distribution of the ratio of predator intrinsic loss to primary productivity $\phi = r/g$, Lower right: 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 centred close to 0 in log scale, suggesting that self-regulation rates are comparable to predation rates.

such as exploitation ecosystems (Oksanen 1981) are in the singular top-down limit $\xi \to \infty$.

The crucial distinction between asking whether cascades are strong and whether they are causally reflected in the biomass distribution, is clearly demonstrated here: top-down cascades can be predicted from the shape of the biomass pyramid if natural predator losses are sufficiently high ($\xi > 1$), but the larger these losses, the weaker the cascades, since the predator population is more depleted, with less potential for further prey release from perturbations.

The existence of a pattern across multiple systems is contingent on low variation of dissipative losses χ, while the pattern's shape depends on the magnitude of dissipative release ξ (Fig. 3). Using ABC, we estimated the distribution of dissipative release compatible with the observed empirical pattern. We found that experimental data were largely compatible with the bottom-up (low dissipative release, 67%) or entangled (25%) scenarios. Only 8% of systems had high enough dissipative release for top-down effects to determine the biomass ratio (Fig. 6). Nonetheless, we did observe a trend between biomass ratios and top-down effects (Fig. 5b). This relationship mainly arose from latent parameters that create an anticorrelation between $A_{\downarrow}$ and $A_{\uparrow}$, and subsequently between $A_{\downarrow}$ and B_r (Appendix S3). Only a small contribution to the trend came from the fraction (25% + 8%) of systems where top-down effects play direct, causal role. Even if we observed a similar relationship between downward responses and biomass ratios in all three groups of systems, our theory proposes that those patterns should be interpreted differently; from a spurious correlation for low dissipation release to an actual causation for high dissipation release.

Beyond hinting at which empirical patterns are causal, our framework may be used to shed light on specific ecological parameters. The ABC analysis suggested that intra- and inter-level interactions are of roughly comparable strength in these pelagic experiments, while the balance of primary productivity and consumer intrinsic losses may be the most important axis of variation in dissipative release between experiments.

Limitations

Our theoretical framework was used to analyse data pooled from multiple experimental pelagic communities. The empirical patterns reported and their interpretation might therefore be specific to pelagic systems. However, our theoretical framework is as general as the notion of food-chain itself (and linear response to perturbations). It has no restriction on the type of system considered, and could thus be used to analyse the drivers of the relationship between trophic cascades and biomass pyramids across ecosystem types.

Only 50% of the empirical systems displayed a consistent chain-like response to either bottom-up or top-down perturbations, and very few had both. This is unfortunate, as using information from both types of perturbations would have allowed us to infer relevant ecological parameters (e.g. self-regulation) in specific communities, rather than only trends across systems.

Different mechanisms could explain this high rate of 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 and Yearsley, 2004; Neutel *et al.*, 2007), and is known to obviate cascading effects (Diehl, 1993; Pringle and Hamazaki, 1998; Polis, 1999; McCauley *et al.*, 2018). Indeed, many 'herbivorous' zooplankton species consume not only phytoplankton but also a substantial amount of microzooplankton, such as rotifers and ciliates (Sprules and Bowerman, 1988; Gilbert, 1988; Brett *et al.*, 1994; Hansson *et al.*, 2004), which can explain some of the non-chain-like responses observed. Similarly, compensation between species or functional groups within one trophic level (Gonzalez and Loreau, 2009) could also attenuate or reverse the expected dynamical response (Leibold, 1989; Hunter and Price, 1992; Strong, 1992; McCann *et al.*, 1998).

Additionally, we may be unable to correctly identify chain-like dynamics when the response of either level to a perturbation is very small, and indistinguishable from measurement noise. Taking a ratio of responses is necessary to eliminate the confounding role of perturbation intensity, but this ratio becomes poorly defined when either response is close to zero.

We obtained the largest fraction of chain-like responses when considering all zooplankton species and all phytoplankton species as two trophic levels, suggesting that consistent chain dynamics may emerge as a complexity reduction of communities into few interacting levels composed by multiple species or groups of species (Ulanowicz, 1995). This suggests a complementary line of research: identify the conditions under which a food web behaves as a chain, thus allowing our theory to apply.

Influence of primary productivity

A long-standing empirical and theoretical question, is how primary productivity can affect either biomass distribution (McNaughton *et al.*, 1989; Del Giorgio *et al.*, 1999) or trophic cascade strength (Carpenter *et al.*, 1985). Here, we showed how primary productivity can change the *relationship* between biomasses and cascades. Increasing primary productivity lowers the strength of trophic dissipation, leading to biomass pyramids shaped by bottom-up propagation of primary productivity that convey, a priori, no information about top-down cascades. Our ABC approach suggests that the variation in dissipative release across systems was mainly driven by a variation in the ratio of intrinsic rates (consumer mortality over prey productivity) among systems. Thus, variations in primary productivity could be an essential factor explaining the diversity of observed pyramids and dynamical responses in the pelagic systems analysed.

On the importance of self-regulation

Previous research has already pointed at the importance of self-regulatory processes to modulate the strength of bottom-up and top-down effects (McCann *et al.*, 1998; Herendeen, 2004; Heath *et al.*, 2014). Our theoretical framework elucidates how both resource and consumer self-regulation shape the link between static and dynamic properties in a food chain, as they determine the importance of trophic dissipation in the observed biomasses of consumers and resources.

Very few empirical studies, however, provide reliable direct estimates of consumer self-regulation (Skalski and Gilliam, 2001). Furthermore, effects from species or compartments outside of the considered chain could participate in the observed self-regulation (Loreau, 2010). This would make it an emergent property that is not directly accessible from individual behaviour such as predator interference, but could still be estimated indirectly through our framework.

CONCLUSION

Cascading responses to perturbations and the biomass pyramid both reflect some aspects of the dynamical sensitivity of a food chain. Based on this observation, we asked whether the shape of the latter could be used to predict the strength of the former. Our approach was to determine the relative contributions of bottom-up and top-down dynamical effects to the biomass distribution, to then predict the relationship (or lack thereof) between the shape of the biomass pyramid, and the strength of either bottom-up or top-down cascades. We identified trophic dissipation, as the driver of this relationship. Trophic dissipation is the relative contribution of consumer intrinsic losses in the standing biomass distribution. It depends on well-studied ecological parameters, such as primary productivity and attack rates, but also on the less empirically accessible notion of prey and predator self-regulation. We noted that an observed relationship between biomass distribution and upward or downward cascades not only can reflect a common dynamical cause, but can also arise from correlations driven by a common factor. In the case of a common dynamical cause, we can extrapolate this relationship to make new predictions, within or across ecosystems, without additional knowledge of confounding factors. Our results thus provide criteria for when measurements of static properties can be used as reliable indicators to predict food chains' 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, MB and JFA wrote the first draft of the manuscript, and all the authors contributed substantially to revisions.

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