

LETTER

Body Mass–Biomass Scaling Modulates Species Keystone-Ness to Press Perturbations

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ABSTRACT

Identifying species with disproportionate effects on other species under press perturbations is essential, yet how species traits and community context drive their ‘keystone-ness’ remain unclear. We quantified keystone-ness as linearly approximated per capita net effect derived from normalised inverse community matrices and as non-linear per capita community biomass change from simulated perturbations in food webs with varying biomass structure. In bottom-heavy webs (negative relationship between species’ body mass and their biomass within the web), larger species at higher trophic levels tended to be keystone species, whereas in top-heavy webs (positive body mass to biomass relationship), the opposite was true and the relationships between species’ energetic traits and keystone-ness were weakened or reversed compared to bottom-heavy webs. Linear approximations aligned well with non-linear responses in bottom-heavy webs, but were less consistent in top-heavy webs. These findings highlight the importance of community context in shaping species’ keystone-ness and informing effective conservation actions.

1 | Introduction

Press perturbations resulting in sustained changes to species’ vital rates or abundances represent a broad class of disturbances that ecosystems are experiencing worldwide (Bender et al. 1984; Ives and Carpenter 2007; Novak et al. 2016). Whether they represent fishing, species invasions, habitat degradation or climate change, the changes they induce can propagate through intricate

direct and indirect interactions among species and can lead to significant changes in community structure (Schmitz 2004; Yodzis 1988). This is particularly true when so-called keystone species are involved; species for which a given change in abundance leads to disproportionately large community effects (Paine 1969). Knowledge of keystone species is thus essential to effective conservation and ecosystem management (Power et al. 1996).

Pioneer studies have promoted examining the measurable traits of species that contribute to their net effects (combining direct and indirect) on the rest of the food web when subjected to press perturbations to capture their keystone-ness (Montoya et al. 2009). Typically, consumers at higher trophic levels with substantial body mass are found to be more likely to play keystone roles (Berg et al. 2011; Montoya et al. 2005). Press perturbations on these species can even cause the extinctions of species with which they do not directly interact (Säterberg et al. 2013). However, studies have also yielded conflicting results, disagreeing, for example, on whether highly connected or lower connected species are more likely to be keystone species (Berg et al. 2011; O'Gorman et al. 2010). It has therefore been challenging to establish predictive relationships between species' traits and keystone-ness.

We hypothesised that the discrepancy of prior predictions of a species' keystone status depended on the structure of the food web in which species are embedded, as a given species' attributes can be highly dependent on its community context. Prior work assessing how community context influences species keystone status has primarily focused on the roles of species richness, connectance and the frequency distribution of interaction strengths (Cagua et al. 2019; Ebenman and Jonsson 2005; Jonsson et al. 2015; Kawatsu 2024). However, the role of a community's energetic organisation, that is, the relative strength of top-down versus bottom-up effects, has been poorly studied, despite being an inherent property of communities (Trebilco et al. 2013). A consequence of a community's energetic organisation is the directional relationship it exhibits across species between their average individual body mass and their population biomass. This relationship is encapsulated by the scaling exponent of species' body mass to biomass ($\log_{10}\text{Biomass} \sim \log_{10}\text{Body mass}$) (Hatton et al. 2015). As body mass is strongly positively related to trophic position (Brose et al. 2006a), negative scaling indicates a bottom-heavy biomass distribution, which has been widely observed in nature and forms the basis of current theory on how species' traits drive their keystone status. More recently, however, the occurrence of a positive scaling of species' body mass to biomass in food webs has also been recognised in many ecosystems (McCauley et al. 2018). This top-heaviness is typically associated with high trophic transfer efficiency, high predator-to-prey body mass ratios and consumers' generalist behaviour, indicating that it is related to different food web functioning and species self-regulatory processes (Barbier and Loreau 2019; Woodson et al. 2018). It remains unknown whether and how the bottom-heavy or top-heavy biomass structure of food webs influences species' net effects on other species and hence their keystone potential.

Species' net effects have typically been inferred using the approach of the inverse community matrix (Bender et al. 1984), where each matrix element specifies the expected response in the equilibrium abundance of species in the row to a press perturbation applied to the population growth rate of the species in the column. Although powerful and simple, this approach assumes that the system is close to a steady state both before and after a perturbation and that the press perturbation response is small (Yodzis 1988). However, press perturbations in nature can be very strong, which can lead to non-linear (accelerating or saturating) effects of species' perturbed growth rates on populations far from equilibrium. The inverse community matrix captures only linear analytical approximations of these potentially non-linear responses (Novak et al. 2016).

While dynamical models have been employed to simulate press perturbations to more faithfully consider potentially non-linear responses (Binzer et al. 2012; Ryser et al. 2021), this has typically been pursued independently of the predictions arrived at by the inverse community matrix and for much smaller food webs. To what extent linearly approximated net effects accurately capture the impacts of large press perturbations in species-rich communities therefore remains unclear, making it challenging to predict the outcomes of such perturbations and identify the keystone species that contribute most to community change.

In this study, we systematically explored (1) the relationships between species' topological and energetic traits and their keystone status, (2) how these relationships depend on the community biomass structure and (3) how keystone-ness identified by linear approximations corresponds to the potentially non-linear effects that species can have on their communities (Figure 1a). To address these, we used empirical, mass-balanced Ecopath food webs as well as dynamic food web simulations generated using the Allometric Trophic Network (ATN) framework. These varied not only in complexity—such as species richness and connectance—but also in biomass structure, trending either bottom-heavy or top-heavy, that is, scaling exponents of species' body mass to biomass towards negative or positive (Figure 1b). We defined keystone species as those that, when subjected to press perturbations, exert disproportionately large effects on the biomasses of all other species within the community. To quantify species' keystone-ness, we employed two approaches (Figure 1a). First, we derived the normalised inverse community matrix for both empirical and model-generated food webs at equilibrium, quantifying species' keystone-ness as their *per capita net effect*, that is, the net effect of a unit perturbation induced change in the biomass of the perturbed species on the equilibrium biomasses of all other species (Figure 1c). Second, for model food webs, we simulated species-specific press perturbations, by either reducing production gain or increasing metabolic loss, and measured the *per capita community biomass change*. We then examined the relationships between species' topological and energetic traits and their keystone-ness, as well as how these relationships depend on the food webs' biomass structure. We thereby evaluated the consistency between species' (linearly approximated) per capita net effect and (potentially non-linear) per capita community biomass change regarding conclusions on species' keystone status.

2 | Methods

2.1 | Empirical Food Webs

We extracted 144 food webs from the Ecobase database (<http://ecobase.ecopath.org/>) that encompass diverse marine ecosystems (Figure S1); bar/fjord ($n = 20$), channel/strait (5), continental shelf (56), coastal lagoon (15), coral reef (9), estuary (7), open ocean (23) and upwelling (9) (see Table S1). The dataset of each food web comprises a list of species and their annual average measured biomasses (t km^{-2}), consumption/biomass (Q/B) ratios (year^{-1}) and production/biomass (P/B) ratios (year^{-1}). Species sharing the same prey and predators and having similar physiological characteristics are aggregated into trophic species (Christensen and Walters 2004). Each food web provides quantitative mass-balanced fluxes between species ($\text{t km}^{-2} \text{year}^{-1}$) assuming that the

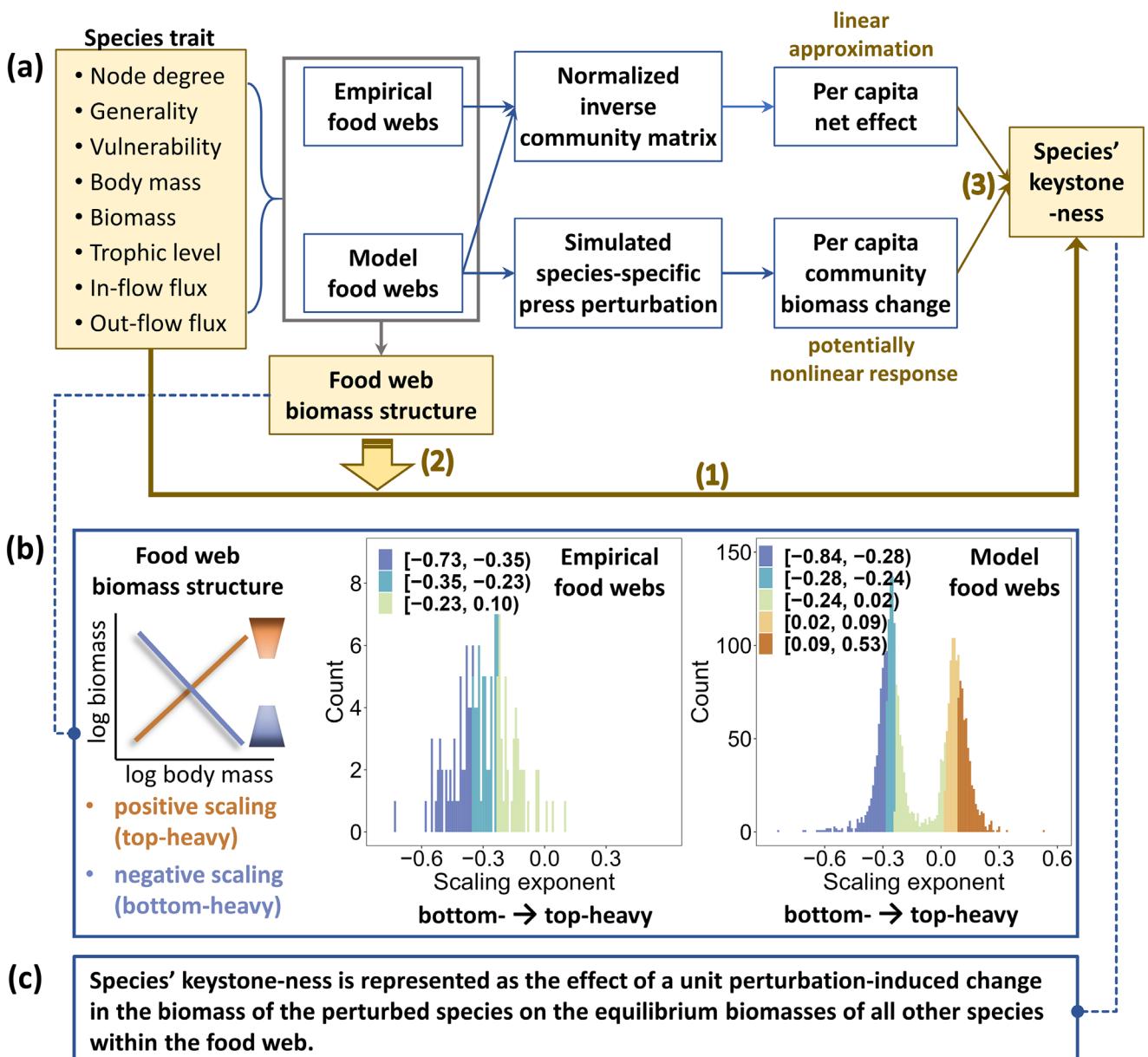


FIGURE 1 | (a) Schematic illustrating the assessment of species' keystone-ness in both empirical and model food webs through three questions (1) how do the traits of a species influence its role as a keystone that disproportionately affects other species, (2) how do these relationships depend on the community biomass structure and (3) how keystone-ness inferred by linear approximation near a locally stable state corresponds to the potentially non-linear effect that species can have on their communities. (b) Community biomass structure is indicated by the scaling exponent of species' body mass to biomass. Histogram distributions show these scaling exponents across 144 empirical food webs (ranging from -0.73 to 0.10) and 2799 model food webs (ranging from -0.84 to 0.53). Empirical and model food webs were respectively divided into three and five groups based on quantiles of the scaling exponent, with each colour-coded group containing an equal number of food webs. (c) Definition of species' keystone-ness in this study.

food web is at a steady state, that is, when for all species, biomass production equals losses due to harvest, predation or other unspecified sources (Christensen and Walters 2004). In most empirical food webs, species body masses (M) were not provided in the original studies. We consistently estimated them by converting species P/B values according to the empirical allometric scaling $P/B = 0.65M^{-0.37}$, which was established for a wide range of species, including phytoplankton, copepods, invertebrates, fishes and mammals (Banse and Mosher 1980). We checked the plausibility of the obtained species' body masses, ensuring that the ranges of body masses for different types of species aligned with those reported in previous studies (Shurin et al. 2012).

The collected empirical food webs exhibit a wide range of complexity, varying in species richness (S , from 10 to 99; Figure S2a), trophic links (L , from 26 to 2612), connectance (L/S^2 , from 0.12 to 0.53; Figure S2b) and maximum flux-based trophic level (from 3.32 to 5.45; Figure S2c). We used Huber regression (Huber 1973) to estimate the scaling exponent of species' body mass to biomass within each food web. These varied from -0.73 to 0.10 (Figure 1b), with 141 of the 144 food webs exhibiting a negative scaling relationship. Hence, in the majority of the collected food webs, larger consumers at higher trophic levels have lower biomass compared to smaller consumers at lower trophic levels (Figure S2d,e).

To assess species' keystone-ness, we applied the inverse community matrix approach (Figure 1) (Bender et al. 1984; Yodzis 1988). An empirically parameterised community matrix \mathbf{A} was constructed for each food web following the methods of de Ruiter et al. (1995). The per capita top-down effects of predator j on its prey i (α_{ij}) were calculated as:

$$\alpha_{ij} = \frac{\partial(dB_i/dt)}{\partial B_j} \Big|_{B=B^*} = -\frac{F_{ij}}{B_j} \quad (1)$$

where B_j is the annual average measured biomass of predator j , * is the equilibrium and F_{ij} is the mass-balanced flux from prey i to predator j . Effects of prey on predators reflect predator growth resulting from this predation, hence the per capita bottom-up effects of prey i on predator j (α_{ji}) can be expressed as:

$$\alpha_{ji} = \frac{\partial(dB_j/dt)}{\partial B_i} \Big|_{B=B^*} = \frac{e_j F_{ij}}{B_i} \quad (2)$$

where e_j is the efficiency with which predator j converts feeding on prey i into predator biomass: $e_j = \frac{(P/B_j)}{(Q/B_j)}$.

Since Ecopath models only depict inter-specific interactions, we had no empirical information about the strength of intraspecific interactions (α_{ii}). Hence, following Neutel et al. (2002), we assumed that α_{ii} is proportional to the species' total natural specific death rate (d_i). Specifically, $\alpha_{ii} = -s_i d_i$, where d_i was calculated by dividing the flux from species i to detritus by its biomass (Zhao et al. 2016) and s_i is the proportion of the natural specific death rate attributed to density-dependent competition ($0 < s_i < 1$). For simplicity and due to limited data availability, we assumed this proportion was equal for all species (Neutel et al. 2002). Given that the inverse community matrix approach assumes the system is at equilibrium, we determined the minimum value of s required for local stability, that is, ensuring that the leading eigenvalue of the matrix has a negative real part (Neutel et al. 2002). This conservative assumption produced qualitatively robust results compared to the less conservative assumption of setting the diagonal elements to $-1 \bullet d_i$ (see Appendix S1).

We then derived the normalised inverse community matrix, $\check{\mathbf{A}}^{-1}$, to obtain linear approximations of species' net effects without directly introducing press perturbations. $\check{\mathbf{A}}^{-1}$ is obtained by dividing each column of the inverse community matrix \mathbf{A}^{-1} by that column's diagonal element (Novak et al. 2016), denoted by $\check{\gamma}_{ij} = \gamma_{ij} / \gamma_{jj}$. The element $\check{\gamma}_{ij}$ represents the net effect of a unit perturbation induced biomass change in species j on the equilibrium biomass of species i . Herewith, the keystone-ness of each individual species j was calculated as $\sum_{i=1(i \neq j)}^S |\check{\gamma}_{ij}|$, which we refer to as the species' *per capita net effect*, reflecting the linearly approximated net effect of the per unit perturbation induced biomass change in species j on the equilibrium biomasses of all other species.

2.2 | Model-Generated Food Webs

To generalise our findings and investigate the underlying mechanisms, we developed a dynamic food web model following the ATN framework (Yodzis and Innes 1992). The model structure involved

two nutrients that support the basal species and a variable number of consumers feeding on these basal species and each other. We conducted simulations across a gradient of initial species richness, ranging from 20 to 100 in steps of 20, and performed 500 replicates for each richness level. Each food web was initially composed of 30% basal species and 70% consumers. Log₁₀-transformed values of species' body masses were sampled from uniformly distributed ranges: [0, 6] for basal species and [2, 12] for consumers, ensuring that the smallest possible body mass for a basal species was 1 and the largest possible body mass for a consumer species was 10¹². The distribution of species body masses was used to determine the initial feeding structure. It was assumed that the probability of a predator j to attack and capture an encountered prey i , defined as an asymmetrical hump-shaped curve (i.e., Ricker function, refer to ψ_{ij} in Table 1), centred around an assumed optimal predator-to-prey body mass ratio of 100 (Schneider et al. 2016). Weak links, that is, $\psi_{ij} < 0.01$ were removed from the feeding networks.

The dynamics in the biomass density of a consumer species (B_j) reflected its production from feeding on prey, minus its loss due to consumption by its predators and its basal maintenance loss, expressed as:

$$\frac{dB_j}{dt} = \underbrace{f_R e_R B_j \sum_i g_{ij}}_{\text{consumption on basal species } i} + \underbrace{f_C e_C B_j \sum_k g_{kj}}_{\text{consumption on consumer } k} - \underbrace{\sum_n g_{jn} B_n}_{\text{loss by predator } n} - \underbrace{f_m x_j B_j}_{\text{basal maintenance loss}} \quad (3)$$

Dynamics in the biomass density of basal species (B_i) were similar except that their growth followed a Monod growth function that depended on nutrient concentrations (G , Table 1), expressed as:

$$\frac{dB_i}{dt} = \underbrace{r_i G_i B_i}_{\text{producer growth}} - \underbrace{\sum_j g_{ij} B_j}_{\text{loss by predator } j} - \underbrace{f_m x_i B_i}_{\text{basal maintenance loss}} \quad (4)$$

The rates of concentration changes of nutrients were defined as:

$$\frac{dN_l}{dt} = D(S_l - N_l) - v_l \sum_i r_i G_i B_i \quad (5)$$

For detailed descriptions, definitions and values of all parameters, see Table 1.

Our model extends the original ATN model (e.g., used in Brose et al. 2006b; Yodzis and Innes 1992) to separately account for basal and activity respiration. Specifically, we introduced three factors: f_R and f_C (Equation 3), the fraction of assimilated energy used for production when feeding on basal species and consumers, respectively; and f_m (Equations 3 and 4), the proportion of basal maintenance loss relative to total metabolic loss. For details see Appendix S2. Previous studies have shown the benefit of incorporating such factors into the original ATN model reflecting the energy transfer through pelagic food webs more realistically (Boit et al. 2012; Kath et al. 2018; Kuparinen et al. 2016; Martinez 2020). We used two combinations of these three factors (Table 1), along with different attack rates and handling times, to regulate how biomass scales from smaller to

TABLE 1 | Parameter descriptions and definitions for the model-generated food webs.

Term	Parameter description	Abbreviation	Definition
Consumer's consumption	Multi-prey Holling-type functional response of consumer species j on prey species i	g_{ij}	$g_{ij} = \frac{w_j a_{ij} B_i^q}{1 + \sum_l c_{lj} B_l + w_j \sum_{k \in \text{prey}} h_{kj} a_{kj} B_k^q} \times \frac{1}{m_j}$ m , species body mass
	Relative consumption rate of consumer j	w_j	1/(number of prey species)
	Specific capture coefficient of consumer species j on prey species i	a_{ij}	$a_{ij} = a_0 m_i^{\beta_i} m_j^{\beta_j} \psi_{ij}$ Combination (1) Scaling constant $a_0 = 50$ $\beta_i \sim \mathbf{N}(\mu = 0.15, \sigma = 0.05)^b$ $\beta_j \sim \mathbf{N}(\mu = 0.47, \sigma = 0.05)^b$ if i is a basal species, $m_i^{\beta_i}$ is replaced by 20 Combination (2) Scaling constant $a_0 = 10$ $\beta_i \sim \mathbf{N}(\mu = 0.09, \sigma = 0.05)^c$ $\beta_j \sim \mathbf{N}(\mu = 0.85, \sigma = 0.05)^c$ if i is a basal species, $m_i^{\beta_i}$ is replaced by 1
	Asymmetrical hump-shaped curve (Ricker function), i.e., the probability of a consumer j to successfully attack and capture an encountered prey i	ψ_{ij}	$\psi_{ij} = \left(\frac{m_j}{m_i R_{\text{opt}}} e^{1 - \frac{m_j}{m_i R_{\text{opt}}}} \right)^\gamma$ Optimal predator-to-prey body mass ratio $R_{\text{opt}} = 100$ Width of the Ricker function $\gamma = 2$
	Hill exponent that varied the functional response between classic type II ($q = 1$) and type III ($q = 2$)	q	$\mathbf{N}(\mu = 1.5, \sigma = 0.3)$
	Interference competition among consumer l and consumer j depending on the similarity between their body masses	c_{lj}	$c_{lj} = c_0 \exp\left(\frac{-(\log_{10}(m_l) - \log_{10}(m_j))^2}{2\sigma_m^2} \right)$ Scaling constant $c_0 \sim \mathbf{N}(\mu = 0.8, \sigma = 0.2)$ Width of inter-specific interference $\sigma_m = 0.4$
	Handling time of consumer j feeding on its prey i	h_{ij}	$h_{ij} = h_0 m_i^{\eta_i} m_j^{\eta_j}$ Scaling constant $h_0 = 0.4$ Combination (1) $\eta_i \sim \mathbf{N}(\mu = -0.66, \sigma = 0.02)^b$ $\eta_j \sim \mathbf{N}(\mu = -0.48, \sigma = 0.03)^b$ Combination (2) $\eta_i \sim \mathbf{N}(\mu = -0.24, \sigma = 0.02)^c$ $\eta_j \sim \mathbf{N}(\mu = -0.76, \sigma = 0.03)^c$
	Assimilation efficiency for herbivorous consumption	e_R	0.45
	Assimilation efficiency for carnivorous consumption	e_C	0.85
	Fraction of assimilated herbivorous consumption used for production	f_R	0.4
	Fraction of assimilated carnivorous consumption used for production	f_C	Combination (1) 0.4 ^d Combination (2) 0.05 ^e

(Continues)

TABLE 1 | (Continued)

Term	Parameter description	Abbreviation	Definition
Basal maintenance loss	Fraction of assimilated carbon resired by the maintenance of basic bodily functions	f_m	0.1
	Metabolic rate of species i scaled by its body mass	x_i	For basal species: $x_i = 0.138 \times m_i^{-0.25}$ For consumers: $x_i = 0.314 \times m_i^{-0.25}$
Producer growth	Loss of a specific nutrient l is limited by its relative content in the biomass of basal species	v_l	$v_1 = 1$ and $v_2 = 0.5$
	Intrinsic growth rate of basal species i	r_i	$r_i = m_i^{-0.25}$
	Species-specific growth factor determined by the limited nutrient	G_i	$G_i = \min\left(\frac{N_1}{K_{1i} + N_1}, \frac{N_2}{K_{2i} + N_2}\right)$
	Half-saturation densities determine the nutrient uptake efficiency	K_{il}	$\mathbf{N}(\mu = 0.1, \sigma = 0.2)$

Note: The parameter combination (1) often generated top-heavy food webs, while the combination (2) more frequently resulted in bottom-heavy food webs (see Appendix S3).

^aN indicates that the parameter was drawn from a normal distribution with a mean (μ) and a standard deviation (σ).

^bExponents established in an empirical study based on various species, including ectotherm vertebrates, invertebrates and unicells in both freshwater and marine ecosystems (Rall et al. 2012).

^cExponents established in an empirical study based on marine invertebrate species (Rall et al. 2012).

^dKeep both f_R and f_C at 0.4 for all types of consumption, as used in previous studies (Boit et al. 2012; Kath et al. 2018; Kuparinen et al. 2016).

^eAssign different values based on the type of consumption: set f_R to 0.4 for herbivory and f_C to 0.05 for carnivory.

larger species, influencing the biomass structure towards either bottom-heavy or top-heavy. For details of these parameter settings and sensitivity analysis see Appendix S3. Generally, top-heaviness mainly resulted from altered allometric parameters that enhance trophic transfer efficiency.

Dynamics were simulated in C using the SUNDIALSCVODE solver (backward differentiation formula; absolute and relative error tolerances of 10^{-10}) over 150,000 time steps to ensure stationary dynamics. A species was assumed to be extinct (its biomass set to 0 and all its feeding links to both prey and predator species removed) when its biomass fell below 10^{-6} . For persisting species, equilibrium biomass was calculated as the average biomass over 10,000 time steps in the stationary state. We then filtered the resulting food webs (details in Appendix S4), selecting only those that displayed sufficient complexity and a leading eigenvalue with a negative real part in the resulting community matrix. Of the 5000 initial simulations (5 initial richness levels \times 500 replicates \times 2 parameter combinations), we retained 2799 food webs (56%). These accepted food webs had species richness ranging from 6 to 100, connectance ranging from 0.06 to 0.27 and consumers' maximum trophic level ranging from 4 to 6 (Figure S3). Importantly, their scaling exponents of species' body mass to biomass ranged from -0.84 to 0.53 (Figure 1b; 1595 with negative scaling and 1204 with positive scaling), extending the examined range of scaling exponents in the empirical food webs.

For each accepted food web, we employed two approaches to assess species' keystone-ness (Figure 1a):

First, we assessed the per capita net effect of each species exerted on all other species, as we did for empirical food webs (i.e., based on the normalised inverse community matrix, see Appendix S5).

Second, we extended each simulation by applying species-specific press perturbations. For each food web, we

manipulated the parameters of each focal species while keeping the parameters of other species unchanged. Specifically, we reduced the production gain of the perturbed species proportionally (the sum of the first two terms in Equation 3 for consumers; the first term in Equation 4 for basal species). In total, we introduced five levels of perturbation intensity, reducing production gains between approximately 10% and 90% compared to the pre-perturbation values ($P^{post} = P^{pre} \times \frac{1}{1+\theta}$, P^{pre} and P^{post} are the rates of production gain of the perturbed species before and after press perturbation, respectively, and $\theta \in \{0.1, 0.5, 1, 5, 10\}$ is the size of the press perturbation). Alternatively, we also applied species-specific press perturbations that increased the basal maintenance loss (the last term in both Equations 3 and 4) of the perturbed species. In this case, we multiplied the original basal maintenance loss of the perturbed species by a factor of $1 + \theta$ ($M^{post} = M^{pre} \times (1 + \theta)$, M^{pre} and M^{post} are the basal maintenance loss of the perturbed species before and after press perturbation respectively). For each perturbation, we calculated the keystone-ness of each perturbed species j as the per capita community biomass change $\sum_{i=1}^S (i \neq j) \left| \frac{B_i^{post} - B_i^{pre}}{B_j^{post} - B_j^{pre}} \right|$, where B^{pre} and B^{post} represent the biomass of the species before and after perturbation, respectively, and S denotes species richness of the food web. This metric quantifies the potentially non-linear responses of species subject to no linear approximation error.

2.3 | Species' Topological and Energetic Traits

To identify traits predictive of keystone-ness, we examined topological and energetic traits based on previously suggested important factors in identifying keystone species (Figure 1a; Jonsson et al. 2015; Jordán 2009). The topological traits considered were node degree (the number of prey and predators of a species),

generality (the number of prey items of a species) and vulnerability (the number of predators that a species has). Energetic traits included body mass, biomass, flow-based trophic level, total in-flow (IF) flux and total out-flow (OF) flux. In empirical food webs, IF and OF were calculated as the sum of fluxes going in and out of the given species respectively. In model food webs, IF and OF were determined by the rate of ingestion and predation loss per unit of time, calculated as average biomass transfer per time step over the same evaluation period (Schneider et al. 2016).

2.4 | Data Analysis

We first performed Huber regression to investigate whether the relationships between species traits and keystone-ness are influenced by the community biomass structure. These analyses examined the effects of individual species traits as well as the interaction between the trait and the scaling exponent of the respective food web on species' per capita net effect.

To gain further insight into how these relationships varied across food webs with different biomass structures. We categorised the empirical food webs into three groups based on the quantiles of the scaling exponent of species' body mass to biomass, with each group containing an equal number of food webs ($n=48$) (Figure 1b). We similarly categorised the model food webs into five groups ($n=559$ or 560) (Figure 1b), where the first three groups approximately matched those of the empirical food webs, and two additional groups extended the top-heavy range. We used Huber regression within each group to analyse the relationship between each species' trait and their per capita net effect, as well as species' per capita community biomass change. In addition, we examined the Spearman's rank correlation between each trait and keystone-ness within each individual food web to demonstrate the influence of community biomass structure.

Finally, to assess the consistency between linear approximations and potentially non-linear responses, we determined the Spearman's rank correlation between species' per capita net effect and per capita community biomass change within each model food web.

All statistics were carried out in R program version 4.1.1 (R Core Team 2021). Huber regressions were performed using the *rlm* function from the *MASS* package (Venables and Ripley 2002). We obtained 95% confidence intervals for the regression estimates by bootstrapping.

3 | Results

3.1 | Species Per Capita Net Effects

In empirical food webs, energetic traits generally had stronger effects on species' per capita net effects than their topological traits (Table S2). Interactions between species' energetic traits and the scaling exponents of species' body mass to biomass in their respective food webs also had stronger effects on species' per capita net effects than interactions involving topological traits (Table S2). These effects were particularly pronounced for

interactions involving trophic level and body mass, followed by in-flow flux, out-flow flux and species' biomass.

Across all empirical food webs, species' node degree had a negligible effect on their per capita net effects (Figure 2a). Spearman's rank correlations between species' node degree and their per capita net effects were often inconsistent within individual food webs, with coefficients ranging from -0.22 to 0.12 (interquartile range [IR]; Figure S4a). By contrast, species' generality and vulnerability showed more consistent patterns: species with higher generality and lower vulnerability tended to exert stronger effects (Figure 2b,c, Figures S4b,c). Larger species occupying higher trophic levels were found to have stronger per capita net effects (Figure 2d,f), but these relationships weakened in food webs with higher scaling exponents (i.e., slopes closer to 0; Table S3, Figure S4d,f). Conversely, species' biomass, in-flow flux and out-flow flux had negative correlations with their per capita net effect (Figure 2e,g,h) such that species with higher biomass and energy fluxes tended to have weaker per capita net effects. These relationships also weakened in food webs with higher positive scaling exponents (Table S3, Figure S4e,g,h).

Compared to empirical food webs, interactions between species' energetic traits and the scaling exponents of model food webs had stronger influences on species' per capita net effects (Table S4) due to the higher frequency of top-heavy food webs (Figure 1b). Species' per capita net effects showed minimal variation and had very limited explanatory power by topological traits, regardless of scaling exponents (Figure 3, Table S5). For energetic traits, model food webs with negative scaling exhibited relationships between species' energetic traits and per capita net effect that closely resembled the relationships observed in empirical food webs (Figure 3). However, in model food webs with positive scaling exponents, the directionality of these relationships reversed for traits such as body mass, trophic level, in-flow flux and out-flow flux (Figure 3d,f-h), while the relationship with biomass weakened (Figure 3e). Across individual model food webs, as the scaling exponent increased, Spearman's rank correlations between species traits and per capita net effects within individual food webs shifted from positive to weak or even negative for node degree, generality, body mass and trophic level (Figure S5a,b,d,f). Conversely, correlations for vulnerability, biomass, in-flow flux and out-flow flux shifted from negative to weak or even positive (Figure S5e,g,h).

3.2 | Linear Versus Non-Linear Responses

Across the model food webs with negative scaling, the non-linear species' per capita community biomass change, resulting from simulated species-specific press perturbations by proportionally decreasing production gain of the perturbed species, was highly correlated with their linear per capita net effect approximations (IR of Spearman's rank correlation coefficients from 0.72 to 0.91) (Figure 4a,b). In contrast, the correlation between these decreased and had high variability (IR from 0.27 to 0.71) across the model food webs with positive scaling (Figure 4c,d). Linear approximations were therefore more effective in capturing non-linear responses in bottom-heavy food webs than in top-heavy ones. This also held for perturbations that increased species basal maintenance loss and resulted in correlations ranging

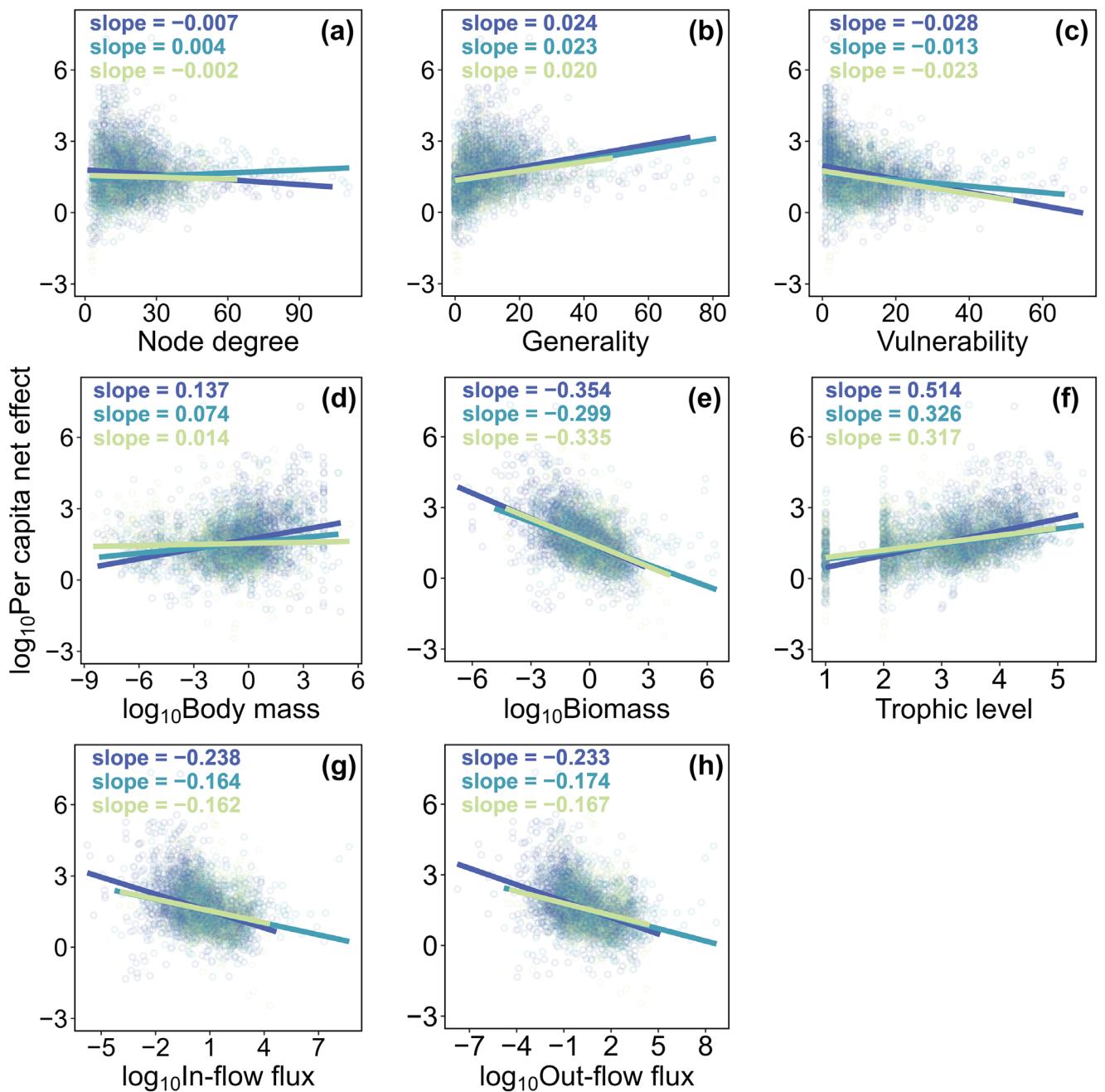


FIGURE 2 | Relationships between species' topological and energetic traits and their keystone-ness in the empirical food webs. The keystone-ness of a species was defined as its per capita net effect derived from the approach of normalised inverse community matrix. Random jitter was applied along the x-axis (a–c, ± 0.2 ; d–h, ± 0.02) to avoid illustrative overlap. Huber regression lines and slope coefficients are shown (see Table S3 for details), with colours corresponding to different groups of empirical food webs (as in Figure 1b), categorised based on quantiles of the scaling exponent of species' body mass to biomass, with each group containing an equal number of food webs ($n=48$).

from 0.62 to 0.89 for negative scaling and 0.36 to 0.73 for positive scaling (Figure S6). Varying the intensity of the press perturbations had little impact on these correlations (Table S6), even though these perturbations could be severe enough to cause the collapse of the entire food web (Figure S7).

The effects of species' topological and energetic traits on their per capita community biomass change were similar to their effects on per capita net effect, except for species biomass (Figures S8 and S9 compared to Figure 3). Hence, in model food webs characterised by negative scaling species energetic traits were more

predictive of their per capita community biomass. In contrast, in model food webs with positive scaling, this predictive capability was notably reduced for species body mass, in-flow flux and out-flow flux, and even revealing contrasting patterns concerning species trophic level (Table S7).

4 | Discussion

This study highlights the critical role of community biomass structure in determining how species' energetic traits influence their

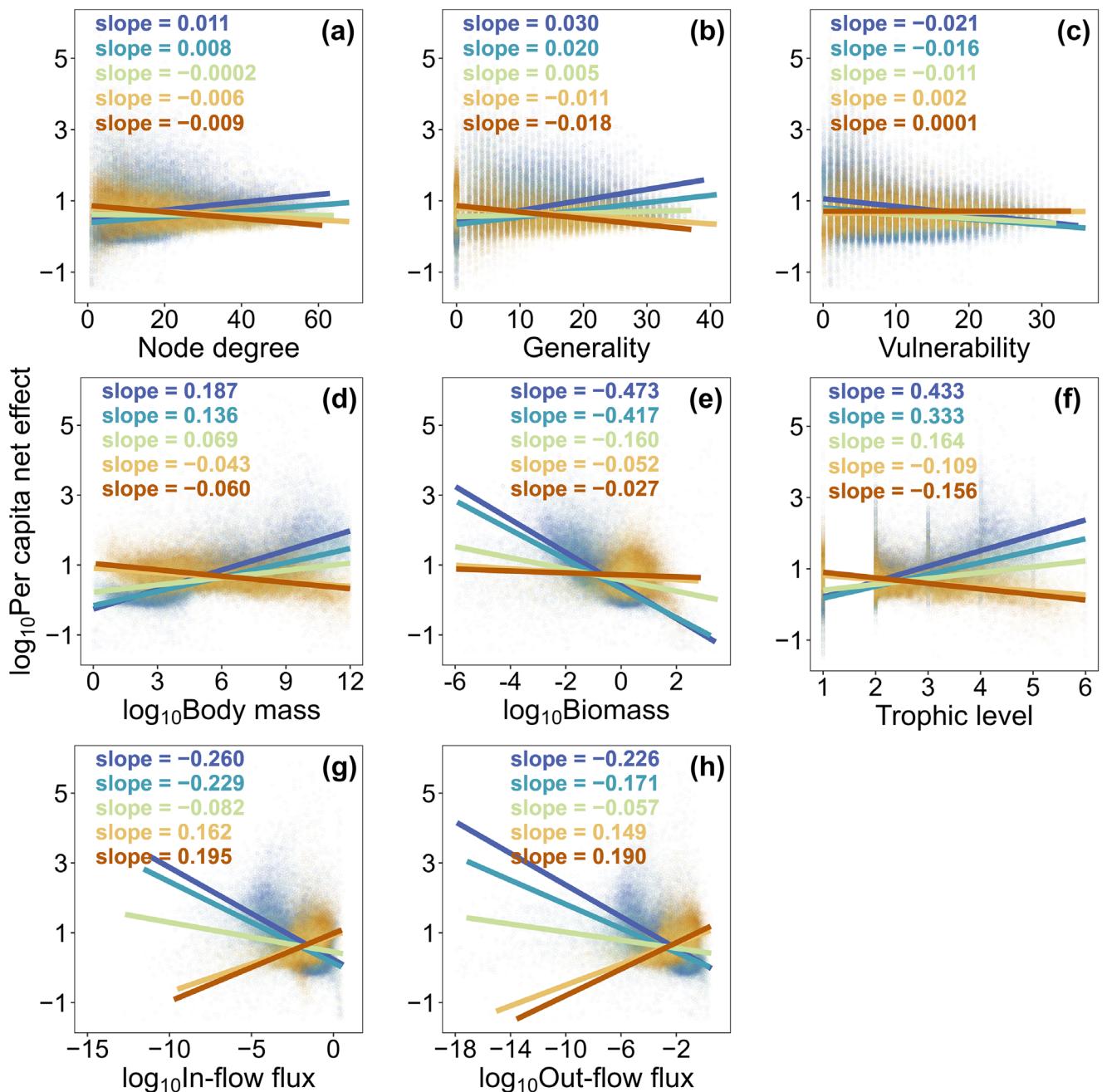


FIGURE 3 | Relationships between species' topological and energetic traits and their keystone-ness in the model food webs. Random variation was applied along the x-axis (a–c, ± 0.2 ; d–h, ± 0.02) to avoid illustrative overlap. Huber regression lines and slope coefficients are shown (see Table S5 for details), with colours corresponding to food webs categorised by their scaling exponent of species' body mass to biomass (as in Figure 1b).

keystone-ness. In bottom-heavy food webs, species traits provide stronger explanatory power for their keystone-ness. Species with larger body mass, lower biomass, higher trophic levels and lower total in- and outgoing fluxes tend to exhibit higher keystone-ness. These relationships weaken or reverse in top-heavy food webs. Furthermore, while high consistency in species keystone-ness is observed between linear approximations and actual non-linear responses in bottom-heavy food webs, this consistency decreases and becomes more variable in top-heavy food webs.

Almost all of the empirical food webs we analysed exhibited bottom-heavy biomass distributions (see also Valls et al. 2015). This presents a potential bias in our empirical dataset due to a

lack of representation of top-heavy food webs. Furthermore, inherent uncertainties in scaling exponents of species' body mass to biomass in empirical food webs arise from data limitations, as species body mass estimates were inferred indirectly from species P/B ratios. While additional uncertainties are also inevitable, including variability in field-based biomass and flux-rate estimates and incomplete knowledge of species' self-effects (i.e., the community matrix diagonal elements), our model food webs with negative scaling closely resembled the empirical food webs (Figure 1b). Indeed, our model-generated food webs exhibited a much broader range of scaling exponents, with only those having negative scaling creating relationships between species' traits and keystone-ness that resembled those of the empirical

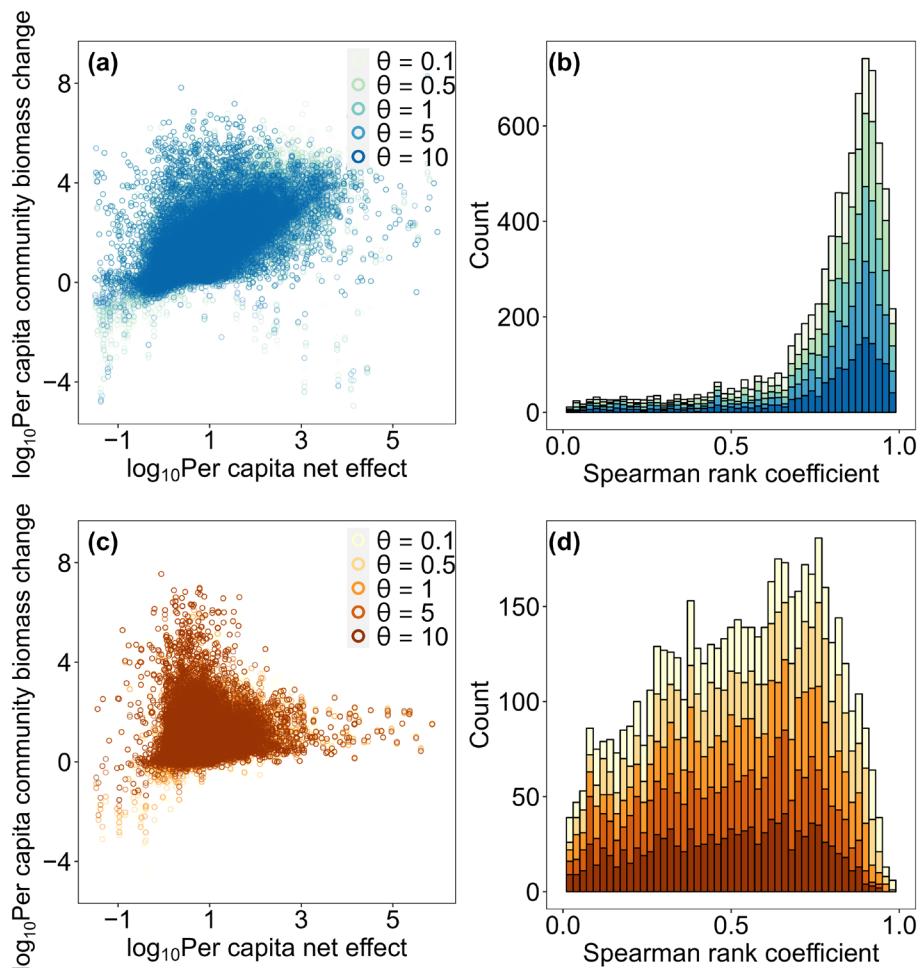


FIGURE 4 | Relationships between the linearly approximating per capita net effect and the potentially non-linear per capita community biomass change of species across simulated model food webs, differentiated by (a, b) negative and (c, d) positive species' body mass–biomass scaling. Species' per capita net effect was predicted by the approach of normalised inverse community matrix. Species' per capita change in biomass of all other species after each species-specific press perturbation, named per capita community biomass change captures potentially non-linear responses. Such species-specific press perturbation was repeated for each species within a food web by multiplying the pre-perturbation production gain of a target species by a factor of $1/(1+\theta)$, where θ values of 0.1, 0.5, 1, 5 and 10 are represented in different colours. (b, d) Histograms of the Spearman's rank correlation coefficient between the per capita net and the per capita community biomass change of species within each model food web. For perturbations by increasing the target species' pre-perturbation basal maintenance loss, see Figure S6. Both implementations of species-specific press perturbations did not result in qualitative differences.

food webs. Generally, top-heaviness in our models resulted from changed allometric parameters that enhance trophic transfer efficiency (Figure S10). Other factors like spatial emigration and resource subsidies may also drive top-heaviness (McCauley et al. 2018), but were not included in our study.

In bottom-heavy food webs, certain traits contribute more to capturing species' keystone-ness than others (Figures 2 and 3). Previous research has shown that press perturbations on highly connected species typically have smaller effects on other species than perturbations on lower connected species (Montoya et al. 2005, 2009; O'Gorman et al. 2010), consistent with the direct and indirect effects cancelling out for highly connected species (Montoya et al. 2009). Our analysis found that species' node degree had a negligible effect on keystone-ness accounting for all food webs (Figures 2a and 3a), displaying either positive or negative correlations within individual webs (Figures S4a and S5a). However, our study demonstrated that the components of species' node degree, that is, generality and vulnerability, were

more reliable predictors. Similarly, generalist consumers have been found to cause more non-focal extinctions within a community than specialists due to their strong cascading effects on a larger proportion of species (Aufderheide et al. 2013; Gutgesell et al. 2022). Species body mass is generally a dependable predictor of keystone-ness (Berg et al. 2011), with recent research showing that the removal of large consumer species causes substantial cascading effects down the food web (Borer et al. 2006; Säterberg et al. 2013). Our findings on bottom-heavy food webs support this, reinforcing the notion that large apex predators, which are often highly susceptible to accelerating environmental changes and anthropogenic pressures, warrant increased attention for conservation and management efforts (Häussler et al. 2020; Heithaus et al. 2008; Ryser et al. 2019). Additionally, our findings highlight the keystone roles of species with low population biomass and low fluxes, which is in line with recent research suggesting that targeted perturbations to species with low biomass have a higher impact on community asymptotic stability due to the strong indirect effects (Säterberg et al. 2019).

Our work demonstrates that species traits exhibited either limited explanatory power or even reversed relationships with keystone-ness in top-heavy compared to bottom-heavy food webs. The mechanisms for this are likely complex, but may be attributed to two potential reasons.

First, we quantified species keystone-ness by the per capita net effect and the per capita community biomass change, aligning with the keystone species concept emphasising impacts disproportionate to a species' abundance (Power et al. 1996). We hence applied the approach of the normalised inverse community matrix (Novak et al. 2016), which specifies the per unit biomass net effect of the perturbed species on the equilibrium biomasses of all other species. Previously, studies employing the inverse community matrix did not use this normalisation, and therefore, assessed the net effect a species' whole population or unit change in the whole population's growth rate exerts on the food web (Berg et al. 2011; Jonsson et al. 2015; Montoya et al. 2009). To test the influence of per capita effects, we repeated our analysis using the non-normalised inverse community matrix (for details see Appendix S6). For these analyses, different food web biomass structures had little influence on species' net effects, with the relationships between species traits and community effects remaining unchanged between bottom-heavy and top-heavy food webs (Appendix S6). The weak or even inverted relationships between species' traits and keystone-ness in food webs with positive scaling seen in our main analysis that accounted for differences in species' biomass therefore stemmed from the per capita basis that is central to the keystone concept (Paine 1969; Power et al. 1996). It is thus, in part, due to their lower biomass that larger species at higher trophic levels demonstrate stronger per capita net effects on other species in bottom-heavy food webs (Figure 3). Conversely, in top-heavy webs, their keystone-ness is markedly reduced as their impacts are not disproportionate to their high biomass.

Second, top-heavy food webs likely exhibit higher internal energy fluxes, less dissipation and weaker energetic constraints than bottom-heavy food webs. As a consequence, while a perturbation on the top predator in a bottom-heavy food web may significantly impact both its direct prey and indirectly linked species, the same perturbation in a top-heavy food web primarily affects only the predator itself, with minimal effects propagating to other species (Figure S11). Therefore, on average, species' per capita net effects in top-heavy food webs were lower than in bottom-heavy food webs (Figure 3). This is likely because the total loss of prey species due to a perturbed predator is less influenced by the predator's biomass in top-heavy than in bottom-heavy food webs (Figure S11f) since the reduced predation loss (due to the decreased biomass of the perturbed predator) is relatively low compared to its metabolic loss at high biomass levels. Top-heavy food webs are also likely to experience greater interference competition among predators to reduce the per predator feeding rates (Allhoff et al. 2015). These hypotheses aside, the response of top-heavy empirical food webs to press perturbations should be considered to remain uncertain, especially considering that top heaviness was likely associated with reduced stability and biomass oscillations (Gutgesell et al. 2022) in our simulations and were hence more likely to be excluded from our analysis due to the requirement that simulations reach a stable equilibrium. These complexities underline the need for

additional research on the response of top-heavy food webs to press perturbations.

The suitability of the linear analytical approach of the inverse community matrix for predicting potentially non-linear effects of perturbations has been debated for some time, with some studies arguing against (Berlow et al. 2004) and others supporting (Jonsson et al. 2015; O'Gorman et al. 2010) its applicability. Our study found relatively high consistency between them in their within-food-web magnitude rankings for bottom-heavy food webs (Figures 4 and S6). Similarly, recent research highlights a high consistency between species' net effects inferred from the inverse community matrix and the proportion of secondary extinctions resulting from species removal (Jonsson et al. 2015). However, our findings highlight the challenge of using linear approximations to predict effects in top-heavy food webs where consistency between the two approaches is lower and highly variable. Pressing top-heavy systems is more likely to perturb them away from exhibiting fixed point equilibria, potentially leading to greater response variation including both more pronounced non-linear responses on the one hand (due to lower asymptotic stability) and diminished responses on the other (possibly due to high trophic transfer efficiency and hence low energetic constraints) as reflected in the Delta-distributed shape in Figure 4c and Figure S6c. Therefore, taken as whole, our work underscores the necessity of considering biomass structure in the planning of robust conservation strategies, particularly given evidence suggesting that climate change can increase top-heaviness in aquatic ecosystems (McCauley et al. 2018; Shurin et al. 2012).

Author Contributions

Xiaoxiao Li, Christian Guill, Wei Yang, Zhifeng Yang and Mark Novak designed the research. Xiaoxiao Li collected the empirical food webs with assistance from Lei Zhao and Wei Yang. Christian Guill developed the initial dynamic model, which was revised by Xiaoxiao Li. Xiaoxiao Li conducted data analysis with valuable input from Christian Guill, Mark Novak, Peter C. de Ruiter, Wei Yang and Zhifeng Yang. The manuscript was written by Xiaoxiao Li with contributions from Christian Guill, Mark Novak, Peter C. de Ruiter, and input from all other authors. All authors gave their final approval for publication.

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Data Availability Statement

All data and codes used in this study are available on Figshare at <https://doi.org/10.6084/m9.figshare.26061349.v2>.

Peer Review

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.70086>.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.