



HAL
open science

Indirect effects of temperature drive gradients in fish food web properties

Azenor Bideault, Matthieu Barbier, Arnaud Sentis, Michel Loreau, Dominique Gravel

► **To cite this version:**

Azenor Bideault, Matthieu Barbier, Arnaud Sentis, Michel Loreau, Dominique Gravel. Indirect effects of temperature drive gradients in fish food web properties. *Global Ecology and Biogeography*, 2025, 34 (9), pp.e70110. <10.1111/geb.70110>. <hal-05412639>

HAL Id: hal-05412639

<https://hal.science/hal-05412639v1>

Submitted on 12 Dec 2025

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons CC BY-NC-ND 4.0 - Attribution - Non-commercial use - No Derivative Works - International License

RESEARCH ARTICLE OPEN ACCESS

Indirect Effects of Temperature Drive Gradients in Fish Food Web Properties

Azenor Bideault^{1,2}  | Matthieu Barbier^{3,4} | Arnaud Sentis⁵ | Michel Loreau⁶ | Dominique Gravel¹

¹Département de Biologie, Université de Sherbrooke, Sherbrooke, Quebec, Canada | ²Département de Biologie, Centre d'Études Nordiques, Université Laval, Quebec, Quebec, Canada | ³CIRAD, UMR PHIM, Montpellier, France | ⁴PHIM Plant Health Institute, University of Montpellier, CIRAD, INRAE, Institut Agro, IRD, Montpellier, France | ⁵INRAE, Aix Marseille University, UMR RECOVER, Aix-en-Provence, France | ⁶Centre for Biodiversity Theory and Modelling, Theoretical and Experimental Ecology Station, CNRS, Moulis, France

Correspondence: Azenor Bideault (azenor.bideault@usherbrooke.ca)

Received: 18 March 2025 | **Revised:** 22 July 2025 | **Accepted:** 30 July 2025

Handling Editor: Jonathan Belmaker

Funding: M.B. and M.L. were supported by the TULIP Laboratory of Excellence (ANR-10-LABX-41). A.B. and D.G. were supported by the Discovery Grant program of the NSERC. A.S. was supported by the ANR project EcoTeBo (ANR-19-CE02-0001) from the French National Research Agency (ANR). This research was co-funded by the European Union (GA#101059915—BIOcean5D).

Keywords: allometric model | dynamics | food web | latitude | metabolic theory in ecology | temperature

ABSTRACT

Aim: Understanding the direct (e.g., on biological rates) and indirect (e.g., through changes in species richness) effects of temperature on food web properties, in the context of latitudinal gradients and climate warming. We focus on species interactions and predict variations in two metrics of food web properties: trophic control and temporal variability.

Location: Global oceans.

Time Period: 2001–2018.

Major Taxa Studied: Marine fish species.

Methods: We use a modelling approach coupled with a global dataset of fish food webs. Species occurrences are obtained from data sources, while trophic interactions are predicted by a size-based niche model calibrated with a global interaction dataset. Interaction strengths are constrained by allometric scaling laws for predation and biomass. We investigate how predictors varying with latitude (temperature, species richness, productivity, food web structure) drive latitudinal variations in trophic regulation and variability.

Results: Our results suggest a latitudinal gradient in two metrics of community dynamics, with both trophic feedback strength (underlying phenomena such as cycles and cascades) and temporal stability increasing with latitude. In our model, this variation is tied directly and indirectly to temperature, and we find that direct effects of temperature are weaker than (or at most equal to) indirect effects. The direct effect on interaction rates decreases trophic feedbacks yet increases variability. The organism-level temperature–size rule is found to increase both feedback and variability. Finally, community-level indirect effects (species richness and connectance) impact trophic control but not variability. Climate warming moderately affects trophic control, variability and total biomass, but more strongly alters individual species biomass.

Main Conclusions: Our study improves understanding of the drivers of latitudinal variation in food web properties and helps disentangle the direct and indirect effects of temperature. Indirect effects are predicted to drive biogeographic variation in food web properties, while direct effects such as short-term warming could have stronger consequences at the species level.

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial-NoDerivs](https://creativecommons.org/licenses/by-nc-nd/4.0/) License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

© 2025 The Author(s). *Global Ecology and Biogeography* published by John Wiley & Sons Ltd.

1 | Introduction

Trophic interactions shape the structure of communities across biogeographic gradients (Jordano 2016). These interactions are also temperature-dependent, and hence vary in space and time with temperature changes (e.g., Bideault et al. 2021; Binzer et al. 2012; Amarasekare 2019). Understanding both the effects of the latitudinal temperature gradient and of warming on food web dynamics is crucial to explain the latitudinal distribution of biodiversity and to predict its changes due to climate warming.

Temperature has various direct, that is, physiological short-term effects, and indirect effects, that is, delayed responses on body size and interactions, at different levels of organisation (Boukal et al. 2019). For ectotherms, temperature has substantial effects on biological rates such as organism metabolism (Gillooly et al. 2001; Brown et al. 2004), growth rate (Savage et al. 2004) or feeding rates (Sentis et al. 2012).

The temperature–size rule (TSR) stipulates that ectothermic organisms typically mature at a smaller body mass when reared in warmer conditions (Forster and Hirst 2012; Horne et al. 2015). It is hypothesised to be driven by different thermal sensitivities in growth and development rates (Forster et al. 2011; Zuo et al. 2012) or to a better maintenance of aerobic scope at smaller sizes (Forster et al. 2012). Temperature is hence an important driver of ecological processes through its various effects on biological rates (Gillooly et al. 2001; Kleiber 1932) and body mass (Atkinson 1994), which in turn affect abundances, interaction strength, food web topology and community stability and functioning (e.g., Brose et al. 2012; Beveridge et al. 2010; Rodríguez-Castañeda 2013; Post and Pedersen 2008). The latitudinal gradient of temperature and ongoing climate warming are thus both expected to affect many facets of food webs (Albouy et al. 2019; Binzer et al. 2012; Bideault et al. 2021).

While the latitudinal gradients of species richness (Fischer 1960) and productivity (Huston and Wolverton 2009) have motivated macroecological studies for decades, the variation in food web structure and dynamics has received less attention at the global scale (Schemske et al. 2009; Albouy et al. 2019; Baiser et al. 2019). Yet, it has recently been shown that food chain length, vulnerability and connectance of marine fish food webs are all correlated to sea surface temperature (Albouy et al. 2019). There is also evidence of spatial variation in trophic control, that is, whether the dynamics of a species are mainly determined by its resources (bottom-up control) or by its consumers (top-down control) (Boyce et al. 2015; Frank et al. 2006; Legagneux et al. 2014; Whalen et al. 2020). This result has come to nuance the dominant picture that marine ecosystems were resource-controlled, with phytoplankton dynamics being the drivers of production and biomass variability of higher trophic levels (Frank et al. 2007). A synthetic analysis of 52 observational field studies from marine ecosystems from the Northern Hemisphere demonstrated that trophic control varied from top-down to bottom-up control with decreasing latitudes, temperature being the strongest predictor of this variation (Boyce et al. 2015). Similarly, an analysis of empirical time-series from communities in the western North Atlantic indicated that top-down control was prevailing in northern areas whilst bottom-up control governed southern areas (Frank et al. 2006).

Hence, there is mounting evidence of variation in community structural and dynamical properties at the global scale, but the causes of such variation remain elusive, notably because many interdependent variables covary with latitude, such as species richness, productivity and temperature (Baiser et al. 2019; Leclerc et al. 2023). Their isolated effects are then difficult to disentangle, and contradictory conclusions abound on the importance of these drivers. For instance, some studies indicated a correlation between water temperature and food webs structure (Albouy et al. 2019; Bonnaffé et al. 2024) whilst another study on marine rock-pool food webs demonstrated that food web structure was not correlated to abiotic characteristics such as pool temperature, latitude or elevation (Gauzens et al. 2020). Other studies highlighted that temperature might have indirect effects on trophic control through its influence on consumer community composition (Whalen et al. 2020), biodiversity or average resource body mass and community turnover (Boyce et al. 2015). Identifying the main drivers of the variation in food web properties, and the contribution of the direct and indirect effects of temperature, is key in understanding the functioning of communities and, importantly, how they are affected by global warming. A mechanistic approach can help to better understand the macroecology of food webs and to disentangle the effect of temperature and other variables.

The objective of this study is to investigate how food web properties vary across latitudes and how they will be impacted by a 2°C warming. We use a global fish food web dataset (Figure 1) and represent community dynamics with allometric Lotka-Volterra equations, with temperature impacting biological rates and body mass. We focus on the effect of temperature on species interactions, leaving aside species range shifts and extinctions resulting from increased species mortality and metabolic requirements at higher temperatures (Fussmann et al. 2014; Synodinos et al. 2021). We explore two metrics characterising different facets of food web dynamics: temporal variability V , reflecting the overall community stability in response to perturbations (Arnoldi et al. 2019), and trophic regulation λ , describing the vertical dimension of the food web (bottom-up and top-down control) (Barbier and Loreau 2019). We first explore how these metrics vary with latitude, and whether that variation can be related to four predictors: (1) a direct organism-level effect of temperature, (2) body mass, an indirect organism-level effect through the TSR, (3) species richness and (4) connectance, two community-level variables resulting from ecological assembly. This method allows us to distinguish the effects of each of these variables and to capture the impact of the direct effect of temperature on species biological rates on food web properties. We then investigate how our model predicts that warming will affect trophic control, variability and total biomass in the same food webs.

2 | Material and Methods

2.1 | Global Dataset of Fish Marine Food Webs

We used datasets of species occurrences and interactions from Albouy et al. (2019), where data processing methods are detailed. Species occurrences were initially obtained from the Ocean Biogeographic Information System (OBIS) Intergovernmental Oceanographic Commission of UNESCO (2014), covering all

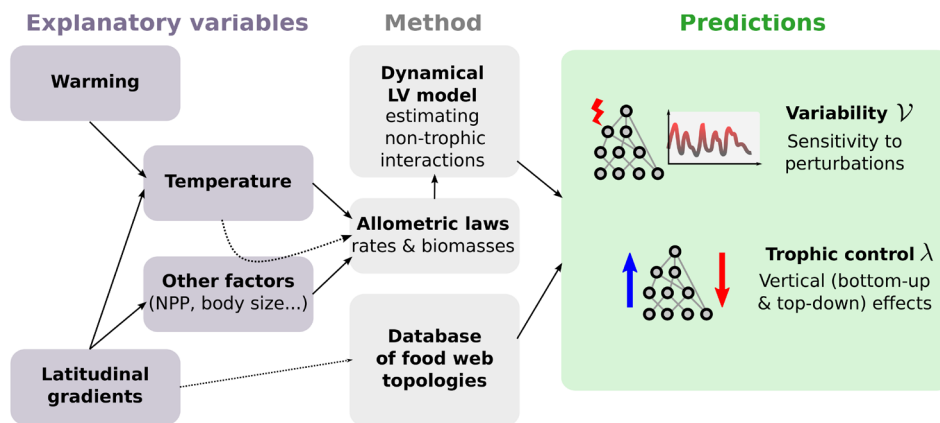


FIGURE 1 | Conceptual schema of our study. Investigation of the effects of temperature on marine food web properties over space (latitude) and time (warming). We aim to disentangle several direct and indirect effects of temperature as well as other predictors that vary across latitudes. All these factors affect expected feeding rates and species biomasses, from which we deduce the interaction coefficients in our dynamical models. We then predict two facets of food web dynamics: its overall sensitivity to perturbations V and the strength of vertical effects λ . Dotted lines represent implicit or indirect effects (e.g., those mediated by other factors, or not modelled explicitly but contained in the structure of our data).

oceans at depths ranging from the surface to 10,900 m. To minimise biases in the occurrence data, distribution maps were reconstructed for each species, and the final distribution maps for a randomly selected sample of 500 species were verified visually and reviewed by experts.

Fish distributions were initially aggregated on a grid with 1° resolution in latitude and longitude. 13,916,517 occurrences for 11,365 fish species were considered. Body mass for each species was estimated from body length–mass relationships (data on body length were obtained from Fish Base). Pairwise interaction data from Barnes et al. (2008) was used to calibrate a model of trophic interactions using the observed body size for predators and prey (34,931 marine predator and prey interactions). The probability of interactions was inferred using a trait-matching function based on the niche model for food web structure (Williams and Martinez 2000; Gravel et al. 2013). This size-based network of potential interactions was subsequently pruned with the removal of forbidden interactions (based on diet) and range overlap, leading to a single deterministic global ‘meta-web’ representing plausible interactions between all the considered fish species. For each spatial cell of the species distribution grid, the local food web was then obtained by restricting the global meta-web to the species present in that cell. For the rest of this study, we restrict ourselves to 1% of the cells, chosen uniformly at random, yielding 431 food webs distributed across the world, as preliminary explorations proved this number of cells to be sufficient to conduct representative analyses. Out of these 431 food webs, 243 have more than nine species for which at least one trophic link is known, and are retained for our analysis.

2.2 | Modelling Framework

Dynamics within each local food web (geographic grid cell) are represented using a Lotka-Volterra model:

$$\frac{1}{B_i} \frac{dB_i}{dt} = g_i + \sum_j \epsilon a_{ij} B_j - \sum_k a_{ki} B_k - D_i B_i$$

with B_i the biomass of species i , g_i its intrinsic growth rate ($g_i = 0$ for species at trophic levels > 1), ϵ the conversion efficiency of consumed into produced biomass, a_{ij} the attack rate of consumer i on resource j and a_{ki} the attack rate of consumer k on consumer i . Finally, D_i is self-regulation, defined as the direct effect of a species on itself, such that its growth rate decreases with its own density.

Further justification is given below for our modelling choices; at first, the equation can be viewed simply as a way of adding dynamics to the static linear mass-balance equations that are often used for large-scale marine ecosystems, for example, Ecopath models (Coll  ter et al. 2015). Here, mass-balance corresponds to the right-hand side of the equation summing to zero, that is, assuming that large-scale food webs are effectively near some dynamical equilibrium that may average out complex smaller scale dynamics. We thus focus chiefly on ecological interactions, both intra- and inter-specific, to explain observed species biomasses, setting aside the effects of spatial fluxes, environmental factors and physiology (such as the metabolic losses often included in other allometric models, which were found here to be of limited importance, see Appendix S2).

We do not have access to direct measurements of biological rates such as g_i and a_{ij} for all species in large food webs (Berlow et al. 2004), and thus resort to an allometric parameterisation. Consumers are assumed to feed proportionally to the total biomass of each prey species, since we lack detailed knowledge on their consumption preferences.

The body mass and temperature dependencies of these rates were obtained from the empirical literature (Savage et al. 2004; Gillooly et al. 2001; Li et al. 2018). Parameters for fish growth rates were initially compiled from estimates from field studies (Savage et al. 2004) and parameters for attack rates were obtained from analyses of functional responses from empirical studies (Li et al. 2018) (see Tables S1 and S2).

Resource growth rate g_i and consumer attack rate a_{ij} are temperature and body mass dependent following the

Boltzmann–Arrhenius model (Gillooly et al. 2001; Brown et al. 2004; Savage et al. 2004):

$$g_i(m_i, T) = g_0 m_i^{\beta_g} e^{E_g(T-T_0)/(k_b T T_0)}$$

$$a_{ij}(m_i, T) = a_0 m_i^{\beta_a} e^{E_a(T-T_0)/(k_b T T_0)}$$

where g_0 and a_0 are scaling coefficients, and m_i is the body mass of species i . For each biological rate, β is the allometric scaling exponent while E is the activation energy in eV (electronvolts). Finally T is sea surface temperature in Kelvin (note that ‘temperature’ is used throughout the study to refer to ‘sea surface temperature’) and T_0 is the temperature of reference. k_b is the Boltzmann constant ($8.617 \times 10^{-5} \text{ eV K}^{-1}$). The attack rate depends here on consumer body mass but not on resource body mass, following a common choice in the literature (Pawar et al. 2012; Andersen et al. 2016; Li et al. 2018) and the empirical observation of shallow scaling of attack rates with resource mass (Rall et al. 2012). We note, however, that the effects of consumer mass in the literature could in fact correspond to entangled effects of both consumer and resource body masses, since these two variables are strongly correlated: the predator–prey body mass ratio plays a key role in determining which interactions are possible.

Self-regulation D_i is a key phenomenological parameter, capturing all the non-trophic interactions (e.g., direct competition or diseases) and other unmodelled processes that create a density-dependence or feedback between species biomass and growth. As discussed in the next section, the dynamics of our model in the absence of self-regulation ($D_i = 0$) are typically highly unstable, and rarely allow all observed species to coexist (Barabás et al. 2017; Barbier and Loreau 2019).

The most classic fix to this perceived model failure is not adding self-regulation, but rather assuming nonlinear functional responses, that is, an expression for the total trophic flux from prey j to predator i that deviates from $a_{ij} B_i B_j$, usually involving saturation with prey density (i.e., sublinear dependence on B_j) and predator interference (i.e., sublinear dependence on B_i) (see e.g., Brose et al. 2006; Barbier et al. 2021). Predator interference, including ratio-dependence (Arditi and Ginzburg 1989), can act as self-regulation for the predators, while prey saturation leads to self-facilitation (the opposite of self-regulation) among the prey. Thus, predator interference tends to attenuate the impacts of trophic interactions, stabilise dynamics and favour coexistence at the food web level like our parameter D_i (Sentis and Boukal 2018), whereas prey saturation can have opposite effects (Johnson and Amarasekare 2015). Barbier et al. (2021) provide some discussion of the similarities between predator interference and phenomenological self-regulation D_i , and we will see below that our approach could use either.

As there is more available information on species biomass than on self-regulation in the literature, we use information on species biomass to subsequently estimate self-regulation. We first use an empirical relationship between primary production and fish biomass from Irigoien et al. (2014) to estimate the total biomass of each local community:

$$B_{\text{tot}} = 0.185\text{PP} - 6.66$$

and subsequently compute the biomass of each species in a given community, using the scaling relationship between body mass and biomass from Hatton et al. (2019):

$$B_i = B_{\text{tot}} \frac{m_i^k}{\sum_j m_j^k}$$

Empirical data suggest that the total biomass in a body mass compartment is independent of body mass, that is, $k = 0$, a striking pattern known as Sheldon’s law (Hatton et al. 2019). If we assume that the equation admits an equilibrium with these biomasses B_i , the self-regulation parameter D_i is then the only unknown in the equation and we can solve for it. However, we usually do not find a solution with all $D_i \geq 0$, as some species may experience stronger predation mortality than their growth with the baseline parameters, even in the absence of self-regulation, and are thus predicted to go extinct. One possible solution is to posit some nonlinear functional response (see above) that would reduce predation mortality and thus allow the assumed equilibrium to exist.

We make a different choice here, as the overall strength of self-regulation is unknown empirically, and we wish to better understand which values would be compatible with the allometric scaling laws that we used. For each species i , we assume that a fixed fraction f of its production is lost to self-regulation (see de Ruiter et al. 1995, where a similar method was used), and we then either decrease or increase the attack rates a_{ji} of its predators (in the same proportion for all of them) in order to balance i ’s equilibrium condition. We expect that an appropriate choice of f should not require large or biased adjustments in the attack rates, but a narrow and symmetrical distribution of changes.

This method (explained in more detail in the [Supporting Information](#)) provides self-regulation estimates for each species in each community. We choose a fixed value of $f = 0.1$ for the fraction of production that is lost to self-regulation, as this value gives reasonable consistency between different parameters (see Appendix S2 for an exploration of values of f), and turns out to suffice to ensure not only the feasibility of the communities, but also their stability. We however note that those criteria are heuristic, and other assumptions may be investigated.

Finally, body masses of aquatic species are observed to decrease with both warmer temperatures and lower latitudes (Horne et al. 2015). Hence, we also consider decreasing body mass with temperature as predicted by the TSR. Following Forster et al. (2012), the temperature dependence of body mass is given by:

$$m_i = m_{20} e^{s(T-20)}$$

where m_{20} is species body mass at 20°C and T is sea surface temperature in Celsius, while s determines the sign and magnitude of the temperature–size response and is determined by the percentage change in body mass per °C (PCM) given by $\text{PCM} = (e^s - 1) \times 100$. For aquatic species (freshwater and marine metazoa), we take from Forster et al. (2012) the following relationship:

$$\text{PCM} = -3.90 - 0.53 \log_{10}(m_{20})$$

We use the initial species body masses as reference body masses at 20°C. Hence, in our model, body masses decrease above 20°C and increase under 20°C according to the equation above.

We first consider the effect of the temperature gradient (sea surface temperature) on biological rates and body mass, and, second, we simulate a warming of 2°C, following one of the predictions of the IPCC according to the high and very high greenhouse gas emissions scenarios (IPCC, Masson-Delmotte et al. 2021).

2.3 | Metrics of Food Web Properties

We focus on two metrics describing distinct and complementary facets of the properties of food webs.

Many food web studies try to find evidence of either bottom-up or top-down control, for example, as positive or negative correlation between predator and prey abundances (Frank et al. 2006). However, bottom-up and top-down control can also be defined in ways that are not mutually exclusive, for example, how strongly an external disturbance of prey (predator) dynamics subsequently impacts predator (prey) species, respectively (Galiana et al. 2021). To avoid potentially misleading conclusions, we propose a more integrative notion of ‘trophic control’, captured by the variable λ , that is, the feedback of a species on itself through its predators or prey (Barbier and Loreau 2019), given by:

$$\lambda_{ij} = \frac{\epsilon a_{ij}^2}{D_i D_j} = - \frac{M_{ij} M_{ji}}{M_{ii} M_{jj}}$$

where a_{ij} is attack rate, D_i is self-regulation of species i and ϵ is conversion efficiency, or equivalently, M_{ij} is the interaction matrix given by $M_{ii} = D_i$, $M_{ij} = \epsilon a_{ij}$ if i consumes j , $M_{ij} = -a_{ji}$ if i is consumed by j .

λ is thus the ratio of consumptive interactions between trophic levels over non-trophic interactions within both levels. Initially derived for a pair of consumer j and resource i , we use here the median value over all pairs of species for each local community (i.e., cell) and discuss alternate definitions in Appendix S3.

An increase in λ indicates stronger overall dynamical effects of predation, such as predator–prey cycles or trophic cascades. As noted by Barbier and Loreau (2019), these effects are often understood as indicators of stronger top-down control, but in fact large λ implies that both bottom-up and top-down effects are strong and cause feedbacks on both predator and prey. Small λ implies the absence of these feedbacks—removing a species altogether could still have an effect on the other (in particular, predators still require prey to persist), but smaller dynamical variations in one species’ biomass are not amplified in the other, thus cycles are absent and trophic cascades are attenuated.

We also look at variability V , which is a metric of sensitivity of the community to perturbations, defined as how strongly species

abundances in the community respond on average to randomly adding or removing individuals. Following Arnoldi et al. (2019), it is computed as the community average of the temporal variance of biomass in response to demographic perturbations for dynamics linearised around equilibrium,

$$V = \text{tr}(C)$$

where $\text{tr}(C)$ is the trace of the covariance matrix C of species temporal fluctuations, which is the solution of the Lyapunov equation $JC + CJ^T = -\bar{B}$, where $\bar{B}_{ij} = B_i$ if $i = j$ is the covariance of the stochastic perturbation (which is assumed diagonal and proportional to equilibrium biomasses) and $J_{ij} = B_i M_{ij}$ is the Jacobian matrix for the dynamics at equilibrium, with M_{ij} the interaction matrix defined earlier in this section. A lower temporal variability of populations is interpreted as higher stability *ceteris paribus*, with the caveat that different communities may be exposed to stronger or weaker perturbations, and thus display smaller or larger biomass fluctuations, even if they are equally sensitive to these perturbations.

2.4 | Latitudinal Variation in Food Web Properties

Food web properties λ and V depend on latitude Lat indirectly, through various drivers. We therefore investigate the relationship between these properties and four variables that vary with latitude: T is sea surface temperature, B_{tot} is the total biomass in g m^{-2} estimated from primary productivity, m is the average body mass in g, S is the number of species in each community, and $C = L/S^2$ is the connectance, computed from L the number of links in the food web. We want to understand how important each of these indirect effects of latitude is in shaping the gradient of food web properties. Since all of these vary over orders of magnitude, the calculations are performed with the log of parameters and variables (i.e., $\log_{10}(\lambda)$ instead of λ , etc.), except for temperature.

Path analysis, Structural Equation Modelling and similar statistical methods could be used to infer the respective partial effects of each predictor on each predicted food web property. However, since we have a simulation model, we can directly compute causal effects such as $\partial \lambda / \partial \log S$ by changing the relevant model parameter in the simulation, here $\log S$, and computing the resulting change in outcome λ (see Figure 2).

More generally, if a variable of interest x depends on the variables $\log S, T, \dots$, which themselves depends on the variable Lat, then we can use the chain rule below for the total dependence of x on Lat.

$$\frac{dx}{d\text{Lat}} = \frac{\partial x}{\partial \log S} \frac{d \log S}{d\text{Lat}} + \frac{\partial x}{\partial T} \frac{dT}{d\text{Lat}} + \dots$$

where $\frac{\partial x}{\partial \log S}$ for instance is the rate of change of x relative to $\log S$, while the variation with latitude (e.g., $dS/d\text{Lat}$) can be measured from the source data. This can be expanded to include any dependence of some variable on some other variable (e.g., body mass m could depend on temperature as $m(T)$). This rule allows us to reveal how much of the variation of x with latitude is due to paths that go through $\log S, T$ or other variables.

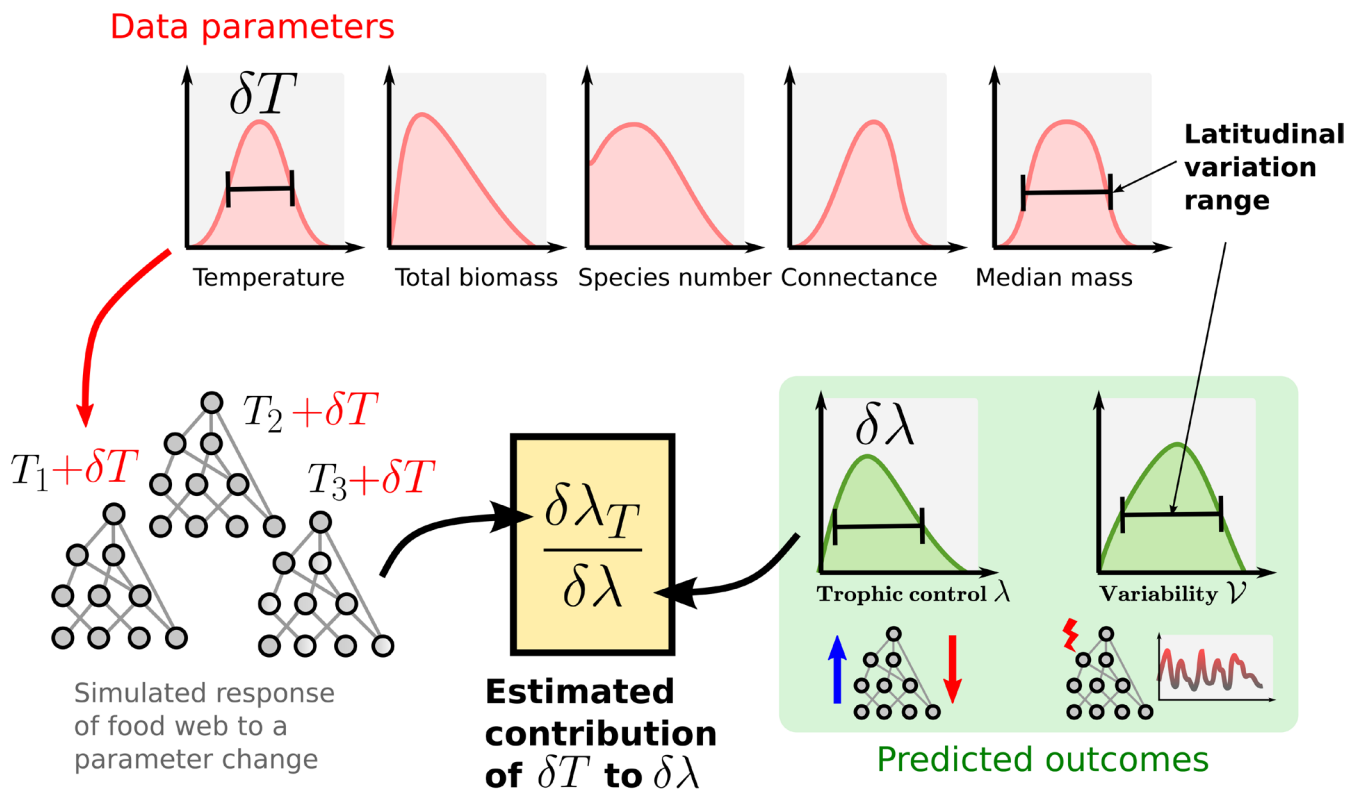


FIGURE 2 | Analysis of the latitudinal variation of food web properties. We observe a latitudinal gradient of many properties, both parameters in our data (e.g., species number) and outcomes of our simulation model (e.g., trophic control). To coarsely understand which parameters mediate the changes in outcomes, we must ask: first, do those parameters vary a lot (e.g., how large is the typical range δT of temperature variation), and second, how much does such a variation impact simulated outcomes (e.g., how large is the change $\delta\lambda_T$ of trophic control λ if we were to increase temperature by δT in every food web)? We finally compare the change in some predicted food web property (e.g., λ) when actively changing a predictor (e.g., T) in each local community to the standing variation of the same property in food webs with parameters drawn from the original data, and use this ratio as a rough estimate of the importance of that predictor in the latitudinal variation of that predicted property.

Yet, these causal effects will be different for every local food web (due to them having different initial parameters and structure), and the chain rule is valid for small variations. Nevertheless, we take inspiration from it to approximately estimate how much the total variation with latitude of each parameter contributes to the total variation in each predicted food web property (Figure 2).

For every quantity y (including both the outcomes x and the explanatory variables $\log S$, T etc.), we compute its median for each latitude $y_{\text{med}}(\text{Lat})$, and then compute δy as the difference between the 75th and 25th percentiles of $y_{\text{med}}(\text{Lat})$, that is, the typical variation of y across latitudes ($\delta y = P_{75\%}(y_{\text{med}}(\text{Lat})) - P_{25\%}(y_{\text{med}}(\text{Lat}))$).

Inspired by the above expression, we approximately decompose the total variation of some predicted outcome x (either λ or V) into contributions from the various parameters:

$$\delta x \approx \delta x_T + \delta x_S + \dots$$

where $\delta x_T = E[x(T) - x(T + \delta T)]$ is computed as the average change of metric x when we simulate each community and change its temperature by the quantity δT (which is not a small change, thus the chain rule does not truly apply). For species number and connectance, we cannot increase them, but only reduce

them by removing species or links at random, and therefore we use a negative δS and δC instead.

We finally roughly approximate the relative contribution (averaged over all communities) of T to the variation of x as:

$$\frac{\delta x_T}{\delta x}$$

and we proceed similarly for the other quantities: $\log S$, $\log B_{\text{tot}}$, C and $\log m$. These approximate coefficients need not sum exactly to 1, but they can give a qualitative sense of how important the parameters are in explaining the total latitudinal variation of food web properties. Empirically, some of the parameters might be interdependent such as species richness and temperature; in our model, however, those variables can be varied independently and we hence focus on their direct effects.

2.5 | Simulating a 2°C Warming

Finally, we simulate for each local community a 2°C warming and compute the relative difference in food web properties and in biomasses with and without warming. We only include here an effect of warming on species biological rates, and

TABLE 1 | Description of the food web model parameters.

Symbol	Description	Unit	Value	References
ϵ	Conversion efficiency	—	0.15	Welch (1968)
T	Sea surface temperature	Kelvin	272–302	—
k_B	Boltzmann constant	eV K ⁻¹	8.617×10^{-5}	—
m	Body mass	g	—	—
g	Growth rate	day ⁻¹	$f(T, m_i)$	Savage et al. (2004)
a	Attack rate	md ⁻¹	$f(T, m_i)$	Li et al. (2018)
T_0	Normalisation temperature	Kelvin	298.15	—
β_g	Allometric scaling exponent for g	—	-0.25	Savage et al. (2004)
E_g	Activation energy for g	eV	-0.35	Savage et al. (2004)
g_0	Scaling coefficient for g	day ⁻¹	0.35	Savage et al. (2004)
β_a	Allometric scaling exponent for a	—	-0.51	Li et al. (2018)
E_a	Activation energy for a	eV	-0.43	Li et al. (2018)
a_0	Scaling coefficient for a	md ⁻¹	2.17	Li et al. (2018)

possibly body mass via the TSR described above. Our analysis should therefore be interpreted as a first-level impact of warming, not accounting for changes in primary productivity, biomass allometry or species ranges. Growth rate, attack rate and self-regulation are changed with warming according to the equations described earlier; parameter values are described in Table 1. Self-regulation, for which the temperature dependence is not known, is assumed to scale with temperature in the same way as the growth rate; see discussion in Bideault et al. (2021). Everything else (e.g., productivity) remains unchanged. We also take a closer look at the relative change in community biomass and individual species biomass for each trophic level with warming.

For each metric x , the relative change with warming is computed as:

$$\Delta(x) = \log_{10}(x_{\text{warm}}) - \log_{10}(x) \approx (x_{\text{warm}} - x) / x$$

Hence $\Delta(x) = 0.2$ means an increase of approximately 20% with warming in the value of x , for example.

2.6 | Calculating Trophic Levels

Trophic levels T_i are computed recursively for each species i according to the following rule: if the set of its prey species, $\text{Prey}(i)$, is empty, then the trophic level of i is 1; otherwise, we compute the trophic level of all prey species $j \in \text{Prey}(i)$, compute its average weighted by each prey species' biomass B_j (which we use as a proxy for their relative contribution to the consumer's diet), and add one to obtain the trophic level of their predator i . This is recapitulated in the following equation:

$$T_i = 1 + \sum_{j \in \text{Prey}(i)} T_j \frac{B_j}{\sum_{k \in \text{Prey}(i)} B_k}$$

This simple calculation can fail if there are loops in the food web (i.e., i eats j which eats i , potentially leading to infinite T_i if calculated this way), but such loops do not occur in our data.

3 | Results

3.1 | Food Web Properties Along the Latitudinal Gradient

We first investigate the variation in food web properties with latitude. We find that trophic control and variability vary at large spatial scales (Figure 3). On average, trophic control decreases towards the equator, indicating weaker trophic phenomena (e.g., cycles and cascades). This trend should be robust to different methods of estimating self-regulation (see Bideault et al. 2021). The map indicates that λ is particularly small for communities near the coast around the equator. The temporal variability of species abundances, V , decreases towards the poles, indicating an increase in stability at colder sites (Figure 3 bottom panel). V does not vary significantly with latitude around the equator but drops at latitudes above |50|.

We show in Appendix S3 that both λ and V steadily decline if we assume a larger fraction $f > 0.1$ of production lost to self-regulation; however, most of our analysis is about relative variations across latitudes or with warming, that are minimally affected by the precise value of f unless it is large (e.g., $f = 0.7$ leads to significantly different parameter estimates and thus different results).

We decompose how different factors, covarying with latitude, influence food web properties (see Section 2.4). Links between the explanatory variables and the metrics are illustrated in Figure 4, and the coefficients are provided in Table 2.

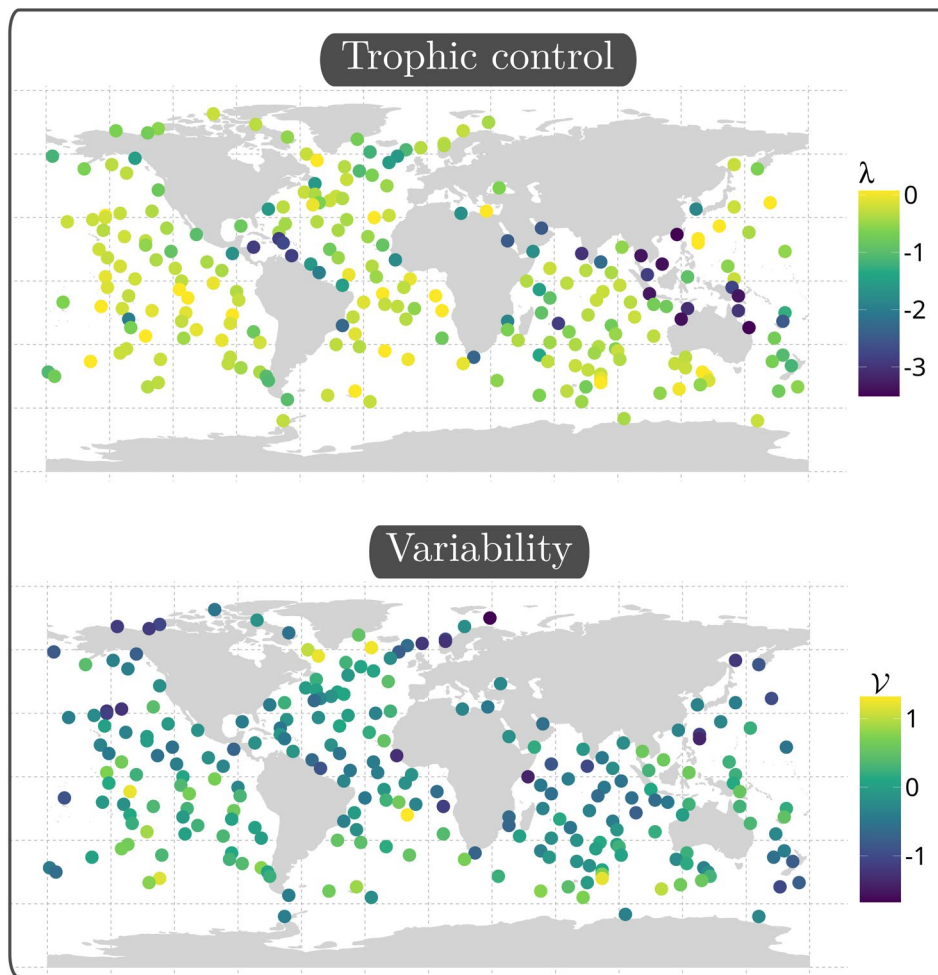


FIGURE 3 | Maps of the metrics of food web properties. Maps of trophic control λ and variability V for fish food webs in saltwater. Each dot corresponds to the food web for a cell representing 1° of latitude and longitude (only 1% of the cells are sampled here, see Section 2). Metrics are computed for each food web as described in Section 2.3. Values are indicated in \log_{10} and colour coded (see colour key).

Trophic control λ is negatively affected by species richness, connectance and body mass, and positively affected by temperature. Species richness and connectance mainly drive variation in λ , with species rich food webs having a weaker trophic control than species poor food webs. Variability V is negatively affected by temperature and body mass. Variability is here mainly driven by body mass and temperature, either of them inducing an increase in stability.

Note that here, temperature refers to a direct effect of temperature on species biological rates only (the TSR is not included, we manipulated body mass separately).

3.2 | Warming

We also explore the impacts of a 2°C warming on food web properties and species biomasses, keeping composition and body mass distribution constant.

If we assume that heating only changes biological rates (see Figure S1), the equations immediately yield (without need of a simulation) an increase of rates by the same fraction for all

species in all communities depending on their original temperature: for T ranging from 0°C to 30°C , attack rates increase by 11%–14%, while basal species growth rates increase by 9%–11% (the relative increase is smaller when the original T is higher). Adding the TSR, species become smaller, leading to an additional 2%–7% increase of the rates, as these are rates per unit mass, decreasing for larger bodied organisms. We could thus expect large dynamical effects due to this notable increase in rates.

Yet, the effects of warming on our food web metrics are noticeably weaker. Without the TSR, the median λ increases on average by 5% indicating that warming promotes moderately stronger trophic effects (Figure S1A, green histogram). Warming also increases stability, with variability V decreasing by up to 10% (Figure S1A, orange histogram). The effect on λ is amplified by adding the TSR (Figure 5A, green histogram), whereas the effect on variability is drastically decreased (Figure 5A, orange histogram).

The reason for these discrepancies, especially compared to the expectation of larger changes suggested by the previous paragraph, is the fact that the food web metrics depend on ratios

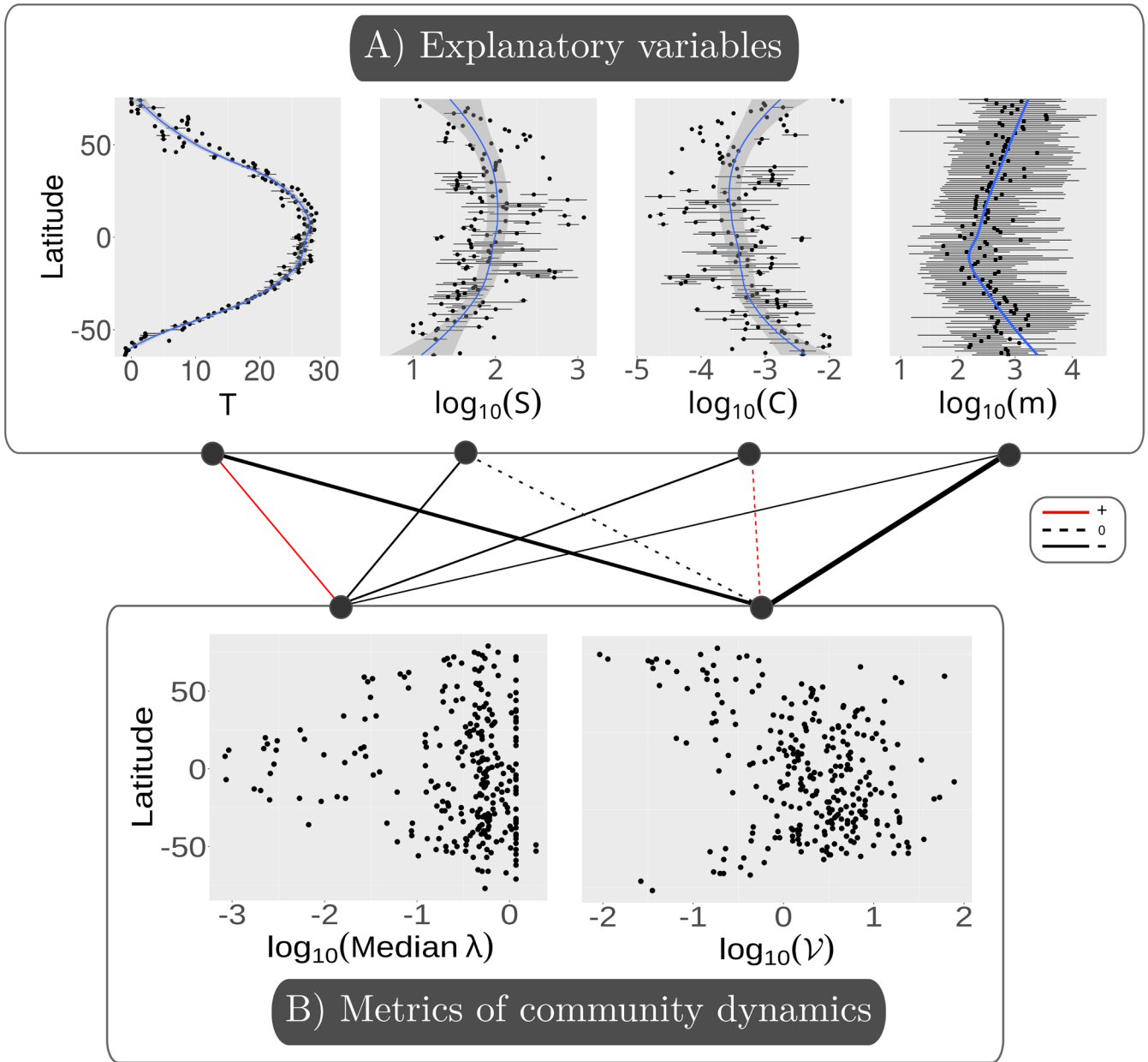


FIGURE 4 | Latitudinal variation in food web properties. (A) Explanatory variables of the latitudinal variation in food web properties. For each latitude, the median and the quartiles are plotted for temperature T in $^{\circ}\text{C}$, species richness $\log_{10}(S)$, connectance $\log_{10}(C)$ and species body mass $\log_{10}(m)$ in g (smoothed by a GAM or a LOESS model). (B) Latitudinal variation in median λ per community and variability V (metrics are in \log_{10}). Following the method presented in Figure 2, links between the explanatory variables and the metrics of food web properties represent approximate relative contributions of each variable in the latitudinal variation of each metric. A red line indicates a positive effect, a dotted line indicates no effect (confidence interval crossing zero) and a full black line indicates a negative effect (see legend). The size of the lines is proportional to the effect size. Coefficients and confidence intervals are indicated in Table 2.

TABLE 2 | Coefficients for the relative contributions of the variables on the latitudinal variation of λ and V . Mean across communities [80% confidence interval].

Explanatory variables	Trophic control, λ	Variability, V
Temperature	0.18 [0.0013, 0.49]	-0.41 [-0.64, -0.075]
Species richness	-0.22 [-0.61, -0.012]	-0.22 [-0.63, 0.6]
Connectance	-0.22 [-0.52, -0.0057]	0.16 [-0.07, 0.51]
Species body mass	-0.16 [-0.45, -0.0012]	-0.59 [-0.99, -0.13]

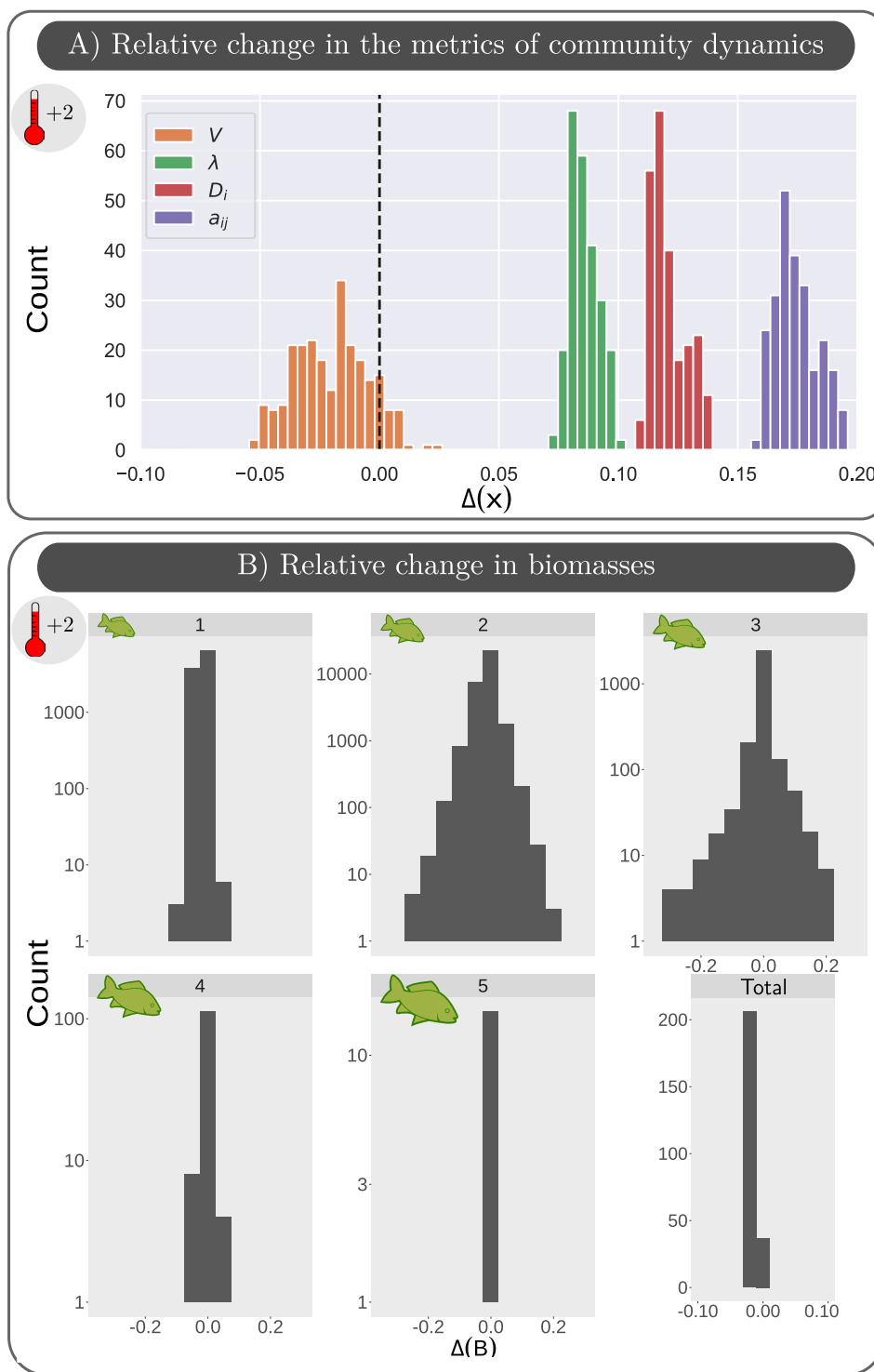


FIGURE 5 | Effect of warming at the community and species level. Histograms of the relative change $\Delta(x)$ in parameters, food web dynamical properties and species biomass with a 2°C warming, including the TSR. (A) Relative change in parameters and in the metrics of food web properties: self-regulation D_i in red, attack rate a_{ij} in purple, trophic control λ in green and variability V in orange. The dotted line corresponds to $\Delta(x)=0$, and indicates no effect of warming. (B) Relative change in total community biomass and species biomass for trophic levels 1, 2, 3, 4 and 5 respectively (trophic levels are computed from the equation in Section 2.6 and rounded to the nearest integer).

of various quantities that are impacted by warming, and these changes can cancel each other out unless there are significant mismatches in their size exponents (when sizes change according to the TSR) and activation energies (Bideault et al. 2021). We show in [Supporting Information](#) that a different metric of

stability, the variability in response to environmental rather than demographic stochasticity, remains impacted by warming even with the TSR. We conclude that, while individual rates change a lot under warming, various composite metrics that can be defined at the community level appear to change less.

We subsequently explore how warming affects both community and species biomasses (Figure 5B). The total biomass of communities does not vary much with warming (Figure 5B last panel). However, individual species biomasses can be more strongly affected by warming. The greatest variation in biomass occurs for species at intermediate trophic levels, and especially for trophic levels 2 and 3. The biomasses of species at trophic levels 5 (and above) appear not to be affected by warming.

4 | Discussion

We aimed at better characterising latitudinal variations in food web properties and identifying their main drivers. Our results indicate that trophic control is mainly driven by variation in species richness and connectance, indicating weaker trophic phenomena (e.g., cycles and cascades) in species-rich communities that are typically found around the equator. Temporal variability is predicted to decrease towards the poles and seems mainly driven by median species body mass. Simulating a 2°C warming induces moderate effects on food web, consistent with the predicted driving role of temperature: warming triggers stronger trophic dynamics yet decreases variability (Figure 5A). Our results also indicate that individual species biomass varies significantly more than total biomass with warming, with some species biomasses increasing whilst others decrease.

4.1 | Latitudinal Gradients of Two Community Metrics

Previous studies have put forward that top-down control is more prevalent in high latitude marine ecosystems and bottom-up control in lower ones (Boyce et al. 2015; Frank et al. 2006). Different hypotheses have been proposed to explain such variation. On the one hand, latitudinal changes in the intensity of biotic interactions have been considered both as a cause and a consequence of the latitudinal biodiversity gradient (Zvereva and Kozlov 2021), and bottom-up regulation has indeed been associated with areas with higher species richness (Frank et al. 2006). On the other hand, a recent study found that predation was higher at mid-range latitudes due to temperature-associated turnover in consumer composition, with no association with species richness (Whalen et al. 2020). We did not investigate how consumer composition varies with latitude, which could possibly explain the observed variation in trophic control, if higher species richness is associated with the presence of specific consumers, for instance.

While we move away from a binary opposition between bottom-up and top-down control, towards a metric of trophic control λ that integrates both, our results are more in line with Frank et al. (2006), as we find a decrease in trophic control towards lower latitudes which would lead to a phenomenology more traditionally associated with bottom-up control (Polis and Strong 1996). This decrease in trophic control arises from the fact that, in our model, consumer attack rates must decrease with species richness: the mortality of prey species is otherwise too large when they have many predators, thus the assumed equilibrium biomasses require a reduction in attack rates that

can be interpreted as multi-species predator interference (Sentis et al. 2012).

Previous studies on real food webs indicated that the spread of interaction strength was negatively correlated to species richness (Jacquet et al. 2016) and that food webs were characterised by many weak interactions and long loops (Neutel et al. 2002). Theoretical studies also demonstrated that weak interactions tend to enhance food web stability (Yodzis 1981; McCann et al. 1998; Neutel et al. 2002). Here, increasing species richness leads to a decrease in trophic control. On the contrary, the direct effect of warming is often observed to increase top-down control in consumer-resource systems (Sentis et al. 2014; Kratina et al. 2012; Bideault et al. 2019, 2021). Our model also shows that warming food webs while keeping a constant species richness induces an increase in trophic control. This suggests that, when considering latitudinal gradients, the direct effect of temperature on trophic control might be counteracted by its indirect effect through species richness.

The constraint imposed by our equilibrium assumption on interaction coefficients (our effective predator interference) can also affect stability, as well as other features of ecosystems such as food web structure (Ives and Carpenter 2007). There is a long-standing debate on the diversity–stability relationship in ecology (May 1974; McCann 2000; Ives and Carpenter 2007; Loreau et al. 2002; Jacquet et al. 2016) but the dominant idea in the field is that there is a stabilising effect of diversity on ecosystem functioning (Loreau and De Mazancourt 2013). There are many different ways to quantify stability (Arnoldi et al. 2016). We here take a particular interest in temporal variability of species abundances in response to demographic perturbations and find that it is mainly driven by body mass and, to a lesser extent, by temperature, with both variables increasing stability (decreasing variability). As body mass is known to decrease with temperature (Forster et al. 2012), there could be indirect effects of temperature on variability (Sentis et al. 2017).

4.2 | Impacts of Warming on Food Web Properties

Latitudinal variation in temperature is not necessarily equivalent to the same amount of warming because of the several indirect effects of temperature on food webs. Warming up communities by 2°C can have strong (up to 20%) effects on individual biological rates, but more moderate impacts on community properties. It still induces an increase in stability and trophic control by up to 10%. An interesting point of our simulations is that it focuses on the direct effect of temperature on biological rates (and on body sizes that intervene in the metabolic scaling), controlling for other variables known to covary with temperature, such as species richness and primary productivity. Many studies demonstrated that warming can significantly increase trophic control (Kratina et al. 2012; Gray et al. 2016; O'Connor et al. 2009; Bideault et al. 2021) or stabilise predator–prey dynamics by damping oscillations (Fussmann et al. 2014), whereas predators become extinct at high temperatures (Rall et al. 2010; Petchey et al. 1999; Fussmann et al. 2014). The extinction of species from top-trophic levels is often due to metabolic demands exceeding ingestion rates, which leads to consumer starvation. We focus here on the effect of density-dependent interactions on

community dynamics, whereby warming does not trigger many extinctions and mainly affects species from mid-trophic levels. Warming can moderately decrease as well as increase species biomass, but induces negligible effects on community total biomass. This result indicates that consumers may not become extinct due to interactions (e.g., competition) and suggests that a mismatch between metabolic requirements and feeding rates might indeed be the cause of consumer extinction (Fussmann et al. 2014). The addition of self-regulation in our model, and the method used to estimate it, might also stabilise food web dynamics and prevent extinctions. Including metabolic rates in the model could lead to stronger effects of warming as species extinctions due to starvation could induce secondary extinctions and change the structure of the food web, which could in turn affect food web properties.

Under our model assumptions, we thus find that food web properties are relatively robust to warming whilst individual species can be strongly affected in a positive or negative way. This may concur with the fact that strong effects of warming have been observed in consumer-resource systems with two or three species, either in experimental or theoretical studies (Sentis et al. 2013; Bideault et al. 2019, 2021; Fussmann et al. 2014). The more modest response at the food web level appears to be due to the fact that properties of interest (metrics that are dimensionless or otherwise constructed to be easily comparable across different systems) are often ratios combining several species-level rates and variables, whose temperature dependence may partially or totally cancel out unless there are mismatches in their allometric parameters (Bideault et al. 2021).

4.3 | Model Parameterisation and Assumptions

The key ingredients of our modelling approach, as shown in Figure 1, are the food web topologies derived from Albouy et al. (2019), the allometric relationships between temperature, body mass and biological rates, and the model structure focusing on trophic interactions and self-regulation. We now discuss these ingredients and the limits of our assumptions.

Food web structures are only partially known and often supplemented with general expectations such as size-based structure. Yet, a recent study demonstrated that using either the natural structure of food webs or synthetic food webs (i.e., food webs drawn from the niche model) leads to different conclusions regarding species persistence under warming (Gauzens et al. 2020). This observation may come from differences in body mass structure or in network topologies between synthetic and natural communities. We used here food webs in which species occurrences were empirically observed and species interactions were derived following allometric laws and subsequently corrected based on species habitat requirements and fish diet (Albouy et al. 2019). The real food web structure might thus be different, but it has been demonstrated that allometric relationships accurately predict trophic interactions among fishes (Leclerc et al. 2023), which might be less the case in food webs with plants and invertebrates as those used in Gauzens et al. (2020).

The core challenge in modelling food web dynamics is that, even assuming that we have a good approximation of the network's

topology, we usually do not have access to more quantitative information: the strength of the trophic interactions (Berlow et al. 2004), and even more importantly, their relative importance compared to other ecological processes such as non-trophic interactions, population structure, spatial fluxes and so on. Modelling only trophic interactions may thus dramatically overestimate and bias their impacts. For the first issue, we follow a large literature, for example, Brose et al. (2012), in using allometric relationships for predation rates. The more novel choice in our approach is the reliance on phenomenological self-regulation coefficients D_i to capture all the non-trophic (and possibly some unmodelled trophic) processes that may jointly act to attenuate the effects of the modelled trophic interactions. Because this self-regulation may only be a phenomenological outcome of many processes, it is understudied in food webs (Barbier and Loreau 2019). Yet, it is a cornerstone of coexistence theory, and essential to obtain stability levels consistent with observation in nature (Barabás et al. 2017). We employ it as the most consistent way to incorporate unmodelled phenomena at the level of approximation of a community-wide Lotka-Volterra model. We do not necessarily expect this model form to be realistic, but only to allow us to modulate food web dynamics: all else being equal, increasing self-regulation means that all direct and indirect effects of predation are weaker.

As no reliable information was available on the magnitude of self-regulation, we adjusted it (and trophic interactions when necessary, see [Supporting Information](#)) in our dynamical model so that its equilibrium biomasses would match a general and robust scaling relationship between species abundance and body size (Hatton et al. 2019). Despite the good fit of these empirical relationships, there is a relatively important spread around the general trend. Taking into account this variation between taxonomic orders or species might lead to different results. It remains, however, difficult to get accurate data for numerous species, and we were mainly interested in global patterns which we expect to be governed by the central trends. Similarly, activation energies for temperature-dependence vary across biological rates and taxonomic groups (Dell et al. 2011) and it has previously been shown that thermal mismatches in activation energies between biological rates of consumers and resources can drive variation in trophic control and biomass structure (Bideault et al. 2021). We nevertheless used the same activation energies across all species. The rationale for this choice is that we consider fish species which are part of the same broad taxonomic group, and we thus expect that there is less variation between different species, while getting activation energies at the species level is difficult (Dell et al. 2011). In any case, parameterising models with numerous species at the global scale remains challenging, and we specifically chose some metrics of food web properties that we expect to be more robust to modelling choices.

5 | Conclusion

In conclusion, our model predicts latitudinal variation in trophic control and temporal variability. We find that indirect temperature effects on this variation, such as those mediated through the TSR and community assembly processes, play a stronger or equal role compared to direct effects like temperature-driven

changes in interaction rates. While direct effects tend to weaken trophic feedbacks and increase variability, indirect effects through changes in body size enhance both. Furthermore, community-level indirect effects, such as variation in species richness and connectance, modulate feedback strength but not variability. These results highlight that although organism-level thermal performance remains important, it is insufficient alone to predict large-scale patterns in community dynamics.

Even as our global knowledge of marine food web composition and topology increases, our understanding of the dynamics of these food webs is limited. The relative importance of trophic interactions compared to other processes in determining population abundances and growth, which species impact which others, or how sensitive the community is to perturbations remains difficult to determine. Our study aims to provide a baseline expectation for how these properties can vary in fish communities across latitudes, and how they might be affected by warming. Being acquainted with the main drivers of food web properties, and the direct and indirect effects of temperature, is crucial to predict how ecological systems will respond to climate warming. We have focused here on the effects of temperature that are mediated by species interactions and community-level dynamics, as a complementary perspective to the vast literature focusing on individual species and their thermal preferences (Grenouillet et al. 2011). Our approach suggests that getting quantitative information on self-regulation is also crucial in understanding community structure and dynamics, and opens new avenues to better capture how food webs vary from one pole to another.

Acknowledgements

Our gratitude goes to Camille Albouy and his co-authors and sources for collecting and sharing the data. We are also grateful to Eva Delmas for help with preliminary modelling work.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The source data on fish presence are available at <https://obis.org/> and the presence/absence data extrapolated from these data are available at <https://doi.org/10.6084/m9.figshare.7034789.v2>. The code to create the meta-web has been published and is available at <https://doi.org/10.6084/m9.figshare.650228.v1>. See Albouy et al. (2019) at <https://doi.org/10.1038/s41559-019-0950-y>. Codes for the simulation and the path analysis are available at <https://doi.org/10.5281/zenodo.15031867>.

References

Albouy, C., P. Archambault, W. Appeltans, et al. 2019. "The Marine Fish Food Web Is Globally Connected." *Nature Ecology & Evolution* 3, no. 8: 1153–1161.

Amarasekare, P. 2019. "Effects of Climate Warming on Consumer-Resource Interactions: A Latitudinal Perspective." *Frontiers in Ecology and Evolution* 7: 146.

Andersen, K. H., N. S. Jacobsen, and K. D. Farnsworth. 2016. "The Theoretical Foundations for Size Spectrum Models of Fish Communities." *Canadian Journal of Fisheries and Aquatic Sciences* 73, no. 4: 575–588.

Arditi, R., and L. R. Ginzburg. 1989. "Coupling in Predator-Prey Dynamics: Ratio-Dependence." *Journal of Theoretical Biology* 139, no. 3: 311–326.

Arnoldi, J.-F., M. Loreau, and B. Haegeman. 2016. "Resilience, Reactivity and Variability: A Mathematical Comparison of Ecological Stability Measures." *Journal of Theoretical Biology* 389: 47–59.

Arnoldi, J.-F., M. Loreau, and B. Haegeman. 2019. "The Inherent Multidimensionality of Temporal Variability: How Common and Rare Species Shape Stability Patterns." *Ecology Letters* 22, no. 10: 1557–1567.

Atkinson, D. 1994. "Temperature and Organism Size: A Biological Law for Ectotherms?" *Advances in Ecological Research* 25: 1.

Baiser, B., D. Gravel, A. R. Cirtwill, et al. 2019. "Ecogeographical Rules and the Macroecology of Food Webs." *Global Ecology and Biogeography* 28, no. 9: 1204–1218.

Barabás, G., M. J. Michalska-Smith, and S. Allesina. 2017. "Self-Regulation and the Stability of Large Ecological Networks." *Nature Ecology & Evolution* 1, no. 12: 1870–1875.

Barbier, M., and M. Loreau. 2019. "Pyramids and Cascades: A Synthesis of Food Chain Functioning and Stability." *Ecology Letters* 22, no. 2: 405–419.

Barbier, M., L. Wojcik, and M. Loreau. 2021. "A Macro-Ecological Approach to Predation Density-Dependence." *Oikos* 130, no. 4: 553–570.

Barnes, C., D. M. Bethea, R. D. Brodeur, et al. 2008. "Predator and Prey Body Sizes in Marine Food Webs: Ecological Archives e089-051." *Ecology* 89, no. 3: 881.

Berlow, E. L., A.-M. Neutel, J. E. Cohen, et al. 2004. "Interaction Strengths in Food Webs: Issues and Opportunities." *Journal of Animal Ecology* 73, no. 3: 585–598.

Beveridge, O. S., S. Humphries, and O. L. Petchey. 2010. "The Interacting Effects of Temperature and Food Chain Length on Trophic Abundance and Ecosystem Function." *Journal of Animal Ecology* 79, no. 3: 693–700.

Bideault, A., N. Galiana, Y. R. Zelnik, et al. 2021. "Thermal Mismatches in Biological Rates Determine Trophic Control and Biomass Distribution Under Warming." *Global Change Biology* 27, no. 2: 257–269.

Bideault, A., M. Loreau, and D. Gravel. 2019. "Temperature Modifies Consumer-Resource Interaction Strength Through Its Effects on Biological Rates and Body Mass." *Frontiers in Ecology and Evolution* 7: 45.

Binzer, A., C. Guill, U. Brose, and B. C. Rall. 2012. "The Dynamics of Food Chains Under Climate Change and Nutrient Enrichment." *Philosophical Transactions of the Royal Society B: Biological Sciences* 367, no. 1605: 2935–2944.

Bonnauffé, W., A. Danet, C. Leclerc, V. Frossard, E. Edeline, and A. Sentis. 2024. "The Interaction Between Warming and Enrichment Accelerates Food-Web Simplification in Freshwater Systems." *Ecology Letters* 27, no. 8: e14480.

Boukal, D. S., A. Bideault, B. M. Carreira, and A. Sentis. 2019. "Species Interactions Under Climate Change: Connecting Kinetic Effects of Temperature on Individuals to Community Dynamics." *Current Opinion in Insect Science* 35: 88–95.

Boyce, D. G., K. T. Frank, B. Worm, and W. C. Leggett. 2015. "Spatial Patterns and Predictors of Trophic Control in Marine Ecosystems." *Ecology Letters* 18, no. 10: 1001–1011.

Brose, U., J. A. Dunne, J. M. Montoya, O. L. Petchey, F. D. Schneider, and U. Jacob. 2012. "Climate Change in Size-Structured Ecosystems." *Philosophical Transactions of the Royal Society B* 367: 2903–2912. <https://doi.org/10.1098/rstb.2012.0232>.

- Brose, U., R. J. Williams, and N. D. Martinez. 2006. "Allometric Scaling Enhances Stability in Complex Food Webs." *Ecology Letters* 9, no. 11: 1228–1236.
- Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. "Toward a Metabolic Theory of Ecology." *Ecology* 85, no. 7: 1771–1789.
- Colléter, M., A. Valls, J. Guitton, D. Gascuel, D. Pauly, and V. Christensen. 2015. "Global Overview of the Applications of the Ecopath With Ecosim Modeling Approach Using the Ecobase Models Repository." *Ecological Modelling* 302: 42–53.
- de Ruiter, P. C., A.-M. Neutel, and J. C. Moore. 1995. "Energetics, Patterns of Interaction Strengths, and Stability in Real Ecosystems." *Science* 269, no. 5228: 1257–1260.
- Dell, A. I., S. Pawar, and V. M. Savage. 2011. "Systematic Variation in the Temperature Dependence of Physiological and Ecological Traits." *Proceedings of the National Academy of Sciences of the United States of America* 108, no. 26: 10591–10596.
- Fischer, A. G. 1960. "Latitudinal Variations in Organic Diversity." *Evolution* 14, no. 1: 64–81.
- Forster, J., and A. G. Hirst. 2012. "The Temperature-Size Rule Emerges From Ontogenetic Differences Between Growth and Development Rates." *Functional Ecology* 26, no. 2: 483–492. <https://doi.org/10.1111/j.1365-2435.2011.01958.x>.
- Forster, J., A. G. Hirst, and D. Atkinson. 2012. "Warming-Induced Reductions in Body Size Are Greater in Aquatic Than Terrestrial Species." *Proceedings of the National Academy of Sciences of the United States of America* 109, no. 47: 19310–19314.
- Forster, J., A. G. Hirst, and G. Woodward. 2011. "Growth and Development Rates Have Different Thermal Responses." *American Naturalist* 178, no. 5: 668–678.
- Frank, K. T., B. Petrie, and N. L. Shackell. 2007. "The Ups and Downs of Trophic Control in Continental Shelf Ecosystems." *Trends in Ecology & Evolution* 22, no. 5: 236–242.
- Frank, K. T., B. Petrie, N. L. Shackell, and J. S. Choi. 2006. "Reconciling Differences in Trophic Control in Mid-Latitude Marine Ecosystems." *Ecology Letters* 9, no. 10: 1096–1105.
- Fussmann, K. E., F. Schwarzmüller, U. Brose, A. Jousset, and B. C. Rall. 2014. "Ecological Stability in Response to Warming." *Nature Climate Change* 4, no. 3: 206–210.
- Galiana, N., J.-F. Arnoldi, M. Barbier, A. Acloque, C. de Mazancourt, and M. Loreau. 2021. "Can Biomass Distribution Across Trophic Levels Predict Trophic Cascades?" *Ecology Letters* 24, no. 3: 464–476.
- Gauzens, B., B. C. Rall, V. Mendonça, C. Vinagre, and U. Brose. 2020. "Biodiversity of Intertidal Food Webs in Response to Warming Across Latitudes." *Nature Climate Change* 10, no. 3: 264–269.
- Gillooly, J. F., J. H. Brown, G. B. West, V. M. Savage, and E. L. Charnov. 2001. "Effects of Size and Temperature on Metabolic Rate." *Science* 293, no. 5538: 2248–2251.
- Gravel, D., T. Poisot, C. Albouy, L. Velez, and D. Mouillot. 2013. "Inferring Food Web Structure From Predator–Prey Body Size Relationships." *Methods in Ecology and Evolution* 4, no. 11: 1083–1090.
- Gray, S. M., T. Poisot, E. Harvey, N. Mouquet, T. E. Miller, and D. Gravel. 2016. "Temperature and Trophic Structure Are Driving Microbial Productivity Along a Biogeographical Gradient." *Ecography* 39, no. 10: 981–989.
- Grenouillet, G., L. Buisson, N. Casajus, and S. Lek. 2011. "Ensemble Modelling of Species Distribution: The Effects of Geographical and Environmental Ranges." *Ecography* 34, no. 1: 9–17.
- Hatton, I. A., A. P. Dobson, D. Storch, E. D. Galbraith, and M. Loreau. 2019. "Linking Scaling Laws Across Eukaryotes." *Proceedings of the National Academy of Sciences of the United States of America* 116, no. 43: 21616–21622.
- Horne, C. R., A. G. Hirst, and D. Atkinson. 2015. "Temperature-Size Responses Match Latitudinal-Size Clines in Arthropods, Revealing Critical Differences Between Aquatic and Terrestrial Species." *Ecology Letters* 18, no. 4: 327–335. <https://doi.org/10.1111/ele.12413>.
- Huston, M. A., and S. Wolverton. 2009. "The Global Distribution of Net Primary Production: Resolving the Paradox." *Ecological Monographs* 79, no. 3: 343–377.
- Intergovernmental Oceanographic Commission of UNESCO. 2014. "Ocean Biodiversity Information System." OBIS. www.obis.org.
- Irigoien, X., T. A. Klevjer, A. Røstad, et al. 2014. "Large Mesopelagic Fishes Biomass and Trophic Efficiency in the Open Ocean." *Nature Communications* 5: 3271.
- Ives, A. R., and S. R. Carpenter. 2007. "Stability and Diversity of Ecosystems." *Science* 317, no. 5834: 58–62.
- Jacquet, C., C. Moritz, L. Morissette, et al. 2016. "No Complexity–Stability Relationship in Empirical Ecosystems." *Nature Communications* 7, no. 1: 1–8.
- Johnson, C. A., and P. Amarasekare. 2015. "A Metric for Quantifying the Oscillatory Tendency of Consumer-Resource Interactions." *American Naturalist* 185, no. 1: 87–99.
- Jordano, P. 2016. "Sampling Networks of Ecological Interactions." *Functional Ecology* 30, no. 12: 1883–1893.
- Kleiber, M. 1932. "Body Size and Metabolism." *Hilgardia* 6: 315.
- Kratina, P., H. S. Greig, P. L. Thompson, T. S. A. Carvalho-Pereira, and J. B. Shurin. 2012. "Warming Modifies Trophic Cascades and Eutrophication in Experimental Freshwater Communities." *Ecology* 93, no. 6: 1421–1430.
- Leclerc, C., N. Reynaud, P.-a. Danis, et al. 2023. "Temperature, Productivity, and Habitat Characteristics Collectively Drive Lake Food Web Structure." *Global Change Biology* 29, no. 9: 2450–2465.
- Legagneux, P., G. Gauthier, N. Lecomte, et al. 2014. "Arctic Ecosystem Structure and Functioning Shaped by Climate and Herbivore Body Size." *Nature Climate Change* 4, no. 5: 379–383.
- Li, Y., B. C. Rall, and G. Kalinkat. 2018. "Experimental Duration and Predator Satiation Levels Systematically Affect Functional Response Parameters." *Oikos* 127, no. 4: 590–598.
- Loreau, M., and C. De Mazancourt. 2013. "Biodiversity and Ecosystem Stability: A Synthesis of Underlying Mechanisms." *Ecology Letters* 16: 106–115.
- Loreau, M., A. Downing, M. Emmerson, et al. 2002. "A New Look at the Relationship Between Diversity and Stability." In *Biodiversity and Ecosystem Functioning: Synthesis and Perspectives*, 79–91. Oxford University Press.
- Masson-Delmotte, V., P. Zhai, A. Pirani, et al. 2021. *IPCC, Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press.
- May, R. M. C. 1974. *Stability and Complexity in Model Ecosystems*, Vol. 6. Princeton University Press.
- McCann, K., A. Hastings, and G. R. Huxel. 1998. "Weak Trophic Interactions and the Balance of Nature." *Nature* 395, no. 6704: 794–798.
- McCann, K. S. 2000. "The Diversity–Stability Debate." *Nature* 405, no. 6783: 228–233.
- Neutel, A.-M., J. A. P. Heesterbeek, and P. C. De Ruiter. 2002. "Stability in Real Food Webs: Weak Links in Long Loops." *Science* 296, no. 5570: 1120–1123.
- O'Connor, M. I., M. F. Piehler, D. M. Leech, A. Anton, and J. F. Bruno. 2009. "Warming and Resource Availability Shift Food Web Structure

- and Metabolism." *PLoS Biology* 7, no. 8: e1000178. <https://doi.org/10.1371/journal.pbio.1000178>.
- Pawar, S., A. I. Dell, and V. M. Savage. 2012. "Dimensionality of Consumer Search Space Drives Trophic Interaction Strengths." *Nature* 486, no. 7404: 485–489.
- Petchey, O. L., P. T. McPhearson, T. M. Casey, and P. J. Morin. 1999. "Environmental Warming Alters Food-Web Structure and Ecosystem Function." *Nature* 402, no. 6757: 69–72.
- Polis, G. A., and D. R. Strong. 1996. "Food Web Complexity and Community Dynamics." *American Naturalist* 147, no. 5: 813–846.
- Post, E., and C. Pedersen. 2008. "Opposing Plant Community Responses to Warming With and Without Herbivores." *Proceedings of the National Academy of Sciences of the United States of America* 105, no. 34: 12353–12358. <https://doi.org/10.1073/pnas.0802421105>.
- Rall, B. C., U. Brose, M. Hartvig, et al. 2012. "Universal Temperature and Body-Mass Scaling of Feeding Rates." *Philosophical Transactions of the Royal Society, B: Biological Sciences* 367, no. 1605: 2923–2934.
- Rall, B. C., O. Vucic-Pestic, R. B. Ehnes, M. Emmerson, and U. Brose. 2010. "Temperature, Predator–Prey Interaction Strength and Population Stability." *Global Change Biology* 16, no. 8: 2145–2157.
- Rodríguez-Castañeda, G. 2013. "The World and Its Shades of Green: A Meta-Analysis on Trophic Cascades Across Temperature and Precipitation Gradients." *Global Ecology and Biogeography* 22, no. 1: 118–130.
- Savage, V. M., J. F. Gillooly, J. H. Brown, G. B. West, and E. L. Charnov. 2004. "Effects of Body Size and Temperature on Population Growth." *American Naturalist* 163, no. 3: 429–441.
- Schemske, D. W., G. G. Mittelbach, H. V. Cornell, J. M. Sobel, and K. Roy. 2009. "Is There a Latitudinal Gradient in the Importance of Biotic Interactions?" *Annual Review of Ecology, Evolution, and Systematics* 40: 245–269.
- Sentis, A., A. Binzer, and D. S. Boukal. 2017. "Temperature-Size Responses Alter Food Chain Persistence Across Environmental Gradients." *Ecology Letters* 20: 852–862. <https://doi.org/10.1111/ele.12779>.
- Sentis, A., and D. S. Boukal. 2018. "On the Use of Functional Responses to Quantify Emergent Multiple Predator Effects." *Scientific Reports* 8, no. 1: 11787.
- Sentis, A., J.-L. Hemptinne, and J. Brodeur. 2012. "Using Functional Response Modeling to Investigate the Effect of Temperature on Predator Feeding Rate and Energetic Efficiency." *Oecologia* 169, no. 4: 1117–1125.
- Sentis, A., J.-L. Hemptinne, and J. Brodeur. 2013. "Effects of Simulated Heat Waves on an Experimental Plant–Herbivore–Predator Food Chain." *Global Change Biology* 19, no. 3: 833–842.
- Sentis, A., J.-L. Hemptinne, and J. Brodeur. 2014. "Towards a Mechanistic Understanding of Temperature and Enrichment Effects on Species Interaction Strength, Omnivory and Food-Web Structure." *Ecology Letters* 17, no. 7: 785–793.
- Synodinos, A. D., B. Haegeman, A. Sentis, and J. M. Montoya. 2021. "Theory of Temperature-Dependent Consumer–Resource Interactions." *Ecology Letters* 24, no. 8: 1539–1555.
- Welch, H. E. 1968. "Relationships Between Assimilation Efficiencies and Growth Efficiencies for Aquatic Consumers." *Ecology* 49, no. 4: 755–759.
- Whalen, M. A., R. D. B. Whippo, J. J. Stachowicz, et al. 2020. "Climate Drives the Geography of Marine Consumption by Changing Predator Communities." *Proceedings of the National Academy of Sciences of the United States of America* 117, no. 45: 28160–28166.
- Williams, R. J., and N. D. Martinez. 2000. "Simple Rules Yield Complex Food Webs." *Nature* 404, no. 6774: 180–183.
- Yodzis, P. 1981. "The Stability of Real Ecosystems." *Nature* 289, no. 5799: 674–676.
- Zuo, W., M. E. Moses, G. B. West, C. Hou, and J. H. Brown. 2012. "A General Model for Effects of Temperature on Ectotherm Ontogenetic Growth and Development." *Proceedings of the Royal Society B: Biological Sciences* 279, no. 1734: 1840–1846. <https://doi.org/10.1098/rspb.2011.2000>.
- Zvereva, E. L., and M. V. Kozlov. 2021. "Latitudinal Gradient in the Intensity of Biotic Interactions in Terrestrial Ecosystems: Sources of Variation and Differences From the Diversity Gradient Revealed by Meta-Analysis." *Ecology Letters* 24: 2506–2520.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendices S1–S3:** [geb70110-sup-0001-AppendicesS1-S3.pdf](#).