



## PRIMARY RESEARCH ARTICLE

# Thermal mismatches in biological rates determine trophic control and biomass distribution under warming

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## Abstract

Temperature has numerous effects on the structure and dynamics of ecological communities. Yet, there is no general trend or consensus on the magnitude and directions of these effects. To fill this gap, we propose a mechanistic framework based on key biological rates that predicts how temperature influences biomass distribution and trophic control in food webs. We show that these predictions arise from thermal mismatches between biological rates and across trophic levels. We couple our theory with experimental data for a wide range of species and find that warming should lead to top-heavier terrestrial food chains and stronger top-down control in aquatic environments. We then derive predictions for the effects of temperature on herbivory and validate them with data on stream grazers. Our study provides a mechanistic explanation of thermal effects on consumer–resource systems which is crucial to better understand the biogeography and the consequences of global warming on trophic dynamics.

## KEYWORDS

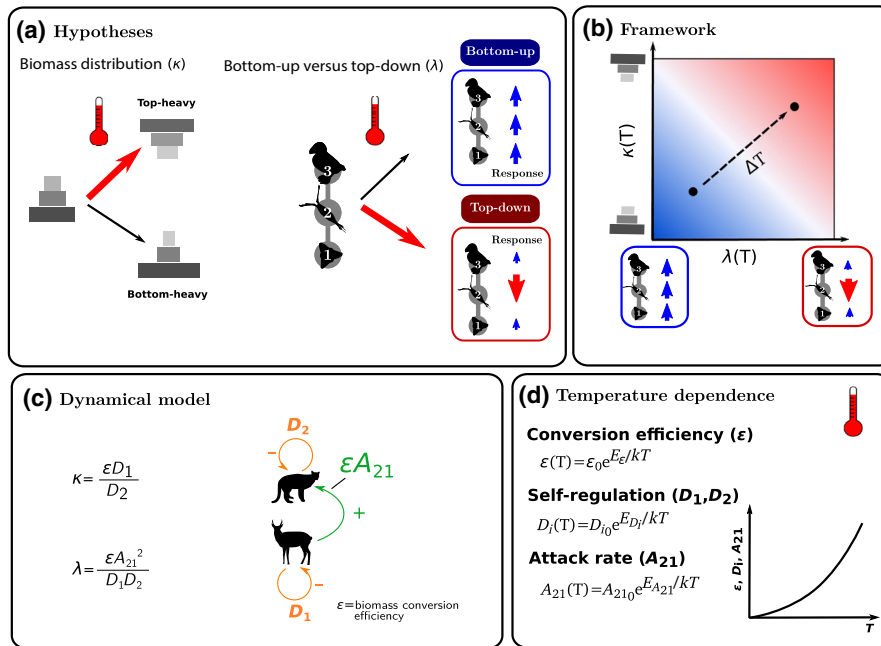
biological rates, biomass distribution, consumer–resource interaction, temperature, thermal mismatches, trophic control

## 1 | INTRODUCTION

Temperature is a major abiotic factor driving many ecological processes, from physiological rates to species geographic distribution and community dynamics (Arrhenius, 1889; Brown et al., 2004; Legagneux et al., 2014). It can alter the strength of trophic interactions (Sentis et al., 2014) and modify the distribution of biomass across trophic levels (Gilbert et al., 2014; Sentis et al., 2019). Empirical and theoretical studies have reported contrasting results regarding temperature effects on both the structural (i.e., biomass distribution across trophic levels) and dynamical (i.e., trophic control; bottom-up vs. top-down) properties of ecological communities (Marino et al., 2018; Figure 1a). For instance, warming can magnify trophic cascades as shown by the positive indirect effects

of spiders on plant biomass (Barton et al., 2009), fishes on phytoplankton density (Kratina et al., 2012; Shurin et al., 2002) and mosquito larvae on protozoa density (Hoekman, 2010). Conversely, warming can also decrease (Barton, 2010; Rall et al., 2010) or have no effect (Van De Velde et al., 2017) on long-term trophic interaction strength in terrestrial arthropods. Empirical studies also reported that warming can lead to the reorganization of biomass structure in food webs (de Sassi & Tylianakis, 2012; Shurin et al., 2012), resulting in top-heavier biomass distribution (i.e., inverted biomass pyramids; Morán et al., 2010; Müren et al., 2005; O'Connor et al., 2009; Romero et al., 2016; Shurin et al., 2012; Yvon-Durocher et al., 2011), or have no effect on population biomass (McKee et al., 2003; Moss et al., 2003; O'Connor et al., 2011; Özen et al., 2013; Tabi et al., 2019). Different explanations have been proposed to explain this diversity of thermal effects (Amarasekare, 2015; Marino et al., 2018). Notably, the

Matthieu Barbier and Arnaud Sentis contributed equally to this work.



**FIGURE 1** Conceptual figure describing: (a) How biomass distribution and trophic control may change with an increase in temperature. Red arrows highlight the hypotheses most supported by empirical studies of experimental warming. Trophic chains may vary between top-heaviness or bottom-heaviness while trophic control may vary between bottom-up or top-down. (b) A graphical summary of the framework developed by Barbier and Loreau (2019), to which we add temperature dependence. The two synthetic parameters defining the structural properties and the dynamical features of the food chain (i.e.,  $\lambda$  and  $\kappa$ ) are temperature-dependent. Along the x-axis,  $\lambda$  defines the regions of bottom-up control with pyramids and of top-down control with alternating cascades and along the y-axis,  $\kappa$  defines the top-heaviness of the biomass distribution. Warming is expected to influence the values of  $\lambda$  and  $\kappa$  toward more top-down control (i.e., right side of the two-dimensional space) and top-heaviness biomass distribution (i.e., upper side of the two-dimensional space). (c) Graphical representation of the dynamical model.  $\lambda$  represents the strength of top-down control in the interaction. It is given by  $\lambda = (\epsilon A_{21}^2) / (D_1 D_2)$ , where  $A_{ij}$  is the strength of trophic interactions between consumer  $j$  and resource  $i$  and  $D_i$  self-regulation of species  $i$ .  $\kappa$  denotes how much biomass is gained by consumers per unit biomass lost by resources and is given by  $\kappa = (A_{21} D_1) / (A_{12} D_2) = \epsilon D_1 / D_2$ . (d) The temperature dependence of parameters. Conversion efficiency  $\epsilon$ , self-regulation  $D_i$  and attack rate  $A_{ij}$  follow an exponential relationship with temperature as described by the Arrhenius equation, commonly used to define the temperature dependence of biological rates below the optimal temperature (we also consider a hump-shaped thermal curve in Section 3.1.2 that includes above optimal temperatures) [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

effect of temperature on interacting species could vary due to the identity of the species (Marino et al., 2018), and, as shown by theoretical studies, to the relative temperature sensitivity of their biological rates (Bideault et al., 2019; Gilbert et al., 2014; Gounand et al., 2016; Sentis, G emard, et al., 2017; Sentis et al., 2015). Species from different habitats (e.g., marine vs. terrestrial; Pinsky et al., 2019; Shurin et al., 2002), geographic origin (Rodr iguez-Casta neda, 2013), metabolic type (Grady et al., 2019), or taxonomic groups (Dell et al., 2011) may thus react differently to increasing temperatures. Here, we argue that a mechanistic framework based on the thermal dependences of key biological rates could help to better understand how thermal effects at the individual and population levels translate into altered biomass distribution and trophic control.

Biological rates of ectotherm species typically increase exponentially with warming, up to an optimal temperature, above which they decrease due possibly to the denaturation of enzymes and lipid membranes (Boukal et al., 2019; P ortner & Farrell, 2008). This relationship between temperature and biological rates, the so-called thermal performance curve, strongly influences the

physiology and behavior of individuals (Dell et al., 2011; Gillooly et al., 2001). There are however considerable differences in thermal sensitivities of biological rates within and between organisms (Dell et al., 2014; R eveillon et al., 2019), which induce mismatches in the response of biological rates to temperature changes (Dell et al., 2014). *Intra-level* mismatches arise when, for a given individual, biological rates exhibit different thermal sensitivities, whereas *inter-level* mismatches arise when the biological rates of a consumer and its resource exhibit different thermal sensitivities. Such mismatches in thermal curves of interacting species have been widely reported (Dell et al., 2011) and shown to strongly influence species interactions under warming (Archer et al., 2019; Betini et al., 2019; Bideault et al., 2019; Dell et al., 2014; Laws & Joern, 2013; Sentis, Binzer, et al., 2017). For instance, autotrophic and heterotrophic biological processes have been shown to exhibit different thermal sensitivities which can lead to increased grazing pressure and reduced primary producers standing biomass in aquatic systems (O'Connor et al., 2009). There is hence some evidence that thermal mismatches in biological rates drive changes in consumer–resource systems but we still lack a

mechanistic understanding of how they affect both biomass structure and trophic control.

Furthermore, it is currently difficult to draw general conclusions on the effects of temperature on ecological interactions because most studies investigate one process at a time (Hoekman, 2010; O'Connor et al., 2009, 2011), studying biomass structure or trophic control in isolation. We argue that a mechanistic understanding of the integrated effects of temperature on both the structural and dynamical properties of ecological communities is crucial to identify generalities in the way temperature impacts communities. A recent study (Barbier & Loreau, 2019) showed that the structural and dynamical features of a trophic chain are controlled by the same key physiological and ecological variables. In particular, two synthetic parameters can be derived:  $\kappa$ , capturing biomass distribution in a chain, and,  $\lambda$ , denoting the strength of top-down control (Figure 1b,c). These two parameters are derived from three biological rates: attack rate, biomass conversion efficiency and self-regulation. Self-regulation is defined by a direct effect of a species on itself such that its growth rate decreases with its own density by, for example, direct interference or cannibalism. Importantly, these biological rates all exhibit rate- and species-specific thermal sensitivities (Figure 1d; Dell et al., 2011; Gillooly et al., 2001), suggesting that trophic control and biomass distribution are temperature sensitive. Note that these three rates are characteristic of interactions between and within trophic levels (consumption and competition). There are also intrinsic rates, such as predator mortality and primary productivity, that can affect trophic structure in a temperature-sensitive way, as studied by Gilbert et al. (2014). These intrinsic rates can be theoretically encapsulated into a third synthetic parameter (Barbier & Loreau, 2019). Galiana et al. (2020) recently showed that this parameter is important but not sufficient by itself to predict trophic phenomena. Hence, we focus here on the interaction-related parameters  $\kappa$  and  $\lambda$ , as their role is both crucial and not currently understood. The theory of Barbier and Loreau (2019) thus opens a promising avenue to tackle unsolved questions about the influence of temperature on the distribution of biomass across trophic levels and the likelihood of trophic cascades.

Our objective is to investigate how the thermal dependences of biological rates affect biomass distribution and trophic control in consumer–resource systems. We first present the modeling framework and derive a theory based on key biological rates and their thermal mismatches underlying the thermal dependences of the synthetic parameters  $\kappa$  and  $\lambda$ , that govern biomass distribution and trophic control. Using a dataset of thermal sensitivities (i.e., activation energy values) for different biological rates, we then demonstrate how thermal mismatches can drive the changes in biomass distribution and trophic control with warming in consumer–resource systems. Additionally, we use two case studies to, first, illustrate the applicability of our framework for predicting warming impacts across terrestrial and marine herbivores at the global scale, and second, to validate the accuracy and limits of our predictions using experimental data on stream organisms. Our study provides

a mechanistic understanding of how food chain structural and dynamical properties depend on temperature and offers new perspectives to better anticipate the functioning of communities under climate warming.

## 2 | THEORY

### 2.1 | Model

We follow the approach of Barbier and Loreau (2019) to represent a consumer–resource system and analyze its macroscopic features. We start from the classic Lindeman representation of trophic dynamics (Lindeman, 1942),

$$\frac{dB_i}{dt} = \underbrace{P_i}_{\text{production}} - \underbrace{L_i}_{\text{internal losses}} - \underbrace{C_{i+1,i}}_{\text{predation losses}}, \quad (1)$$

where  $B_i$  is the biomass of trophic level  $i$ . Production  $P$  is externally driven for primary producers, and determined by consumption  $C$  for consumers,

$$P_1 = g_1 B_1, \quad P_{i+1} = \varepsilon C_{i+1,i}, \quad (2)$$

where  $g_1$  represents the intrinsic biomass growth,  $\varepsilon$  is the conversion efficiency of consumed biomass into population growth (which can be notably lower than the immediate assimilation efficiency, for example, estimates in models parameterized from experiments can range from 0.004 to 0.010; Daugaard et al., 2019).

We define non-trophic losses (internal to one trophic level) as

$$L_i = -q_i B_i - D_i B_i^2, \quad (3)$$

where  $q_i$  is the individual (metabolic) mortality and  $D_i$  is the self-regulation (density-dependent mortality, e.g., direct competition). Note that we include self-regulation at all trophic levels.

We consider a Type I Lotka–Volterra functional response,

$$C_{i+1,i} = A_{i+1,i} B_i B_{i+1}, \quad (4)$$

with  $A_{i+1,i}$  being the attack rate.

From this system of consumer–resource at equilibrium, two synthetic parameters,  $\kappa$  and  $\lambda$ , summarize the structure (i.e., biomass distribution across trophic levels) and the dynamics (i.e., trophic control), respectively (see Figure 1b,c).  $\kappa$  is the ratio of the non-trophic interactions (self-regulation) of trophic level  $i + 1$  over the one for trophic level  $i$  and  $\lambda$  is the ratio of the between-trophic levels interactions (attack rate) over the within-level non-trophic interactions. More formally, they are defined as

$$\kappa = \varepsilon \frac{D_1}{D_2}, \quad \lambda = \varepsilon \frac{A_{21}^2}{D_1 D_2}, \quad (5)$$

$\kappa$  denotes how much biomass is gained by consumers per unit biomass lost by resources; large  $\kappa$  indicating top-heavy distributions.  $\lambda$  describes the feedback of a trophic level on itself through its predators, and therefore it indicates the strength of top-down control (Figure 1b,c). These parameters are derived from attack rate, self-regulation and biomass conversion efficiency, which may be temperature-dependent. The temperature dependence of  $\kappa$  and  $\lambda$  can thus be directly obtained by incorporating the temperature dependence of these biological rates.

## 2.2 | Temperature dependence of the synthetic parameters $\kappa$ and $\lambda$

The temperature dependence of biological rates is typically described by the exponential Arrhenius equation (Arrhenius, 1889; Brown et al., 2004; Gillooly et al., 2001; Savage et al., 2004; at least for temperatures below the optimal temperature, Figure 1d):

$$X(T) = X(T_0) e^{-E_x/(kT)}, \quad (6)$$

where  $X$  stands for a biological rate (e.g.,  $\epsilon$ ,  $D_i$  or  $A_{i+1,i}$ ),  $X(T_0)$  is a rate-dependent normalization constant,  $E_x$  [eV] is the rate's activation energy,  $k$  [ $8.617 \cdot 10^{-5}$  eVK $^{-1}$ ] is the Boltzmann constant and  $T$  [K] is the temperature.

The activation energy, which is rate- and organism-specific, is the slope of the relationship between the biological rate and temperature on a log-log scale and it represents how fast the biological rate increases with temperature. Because  $\kappa$  and  $\lambda$  are products and ratios of biological rates (Equation 5), their activation energies are sums and differences of the activation energies of these biological rates. Hence, substituting the equations for the different biological rates (Equation 6) into Equation (5), the activation energies of the synthetic parameters are defined as

$$\begin{aligned} E_\kappa &= E_\epsilon + E_{D_1} - E_{D_2} \\ &= E_\epsilon - \Delta E_{\text{inter}}, \end{aligned} \quad (7)$$

$$\begin{aligned} E_\lambda &= E_\epsilon + 2E_A - E_{D_1} - E_{D_2} \\ &= E_\epsilon + 2\Delta E_{\text{intra}} + \Delta E_{\text{inter}}, \end{aligned} \quad (8)$$

where we define the *intra-level* mismatch between predator attack rate and self-regulation (i.e., trophic and non-trophic processes) as

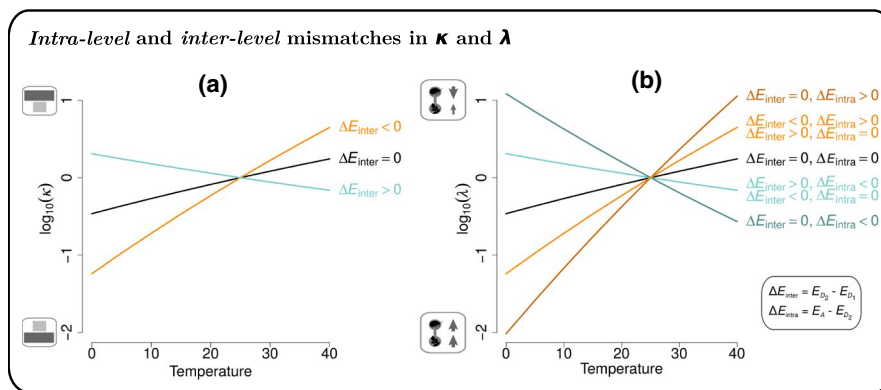
$$\Delta E_{\text{intra}} = E_A - E_{D_2}, \quad (9)$$

and the *inter-level* mismatch as

$$\Delta E_{\text{inter}} = E_{D_2} - E_{D_1}. \quad (10)$$

Thermal mismatches arise when activation energies differ among biological rates or between species. Mismatches are key drivers in the way temperature influences  $\kappa$  and  $\lambda$  (Figure 2). The *inter-level* mismatch,  $\Delta E_{\text{inter}} = E_{D_2} - E_{D_1}$ , is defined as the difference between the activation energies of the consumer and the resource self-regulations. It mainly controls the direction of the thermal response of  $\kappa$  (Figure 2a) and hence of biomass distribution. When the activation energies of the consumer and the resource self-regulations are equal, only  $E_\epsilon$  drives the impact of temperature on  $\kappa$  (i.e., when  $\Delta E_{\text{inter}} = 0$ ,  $E_\kappa = E_\epsilon$ , Equation 7). In that case, if  $E_\epsilon > 0$ , warming increases  $\kappa$  and thus triggers top-heavier biomass distribution. When the activation energy of self-regulation is higher for the resource than for the consumer ( $\Delta E_{\text{inter}} < 0$ ),  $E_\kappa$  is larger and  $\kappa$  increases faster with temperature (i.e., leading to top-heavier biomass distribution), while when the activation energy of self-regulation is smaller for the resource than for the consumer ( $\Delta E_{\text{inter}} > 0$ ),  $E_\kappa < 0$  which yields a decrease in  $\kappa$  with temperature leading to bottom-heavier biomass distribution.

The *intra-level* mismatch,  $\Delta E_{\text{intra}} = E_A - E_{D_2}$ , is defined as the difference between the activation energies of the consumer attack



**FIGURE 2** Effect of the *intra-level* mismatch,  $\Delta E_{\text{intra}}$ , and the *inter-level* mismatch,  $\Delta E_{\text{inter}}$ , on the thermal responses of the synthetic parameters  $\kappa$  (panel a) and  $\lambda$  (panel b). The activation energies of self-regulation and attack rate are varied ( $E_{D_1}$ ,  $E_{D_2}$  and  $E_A \in \{0.5, 1\}$ ) to represent mismatches. The activation energy of conversion efficiency  $E_\epsilon$  is fixed at 0.3 as the thermal dependence of  $E_\epsilon$  is often reported as weak.  $E_\kappa$  and  $E_\lambda$  are computed following Equations (7) and (8) for every possible combination of  $E_{D_1}$ ,  $E_{D_2}$  and  $E_A$ .  $\kappa$  and  $\lambda$  follow an exponential Arrhenius function (Equation 6) and are set at 1 at a temperature of reference of 25°C. When the mismatches are equal to 0 or when they cancel each other, it is  $E_\epsilon$  that drives the variation in  $\kappa$  and  $\lambda$  with temperature changes [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

rate and of its self-regulation. The *inter-level* and the *intra-level* mismatches both determine the response of  $\lambda$  (i.e., trophic control) to temperature changes (Figure 2b). As for  $\kappa$ ,  $E_\lambda = E_\kappa$  when the activation energies of attack rate and self-regulation (of both trophic levels) are equal ( $\Delta E_{\text{intra}} = \Delta E_{\text{inter}} = 0$ , see Equation 8). Generally, the sign of  $\Delta E_{\text{intra}}$  defines whether  $\lambda$  increases or decreases with temperature. When the activation energy of the consumer attack rate is greater than the one of its self-regulation ( $\Delta E_{\text{intra}} > 0$ ),  $\lambda$  increases with temperature leading to stronger top-down control. On the contrary, when  $\Delta E_{\text{intra}} < 0$ , top-down control decreases with temperature. When the activation energies of attack rate and self-regulation are equal ( $\Delta E_{\text{intra}} = 0$ ), the sign of  $\Delta E_{\text{inter}}$  determines the direction of the thermal response of  $\lambda$  (e.g., when  $\Delta E_{\text{intra}} > 0$ ,  $\lambda$ , and hence top-down control, increases with warming). Therefore, the effect of temperature on biomass distribution and trophic control can be system-dependent if activation energies of biological rates differ among species as reported in previous studies (Dell et al., 2011). We subsequently illustrate this variation with empirical applications.

### 3 | EMPIRICAL APPLICATIONS

#### 3.1 | Methods

##### 3.1.1 | Database of activation energies

We collected the values of activation energies from previous meta-analyses with the objective of depicting a general overview of the temperature sensitivity of biomass distribution and trophic control in food chains for various consumer–resource systems. We used the meta-analyses from Dell et al. (2011), Burnside et al. (2014) and Fussmann et al. (2014), reporting activation energies for different biological rates and types of organisms. In these studies, activation energies are estimated by fitting the linearized Arrhenius equation (Equation 6) to the log-transformed biological rates. We included activation energy values only when the linear coefficient (i.e., the activation energy) of the linear model was statistically significant ( $p < .05$ ) to get reliable estimates of activation energies.

We could not find values of activation energy for self-regulation since this parameter is seldom measured empirically and, to our knowledge, its activation energy has never been reported. Indeed, even though growth rate and abundance usually exhibit a negative relationship, the causes of such a relationship are difficult to disentangle. In Barbier and Loreau (2019), biological rates (e.g., self-regulation and attack rate) are assumed to depend on metabolic rates. However, interacting species from different taxonomic groups may exhibit different physiologies. Species' biological rates may thus be related to different ecological processes and might not follow the same scaling. For instance, if self-regulation is driven by predator interference or cannibalism, it could scale with attack rate. A recent study analyzing a large dataset on eukaryotes organisms also indicates that self-regulation should scale strongly with growth

rates (Hatton et al., 2019). Hence, given this limited knowledge on self-regulation, we explore here three options for the scaling of self-regulation in our analyses: growth rate, metabolic rate, or attack rate.

We hence gathered values of activation energies for conversion efficiency, growth, metabolic and attack rates for various ectotherm species (ranging from bacteria to arthropods and fish) and classified them by habitat (aquatic vs. terrestrial), diet (primary producers, herbivores and carnivores) and taxonomic groups (class or phylum). In the analyses for which we consider groups of species (e.g., taxonomic groups), we only account for the groups for which we have a significant number of species (i.e., minimum seven species), to avoid biases in the distributions of activation energies due to low sample size.

From this database and for the different scaling assumptions of self-regulation, we compute activation energies of  $\kappa$  and  $\lambda$  (Equations 7 and 8) for each combination of prey and predator (pairwise interactions) within the different taxonomic groups and habitat types (terrestrial vs. aquatic). Activation energies for attack rates were originally defined for each pair of interacting species in the meta-analyses considered. When we have multiple values of activation energies for the other rates (i.e., growth rate or metabolic rate) for a given species, we compute all possible combinations to derive  $E_\kappa$  and  $E_\lambda$ .

We illustrate the temperature sensitivity of  $\kappa$  and  $\lambda$  for different taxonomic groups and describe more specifically the *intra-* and *inter-level* mismatches of two taxonomic groups from marine and terrestrial environments to clarify the origin of the variation in  $E_\kappa$  and  $E_\lambda$ . As the different groups (i.e., taxonomic groups or habitat) are not equally represented in the database, we compute the weighted means when necessary.

##### 3.1.2 | Case studies

The normalization constant (i.e., the intercept of the Arrhenius equation) is also needed to document the effect of temperature on a specific system. This information is essential to calculate the absolute values of  $\kappa$  and  $\lambda$  and thus place a specific system in the  $\lambda$ – $\kappa$  space (Figure 1b). Unfortunately, our database does not include enough information on the values of normalization constants to compute the values of  $\kappa$  and  $\lambda$  across all systems and species pairs. We therefore use two specific ecological systems for which we have sufficient information on biological rates to compute the values of  $\kappa$  and  $\lambda$  at a given temperature and predict how their values should shift with temperature changes. In the first case study, we generate large-scale predictions for marine and terrestrial herbivory. In the second case study, we use an experiment on stream organisms (Kishi et al., 2005) to validate the accuracy of our predictions by comparing the predicted effects of temperature derived from  $\kappa$  and  $\lambda$  with the empirically measured effects.

##### *Large-scale predictions for terrestrial and marine herbivory*

In a recent meta-analysis, Bar-On et al. (2018) estimated biomasses in carbon mass for the major taxonomic groups on Earth. We take

advantage of their study to investigate the biomass distribution and trophic control of herbivores and primary producers at the global scale. We use their estimates of global distributions of biomasses to compute  $\kappa$  and  $\lambda$  for marine and terrestrial herbivory and predict how they shift with temperature changes.

Bar-On et al.'s (2018) estimates of biomass (in petagrams of carbon [Pg C]) for herbivores and primary producers are  $B_1 = 450$  and  $B_2 = 20$  for terrestrial systems, and  $B_1 = 1$  and  $B_2 = 5$  for marine systems, which yield a regular pyramid in terrestrial systems and an inverted one in marine systems. From the consumer-resource system at equilibrium (Section 2.1) we obtain,

$$\frac{B_2}{B_1} = \frac{\epsilon A_{21}}{D_2} = \sqrt{\kappa \lambda}. \quad (11)$$

Following the above theory, we use the relationships between biomass ratios, metabolic ratios and  $\kappa$  and  $\lambda$  to compute the synthetic parameters for terrestrial and marine herbivory (See Supporting Information for detailed calculations). This leads us to the following estimates of  $\kappa$  and  $\lambda$ :

$$\kappa \sim 2.5, \quad \lambda \sim 10, \quad \text{for marine organisms,} \quad (12)$$

and

$$\kappa = 0.02, \quad \lambda = 0.1, \quad \text{for terrestrial organisms.} \quad (13)$$

We then predict how  $\kappa$  and  $\lambda$  would shift with warming using the corresponding activation energies for marine and terrestrial herbivores from our database (Equations 7 and 8), and considering different scalings for self-regulation. We assume that  $\kappa$  and  $\lambda$  increase exponentially with temperature following the Arrhenius model (Equation 6). We present the variation of  $\kappa$  and  $\lambda$  with temperature, which is similar between the different scaling scenarios, and provide a more specific example for the case where self-regulation scales with growth rate.

#### *Validation of the theory with a stream grazer experiment*

With the second case study, we aim to validate the accuracy of our predictions by focusing on an experiment carried out by Kishi et al. (2005) on a food chain of stream organisms. Kishi et al. (2005) investigated the effects of water temperature on the community structure of fish, grazing caddisfly larvae and periphyton. They performed top-down control experiments (assessment of resource biomass in the absence and the presence of consumers) at three different temperatures (3, 12 and 21°C) and experimentally measured consumer feeding activities (i.e., scar area grazed by larvae) and periphyton production at seven temperatures ranging from 3 to 21°C.

Using the data of their top-down experiment, we first compute  $\kappa$  and  $\lambda$  for this system at a given temperature (12°C) for which we are able to obtain all the parameter values needed. We then estimate the variation in  $\kappa$  and  $\lambda$  with temperature changes relative to their values at 12°C. To do so, we assume that biomass conversion efficiency increases exponentially with temperature with an

activation energy of 0.3 obtained from our database. We also assume that self-regulation of the bottom level (periphyton) scales with their production and that attack rate and self-regulation of the consumers (caddisfly larvae) scale with their grazed scar area, as periphyton production and grazed scar area were both experimentally measured in Kishi et al. (2005). We hence obtain estimates of  $\kappa$  and  $\lambda$  at the seven different temperatures from the data. Moreover, we fit an Arrhenius function and a quadratic Arrhenius function to the thermal performance curves of production and grazed scar area to describe the relationship between biological rates and temperature (for more details, see Englund et al., 2011; Gillooly et al., 2001). We obtain estimates of  $\kappa$  and  $\lambda$  at the seven temperatures from the fitted data, using the same reasoning as above. Finally, we compute the biomass ratios at three different temperatures from our estimates of  $\kappa$  and  $\lambda$  using Equation (10) to compare the data of biomass ratios measured in Kishi et al. (2005) with our predictions. See Supporting Information for details on the calculations for this section.

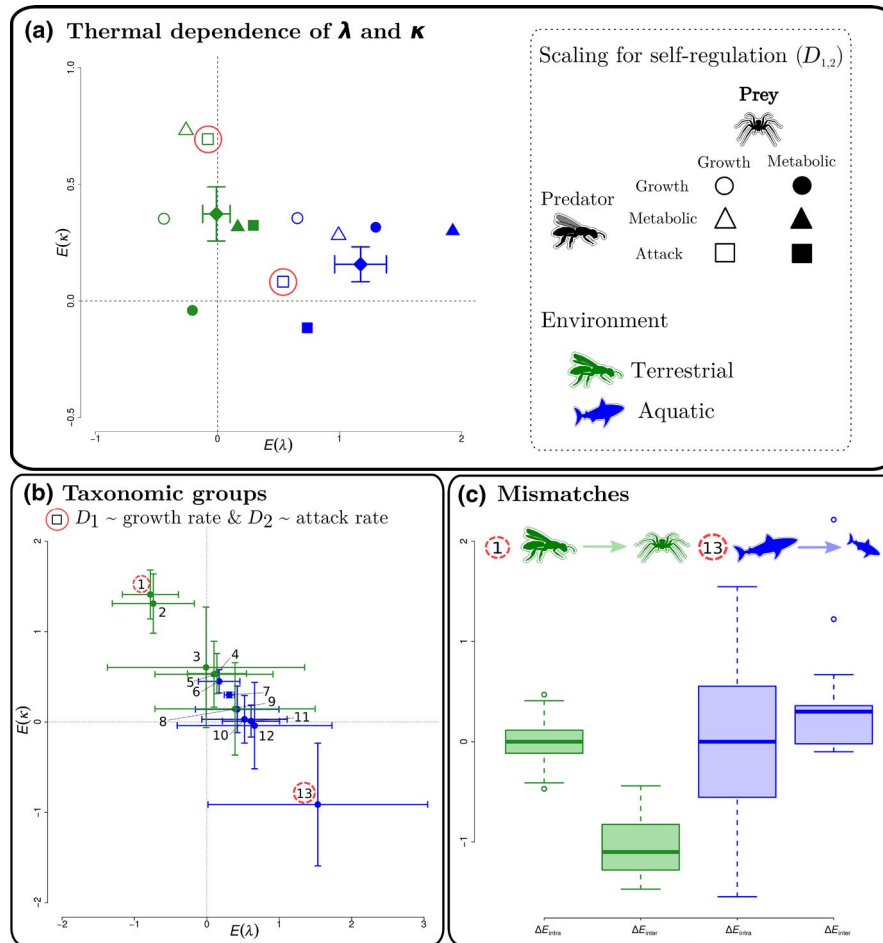
## 3.2 | Results

### 3.2.1 | Thermal dependence of $\kappa$ and $\lambda$ across habitats and taxonomic groups

Marine and terrestrial consumer-resource systems show different temperature dependences in  $\kappa$  and  $\lambda$  (Figure 3a), due to the variation in biological rates' activation energies across taxonomic groups (Figure 3b). When averaging across the six scaling assumptions for self-regulation,  $E_\kappa$  is positive for terrestrial environments. Warming should thus increase  $\kappa$ , and hence shift biomass distribution toward more top-heaviness.  $E_\lambda$  is on average approximately zero, implying that temperature does not alter top-down control. In aquatic environments,  $\lambda$  exhibits a strong temperature dependence ( $E_\lambda > 1$  on average) so that warming increases top-down control and induces cascade patterns.  $\kappa$  is less sensitive to temperature changes, but  $E_\kappa > 0$  shows that food chains become moderately more top-heavy with warming. Although the dissociation between marine and terrestrial environments is consistent across the different scaling assumptions of self-regulation, the variation around this general trend highlights the importance of finding the temperature dependence of this key parameter.

We detail the temperature dependence of  $\kappa$  and  $\lambda$  for species from different taxonomic groups for a given scaling scenario for self-regulation, namely when  $D_1$  (resource self-regulation) scales with growth rate and  $D_2$  (consumer self-regulation) with attack rate (Figure 3b), as supported by previous studies (Barbier & Loreau, 2019; Hatton et al., 2019). We recover the general trend, with  $\kappa$  being more sensitive to temperature changes for terrestrial organisms, whereas  $\lambda$  is more sensitive to temperature changes for aquatic organisms but also find that there is variation between the different taxonomic groups. For instance, for the taxonomic groups Insecta-Arachnida, warming leads to more top-heaviness but less





**FIGURE 3** Temperature sensitivity of biomass distribution and trophic control in consumer–resource systems from terrestrial (green) and aquatic (blue) environments. (a) Mean activation energies for  $\kappa$  and  $\lambda$  (Equations 7 and 8) for different assumptions regarding the temperature dependence of self-regulation for prey,  $D_1$ , and predator,  $D_2$ , which either scale with growth, metabolic or attack rates. Each assumption is represented by a different point type (see legend). Rhombuses correspond to the weighted mean per environment type, error bars show the SE. (b) Median values and SD of activation energies of  $\kappa$  and  $\lambda$  for different taxonomic groups, for the case where  $D_1$  scales with growth rates and  $D_2$  with attack rate (empty squares surrounded by red circles in panel a). Taxonomic groups for pairs of predator–prey are as follows: (1) Insecta–Arachnida, (2) Arachnida–Arachnida, (3) Insecta–Insecta, (4) Arachnida–Insecta, (5) Insecta–Tracheophyta, (6) Insecta–Hydropsyche, (7) Insecta–Culicidae, (8) Nematoda–Insecta, (9) Insecta–Insecta, (10) Insecta–Branchiopoda, (11) Actinopterygii–Insecta, (12) Mollusca–Mollusca and (13) Actinopterygii–Actinopterygii. (c) Inter- and intra-level mismatches for two pairs of taxonomic groups: Insecta–Arachnida (1) and Actinopterygii–Actinopterygii (13).  $\Delta E_{intra} = E_A - E_{D_2}$  is the intra-level mismatch between predator attack rate and self-regulation, which is centered around zero by construction as  $D_2 \sim A$ , and  $\Delta E_{inter} = E_{D_2} - E_{D_1}$  is the between-trophic level mismatch, driving the observed variation in  $E_\kappa$  and  $E_\lambda$  [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

top-down control while, for Nematoda–Insecta, warming does not influence biomass distribution but leads to stronger top-down control. This observed variation between taxonomic groups arises from the fact that species exhibit different thermal sensitivities in their biological rates, that are thus altered at different rates by temperature changes, which causes mismatches (Figure 3c).

Mismatches between biological rates drive the variation in  $\kappa$  and  $\lambda$ . Specifically, the *inter-level* mismatch (Equation 10) governs variation in  $\kappa$  (biomass distribution), while both mismatches, the *inter-* and the *intra-level* mismatch (Equation 9), are important in determining variation in  $\lambda$ , and hence in trophic control with temperature changes. We underline this point by showing both mismatches for two pairs of taxonomic groups that have the most extreme values in  $E_\kappa$  or  $E_\lambda$ : predators from the class Insecta and prey from the class

Arachnida for terrestrial environments and predators and prey from the class Actinopterygii for marine environments. Due to the scaling of self-regulation used here ( $D_2 \sim A_{21}$ ), the *intra-level* mismatch (between trophic and non-trophic processes),  $\Delta E_{intra}$ , is centered around 0. It is then the *inter-level* mismatch,  $\Delta E_{inter}$ , that governs  $E_\kappa$  and  $E_\lambda$ , along with its difference with  $E_\epsilon$  (see Equations 7 and 8).  $\Delta E_{inter}$  differs between the two pairs of taxonomic groups considered here. For instance, for the pair Insecta–Arachnida,  $\Delta E_{inter} < 0$ , meaning that the prey's self-regulation increases faster with warming than the predator's one. Because  $E_\epsilon > 0$  we see from Equation (7) that  $E_\kappa$  is positive too, indicating that warming would trigger top-heavier food chains. On the contrary,  $E_\lambda$  is negative because  $E_\epsilon + \Delta E_{inter} < 0$  as  $|E_\epsilon| < |\Delta E_{inter}|$  (Equation 8), showing that, in that case, top-down control would decrease with temperature.

Overall, our results show that warming affects food chains in terrestrial and aquatic environments in different ways. It mainly triggers heavier biomass pyramids in terrestrial systems, while leading to stronger top-down control in aquatic systems. However, our findings also highlight substantial variations across taxonomic groups due to the relative temperature dependence of biological rates, which are key in determining food chain structure and dynamics.

### 3.2.2 | Case studies

In the previous results, we analyzed the variation in food chain patterns with temperature changes. We now first describe a system for which we can estimate specific values of  $\kappa$  and  $\lambda$  and make large-scale predictions on how they will shift with warming, and second, we evaluate the accuracy of our predictions using measurements of temperature effects on a stream grazer community.

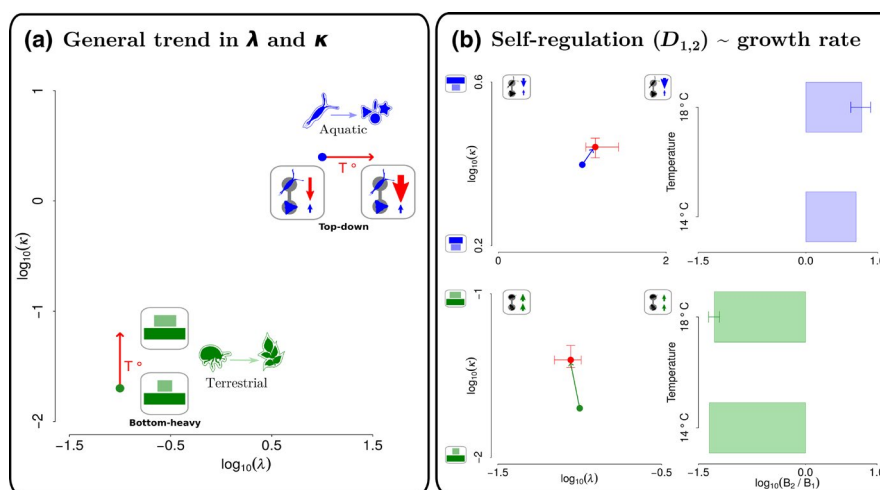
#### Large-scale predictions for terrestrial and marine herbivory

Using the results from Bar-On et al. (2018), we estimate the values of  $\kappa$  and  $\lambda$  for global marine and terrestrial herbivory and then predict their shift with warming (Figure 4). The estimated values of  $\kappa$  and  $\lambda$  show that terrestrial herbivory stands in the region of bottom-up control with a regular biomass pyramid structure while marine herbivory is found in the region of top-down control with cascading patterns. According to our predictions, warming should shift food chain patterns toward more herbivore biomass ( $\kappa$  axis) in terrestrial environments and toward more top-down control ( $\lambda$  axis) in marine environments. This result holds regardless of the specific scaling assumptions for self-regulation. However, when considering

the different scaling assumptions,  $\lambda$  varies in different directions and magnitude for terrestrial herbivory, as does  $\kappa$  for marine herbivory. Hence, we cannot accurately predict these shifts without knowing the temperature dependence of self-regulation. We thus provide a more specific example for the case where self-regulation scales with growth rate (see Figure S1 in Supporting Information for the other scaling scenarios) for a temperature increase of 4°C. Given this particular scaling, food chains from marine environments would exhibit top-heavier biomass distributions along with an increase in the strength of top-down control (Figure 4b, top panel). Food chains from terrestrial environments would become top-heavier too with stronger bottom-up control (Figure 4b, bottom panel).

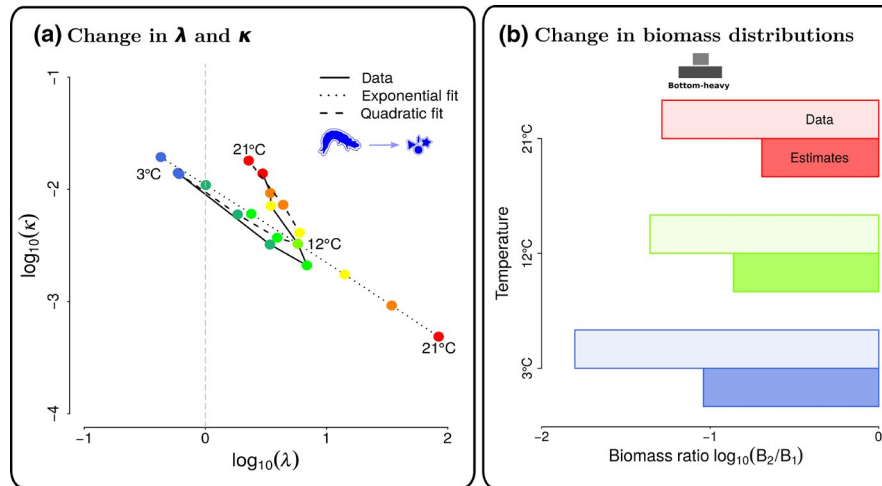
#### Validation of the theory with a stream grazer experiment

Using data from a stream grazer experiment (Kishi et al., 2005), we estimate values of  $\kappa$  and  $\lambda$  along a temperature gradient and show that a change in temperature alters the dynamics of the food chain by (a) increasing top-down control at low temperature and decreasing it at higher ones and (b) inducing cascade patterns (Figure 5a, data). The relationship between temperature and  $\kappa$  or  $\lambda$  estimated from the data follows a unimodal shape with 12°C being the shifting point. Our estimates of  $\kappa$  and  $\lambda$ , computed from the quadratic fits, accurately follow the estimates obtained from the data (Figure 5a, quadratic fit). Using an exponential function to estimate the parameters is a simpler, and widespread derivation of the temperature dependence of biological rates that effectively works at low temperatures (Figure 5a, exponential fit). However, it leads to inaccurate estimates of temperature dependence at higher temperatures, leading to an underestimation of  $\kappa$  and an overestimation of  $\lambda$  for temperatures above 12°C. Thermal performance curves of



**FIGURE 4** Variation in  $\lambda$  and  $\kappa$  and biomass ratios with increasing temperatures for global terrestrial and marine herbivory.  $\lambda$  and  $\kappa$  are estimated from global distributions of biomass (Bar-On et al., 2018; see Section 3.1.2) and their shift due to temperature is predicted using our database of activation energies (Section 3.1.1). (a) General trend in the shift of  $\lambda$  and  $\kappa$  with increasing temperatures across the different scaling scenarios for self-regulation. The direction of change is consistent for  $\lambda$  in marine environments and  $\kappa$  in terrestrial environments across the six scaling scenarios of self-regulation but varies in the other axis (see Supporting Information for details). (b) Example for the case where self-regulation scales with growth rate. Median values for herbivore species along with the 25th and the 75th quantiles are represented. Left panels, the shifts in  $\lambda$  and  $\kappa$  are estimated using our database of activation energies for a 4°C increase. Right panels, biomass ratios are given by  $B_2/B_1 = \sqrt{(\lambda\kappa)}$  [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]





**FIGURE 5** Case study from Kishi et al. (2005) that investigated the effect of water temperature on the structure of a consumer–resource system with caddisfly larvae as consumer and periphyton as basal species. (a) Variation in  $\lambda$  and  $\kappa$  with temperature changes (color points are for 3, 6, 9, 12, 15, 18 and 21°C corresponding to the experimental temperature in Kishi et al. (2005)). Color coding ranges from blue, that is, cold, to red, that is, warm.  $\lambda$  and  $\kappa$  are computed at 12°C as a starting point. Their variation with temperature is then estimated assuming that periphyton self-regulation  $D_1$  scales with their production and that grazers attack rate  $A_{12}$  and self-regulation  $D_2$  scale with their feeding rate. The solid line represents estimations of  $\lambda$  and  $\kappa$  from the parameters experimentally measured in Kishi et al. (2005). The dashed and the dotted lines represent estimations of  $\lambda$  and  $\kappa$  from, respectively, an exponential and a quadratic fit of the data. (b) Biomass ratios computed from the relationship  $B_2/B_1 = \sqrt{\lambda\kappa}$  for  $\lambda$  and  $\kappa$  derived from the data and the fitted functions. See Supporting Information for details on the difference between the estimates from data and  $\lambda$  and  $\kappa$  [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

biological rates are thus prominent in determining how the community varies with warming.

Regarding biomass distribution, periphyton biomass is larger than the one of their larvae consumers but warming decreases this bottom-heavy pattern (Figure 5b, data). Predicting biomass ratio  $B_2/B_1$  from  $\kappa$  and  $\lambda$  indicates that the food chain becomes less bottom-heavy with warming. Although the predicted values are lower than the observed data, our predictions are consistent with the experimental measurements (Figure 5b), demonstrating the reliability of our theoretical framework.

## 4 | DISCUSSION

Investigating how temperature affects the structure of communities and their dynamics is important for understanding how climate change may impact biodiversity and ecosystem functions (Boukal et al., 2019; Woodward et al., 2010). Here, we built on a recent theoretical study (Barbier & Loreau, 2019) to explore mechanistically how the structural and dynamical features of food chains are simultaneously affected by temperature.

We demonstrate that the discrepancies in the thermal response of consumer–resource systems arise through intra- and inter-individual variation in the temperature dependence of biological rates, which induce mismatches between interacting species (Voigt et al., 2003). Such mismatches, measured by differences in the activation energies, have already been shown to strongly impact species interactions (Bideault et al., 2019; Gilbert et al., 2014; O'Connor et al., 2011; Sentis, Binzer, et al., 2017). Here, we focus on three key

parameters: attack rate, self-regulation and conversion efficiency. The *intra-level* mismatch (between the predator's attack rate and self-regulation), the *inter-level* mismatch (between the predator's and prey's self-regulation) and the activation energy of conversion efficiency together govern the thermal response of food chain patterns. For instance, when the *inter-level* mismatch and the activation energy of conversion efficiency are positive, biomass distribution becomes top-heavier with warming.

We further explore how these thermal mismatches drive the biomass distribution and the trophic control in consumer–resource systems across taxonomic groups and habitats using a database of activation energies. Our theory coupled with the data predicts differences between aquatic and terrestrial communities. Warming is expected to trigger top-heavier food chains in both terrestrial and aquatic ecosystems, whereas it might induce stronger top-down control only in aquatic ecosystems. Previous experimental studies have also demonstrated that warming increases consumers biomass in terrestrial systems (de Sassi & Tylianakis, 2012) while enhancing top-down control (Kratina et al., 2012; O'Connor et al., 2009) and decreasing autotroph biomass relative to heterotroph biomass in aquatic systems (Müren et al., 2005; O'Connor et al., 2009; Shurin et al., 2002; Yvon-Durocher et al., 2011). Using the database of activation energies for ectotherm species, we show that there is a substantial variation around these general trends. Our findings could explain the variety of thermal responses in consumer–resource systems previously observed (Marino et al., 2018) between, for example, habitats (terrestrial vs. aquatic) and taxonomic groups, and help understanding how biological rates drive this context dependency. For instance, we do not find, on average,

that top-down control increases with warming in terrestrial systems but our model does predict an increase for the interaction between Arachnida and Insecta taxonomic groups, coherent with empirical findings from Barton et al. (2009). Our predictions should, however, be nuanced as our database of activation energies might be biased toward some taxonomic groups that are more commonly studied. In particular, we do not include data for the thermal sensitivity of endotherm species while their *inter-level* mismatch with ectotherm species might be significant as shown in a recent study (Grady et al., 2019). Better characterizing mismatches between endotherm and ectotherm species is thus an important next step to improve predictions of how warming affects community structure and dynamics.

While our database of activation energies is nevertheless useful to determine the thermal sensitivities of  $\kappa$  and  $\lambda$  across taxonomic groups, it does not contain enough information to compute the values of  $\kappa$  and  $\lambda$  across all species pairs, which is limiting to generate quantitative predictions. To overcome this limitation, we compute values of  $\kappa$  and  $\lambda$  from estimates of herbivores to autotroph biomass ratios in marine and terrestrial environments (Bar-On et al., 2018). Our estimates of biomass ratios are in accordance with previous studies showing regular biomass pyramids in terrestrial environments and inverted pyramids in marine systems where the herbivore to autotroph biomass ratio is greater (Cebrian et al., 2009; Rip & McCann, 2011). Our results thus suggest that herbivores experience bottom-up control in terrestrial environments and trigger top-down control in marine ones. The mechanisms and factors influencing the strength of trophic cascades are still debated (Borer et al., 2005; Schmitz et al., 2000; Sentis et al., 2020; Shurin et al., 2002; Start & Gilbert, 2017), and our results support the claim that top-down control of plants by herbivores is weak in terrestrial systems. We show that warming would trigger less bottom-heavy food chains in terrestrial environments and stronger top-down control in marine environments, which is consistent with our more general predictions discussed above. However, we obtain variable results across the different scaling scenarios of self-regulation regarding the change in trophic control for terrestrial environments and in biomass distribution for aquatic environments, which suggests that we cannot reliably conclude on the direction of change for these other axes. Determining how self-regulation varies with temperature is thus crucial to further explore how food chain structure and dynamics will be affected by temperature changes.

The temperature dependence of conversion efficiency also remains poorly estimated and is still subject to debate (Daugaard et al., 2019), despite the importance of this parameter in determining energy flow between trophic levels (Lang et al., 2017). To overcome this lack of knowledge, we consider different scaling scenarios regarding the temperature dependence of self-regulation and we assume that conversion efficiency increases with temperature following recent outcomes from experimental (Daugaard et al., 2019) and data-driven (Lang et al., 2017). Using existing data on the temperature dependence of these key parameters is a first step in the effort to better understand community functioning under warming

but conducting empirical studies would be essential to better characterize their thermal dependences.

Self-regulation is indeed a key and poorly known parameter. It has often been neglected in theoretical and empirical studies (Amarasekare, 2015; Gilbert et al., 2014), despite its importance in determining network stability (Barabás et al., 2017). For instance, Gilbert et al. (2014) explored the effects of temperature on biomass distribution and stability in consumer–resource systems in the absence of consumer self-regulation (corresponding to the case where  $\lambda$  tends to infinity). In contrast, we consider self-regulation both at the resource and consumer levels and show that the effects of temperature on biomass distribution across trophic levels strongly depend on the consumer self-regulation. Without self-regulation, the model predicts inverted biomass pyramids in most cases whereas, with self-regulation, the cases with non-inverted biomass pyramids are much more frequent. Our study is thus complementary to the work of Gilbert et al. (2014). It extends and generalizes previous works by adding another dimension (i.e., consumer self-regulation) and by testing general and specific effects of temperature using a large database of activation energies and two case studies.

To test specific predictions of our theoretical framework, we thus use experimental parameters on stream organisms (Kishi et al., 2005) to compute values of  $\kappa$  and  $\lambda$  along a temperature gradient and compare our estimations with the observed empirical pattern. We find that the values of  $\kappa$  and  $\lambda$  computed directly from these experimental data and their estimated values are similar for the whole temperature range when the thermal performance curves of biological rates are described by quadratic functions. However, when the thermal performance curves are fitted with exponential Arrhenius functions, the computed values of  $\kappa$  and  $\lambda$  and their estimated values are similar only for the lowest temperatures. The divergence between the quadratic and the exponential model at higher temperatures observed here emerges from the often unimodal relationship between biological rate and temperature (Pörtner & Farrell, 2008). Unimodal thermal responses have more recently been reported (Dell et al., 2014; Englund et al., 2011; Sentis et al., 2012) and shown to cascade up to the community level by inducing nonlinear responses in interaction strength (Betini et al., 2019; Bideault et al., 2019; Sentis, Gémard, et al., 2017; Uszko et al., 2017). A better characterization of the full thermal response of biological rates could thus help to better understand the effects of temperature on trophic interactions beyond optimal temperatures. Nevertheless, most species typically experience temperatures below their optimal temperatures (Martin & Huey, 2008; Pawar et al., 2016; Thomas et al., 2012) and we demonstrate that using an exponential function can be appropriate for these sub-optimal temperatures. The coherence between our estimates of biomass ratios and the data also highlights the reliability of our framework here. This promising example suggests that our theory may be able to predict changes in biomass distribution and trophic control in consumer–resource systems.

Our mechanistic framework allows drawing a comprehensive picture of thermal effects on both the structural and dynamical

properties of consumer–resource systems. We highlight major differences between terrestrial and aquatic habitats and across taxonomic groups and point out the key role of thermal mismatches between biological rates. Although we do not consider some mechanisms that could modify the responses of communities to warming such as thermal adaptation (Kontopoulos et al., 2020), life history or differences in warming scenarios between temperate and tropical regions (Amarasekare, 2019), our study sheds light on the mechanisms driving variations in food chains structure and dynamics with temperature changes, laying foundations to further explore how complex networks will change with warming.

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## AUTHOR CONTRIBUTION

A.B., A.S., M.B., N.G. and Y.R.Z. collected the data, performed the modeling work and analyzed the output data. A.B. wrote the first draft of the manuscript. All authors designed the study and contributed to revisions.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in figshare at <https://doi.org/10.6084/m9.figshare.13077851.v1>.

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## SUPPORTING INFORMATION

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

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