

RESEARCH ARTICLE

Food web consequences of thermal asymmetries

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Abstract

1. Understanding how food webs will respond to globally rising temperatures is a pressing issue. Temperature effects on food webs are likely underpinned by differences in the thermal sensitivity of consumers and resources, or thermal asymmetries. We identify three sources of asymmetry in the rising portion of thermal performance curves: *inter*-thermy variation across thermoregulatory groups, *intra*-thermy variation within a thermoregulatory group and *rate*-dependent variation in how different ecological rates respond to temperature.
2. We use a large empirical dataset on thermal sensitivities across thermoregulatory groups to explore how prevalent thermal asymmetries are in real consumer-resource interactions. We then develop theory to illustrate how food web temperature responses are mediated by the magnitude and direction of these thermal asymmetries. We use this model to show possible conditions under which food webs could respond to warming as currently expected, and when that may not be the case.
3. Our results suggest that *inter*-thermy, *intra*-thermy and *rate*-dependent asymmetries are likely common in natural food webs. We show how all thermal asymmetries have important effects on species abundances across trophic levels as well as the maximum trophic position in the food web. Both the direction of the asymmetries (i.e. which species respond more strongly) and their magnitude (the difference in thermal responses) determine the temperature response of the food web and, consistent with current expectations, top predator abundance almost always declines with temperature, even though maximum trophic position may increase.
4. While our model shows that food web temperature responses can be varied, much of this variation can be explained by considering thermal asymmetries. Our study provides new data and theoretical insights into the widely varying food web effects of warming observed in laboratory, experimental and observational settings, and clarifies how predator and prey thermal ecology may influence overall food web responses in a changing world.

KEYWORDS

activation energies, communities, food web thermal responses, global warming, temperature responses, temperature sensitivities

1 | INTRODUCTION

Understanding how ecosystems will respond to a rapidly changing climate is a major goal of ecology (Barbour & Gibert, 2021; Bonebrake et al., 2018; Pimm, 2009; Rosenblatt & Schmitz, 2016). Global climate change (GCC) is leading to warmer temperatures, which has myriad ecological consequences from individuals (Avery & Bond, 1989; Tsubaki et al., 2010) to ecosystems (Antiqueira et al., 2018; Carr et al., 2018; Maureaud et al., 2017). For example, well-known temperature effects on energetic demands (Brown et al., 2004; Gillooly et al., 2001; Rohr et al., 2018) can ultimately determine the strength and outcome of predator–prey and other types of interactions (Barton et al., 2009; Bertness & Ewanchuk, 2002; Gedan & Bertness, 2009). Because ecological interactions underpin community structure and dynamics, some of the most important effects of GCC are likely to be on entire communities (Garzke et al., 2019; Gibert & DeLong, 2014; O'Connor & Bruno, 2009). Accurately forecasting community responses to GCC thus hinges on a mechanistic understanding of how shifting temperatures will affect networks of ecological interactions.

Food webs are arguably the most important and well-studied interaction network in ecology (e.g. Dunne et al., 2014; May, 1972; McCann, 2000; Paine, 1992). Foundational work showed reductions in the abundance of top predators with warmer temperatures, as basal species abundance increased (Petchey et al., 1999). In addition, the shrinking of body sizes (Atkinson, 1995; Brose et al., 2012; Sentis et al., 2017), and increasingly inefficient energy transfers with increasing temperatures (Barneche et al., 2021), should result in food webs that sustain fewer top predators and trophic levels as temperatures increase. These predictions hold in some systems: rising temperatures lead to inefficient energy transfers in marine food webs (Ullah et al., 2018) and terrestrial pitcher-plant food webs have fewer trophic levels in warmer climates (Baiser et al., 2012). Results vary, however, as body sizes do not always decrease in warmer streams (O'Gorman et al., 2017), the proportion of basal species can decrease (Carr et al., 2018; Garzke et al., 2019; Svensson et al., 2017) or remain unchanged with temperature (Baiser et al., 2012), while an increase (instead of a decrease) in the number of trophic levels with temperature has also been observed (Gibert, 2019; O'Gorman et al., 2017). These diverse findings emphasize the need for a more complete understanding of how temperature jointly influences the abundance of organisms across trophic levels, as well as the number of trophic levels in a food web, to resolve inconsistencies between current expectations and observations.

One path forward to address these issues is to focus on differences in thermal sensitivities between consumers and resources engaged in the feeding interactions that represent the building blocks of food webs. Thermal sensitivities characterize the degree to which biological processes change with temperature and are typically quantified as the activation energy parameter (E_a) of the Arrhenius–Boltzmann model of temperature dependence (Brown et al., 2004; Gibert et al., 2016; Gillooly et al., 2001; Gillooly et al., 2002; O'Connor et al., 2011), reflecting linkages between organismal metabolism and

statistical mechanics. Differences in thermal sensitivities between consumers and resources can lead to asymmetries in their temperature response (Barton & Schmitz, 2009; Dell et al., 2014; Huey & Kingsolver, 1989; O'Connor, 2009; Rall et al., 2010). Such thermal asymmetries can alter the strength and outcome of consumer–resource interactions (Lindmark et al., 2019), precipitating effects at community and global scales (Dell et al., 2014; Grady et al., 2019). We argue that thermal asymmetries between interacting species have important but poorly understood implications for food webs.

Thermal asymmetries in the shape of (unimodal) thermal performance curves (TPCs) have been described in detail elsewhere and are thought to arise from differences in the response magnitude (the height of the TPC), the rate (how strongly the measure of performance responds to temperature) or the peak (how large the response can be; Dell et al., 2014). Here, we build upon these ideas and identify three major sources of asymmetry in the rising portion of TPCs that may affect feeding interactions as temperatures change. First, we hypothesize that the most general form of asymmetry arises from species that differ in their thermoregulatory mode (or *thermy*), which we term *inter-thermy asymmetry*. Most species are ectotherms, where body temperature is driven by external environmental conditions, leading to shifts in metabolism and performance as ambient temperature changes. In contrast, endothermic mammals and birds have a constant body temperature that dampens physiological and behavioural responses to ambient temperature. Wherever endotherms hunt or flee ectotherms, metabolic and performance differences will be greater and more favourable to endotherms in colder environments, where ectotherm metabolism and performance are low, and will converge as temperatures rise (Figure 1a). These *inter-thermy* asymmetries have recently been shown to predict global patterns of diversity and abundance in marine mammals and birds versus sharks and bony fish (Grady et al., 2019) but their broader food web consequences have received little attention.

Second, thermal sensitivities can vary widely within the same thermoregulatory mode (Dell et al., 2011). We hypothesize that this *intra-thermy* variation might lead to thermal asymmetries between interacting species of the same thermoregulatory mode, which we call *intra-thermy asymmetry* (Figure 1b). *Intra-thermy* asymmetry may be especially common between consumers and resources belonging to the same phylogenetic group (e.g. fishes or birds), as organisms from different phylogenetic groups often vary more in their thermal physiology (Kontopoulos et al., 2020). We expect this *intra-thermy* variation to be higher between ectotherms than between endotherms (Figure 1b), owing to tighter physiological controls at play in body temperature regulation among endotherms.

Third, we hypothesize that even within the same species, different biological rates may vary in their thermal sensitivity, thus shaping the ecology of interacting species (Figure 1c; e.g. Amarasekare, 2015; Dell et al., 2014; Lindmark et al., 2019; Osmond et al., 2017). If a consumer and its resources vary in which of their ecological rates are temperature dependent, then this *rate*-dependent variation should result in *rate*-dependent *asymmetry* between the consumer and its resource. For example, temperature could strongly influence the

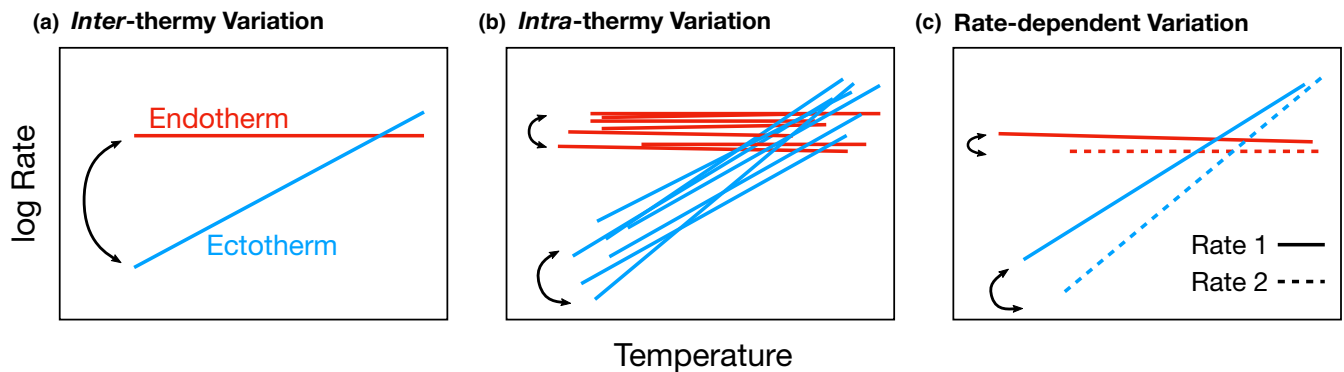


FIGURE 1 Comparative change in performance with temperature. Each line represents a species-specific response to temperature for some population. Three sources of thermal asymmetries are shown: (a) variation between endotherms and ectotherms (*thermy*), (b) variation within endotherms and ectotherms (variation in slopes), as well as, species-specific responses (variation in intercepts), and (c) rate-specific responses (slopes and intercepts). Double-headed arrows indicate the potential for predator–prey interactions among organisms that would lead to temperature asymmetries: (a) Represents predator–prey interactions where one species is an endotherm and the other species an ectotherm, (b) represents interactions between species of equal thermy but different temperature sensitivity and (c) represents interactions between species of equal thermy but where the rates more strongly responding to temperature differ among species (e.g. in one species rates related to energy intake are more sensitive, while, in the other, rates related to energy expenditure may be more sensitive). Shown changes occur within the rising part of the unimodal thermal performance curve. We focus on changes in slopes (thermal sensitivities) throughout this manuscript.

thermal sensitivity of ecological rates relevant to predatory ability or energy transfers, while it may more strongly influence resource traits linked to growth or mortality. *Rate*-dependent asymmetries would be a special type of *intra*-thermy asymmetry because both species need to be able to respond to temperature for this form of asymmetry to arise. The difference in the response is due to which rates more strongly respond to temperature among interacting species, instead of the magnitude of the temperature sensitivity. Recent work has shown that differences in which rates are responding to temperature in consumer–resource pairs lead to vastly different temperature effects on consumer–resource interactions (Bideault et al., 2019), thus supporting the hypothesis that inter-rate asymmetries may have important consequences for food webs.

To test these hypotheses, we compiled published data from multiple species across habitats on the thermal sensitivity of two ecological rates that are central to consumer–resource interactions: attack rate and mortality rate (Rosenzweig & MacArthur, 1963). In the context of these data, (a) the *inter*-thermy asymmetry hypothesis predicts strong, directional differences in the temperature sensitivity of attack and mortality rates between endotherms and ectotherms (Figure 1a). (b) The *intra*-thermy asymmetry hypothesis predicts larger variation in thermal sensitivities among ectotherms than among endotherms (Figure 1b). And, (c) for *rate*-dependent asymmetries to play a role in consumer–resource interactions, interacting organisms of equal thermy should differ in what rates respond more strongly to temperature (Figure 1c).

Published empirical results have not always matched theoretical expectations (Gibert, 2019; O’Gorman et al., 2017) that rising temperatures will increase the abundance of basal species and decrease the abundance of apex species, resulting in a decline in maximum trophic level of the food web. Through their effect on biomass gains and losses (Bideault et al., 2019), attack and mortality rates

will ultimately influence biomass accumulation (Brose, 2010) and, thus, species abundances across trophic levels and the number of trophic levels in a food web. We use a mathematical model to illustrate some of the food web consequences of the identified sources of asymmetry in the rates for which we have data, and assess how these three sources of asymmetry may influence biomass distribution across trophic levels, as well as food web maximum trophic position, as temperatures increase. We expect that these sources of asymmetry will result in different food web responses depending on their magnitude (or how large the asymmetry is), and how thermal sensitivities vary across trophic levels (we call this the ‘direction’ of the asymmetry).

2 | MATERIALS AND METHODS

2.1 | Mortality and attack rate data

Data on endotherm and ectotherm mortality rates were obtained from McCoy and Gilgooly (2008), and attack rates from Li et al. (2018). Attack rate data were only available for ectotherms, and their ambient temperature (T) was reported by the original references. For mortality data, no environmental temperature was provided in the original data for endothermic birds and mammals. An appropriate temperature value should represent the average temperature experienced over a lifetime. Because the temperature of mortality can span the lifetime of an organism and almost all mammal and birds complete their life cycle over at least a year, mean annual temperature within a species’ range provides a reasonable estimate of the temperature of mortality rates. To estimate the mean annual temperature for endotherms, we first obtained species distribution maps from IUCN (2021) and Birdlife International (2017). Each species

range was gridded as 55 km × 55 km cells (~1/2 degree latitude and longitude at the equator) using Behrmann equal area projections. We used coordinates at the centre of each cell to extract annual mean surface temperature from WorldClim (Fick & Hijmans, 2017; Hijmans et al., 2005) on land, and used surface temperature averaged over a 10-year period (2006–2015) from Reynolds et al. (2002) for sea temperatures (available at <http://iridl.ldeo.columbia.edu/>). We then averaged all grid cells in a species' range to get a single temperature value for a given endothermic species. This limited us to one temperature value per endothermic species. Thus, to examine *intra*-thermy variation, we focused on patterns at the genus level rather than at the species level, whereas each endotherm genus analysed had multiple species that spanned a minimum range of 5°C. WorldClim data were accessed through the R package RASTER v3.0-7 (Hijmans, 2019), with an arc-minute resolution of 10 min of a degree. Discrepancies in species names across datasets were standardized using *Taxize* (Chamberlain & Szöcs, 2013), *Rangebuilder* (Rabosky et al., 2016), and manual inspection. Statistical analyses were performed in R 3.6.2 (R Core Team, 2013).

2.2 | Estimating the thermal sensitivity of mortality and attack rates

While many thermal dependencies are unimodal (e.g. Amarasekare, 2015; Dell et al., 2014; Singleton et al., 2021), we focus on the rising portion of temperature performance curves (TPCs) because the physiological and evolutionary controls that shape this portion of the TPC are better understood (Kontopoulos et al., 2020; Pawar et al., 2016). In addition, more data are available in that range to test our hypotheses (Dell et al., 2011), as evidenced by many previous studies that also followed this approach (e.g. Bernhardt et al., 2018; Dell et al., 2014; Gilbert et al., 2014; O'Connor et al., 2011; Savage et al., 2004).

Both mortality rate (m) and attack rate (α) vary with temperature (T) and body mass (M ; Gilbert et al., 2014; Gillooly et al., 2001). To estimate the thermal sensitivity, E , of attack and mortality rates (which we call E_α and E_m , respectively), we modelled the effect of M and T (with T estimates from the previous section) on m or α by assuming that each rate (attack or mortality) was a function of temperature as in the Arrhenius–Boltzmann model, that is, $Ae^{-\frac{E}{k_{bol}T}}$, where A is a pre-exponential term that sets the units of the rate, T is the temperature in degrees Kelvin, E is the thermal sensitivity parameter (or activation energy, in units of electron volts, eV) and k_{bol} is the Boltzmann constant (=8.62 eV K⁻¹). By taking natural logs in both sides of the above expression, E can be estimated from data as the slope of the logarithm of the rate against $\frac{1}{k_{bol}T}$ (see Equations S1 and S2 in Appendix 1 for more details).

To estimate E , we used linear mixed models (Appendix 1), with T and M as fixed effects, and taxonomic information as a random effect. Specifically, species was a random term with random intercepts, accounting for multiple observation per species. In addition, the broad taxonomic categories used by McCoy and Gillooly (2008)—fish,

birds, mammals, invertebrates—were also a random term in which species were nested. For *intra*-thermy analysis of genera, genus was included as a random effect with random slopes and intercepts (Appendix 1, Equations S3 and S5). Statistical analyses, including tests of differences across thermoregulatory groups, were performed using packages LME4 (v1.1-25; Bates et al., 2011), LMERTEST (v3.1-3; Kuznetsova et al., 2017), BRMS (v2.14.4; Bürkner, 2017) and BASE R (R Core Team, 2013). We also considered the role of phylogenetic relatedness of taxa for which comprehensive phylogenies were available: mammals and birds, using a Bayesian mixed model in BRMS (v2.14.4) and BASE R methods (see Appendix 1). Results are quantitatively similar to non-phylogenetic analyses. LME4 output is reported unless otherwise stated.

2.3 | A simple food web model for thermal asymmetries

We model the dynamics of an omnivory module, a highly prevalent building block of larger food webs (McCann et al., 1998; Thompson et al., 2007) whose dynamics have been studied in detail elsewhere (Diehl, 2003; Diehl & Feiße, 2000; Mylius et al., 2001). We track the rate of change in the abundance of an omnivorous top predator (P , 'predator' hereafter) that consumes an intermediate consumer (G , 'grazer' hereafter) and a basal resource (R). We do not assume that G is an actual grazer, we only call it that for simplicity. Indeed, the grazer can be any intermediate consumer, meaning that our results are not necessarily constrained to the dynamics at the bottom of the food web. Importantly, the omnivory module/model is very flexible and encompasses the dynamics of a three-species chain and exploitative competition as special cases. Indeed, if the attack rate of the top predator with the resource is zero (or the handling time is infinitely large), the dynamics of the omnivory module tend to those of the three-species chain while exploitation occurs when the attack rate of the predator with the grazer is zero (or handling time infinite).

The model assumes that the resource population grows logistically with intrinsic growth rate r and carrying capacity K . The grazer eats the resource following a type II functional response with attack rate α_{GR} and handling time η_{GR} , and dies at a background mortality rate, m_G . The predator eats both the grazer and the resource following a type II multi-species functional response (Lawton et al., 1974; Smout et al., 2010) with parameters α_{pi} and η_{pi} (with $i \in \{R, G\}$), and dies at a background mortality rate, m_p . To illustrate the effects of temperature asymmetries, we assumed that both grazers' and predators' attack and mortality rates were temperature dependent. For simplicity, we assume that no other parameter is temperature dependent, although we relax these assumptions in the Appendix. Temperature-dependent parameters are denoted as functions of temperature, T . Taken together, our model reads:

$$\frac{dR}{dt} = rR \left(1 - \frac{R}{K} \right) - \frac{\alpha_{GR}(T)RG}{1 + \alpha_{GR}(T)\eta_{GR}R} - \frac{\alpha_{PR}(T)RP}{1 + \sum_{i \in \{R, G\}} \alpha_{pi}(T)\eta_{pi}i},$$

$$\frac{dG}{dt} = \epsilon_{GR} \frac{\alpha_{GR}(T)RG}{1 + \alpha_{GR}(T)\eta_{GR}R} - \frac{\alpha_{PG}(T)GP}{1 + \sum_{i \in \{R,G\}} \alpha_{Pi}(T)\eta_{Pi}i} - m_G(T)G,$$

$$\frac{dP}{dt} = \epsilon_{PR} \frac{\alpha_{PR}(T)RP}{1 + \sum_{i \in \{R,G\}} \alpha_{Pi}(T)\eta_{Pi}i} + \epsilon_{PG} \frac{\alpha_{PG}(T)PG}{1 + \sum_{i \in \{R,G\}} \alpha_{Pi}(T)\eta_{Pi}i} - m_P(T)P, \quad (1)$$

where the ϵ_{ij} parameters represent the conversion of resources into consumers (G and P).

Across species, mortality rates increase exponentially with temperature (Amarasekare & Savage, 2012; Gillooly et al., 2002; Wieczynski et al., 2021). Other parameters have more complex temperature dependencies, either by significantly departing from the classic Arrhenius functional form (e.g. Amarasekare & Savage, 2012; DeLong et al., 2017), or from its assumptions (Gibert et al., 2016; Pawar et al., 2016). For consistency with our empirical data, we follow previous studies (e.g. Bernhardt et al., 2018; Gilbert et al., 2014; O'Connor et al., 2011; Savage et al., 2004) and focus on the rising portion of the temperature response, which can be modelled as:

$$f(T) = A e^{\frac{E}{k_{bol}} \left(\frac{1}{T_{ref}} - \frac{1}{T} \right)}, \quad (2)$$

where f is the focal parameter (attack or mortality rate), A is the value the parameter takes at the reference temperature T_{ref} (in degrees Kelvin), and T , k_{bol} and E as in the previous section. The larger the value of E (on average ~ 0.65 eV, Dell et al., 2011), the larger the change in f with an equal change in temperature.

2.4 | Modelling thermal asymmetries

By definition, thermal asymmetries in trophic interactions imply that thermal sensitivity changes across trophic levels/positions. *Inter*-rate asymmetries imply differences in thermal sensitivities across trophic levels and across ecological rates. We incorporated asymmetries in mortality and attack rates by allowing the thermal sensitivity parameters (E) to vary across trophic levels and ecological rates. All three sources of asymmetry can occur simultaneously, leading to an exceedingly large parameter space. For simplicity, we grouped analyses into distinct qualitative scenarios for each type of asymmetry. The goal of our modelling was not to explore to exhaustion every possible food web consequence of all combinations of asymmetries, but instead to illustrate their possible food web consequences with respect to abundances/biomass across trophic levels and maximum trophic position (maxTP hereafter). Across all scenarios, we explored 25,200 different parameter combinations.

First, we considered two scenarios with no *rate*-dependent asymmetries ($E_{m_{G,P}} = E_{\alpha_{G,P}}$): (a) *inter*-thermy asymmetries only (grazer or predator was an endotherm, but not both) and (b) *intra*-thermy asymmetries only (both grazer and predator were ectotherms). For the *inter*-thermy asymmetry scenario, we set each species' (grazer or predator) thermal sensitivities to zero (because there only is one

way to be an endotherm, i.e. $E = 0$), and allowed the other species' thermal sensitivities to vary from 0 to 1 (step size = 0.014). These analyses also consider the situation in which both species are endotherms ($E_G = E_P = 0$), which is trivially unresponsive to temperature.

To model the *intra*-thermy asymmetry scenario, we set the grazer's thermal sensitivities to 0.5 (average ectotherm in our dataset) and allowed the predator's thermal sensitivities to vary from 0 to 1 as before. To model the *rate*-dependent asymmetries scenario, we further subdivided parameter space into the following cases: (a) grazer mortality more thermally sensitive than predator mortality ($E_{m_G} = 0.5, E_{m_P} = 0.2$), (b) grazer and predator mortality equally sensitivity to temperature ($E_{m_G} = 0.5, E_{m_P} = 0.5$) and (c) grazer mortality less sensitive to temperature than predator mortality ($E_{m_G} = 0.5, E_{m_P} = 0.8$). Within each case, we set the grazer's attack rate thermal sensitivity to 0.5 and allowed the predator's attack rate thermal sensitivities to vary from 0 to 1.

2.5 | Quantifying species abundances and trophic positions in our model food web

To illustrate the food web consequences of thermal asymmetries, we numerically solved the model for all possible scenarios at different temperatures, which varied in our model from 15 to 30°C, with steps of 0.25°C. We focused on two important metrics of food web structure often reported in empirical studies: species abundances across trophic levels (measured as a density, in individuals/unit area) and the maximum trophic position (maxTP) of the food web. We used the DIFFERENTIALEQUATIONS v6.6 package (Rackauckas & Nie, 2017) in Julia computing language v1.0 (Bezanson et al., 2014) and stored equilibrium densities for all species after 4,000 time steps. While unstable and oscillatory dynamics are possible in this model (Diehl & Feiße, 2000), these were not observed in the range of parameters explored.

The maxTP was calculated as $\max\left(1 + \sum_{j=1}^n p_{ij} TP_j\right)$, $i = \{R, G, P\}$, (Levine, 1980; Williams & Martinez, 2004), where TP_j is the trophic position of each resource item j the focal species i consumes, and p_{ij} is the fractional (energetic) contribution of species j to the diet of species i . The trophic position of the predator (TP_P), which also is the maxTP of the food web, can change over time because the fractional contributions (p_{ij}) are a function of foraging rates (Gibert & DeLong, 2017; Gibert & Yeakel, 2019) as:

$$p_{Pj} = \frac{\epsilon_{Pj} \frac{\alpha_{Pj}(T)p_j}{1 + \sum_{k \in \{R,G\}} \alpha_{Pk}(T)\eta_{Pk}(T)k}}{\epsilon_{PR} \frac{\alpha_{PR}(T)PR}{1 + \sum_{k \in \{R,G\}} \alpha_{Pk}(T)\eta_{Pk}(T)k} + \epsilon_{PG} \frac{\alpha_{PG}(T)PG}{1 + \sum_{k \in \{R,G\}} \alpha_{Pk}(T)\eta_{Pk}(T)k}}, j \in \{R, G\}. \quad (3)$$

Resource and grazer trophic positions, however, are constant ($TP_R = 1$ and $TP_G = 2$). The maxTP approaches a steady state if the abundance of all species approaches a steady state (Gibert & DeLong, 2017). All parameter values were chosen so that, at the reference temperature ($T = T_{ref}$), equilibrium abundances decreased

towards higher trophic position ($R > G > P$, see Table S1), to reduce complexity in model outcome. All other parameter values are found in Table S2, Appendix 2. All data and code can be found at our dedicate repository (Gibert et al., 2022).

3 | RESULTS

3.1 | Sources of thermal asymmetries are common

First, endotherms and ectotherms differed in their temperature responses, consistent with predictions (Figure 2a,b). Across all taxa, the temperature dependence of mortality rates was close to zero among endotherms ($E_m = 0.047$, CI: -0.0066 – 0.087 ; $p = 0.022$, Table S1, Figure 2a) and when restricted to data-rich genera (Figure 2c,d; Figure S2), endotherms slopes were not significantly different from zero ($E_m = -0.012$, CI: -0.05 – 0.074 , $p = 0.70$). Ectotherms were closer to the typical temperature sensitivity of 0.65 ($E_m = 0.53$, CI: 0.41 – 0.67 ; $p < 0.001$, Table S1; Figure 2b), but somewhat lower when analysed at the genus level (ectotherms: $E_m = 0.43$, CI: 0.30 – 0.56 , $p < 0.001$; Figure 2c; Figure S1), indicating the potential for *inter*-thermy asymmetries in consumer–resource interactions. Second, while the data

revealed variation in thermal sensitivities within ectotherms and endotherms (Figure 2d), this variation was significantly lower for endotherms than for ectotherms, as predicted ($p = 0.019$, $F_{12,50} = 2.33$), suggesting that *intra*-thermy asymmetries (in mortality rates) and *intra*-thermy asymmetries are common in nature, at least among ectotherms. Last, average thermal sensitivity across mortality (E_m) and attack rates (E_a) were similar among ectotherms, with overlapping confidence intervals (Figure 2e,f; $t = 0.611$, $p = 0.55$, $df = 16.4$). Contrary to our hypothesis, these results may and suggest that *intra*-rate asymmetries may be less common than *inter*- or *intra*-thermy asymmetries. However, variance differed strongly between rates, with ectothermic attack rates being much more variable than mortality (Figure 2e,f, $F_{14,12} = 13.24$, $p < 0.001$, Table S1), thus making it possible for particular interacting species to still show *inter*-rate asymmetries in the tails of these distributions.

3.2 | Consequences of inter- and intra-thermy asymmetries for food web structure

In the absence of *inter*-rate asymmetries, abundances and maxTP were strongly influenced by *inter*- and *intra*-thermy asymmetries (Figure 3). Both the direction of the asymmetry (which species

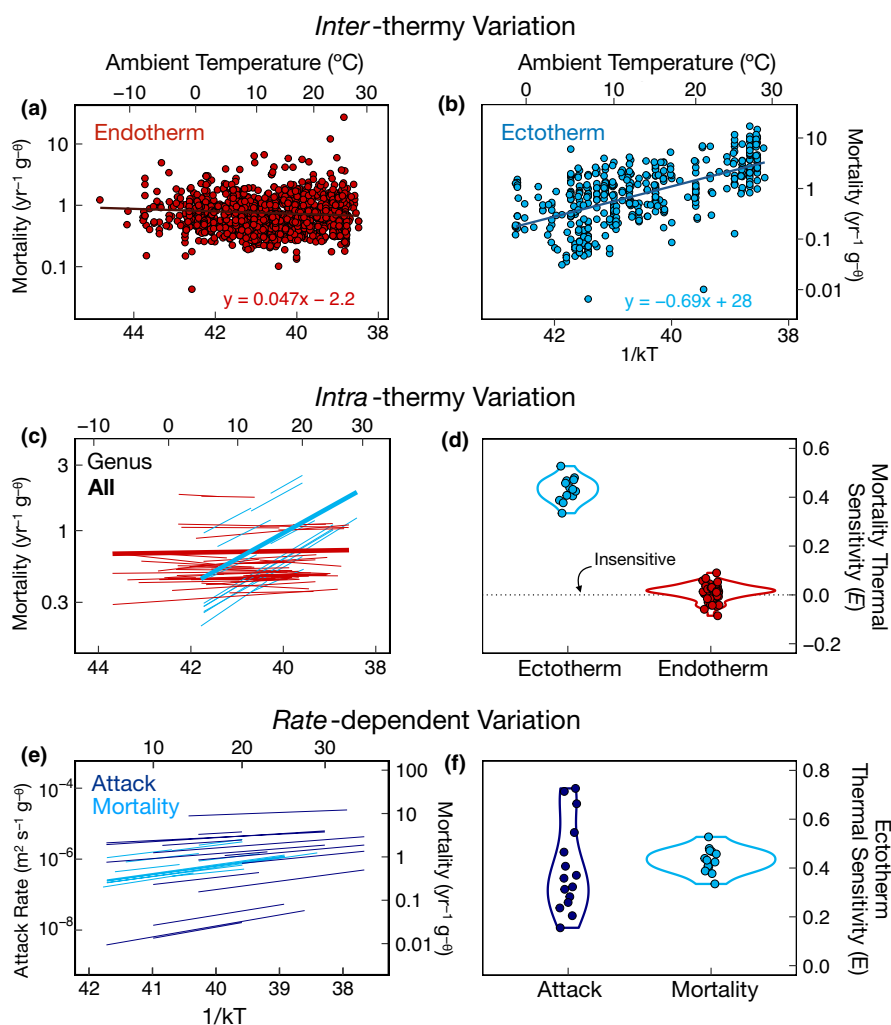


FIGURE 2 Sources of thermal asymmetry. The thermal sensitivity E is calculated by regressing rates against $1/kT$; temperature in °C is also shown for reference. (a) Mortality rates vs $1/kT$ for endotherms (birds and mammals); temperature increases from left to right, with equivalent °C values shown above. Endotherm mortality rates (red) are largely unresponsive to temperature. (b) As in a but for ectotherms (fish and invertebrates; light blue), mortality rates increase strongly with temperature. (c) Mortality rates vs $1/kT$ for both ecto and endotherms on a per genus basis show variation in slopes (thermal sensitivities). Fitted lines in bold show results for all genera per thermy. (d) Violin plots of the fitted thermal sensitivities across genera show thermal sensitivities and variance in thermal sensitivity for ectotherms while endotherms are statistically less variable ($F_{12,50} = 2.33$; $p = 0.019$). (e) Attack rates (navy blue) and mortality rates (light blue) increase with temperature for ectotherms. (f) Violin plots of thermal sensitivities for mortality and attack rates in all ectothermic species; attack rates are more variable than mortality ($F_{14,12} = 13.24$, $p < 0.001$). Y-axes in a–c and e are logged (as in Figure 1).

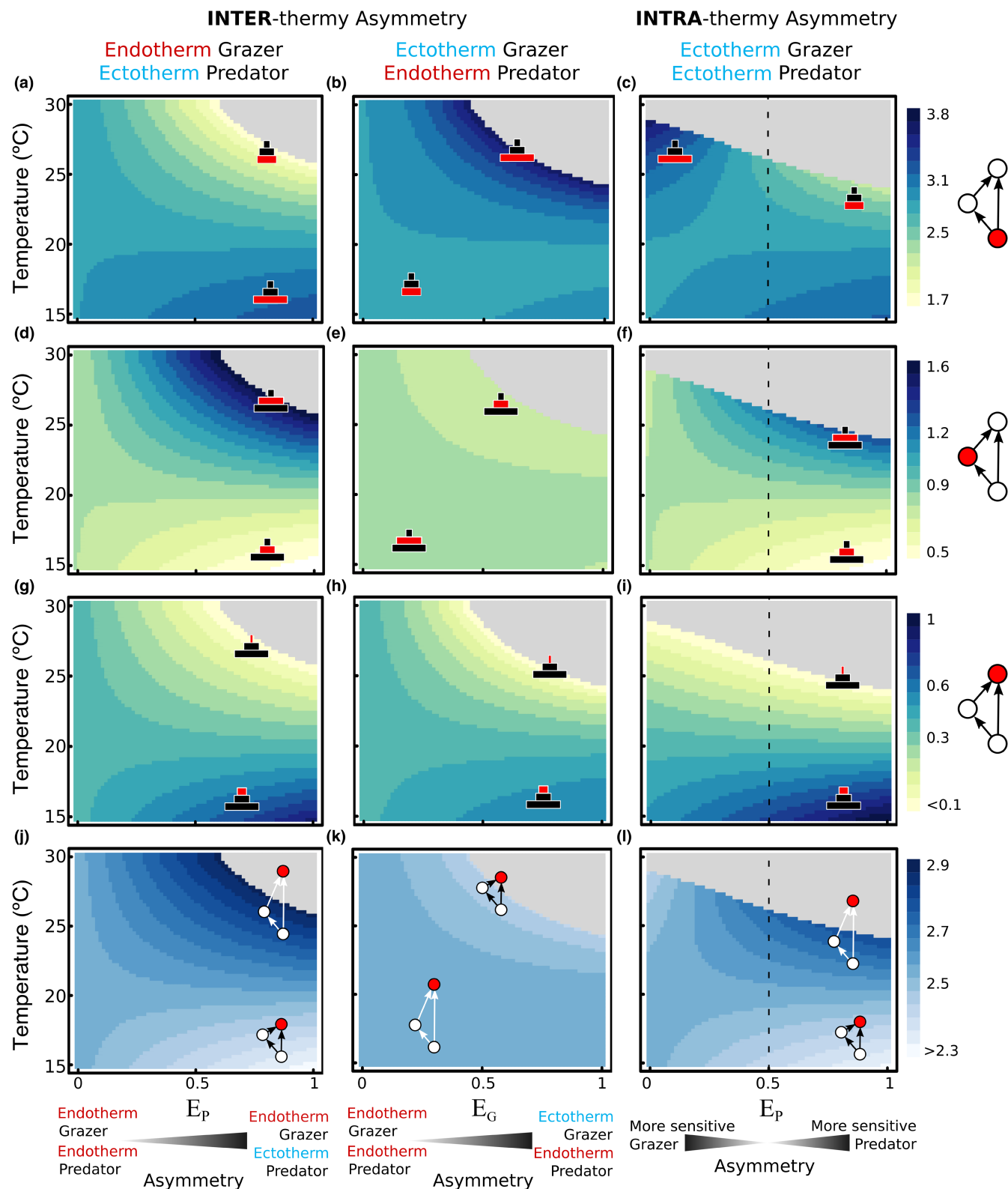


FIGURE 3 Effect of *inter-* and *intra-*thermy asymmetries on species densities and trophic level. Shown are the effects on the densities of resources (a–c), grazers (d–f), predators (g–i) and maxTP (j–l) of the food web (i.e. trophic level of the predator). All metrics are plotted against the relevant thermal sensitivity (either E_p or E_g , assuming that $E_{a_i} = E_m$). In the 1st and 2nd columns, the x-axis can be seen as a measure of the magnitude of the asymmetry (each column implies a different direction: In column 1, thermal sensitivity increases across trophic levels, in column 2, thermal sensitivity decreases with trophic level). In the 3rd column, the dashed line indicates a situation where predators and grazers are equally thermally sensitive ($E_p = E_g = 0.5$), so the x-axis indicates changes in the magnitude and direction of the thermal asymmetry. Numbers indicate equilibrium densities in a–i and maxTP in j–l. Colour coding can be compared across columns within each row but not across rows. Grey areas indicate predator extinction.

responds more strongly, grazer or predator) and its magnitude (how large the difference between thermal sensitivities), influenced abundances across trophic levels and maxTP (Figure 3).

The food web consequences of *inter*-thermy asymmetries largely depended on which species was the endotherm and which was the ectotherm (i.e. the direction of asymmetry). For instance, whenever predators were ectotherms and grazers were endotherms, resources and predators largely decreased in abundance with temperature while grazer abundance increased (Figure 3, 1st column). As a result, maxTP increased with temperature (Figure 3j). However, when grazers were ectotherms and predators were endotherms, resources largely decreased with temperature, grazer abundance was largely unresponsive to changes in temperatures, but predators still decreased in density (Figure 3, 2nd column), which resulted in a mostly unchanging maxTP with temperature (Figure 3k). The magnitude of all those responses depended on how thermally sensitive the species were: large thermal sensitivities almost always led to stronger overall changes in the food web (Figure 3, 1st and 2nd columns).

The effects of *intra*-thermy asymmetries were consistent with those observed for *inter*-thermy asymmetries (Figure 3, 3rd column). For example, resource densities decreased with temperature when predators were more temperature sensitive than the grazers and increased with temperature when the grazers were more sensitive than the predators (Figure 3c), also consistent with results of *inter*-rate asymmetries (Figure 3a,b). Grazer density increased with temperature when predators were more temperature sensitive but remained roughly temperature insensitive when predators were less sensitive (Figure 3f). Also consistent with *inter*-thermy effects, predators consistently decreased in abundance with temperature (Figure 3i). Whether maxTP increased or decreased with temperature was also determined by the direction of the asymmetry, with increases in maxTP with temperature occurring when predators were more thermally sensitive than the grazers and decreases in maxTP with temperature occurring when predators were less thermally sensitive than grazers (Figure 3l).

Different model assumptions did not qualitatively alter these results (Appendix 3). Indeed, a more general model that included temperature effects in resource intrinsic growth rates, carrying capacity, handling times and conversion efficiency parameters, led to similar effects of *inter*- and *intra*-rate asymmetries (Figures S6 and S7). However, larger differences in model behaviour were observed when grazer thermal sensitivities were allowed to vary within the *intra*-thermy asymmetry scenario (Figures S8 and S9). In one case, *intra*-thermy asymmetries had no effect on grazer abundances and maxTP, even as temperature did (Figure S9), suggesting that, under some conditions, temperature may still influence food webs even in the absence of thermal asymmetries.

3.3 | Consequences of rate-dependent asymmetries for food web structure

The food web consequences of *rate*-dependent asymmetries largely depended on which ecological rate and which species was the most

thermally sensitive (Figure 4). The temperature response of resource abundance was the most likely to change qualitatively across all *rate*-dependent asymmetry scenarios analysed (Figure 4a–c). For example, while resource density could decrease or increase with temperature whenever grazer mortality was equally thermally sensitive as predator mortality (Figure 4b), whether resource density increased or decreased also depended on whether the grazer's attack rate was more or less thermally sensitive than the predator's. In contrast, rising temperature generally led to a decrease in resource abundances whenever predator mortality was more thermally sensitive, regardless of the thermal sensitivity of attack rates (Figure 4c).

Grazers and predators, however, showed much more consistent responses across all scenarios explored (Figure 4d–f,g–i). Grazer abundance tended to increase with temperature, except when grazer mortality was the most sensitive and attack rates were less sensitive than the predator's (Figure 4d). Predator abundance, on the other hand, only decreased with rising temperature, consistent with results from *inter*- and *intra*-thermy asymmetries, and showed little to no effect of either the direction or magnitude of *rate*-dependent asymmetries (Figure 4g–i). Changes in maxTP largely mimicked changes in grazer abundance with temperature (Figure 4j–l). The only scenario in which maxTP decreased with temperature, which is the only one consistent with the current paradigm, also led to a decrease in grazer density but an increase in resource density (Figure 4, 1st column).

Once again, our exploration of different model assumptions did not qualitatively alter our results (Appendix 4). Yet, some differences in the effects of *rate*-dependent asymmetries were found when grazer mortality rates were less or equally sensitive to temperature than predator mortality rates (Figures S10 and S11). Finally, allowing the grazer thermal sensitivities in attack rates to vary led to weaker effects of asymmetries and temperature on the grazer, and resource temperature responses were qualitatively different from those presented in the main text under some conditions (e.g. grazer mortality more temperature sensitive than predator mortality), as well as smaller changes in maxTP with temperature (Figures S12 and S13). However, temperature increase still led to consistent decreases in top predator density across the table (Figures S12 and S13).

4 | DISCUSSION

Our empirical analysis of available mortality and attack rate data suggest that *inter*-thermy and *intra*-thermy asymmetries (Figure 1) are likely common in natural food webs (Figure 2a–d), while *rate*-dependent asymmetries may be less so in terms of differences in thermal sensitivities for the rates analysed (Figure 2e,f), but significant differences in the variance of those rates may (Figure 2f) still allow for those asymmetries to occur widely. Furthermore, our modelling indicates that thermal asymmetries constrain how temperature affects species abundances across trophic levels and the maxTP of food webs (Figure 3), both of which have been proposed to respond to temperature in specific ways (e.g. Brose et al., 2012;

Petchey et al., 1999). While thermal symmetries in entire TPCs had been shown to influence predator–prey interactions (Dell et al., 2014), our results also suggest that thermal asymmetries in the rising portion of TPCs play an important role in determining the temperature response of food webs. Previous work has shown that temperature effects on trophic interactions depend on which ecological rates respond most strongly to temperature (Bideault et al., 2019; Uszko et al., 2017). Our results add to this literature by showing that in addition to which ecological rates are responding to temperature, the food web consequences of thermal asymmetries may also depend on the magnitude and direction of these responses (Figures 3 and 4). In what follows, we attempt to generalize our results beyond the rather simple dynamics of the omnivory food web model, by discussing how they may apply, more generally, to larger food webs.

Our results show that increasing temperatures could lead to a consistent decrease in top predator abundance—as currently expected (e.g. Brose et al., 2012; Petchey et al., 1999)—regardless of the existence or nature of any thermal asymmetry (Figures 3 and 4). However, increasing temperatures could result in shifts in basal resource abundances that ultimately depend on thermal asymmetries (Figures 3 and 4). More generally, our model suggests that current expected food web temperature responses (i.e. increase in basal species, decrease in top predators, decrease in maxTP) should occur whenever top predators are endotherms and intermediate consumers are ectotherms (Figure 3, 2nd column). Or, more generally, whenever thermal sensitivities decline with increasing trophic level. Whether thermal sensitivities increase or decrease with trophic level in real food webs, however, has not yet been empirically quantified but is an exciting path for future research.

There is reason to expect thermal sensitivities to be weaker at higher trophic levels. For example, endotherms are generally precluded from small size classes by surface area: volume constraints on heat loss; thus, they are more likely to occupy higher trophic levels (Pauly et al., 1998) as higher trophic levels tend to be occupied by larger animals (Riede et al., 2011). However, even among ectotherms, thermal sensitivity may decrease with trophic level as larger organisms have higher levels of thermal inertia. This indicates that thermal asymmetries may be smaller at higher trophic levels than at the base of the food web. Similar arguments may apply across latitudes. For example, higher (colder) latitudes are often dominated by endothermic predators in the ocean, but waters near the equator are dominated by ecto- and mesothermic predators (Grady et al., 2019). This, in turn, suggests the potential for smaller *inter*-thermy asymmetries in the tropics than in the poles, but perhaps a larger potential for *intra*-thermy or *rate*-dependent asymmetries. As a consequence, the magnitude of asymmetries and its ecological consequences likely varies across latitudes and trophic levels in systematic ways.

In the presence of *inter*-rate asymmetries, however, our model suggests multiple possible food web responses. These include

increases in top predator abundances and decreases in basal resource abundances with concomitant increases in maxTP (Figure 4), consistent with recent studies (Gibert, 2019; O'Gorman et al., 2017), but counter to current expectations (e.g. Brose et al., 2012; Petchey et al., 1999). More generally, our model indicates that in the presence of *inter*-rate asymmetries, current expectations on food web responses are only likely to occur whenever the thermal sensitivity of processes leading to biomass loss (e.g. mortality rates) decreases across trophic levels (in our model, the grazer was more sensitive than predator), but the processes controlling gains (e.g. attack rates) respond in the opposite way. Interestingly, because mortality rates decline with body size (McCoy & Gillooly, 2008) and attack rates increase (Rall et al., 2012), the processes leading to biomass losses are likely to decrease with trophic level and those leading to biomass gains are likely to increase with trophic level. Whether temperature will further strengthen that relationship is unknown. Our data also suggest that *inter*-rate asymmetries in attack and mortality rates should, on average, be small. However, we only analysed a small subset of all possible ecological rates, so the important question of whether *inter*-rate asymmetries are likely among other ecological rates and traits that determine species interactions should still be considered an open question.

Different ecological rates often vary qualitatively in their temperature response: while mortality rates increase exponentially with temperature (e.g. Uszko et al., 2017), attack rates are expected to increase unimodally (Amarasekare, 2015; Englund et al., 2011; Rall et al., 2012). How differences in the shape of unimodal temperature responses influence predator–prey interactions has been analysed extensively elsewhere (Amarasekare, 2015; Dell et al., 2014). However, we expect situations where two interacting species have different rates that respond qualitatively differently to temperature, as is the case in the above example, to represent a form of *intra*-thermy or *inter*-rate asymmetry. Our simple characterization of possible thermal asymmetries extends to situations in which unimodality is present, and thus has the potential to still yield interesting insights even in cases where temperature responses are more complex than the simple exponential increases considered in this paper.

It is possible for different rates within the same species to respond differentially to temperature. While these intraspecific differences do not conform to the definition of thermal asymmetry that is common in the literature (i.e. asymmetries occur between interacting species that respond differentially to temperature, e.g. Huey & Kingsolver, 1989; Barton & Schmitz, 2009; O'Connor, 2009; Rall et al., 2010; Dell et al., 2014; Grady et al., 2019), they can—and likely will—influence the way *rate*-dependent asymmetries affect ecological dynamics. Our own model considers the possibility of mortality and attack rates responding in different ways within each species and suggests that differences in which rates respond to temperature, as well as how strongly they do so, affects how *rate*-dependent asymmetries ultimately influence food web structure (Figure 4). This is in line with other studies (Bideault et al., 2019; Vasseur & McCann, 2005).

Last, multiple lines of evidence now suggest that rapid climate change is leading to increasing levels of phenological mismatch between organisms that depend on each other for survival and reproduction (e.g. plants and pollinators; Visser & Gienapp, 2019). Recent work has shown that climate change is influencing consumer–resource interactions through changes in phenology (Renner & Zohner, 2018), especially between plants and their consumers. These mismatches may represent a form of thermal asymmetry, where consumers and resources respond to temperature differentially, leading to a phenological mismatch that ultimately affects the consumer–resource interaction. However, we suspect that while the more general *intra*- and *inter*-thermy and *rate*-dependent variation may likely influence consumer–resource interactions across trophic levels, those occurring through phenological mismatches may be more likely to occur in the first few trophic levels of food webs.

A caveat of our study is that we do not account for temperature variability within the ranges of the species analysed, or seasonality. Indeed, temperatures may fluctuate over short and long time-scales, possibly influencing the dynamics described here in ways we do not yet understand. We also do not fully explore how changes in nutrient levels (and other parameters) may affect these results. For example, changes in *K* due to changes in nutrients can influence food web dynamics (Diehl, 2003; Diehl & Feiße, 2000) and result in interactive effects with warming (Binzer et al., 2012; Binzer et al., 2016). Thus, understanding how anthropogenic increases in nutrient load may influence the food web consequences of thermal asymmetries remains an interesting but open question. Moreover, our simplified food web model does not account for the actual complexity of structures and dynamics observed in real food webs, so our results should only be considered a possibility, albeit one that strikingly matches current expectations, but also diverges from them in interesting ways. We believe that those divergences are situations that may need to be further explored to advance our current understanding of this complex issue.

Together, our empirical and theoretical results indicate that thermal asymmetries are likely common in natural food webs. We show that the magnitude and direction of these thermal asymmetries drive food web species abundances across trophic levels, as well as the number of trophic positions. We also illustrate possible conditions under which these thermal asymmetries could result in current expectations for food web temperature responses, and situations in which those expectations may be unlikely to occur. Taken together, our results indicate how thermal asymmetries could result in variable food web responses to temperature, thus providing new insights into community-level responses to a rapidly—albeit asymmetrically—warming world.

AUTHORS' CONTRIBUTIONS

J.P.G. conceived the original study; J.P.G., J.M.G. and A.I.D. conceived the empirical approach and J.M.G. analysed the data; J.P.G. did the mathematical modelling and wrote the first version of the manuscript with inputs from all authors; all authors contributed substantially to subsequent versions. J.P.G. and J.M.G. contributed equally and are co-first authors.

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CONFLICT OF INTEREST

None.

DATA AVAILABILITY STATEMENT

All annotated code is available at our dedicated Zenodo repository (10.5281/zenodo.6557571) and on GitHub (https://github.com/JPGibert/Foodweb_thermal_asymmetries). The data used in this manuscript are already freely available elsewhere but can also be found at said repositories.

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SUPPORTING INFORMATION

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