Title

General predictions for the effects of warming on competition

Authors

Kaleigh E. Davis[1], Tess N. Grainger[1], Po-Ju Ke[2], Patrick L. Thompson[3], Mary I. O'Connor[3], Joey R. Bernhardt[1]

Affiliations

1. University of Guelph, Department of Integrative Biology; kaleigh.davis@uoguelph.ca (corresponding author)
2. Institute of Ecology and Evolutionary Biology, National Taiwan University;
3. University of British Columbia, Department of Zoology and Biodiversity Research Centre

Abstract

Understanding the effects of climate change on communities has been hindered by a lack of general theory for how temperature affects competition. To fill this knowledge gap, we integrated Modern Coexistence Theory and the Metabolic Theory of Ecology by incorporating empirically-derived temperature sensitivities into Modern Coexistence Theory's central model. We then simulated warming in two-consumer, two-resource systems and found that warming reduced both niche and fitness differences, making species more ecologically similar, and competitive interactions more neutral. The greatest shifts in competition occurred when thermal responses among consumers or resources were highly asymmetrical. Effects of warming on competition via niche differences were comparable to or stronger than those on fitness differences, suggesting that the emphasis on vital rates in global change research may overlook key biodiversity drivers. Our general theory expands the domains of two prominent ecological theories and contributes to a more predictive understanding of global change.

Introduction

Understanding the effects of climate warming on biodiversity is a central challenge of modern ecology (Parmesan & Yohe, 2003; Peters & Lovejoy, 1992; Román-Palacios & Wiens, 2020). Species interactions, and competition in particular, influence species' responses to the environment, and are thus critical to understanding the effects of warming on biodiversity (Godoy, 2019; Tilman, 1994). While a considerable body of empirical work has demonstrated shifts in competition with changing environments (e.g., Alexander et al., 2015; Germain et al., 2018; Pérez-Ramos et al., 2019), no general patterns in these effects have been demonstrated. Indeed, the nature of these shifts has been variable, and explanations usually context specific. Whether there is any generality in how warming affects competition, or whether these changes are inherently species-specific is a major open question. In the face of rapid environmental change, new theory is needed to address this question.

Modern Coexistence Theory has become the leading framework for understanding competition and coexistence (Chesson, 2000; Godoy & Levine, 2014; Godwin et al., 2020). This theory has the advantage of being agnostic to the specific mechanisms or context of competitive interactions, which allows it to be used to investigate general principles of competition and to be applied across a wide range of systems (Godwin et al., 2020; Grainger et al., 2019). Within Modern Coexistence Theory, species' competitive differences are described along two axes: fitness differences and niche differences (Chesson, 2000). Fitness differences are interspecific differences that give one species a competitive advantage and stem from differences between competing

species in intrinsic growth rate and sensitivity to competition. Niche differences are differences that reduce the strength of interspecific competition relative to intraspecific competition, for example, differences in resource use or susceptibility to predators (Chesson, 2000; Chesson & Kuang, 2008). The balance of these differences determines whether two species can coexist, one species will exclude the other, or whether they are competitively neutral (Adler et al., 2007). In global change research, work to understand the effects of warming on species abundance and distribution has predominantly emphasized shifts in vital rates (fitness differences; e.g. Merow et al 2014, Ehrlen and Morris 2015; but see Adler et al., 2012; Usinowicz & Levine, 2018), while the potential effects of warming on niche differences remain underexplored.

One criticism of Modern Coexistence Theory is that, because it is phenomenological, it is not well-suited to generate a priori predictions about how a given factor will affect competition and coexistence (Terry, 2025). Indeed, the parameters used to estimate niche and fitness differences in classical Modern Coexistence Theory models describe the outcomes of competitive interactions but are not related explicitly to underlying mechanisms (Chesson, 2000). However, niche and fitness differences can be alternatively calculated from their constituent mechanistic processes (Chesson & Kuang, 2008; Letten et al., 2017), for example, parameters related to resource competition (Song et al., 2019). Fortunately, the effects of temperature on many of these mechanistic processes have also been investigated empirically in the field of metabolic ecology (Dell et al., 2011; Rall et al., 2010). To evaluate how these temperature effects shift competitive dynamics with warming, the logical next step is to

integrate empirically-grounded temperature dependencies into Modern Coexistence Theory models.

The Metabolic Theory of Ecology is a widely used framework for understanding the effects of temperature on ecological processes. A central premise of this framework is that ecological processes, such as population growth and species interactions, all stem from metabolic processes, i.e. processes related to the uptake and transformation of resources into maintenance, growth and reproduction (Brown et al., 2004). In this way, metabolism is a fundamental process that constrains higher order processes, and the temperature- and body-size dependence of ecological interactions can be predicted based on the temperature- and body-size dependences of metabolic processes at lower levels of organization. Using this principle of metabolic scaling, the Metabolic Theory of Ecology has been used to predict the effect of temperature on population growth rates (Savage et al., 2004), population carrying capacities (Bernhardt et al., 2018), consumer-resource interactions (O'Connor, 2009; O'Connor et al., 2011), food webs (Gilbert et al., 2014; Vasseur & McCann, 2005), and ecosystem productivity (Enquist et al., 2003; Lopez-Urrutia et al., 2006; Welter et al., 2015). While this theory has been extended to competitive interactions (e.g., Saavedra et al., 2023; Yodzis & Innes, 1992), these studies have largely focused on body size effects, and theory for the effects of warming on competition and coexistence remains to be developed.

Progress in the Metabolic Theory of Ecology in elucidating the effects of temperature on species interactions has primarily been made by exploring the consequences of

differences in average temperature-sensitivities among biological processes, classically termed thermal asymmetries (Dell et al., 2014; here, inter-process thermal asymmetries, Figure 1B). For example, integrating differences in the temperature-dependencies of consumer metabolic rates, driven by respiration rate, and resource metabolic rates, driven by photosynthetic rate, into consumer-resource models revealed general patterns in how trophic interaction strengths change with warming (Gilbert et al., 2014; O'Connor, 2009; O'Connor et al., 2011; Sentis et al., 2015). However, this focus on constraints and consequences of inter-process thermal asymmetries has largely excluded competition. This is because competition deals inherently with intra-process variation in traits among species (e.g. interspecific variation in resource-use traits; Fig. 1C), rather than the inter-process (Fig. 1B) variation that has been the focus of the Metabolic Theory of Ecology (but see Bestion et al., 2018; Lewington-Pearce et al., 2019). Indeed, the Metabolic Theory of Ecology has largely overlooked interspecific trait variation and assumed that processes depending on this variation could not generate general patterns. Combining intra-process variation in thermal traits with metabolic scaling concepts from the Metabolic Theory of Ecology is a necessary next step in understanding shifts in competitive dynamics with warming. Incorporating temperature-dependent metabolic traits into the general governing processes of Modern Coexistence Theory offers a unique opportunity to develop new, general theory for how competition will change with warming and, in the process, test the longstanding assumption that generality cannot emerge from interspecific trait variation.

Here we draw from the Metabolic Theory of Ecology and Modern Coexistence Theory to develop theory for how warming affects competition for shared resources. We use this theory to address three questions: 1) How do the temperature sensitivities of each of the processes underlying competition contribute to changes in niche and fitness differences with warming? 2) How do inter- and intra-process thermal asymmetries affect these changes? 3) Are there general effects of warming on competition that emerge from the combined effects of warming on its suite of underlying mechanistic processes? To answer these questions, we analyzed a MacArthur consumer–resource model (MacArthur, 1970) using the canonical two-species Lotka–Volterra formulation of Modern Coexistence Theory that expresses phenomenological competition coefficients with mechanistic parameters (Chesson, 1990, 2011; Chesson & Kuang, 2008; Song et al., 2019). We modeled the effects of warming on competition by making each parameter in the MacArthur consumer–resource model temperature-sensitive. We synthesized temperature sensitivity data for each model parameter from the published literature to generate an empirical distribution of temperature sensitivities and then used this distribution to simulate effects of warming on competition between species pairs. In doing so, we identified a set of general predictions for how competition is affected by warming, and the conditions under which we expect to see more extreme shifts in competition.

Materials and Methods

The resource competition model

We modeled competition in a two-consumer system (N_1 and N_2) with two substitutable

resources (R_a and R_b) following the classic MacArthur consumer–resource model (MacArthur, 1970):

$$\frac{dN_i}{dt} = \sum_{k=a}^{b} v_{ik}\, c_{ik} R_k N_i - m_i N_i \qquad \text{Eq. 1}$$

$$\frac{dR_k}{dt} = r_k R_k \left(1 - \frac{R_k}{K_k}\right) - \sum_{i=1}^{2} c_{ik}\, R_k N_i \ , \qquad \text{Eq. 2}$$

with *i* = *1* or *2* and *k* = *a* or *b*. Here, the resource follows logistic growth with intrinsic growth rate r_k and carrying capacity K_k. Consumer species *i* utilizes resource *k* following a Holling type-I functional response, with per capita consumption rate (hereafter "consumption rate") parameter c_{ik} and conversion efficiency parameter v_{ik}. Finally, consumers experience per-capita mortality m_i. We converted this model into a two-species Lotka–Volterra competition model by separation of timescales. Specifically, by assuming fast resource dynamics, the quasi-equilibrium of R_k can be solved as:

$$\widehat{R_k} = \frac{K_k}{r_k}\left(r_k - \sum_{i=1}^{2} c_{ik}\, N_i\right) \ , \qquad \text{Eq. 3}$$

which is a function of consumer abundances. Substituting this expression back into the equation of consumer dynamics, we arrive at the following:

$$\frac{dN_i}{dt} = N_i \left[\left(\sum_{k=a}^{b} v_{ik}\, c_{ik} K_k - m_i\right) - \left(\sum_{k=a}^{b} v_{ik} \frac{K_k}{r_k} c_{ik}^2\right) N_i - \left(\sum_{k=a}^{b} v_{ik} \frac{K_k}{r_k} c_{ik} c_{jk}\right) N_j\right] =$$

$$g_i N_i \left[1 - \sum_{j=1}^{2} \alpha_{ij}\, N_j\right] ,$$

Eq. 4

with

$$g_i = \sum_{k=a}^{b} v_{ik}\, c_{ik} K_k - m_i \qquad \text{Eq. 5}$$

$$\alpha_{ij} = \frac{\sum_{k=a}^{b} v_{ik} \frac{K_k}{r_k} c_{ik} c_{jk}}{g_i} = \frac{\sum_{k=a}^{b} v_{ik} \frac{K_k}{r_k} c_{ik} c_{jk}}{\sum_{k=a}^{b} v_{ik} c_{ik} K_k - m_i} \ . \qquad \text{Eq. 6}$$

Here, g_i represents consumer *i* 's intrinsic growth rate, which equals the maximum energy gain by consumption minus the consumer's per-capita mortality rate. On the other hand, α_{ij} represents the relative reduction in consumer species *i* 's intrinsic growth rate caused by competition from species *j* (i.e., relative competition coefficient; *sensu* Song et al., 2019).

Modern Coexistence Theory then defines niche overlap (ρ) and fitness ratio ($\frac{f_2}{f_1}$) as follows:

$$\rho = \sqrt{\frac{\alpha_{12}\alpha_{21}}{\alpha_{11}\alpha_{22}}} \qquad \text{Eq. 7}$$

$$\frac{f_2}{f_1} = \sqrt{\frac{\alpha_{11}\alpha_{12}}{\alpha_{22}\alpha_{21}}} \ . \qquad \text{Eq. 8}$$

Here, ρ quantifies the relative strength of intraspecific and interspecific competition, and $\frac{f_2}{f_1}$ quantifies species' relative sensitivity to competition. Finally, we define niche difference (ND) as $-log(\rho)$ and fitness difference (FD) as $log\left(\frac{f_2}{f_1}\right)$. Under this definition, we can recover the ecologically intuitive condition for species coexistence, i.e., the niche difference between a pair of species needs to be greater than their fitness difference for them to coexist.

Adding temperature sensitivity to model parameters

For each mechanistic process from the MacArthur model (i.e. r_k, K_k, c_{ik}, v_{ik}, m_i; Eq. 4), we modeled temperature sensitivity using an Arrhenius function of the form:

$$Y(T) = Y_{T_{amb}}\, e\left(\frac{E_Y}{k_B T_{amb}} - \frac{E_Y}{k_B T}\right) \quad , \qquad \text{Eq. 9}$$

where Y is any parameter of the consumer-resource model (Eq. 4), T is the environmental temperature in Kelvin (K), T_{amb} is the ambient temperature, here set to 10°C (= 283.15 K), $Y_{T_{amb}}$ is the rate of the process at the ambient temperature, E_Y is the exponential rate of increase in process rate with increasing temperature (Fig. 1B, 1C; hereafter temperature sensitivity), and k_B is the Boltzmann constant (eV/K). The temperature sensitivity parameter used here, E_Y, is equivalent to the activation energy parameter from chemistry's Boltzmann-Arrhenius model, which has been applied to ecological rates within the Metabolic Theory of Ecology (Brown et al., 2004). While it is known that most individual- and population-level temperature responses are unimodal

(Amarasekare & Savage, 2012; Kingsolver, 2009; Michaletz & Garen, 2024) and that exponential models typically overpredict the temperature sensitivity of processes (Knies & Kingsolver, 2010; Michaletz & Garen, 2024; Pawar et al., 2016), many studies have focused on the rate of increase in the exponential portion of the temperature-response curve (Fig. 1B, 1C, grey shaded region) to model scaling effects of temperature (Bernhardt et al., 2018; Gibert et al., 2022; Gilbert et al., 2014). As such, we employed an exponential model to describe shifts in competition with warming when both species were in this exponentially increasing portion of their thermal niche, and where the effects of temperature were non-stressful. We obtained temperature dependence estimates for each parameter from posterior distributions (Fig. 2) generated from an empirical data synthesis for each parameter (see *Supplemental Methods – Data synthesis*).

Simulating effects of warming on competition

Model starting conditions

We answered our three questions by simulating competition across a 15-degree temperature gradient (10°C to 25°C) between consumer species pairs that co-occur or coexist under ambient temperature conditions (T_{amb} = 10°C). All simulations presented in the main text have the same starting conditions at T_{amb} , captured by the set of intercepts in the Arrhenius models ($Y_{T_{amb}}$; Eq. 9, Table S1) that comprise the temperature-dependent consumer-resource model (Eq. 4): at T_{amb}, species are predicted to coexist and consumer species pairs have even and reciprocal resource use preferences, so that each consumer specializes to the same degree on one of two

substitutable resources (given by c_{ik} and v_{ik} in Table S1). At T_{amb} the preferred resource of N_2 (here, r_a) had a faster growth rate than the preferred resource of N_1 (here, r_b; see Table S1). This set of starting conditions placed our species pairs on the boundary between coexistence and competitive exclusion of N_1 by N_2 (Fig. 3, 5). Other starting conditions for competing consumers that co-exist under ambient temperature conditions were explored in supplementary analyses (Table S1, Figs. S3, S4). Although 15°C of warming is unrealistic for changes in average temperatures from a climate change perspective, we used this large thermal gradient to demonstrate our results clearly. Applying a more realistic thermal gradient, from 10°C to 15°C generated qualitatively similar results, but with less contrast (Fig. S1).

Simulation: Questions 1 and 2

To examine the effects of each parameter's temperature sensitivity on niche and fitness differences (Question 1) and the effects of thermal asymmetries on competition (Question 2), we ran 500 warming simulations, where we varied one focal parameter at a time. For each simulation, we drew temperature sensitivity, E_Y, values for the focal parameter at random from its empirical posterior distribution, and we set all other parameters' temperature sensitivities equal to 0. After each draw of temperature sensitivities for a focal parameter was made, we simulated 15°C warming for that set of parameters and calculated niche and fitness differences every 0.1°C, according to Eqs. 7 and 8. For resource growth rate, r_k, resource carrying capacity, K_k, and consumer mortality rate, m_i, temperature sensitivities for each consumer or resource were drawn independently for each simulation. For consumption rate, c_{ik}, we drew temperature

sensitivities independently for each species' consumption rate on each resource (See Fig. S2 for other draw configurations). Finally, for resource conversion efficiency, v_{ik}, we assumed that the temperature sensitivity was the same among both consumers for a given resource (i.e. $E_{v_{1a}} = E_{v_{2a}}$), and drew only two temperature sensitivities, E_{v_a} and E_{v_b}, in each simulation.

To explore the effects of inter- and intra-process thermal asymmetries on competition (Question 2), we quantified the magnitude of the thermal asymmetries from the temperature sensitivities drawn for each simulation and examined the associated shift in ND–FD space. We quantified the magnitude of thermal asymmetry as the absolute difference between the values drawn for the focal parameter in each simulation (e.g. $|E_{r_a} - E_{r_b}|$). We then quantified the shift in ND–FD space as the Euclidean distance between the model's starting position and the position after 15°C simulated warming.

Simulation: Question 3

To identify general effects of warming on competition (Question 3), we allowed all model parameters to vary with temperature simultaneously and simulated warming over a 15°C thermal gradient. For each simulation (N = 500), we drew temperature sensitivity values, E_Y, for all parameters from their respective distributions. At each 0.1°C step, we calculated niche and fitness differences. We quantified the effect of warming on competition based on the distance between the species' starting niche and fitness difference values (at T_{amb}, 10°C) and their median niche and fitness difference values at the final temperature (25 °C).

Data and code for analyses will be made publicly available at the time of publication. In the interim, please reach out to the corresponding author for access.

Results

Empirically-derived temperature sensitivity of parameters

We synthesized consumer-resource parameters' temperature sensitivity estimates from 58 studies, representing 79 ectothermic consumer and resource species. Our dataset of temperature sensitivity estimates for consumption rate, conversion efficiency, and mortality contained data from heterotrophic organisms only, while data for resource carrying capacity and growth rate came from both heterotrophs and autotrophs.

We found considerable variation within and across parameter temperature sensitivity estimates, E_Y (Fig. 2), suggesting both inter-process and intra-process thermal asymmetries were present in our synthesized dataset. Posterior distributions and 95% credible intervals for the temperature sensitivities of resource growth rate, r_k, consumption rate, c_{ik} , and consumer mortality rate, m_i, were positive, indicating that these rates increase with increasing temperature. Posterior means and 95% credible intervals were: E_{r_k}= 0.79 eV (0.62, 0.96 eV; 30 observations); $E_{c_{ik}}$= 0.56 eV (0.50, 0.63 eV; 105 observations); E_{m_i}= 0.49 eV (0.35, 0.62 eV; 8 observations; Fig. 2A, 2B, 2E). Overlapping 95% credible intervals across these three parameters suggests no inter-process thermal asymmetry among them (Fig. 2F). Contrastingly, resource carrying capacity, K_k, had a negative temperature sensitivity, E_{K_k}= -0.65 eV (-0.98, -0.33 eV; 8

observations; Fig. 2C), indicating that carrying capacities decrease with warming. This negative temperature sensitivity was statistically distinct from that of consumption rate, resource growth rate, and mortality rate (Fig. 2F). Finally, the posterior distribution for the temperature sensitivity of conversion efficiency had a 95% credible interval that spanned both negative and positive values and was centered near 0: $E_{v_{ik}}$= 0.0036 eV (-0.41,0.42 eV; 5 observations; Fig. 2D). We did not find an inter-process thermal asymmetry between resource carrying capacity and conversion efficiency, but we did find thermal asymmetries between conversion efficiency and consumption rate and resource growth rate (Fig. 2F).

Question 1: How do temperature sensitive processes underlying competition affect niche and fitness differences?

For competing consumer species able to co-exist under ambient temperature conditions, warming the system caused every process except mortality to have large effects on niche and/or fitness differences (Fig. 3). Effects of warming on resource consumption rate, c_{ik}, drove variation in both niche and fitness differences (Fig. 3A), whereas effects of warming on resource growth rate, r_k, primarily drove variation in fitness differences (Fig. 3B). We found that temperature sensitivity in these two processes have the largest potential to affect competitive outcomes in our model, because their temperature sensitivity can move the species pair along a trajectory that is far from parallel (and in some cases close to perpendicular) to the coexistence boundary as the system warms. In contrast, effects of warming on resource carrying capacity, K_k, and conversion efficiency, v_{ik}, drove variation parallel to the coexistence

boundary (Fig. 3C, 3D, S3, S4). In our focal analysis, where species pairs underwent warming from a starting position on the coexistence boundary, temperature-dependent carrying capacity and conversion efficiency drove the species towards increased functional similarity (i.e. toward the neutral point).

In supplemental analysis of co-existing species pairs with different resource preferences at ambient temperature, and therefore different starting points in ND—FD space (Table S1), effects of temperature-sensitivity in resource consumption rate, c_{ik}, resource growth rate, r_k, and mortality, m_i, were similar, while effects of temperature-sensitivity in resource carrying capacity, K_k, and resource conversion efficiency, v_{ik}, differed (Fig. S3, S4). Specifically, temperature-sensitive resource carrying capacity and conversion efficiency had qualitatively different effects on niche and fitness differences when consumers' resource preferences were sufficiently different at the ambient temperature. That is, when thermal conditions amplified the competitive dominance of one consumer species over the other (e.g. when N_1 had a stronger preference for its preferred resource than N_2, and conversion efficiency of that preferred resource increased with warming), that warming trajectory of conversion efficiency pointed away from neutrality rather than toward neutrality (i.e. increasing niche differences among species; Fig. S3, S4).

Across all analyses, altering the temperature-sensitivity of consumer mortality rate only affected fitness differences (Song et al., 2019), but competitive dynamics were highly

insensitive to variation in the temperature sensitivity of mortality, as indicated by the absence of visible shifts in Fig. 3E (See also Fig. 4E).

Question 2: How do thermal asymmetries contribute to shifts in competition with warming?

We found that when competing species had the same temperature sensitivity value for a given process, there was no effect on competition (Fig. S5), because shifts in ND—FD space depend on relative changes between species. That is, without intra-process thermal asymmetries, the inter-process thermal asymmetries we identified in the data synthesis did not affect competitive dynamics. However, when species differed in their temperature sensitivities for a given process, competitive dynamics shifted with warming. Within each parameter, larger differences in temperature sensitivities between competing species or between their resources (intra-process thermal asymmetries) were associated with larger shifts in competition, i.e. larger Euclidean distances between the species' "start" point at the ambient temperature and the "end" point after 15°C warming (Fig. 4, S6). For consumer mortality rate, m_i, changes in position with warming were too small relative to that of other parameters to be visible in our analysis (Fig. 4E). Thermal asymmetries across species within resource growth rates, r_k, and conversion efficiencies, v_{ik}, were responsible for the largest changes in position with warming (Fig. 4).

For each parameter except consumption rate, warming created two distinct trajectories that moved in opposite directions away from the ambient temperature point (Fig. 4B-E).

Which trajectory a species pair moved along depended on the relative value of the two focal temperature sensitivities, or the directionality of the intra-process thermal asymmetry (Fig. 4B-E). For resource growth rate and consumer mortality rate, these trajectories moved monotonically toward the region of the state space where a consumer's preferred resource was more abundant with warming, or where mortality was minimized for a species, though this latter effect was too small to observe for most species. For example, if the temperature sensitivity for growth rate is higher for resource *a* than for resource *b*, then, when the system is warmed, the coexistence trajectory moves monotonically toward the region of competitive dominance for the species that preferentially consumes resource *a*, here N_2 (e.g. Fig. 3B, 4B). Interestingly, the two trajectories for carrying capacity and conversion efficiency comprise one monotonic trajectory and one non-monotonic trajectory, both of which point ultimately toward neutrality (Fig. 3C, 3D, 4C, 4D, S3). However, when there are large differences in ambient-temperature resource preferences between species, this pattern disappears, and two distinct trajectories leading in opposite directions away from the start point are recovered (Table S1, Fig. S4).

Question 3: How does warming affect competition, via effects on niche and fitness differences?

For consumer species existing at the boundary of coexistence and competitive exclusion, temperature sensitivity of all processes underlying competition generally drove decreases in both niche and fitness differences with warming (Fig. 5A, yellow dot to magenta dot). Effects of warming on competition were skewed, and very large effects

were rare (Fig. 5B). The median decreases in niche and fitness differences were roughly similar in magnitude (Fig. 5C, 5D), leading to a general tendency of competitive dynamics shifting toward neutrality with warming (Fig. 5A). While some competitive dynamics became less neutral, i.e. increased in niche and fitness differences, under 15°C warming, analysis simulating extreme warming of 50°C reveals that many of the trajectories that initially moved away from neutrality bent back toward neutrality with sufficient warming (Fig. S7). When species had similar resource preferences but different starting positions (Figure S3) or had very different resource preferences (Figure S4), we observed the same trend toward neutrality with warming, despite some variation in how warming effects on specific processes (e.g. resource carrying capacity and conversion efficiency; Figs S3C, S3D S4C, S4D).

Discussion

In this study, we drew from two prominent theories in ecology to address a central question in global change biology: how does warming affect competition for shared resources? Using empirically-derived temperature effects on competitive processes, we found three general patterns in how simulated competition responded to warming. First, warming tended to reduce both fitness differences and niche differences, which resulted in a general trend of warming causing species pairs to move toward neutrality. Next, we found that warming-induced increases in mortality had surprisingly little effect on these shifts in competition with warming. Finally, we found that species pairs that underwent the largest shifts in competitive dynamics with warming had highly asymmetric temperature sensitivities in the mechanistic processes underlying competition. Together, these findings suggest that understanding how communities will change with warming requires an understanding of how both population fitness and resource use change with temperature, and how variable these traits are within a community.

While much of the work seeking to understand biodiversity effects of climate change has focused on temperature-induced changes in fitness differences (e.g. growth rates; Ehrlén & Morris, 2015; Kordas et al., 2011; Merow et al., 2014), here we show that understanding the effects of warming on competition requires an equal consideration of niche differences. As expected, resource growth rate had a large effect on competition in our analysis. This effect was near orthogonal to the coexistence boundary, occurring primarily via shifts in fitness differences and allowing resource growth rate to affect

competitive hierarchies (by moving species from one region of ND—FD space to another) under warming. However, in natural systems warming is unlikely to affect resource growth rate in isolation, and when warming was allowed to affect the full suite of competitive mechanisms, species pairs generally experienced a decrease in niche differences with warming (Fig. 5). These shifts were driven primarily by the effects of warming on consumption rate, resource carrying capacity, and consumer conversion efficiency – all of which determine patterns of relative resource use among species. Of these processes, warming effects on consumption rates also had the capacity to alter competitive hierarchies. Together, these results add to a limited body of literature that suggests that temperature effects on niche differences play a key role in how warming affects communities (Adler et al., 2012).

Changes to mortality rates have been another focal point of climate modelling and thermal physiology (Deutsch et al., 2008; Sunday et al., 2014), and have been shown to have effects on competition and, specifically, on fitness differences (Song et al., 2019). In our analysis, despite exponentially increasing consumer mortality rates across the thermal gradient (Amarasekare & Savage, 2012), effects of warming on mortality rate had almost no effect on competition. This effect is due to the independence of consumer mortality rate from density-dependent processes and interspecific competition in consumer-resource models (Eq. 4; Song et al., 2019). This suggests that, when all consumer-resource processes increase exponentially with warming, quantifying thermal responses of mortality may be less important than previously thought. However, mortality may play a more important role in competitive responses to warming when

environmental temperatures cause one or many of these processes to pass their thermal optimum and decline with warming.

Within Modern Coexistence Theory, competition is considered neutral when there is an absence of both niche differences and fitness differences; biologically this means that the two species are functionally equivalent (Adler et al., 2007). In our analysis, warming had a general tendency to shift competing species towards neutrality. This finding is consistent with Grainger et al. (2019), who also observed a shift toward neutrality with changing environmental conditions, in their case more benign environments. The often-non-monotonic shift toward neutrality that we observed is consistent with prior observations that non-independence between niche and fitness differences leads to complex movements of species pairs in ND—FD space (Song et al., 2019). However, the tendency for warming to shift species pairs towards neutrality was reduced when warming benefitted the preferred resource of a species with a much stronger resource preference than its competitor (Table S1, Fig. S4). This finding is consistent with other studies that have identified the magnitude of difference in functional traits as a key determinant of competitive outcomes (Alexander et al., 2015; Song et al., 2019).

Under changing thermal regimes, which types of species pairs are likely to experience large competitive shifts is an open question. While most species experienced relatively small shifts in competitive dynamics with warming, species pairs that experienced large shifts had large intra-process thermal asymmetries (Fig. 4). Within the Metabolic Theory of Ecology, multi-scale effects of thermal asymmetries have primarily been studied

across processes (i.e. inter-process thermal asymmetries; Dell et al., 2014; Gibert et al., 2022; Gilbert et al., 2014), with minimal focus on interspecific (intra-process) variability. Here, inter-process thermal asymmetries required accompanying intra-process thermal asymmetries to have any effect on competition. For example, a higher temperature sensitivity of resource growth rate then conversion efficiency cannot, on its own, cause a shift in competition between species (Fig. S5): there must also be interspecific variation in the temperature sensitivities of the growth rates or conversion efficiencies of the different resources to affect competition. This is consistent with the general predictions of Modern Coexistence Theory (Chesson, 2000), which model competition based on relative differences in species traits, here temperature sensitivities. This result further suggests that consumer species (or their resources) that have the most divergent thermal traits will undergo the largest shifts in competition with warming (Fig. 4, Fig. S6). This is the first example, to our knowledge, of a general prediction for how warming affects communities developed from the metabolic scaling of interspecific (intra-process) variation in thermal traits.

Conclusions

Identifying general effects of warming on communities has been a major challenge in ecology. The Metabolic Theory of Ecology, with its focus on the temperature sensitivity of metabolic processes across biological scales, and Modern Coexistence Theory, through its conceptual framework for species competition, have both advanced our understanding of ecosystem responses to environmental change. However, differences in the domains of these two fields, one of which focuses on interspecific differences and

the other which focuses on macroecological differences in key metabolic processes as drivers of change, have prevented their integration to date. Here we integrated concepts from both fields and combined this with empirical thermal trait data to develop new, general theory for how competition changes with warming and advance a more coherent understanding of global change. The next step will be to test these predictions empirically in natural systems. Doing so will facilitate better linkages between general patterns in biological responses to warming and context-specific stewardship strategies under rapid environmental change.

Acknowledgements

JB was supported by a Natural Science and Engineering Research Council of Canada Discovery Grant and KD was supported by a Centre for Ecosystem Management Postdoctoral Fellowship. We thank Megan Szojka for helpful feedback on the manuscript.

References

Adler, P. B., Dalgleish, H. J., & Ellner, S. P. (2012). Forecasting plant community impacts of climate variability and change: When do competitive interactions matter? *Journal of Ecology*, *100*(2), 478–487. https://doi.org/10.1111/j.1365-2745.2011.01930.x

Adler, P. B., HilleRisLambers, J., & Levine, J. M. (2007). A niche for neutrality. *Ecology Letters*, *10*(2), 95–104. https://doi.org/10.1111/j.1461-0248.2006.00996.x

Alexander, J. M., Diez, J. M., & Levine, J. M. (2015). Novel competitors shape species' responses to climate change. *Nature*, *525*(7570), 515–518. https://doi.org/10.1038/nature14952

Amarasekare, P., & Savage, V. (2012). A Framework for Elucidating the Temperature Dependence of Fitness. *The American Naturalist*, *179*(2), 178–191. https://doi.org/10.1086/663677

Bernhardt, J. R., Sunday, J. M., & O'Connor, M. I. (2018). Metabolic theory and the temperature size rule explain the temperature dependence of population carrying capacity. *American Naturalist*, *In press*(6). https://doi.org/10.1086/700114

Bestion, E., García-Carreras, B., Schaum, C.-E., Pawar, S., & Yvon-Durocher, G. (2018). Metabolic traits predict the effects of warming on phytoplankton competition. *Ecology Letters*, *21*(5), 655–664. https://doi.org/10.1111/ele.12932

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a Metabolic Theory of Ecology. *Ecology*, *85*(7), 1771–1789.

Chesson, P. (1990). MacArthur's consumer-resource model. *Theoretical Population Biology*, *37*(1), 26–38. https://doi.org/10.1016/0040-5809(90)90025-Q

Chesson, P. (2000). General Theory of Competitive Coexistence in Spatially-Varying Environments. *Theoretical Population Biology*, *58*(3), 211–237. https://doi.org/10.1006/tpbi.2000.1486

Chesson, P. (2011). Ecological niches and diversity maintenance. *Research in Biodiversity: Models and Applications. InTech, Rijeka, Croatia*, 43–60.

Chesson, P., & Kuang, J. J. (2008). The interaction between predation and competition. *Nature*, *456*(7219), 235–238. https://doi.org/10.1038/nature07248

Dell, A. I., Pawar, S., & Savage, V. M. (2011). Systematic variation in the temperature dependence of physiological and ecological traits. *Proceedings of the National Academy of Sciences*, *108*(26), 10591–10596. https://doi.org/10.1073/pnas.1015178108

Dell, A. I., Pawar, S., & Savage, V. M. (2014). Temperature dependence of trophic interactions are driven by asymmetry of species responses and foraging strategy. *Journal of Animal Ecology*, *83*(1), 70–84. https://doi.org/10.1111/1365-2656.12081

Deutsch, C. A., Tewksbury, J. J., Huey, R. B., Sheldon, K. S., Ghalambor, C. K., Haak, D. C., & Martin, P. R. (2008). Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences*, *105*(18), 6668–6672. https://doi.org/10.1073/pnas.0709472105

Ehrlén, J., & Morris, W. F. (2015). Predicting changes in the distribution and abundance of species under environmental change. *Ecology Letters*, *18*(3), 303–314. https://doi.org/10.1111/ele.12410

Enquist, B. J., Economo, E. P., Huxman, T. E., Allen, A. P., Ignace, D. D., & Gillooly, J. F. (2003). Scaling Metabolism from organisims to ecosystems. *Nature*, *423*, 639–642.

Germain, R. M., Mayfield, M. M., & Gilbert, B. (2018). The ‘filtering’ metaphor revisited: Competition and environment jointly structure invasibility and coexistence. *Biology Letters*, *14*(8), 20180460. https://doi.org/10.1098/rsbl.2018.0460

Gibert, J. P., Grady, J. M., & Dell, A. I. (2022). Food web consequences of thermal asymmetries. *Functional Ecology*, *36*(8), 1887–1899. https://doi.org/10.1111/1365-2435.14091

Gilbert, B., Tunney, T. D., McCann, K. S., DeLong, J. P., Vasseur, D. A., Savage, V., Shurin, J. B., Dell, A. I., Barton, B. T., Harley, C. D. G., Kharouba, H. M., Kratina, P., Blanchard, J. L., Clements, C., Winder, M., Greig, H. S., & O'Connor, M. I. (2014). A bioenergetic framework for the temperature dependence of trophic interactions. *Ecology Letters*, *17*(8), 902–914. https://doi.org/10.1111/ele.12307

Godoy, O. (2019). Coexistence theory as a tool to understand biological invasions in species interaction networks: Implications for the study of novel ecosystems. *Functional Ecology*, *33*(7), 1190–1201. https://doi.org/10.1111/1365-2435.13343

Godoy, O., & Levine, J. M. (2014). Phenology effects on invasion success: Insights from coupling field experiments to coexistence theory. *Ecology*, *95*(3), 726–736. https://doi.org/10.1890/13-1157.1

Godwin, C. M., Chang, F.-H., & Cardinale, B. J. (2020). An empiricist's guide to modern coexistence theory for competitive communities. *Oikos*, *129*(8), 1109–1127. https://doi.org/10.1111/oik.06957

Grainger, T. N., Levine, J. M., & Gilbert, B. (2019). The Invasion Criterion: A Common Currency for Ecological Research. *Trends in Ecology and Evolution*, *34*(10), 925–935. https://doi.org/10.1016/j.tree.2019.05.007

Kingsolver, J. G. (2009). The Well-Temperatured Biologist: (American Society of Naturalists Presidential Address). *The American Naturalist*, *174*(6), 755–768. https://doi.org/10.1086/648310

Knies, J. L., & Kingsolver, J. G. (2010). Erroneous Arrhenius: Modified Arrhenius Model Best Explains the Temperature Dependence of Ectotherm Fitness. *The American Naturalist*, *176*(2), 227–233. https://doi.org/10.1086/653662

Kordas, R. L., Harley, C. D. G. G., & O'Connor, M. I. (2011). Community ecology in a warming world: The influence of temperature on interspecific interactions in marine systems. *Journal of Experimental Marine Biology and Ecology*, *400*(1–2), 218–226. https://doi.org/10.1016/j.jembe.2011.02.029

Letten, A. D., Ke, P. J., & Fukami, T. (2017). Linking modern coexistence theory and contemporary niche theory. *Ecological Monographs*, *87*(2), 161–177. https://doi.org/10.1002/ecm.1242

Lewington-Pearce, L., Narwani, A., Thomas, M. K., Kremer, C. T., Vogler, H., & Kratina, P. (2019). Temperature-dependence of minimum resource requirements alters competitive hierarchies in phytoplankton. *Oikos*, 1194–1205. https://doi.org/10.1111/oik.06060

Lopez-Urrutia, A., San Martin, E., Harris, R. P., & Irigoien, X. (2006). Scaling the metabolic balance of the oceans. *Proceedings of the National Academy of Sciences*, *103*(23), 8739–8744. https://doi.org/10.1073/pnas.0601137103

MacArthur, R. (1970). Species packing and competitive equilibrium for many species. *Theoretical Population Biology*, *1*(1), 1–11. https://doi.org/10.1016/0040-5809(70)90039-0

Merow, C., Latimer, A. M., Wilson, A. M., McMahon, S. M., Rebelo, A. G., & Silander Jr, J. A. (2014). On using integral projection models to generate demographically

driven predictions of species' distributions: Development and validation using sparse data. *Ecography*, *37*(12), 1167–1183. https://doi.org/10.1111/ecog.00839

Michaletz, S. T., & Garen, J. C. (2024). Hotter is not (always) better: Embracing unimodal scaling of biological rates with temperature. *Ecology Letters*, *27*(2), e14381. https://doi.org/10.1111/ele.14381

O'Connor, M. I. (2009). Warming Strengthens an Herbivore: Plant Interaction. *Ecology*, *90*(2), 388–398. https://doi.org/10.1890/08-0034.1

O'Connor, M. I., Gilbert, B., & Brown, C. (2011). Theoretical Predictions for How Temperature Affects the Dynamics of Interacting Herbivores and Plants. *The American Naturalist*, *178*(5), 626–638. https://doi.org/10.1086/662171

Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, *421*(6918), Article 6918. https://doi.org/10.1038/nature01286

Pawar, S., Dell, A. I., Savage, V. M., & Knies, J. L. (2016). Real versus Artificial Variation in the Thermal Sensitivity of Biological Traits. *The American Naturalist*, *187*(2), E41–E52. https://doi.org/10.1086/684590

Pérez-Ramos, I. M., Matías, L., Gómez-Aparicio, L., & Godoy, Ó. (2019). Functional traits and phenotypic plasticity modulate species coexistence across contrasting climatic conditions. *Nature Communications*, *10*(1), 2555. https://doi.org/10.1038/s41467-019-10453-0

Peters, R. L., & Lovejoy, T. E. (1992). *Global warming and biological diversity*. Yale University Press.

Rall, B. C., Vucic-Pestic, O., Ehnes, R. B., Emmerson, M., & Brose, U. (2010). Temperature, predator-prey interaction strength and population stability: TEMPERATURE AND INTERACTION STRENGTH. *Global Change Biology*, *16*(8), 2145–2157. https://doi.org/10.1111/j.1365-2486.2009.02124.x

Román-Palacios, C., & Wiens, J. J. (2020). Recent responses to climate change reveal the drivers of species extinction and survival. *Proceedings of the National Academy of Sciences of the United States of America*, *117*(8), 4211–4217. https://doi.org/10.1073/pnas.1913007117

Saavedra, S., Arroyo, J. I., Marquet, P. A., & Kempes, C. P. (2023). *Linking metabolic scaling and coexistence theories* [Preprint]. Ecology. https://doi.org/10.1101/2023.02.28.530509

Savage, V. M., Gillooly, J. F., Brown, J. H., West, G. B., & Charnov, E. L. (2004). *Effects of body size and temperature on population growth*. 429–441.

Sentis, A., Morisson, J., & Boukal, D. S. (2015). Thermal acclimation modulates the impacts of temperature and enrichment on trophic interaction strengths and population dynamics. *Global Change Biology*, *21*(9), 3290–3298. https://doi.org/10.1111/gcb.12931

Song, C., Barabás, G., & Saavedra, S. (2019). On the Consequences of the Interdependence of Stabilizing and Equalizing Mechanisms. *The American Naturalist*, *194*(5), 627–639. https://doi.org/10.1086/705347

Sunday, J. M., Bates, A. E., Kearney, M. R., Colwell, R. K., Dulvy, N. K., Longino, J. T., & Huey, R. B. (2014). Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *Proceedings of the*

National Academy of Sciences, *111*(15), 5610–5615. https://doi.org/10.1073/pnas.1316145111

Terry, J. C. D. (2025). An Experimental Validation Test of Ecological Coexistence Theory to Forecast Extinction Under Rising Temperatures. *Ecology Letters*, *28*(1), e70047. https://doi.org/10.1111/ele.70047

Tilman, D. (1994). Competition and Biodiversity in Spatially Structured Habitats. *Ecology*, *75*(1), 2–16. https://doi.org/10.2307/1939377

Usinowicz, J., & Levine, J. M. (2018). Species persistence under climate change: A geographical scale coexistence problem. *Ecology Letters*, *21*(11), 1589–1603. https://doi.org/10.1111/ele.13108

Vasseur, D. A., & McCann, K. S. (2005). A Mechanistic Approach for Modeling Temperature-Dependent Consumer-Resource Dynamics. *The American Naturalist*, *166*(2), 184–198. https://doi.org/10.1086/431285

Welter, J. R., Benstead, J. P., Cross, W. F., Hood, J. M., Huryn, A. D., Johnson, P. W., & Williamson, T. J. (2015). Does N2 fixation amplify the temperature dependence of ecosystem metabolism? *Ecology*, *92*(11), 603–610.

Yodzis, P., & Innes, S. (1992). Body Size and Consumer-Resource Dynamics. *The American Naturalist*, *139*(6), 1151–1175.

Figures

Figure 1

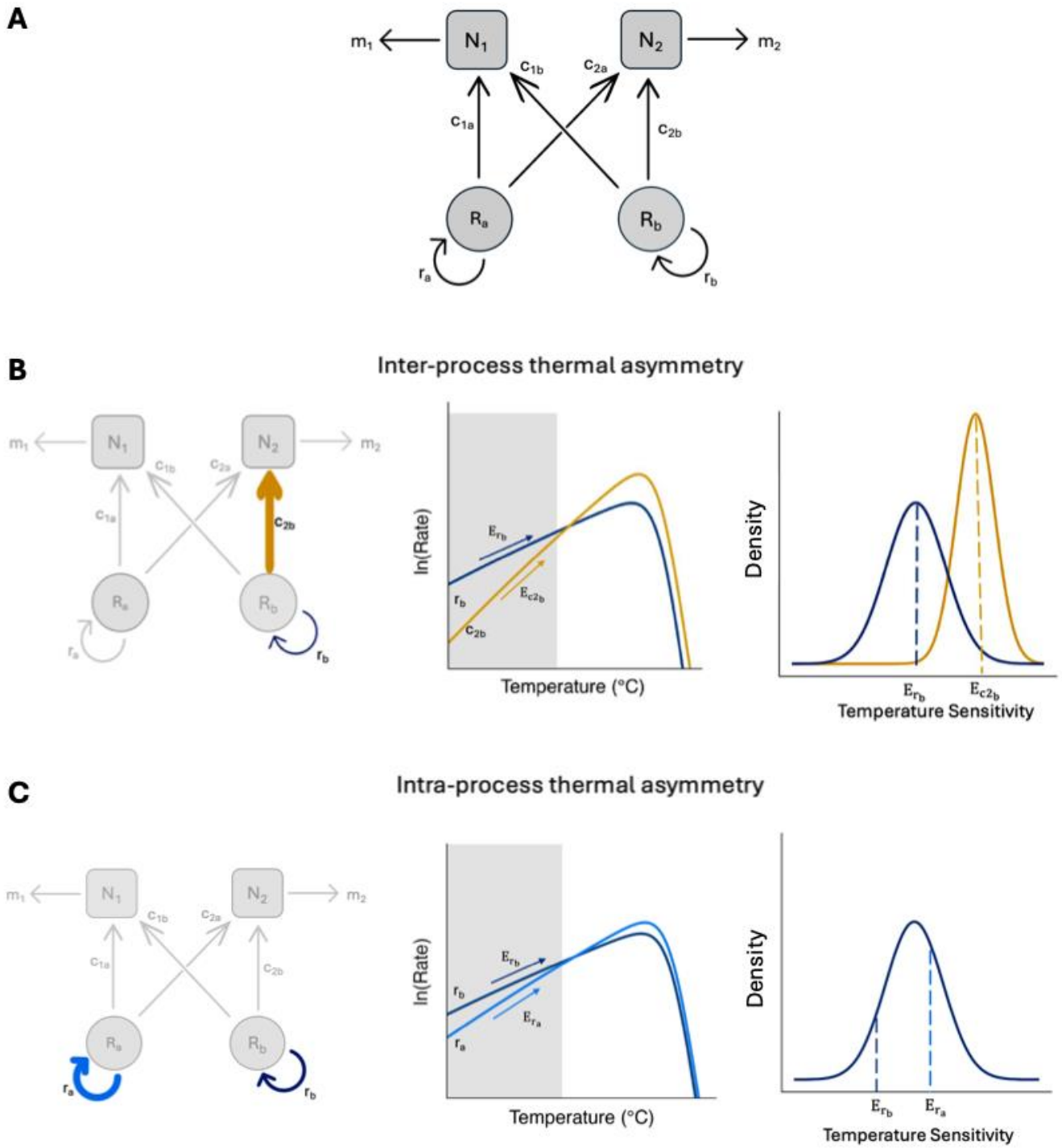

Figure 2

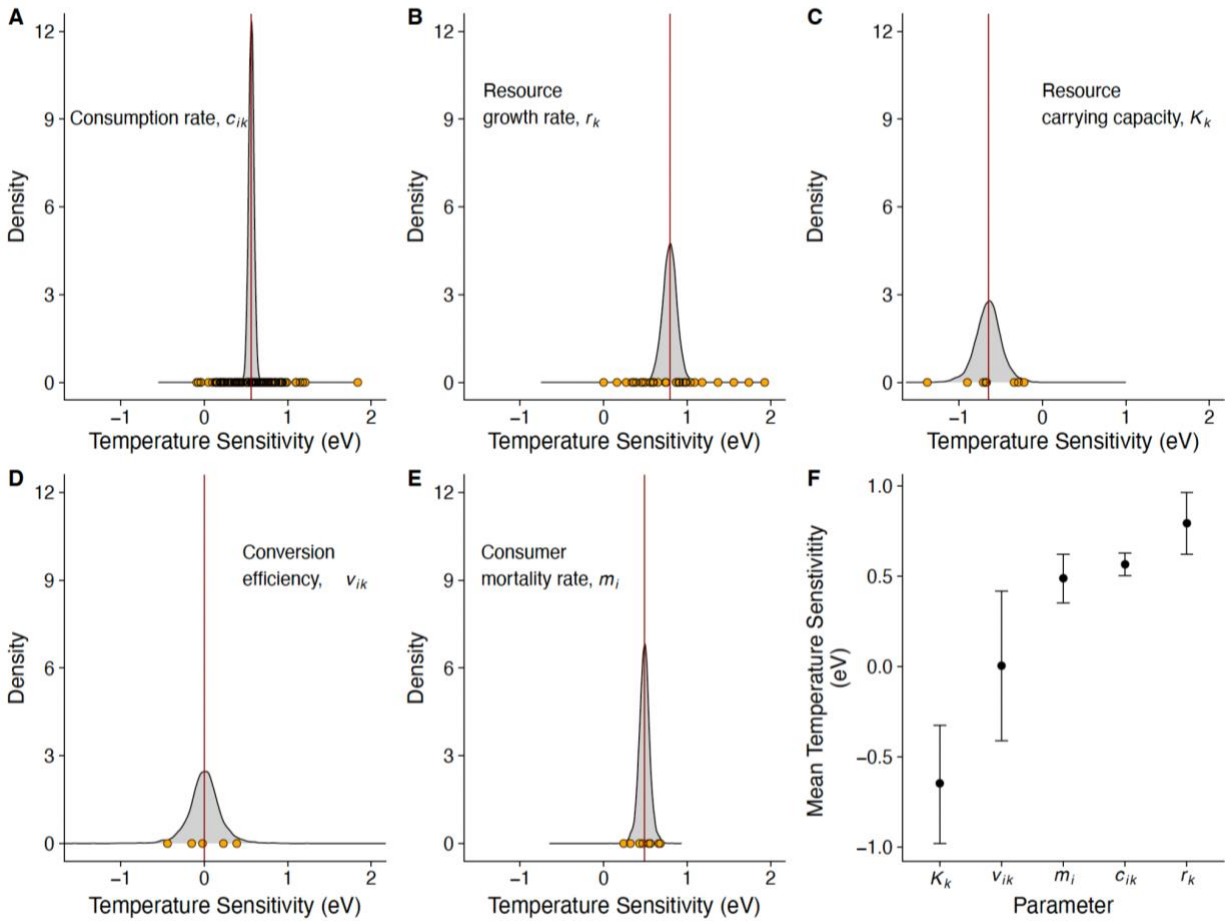
A
Consumption rate, c_{ik}
B
Resource growth rate, r_k
C
Resource carrying capacity, K_k
D
Conversion efficiency, v_{ik}
E
Consumer mortality rate, m_i
F
Density
Temperature Sensitivity (eV)
Mean Temperature Senstivitity (eV)
Parameter
K_k
v_{ik}
m_i
c_{ik}
r_k

Figure 3

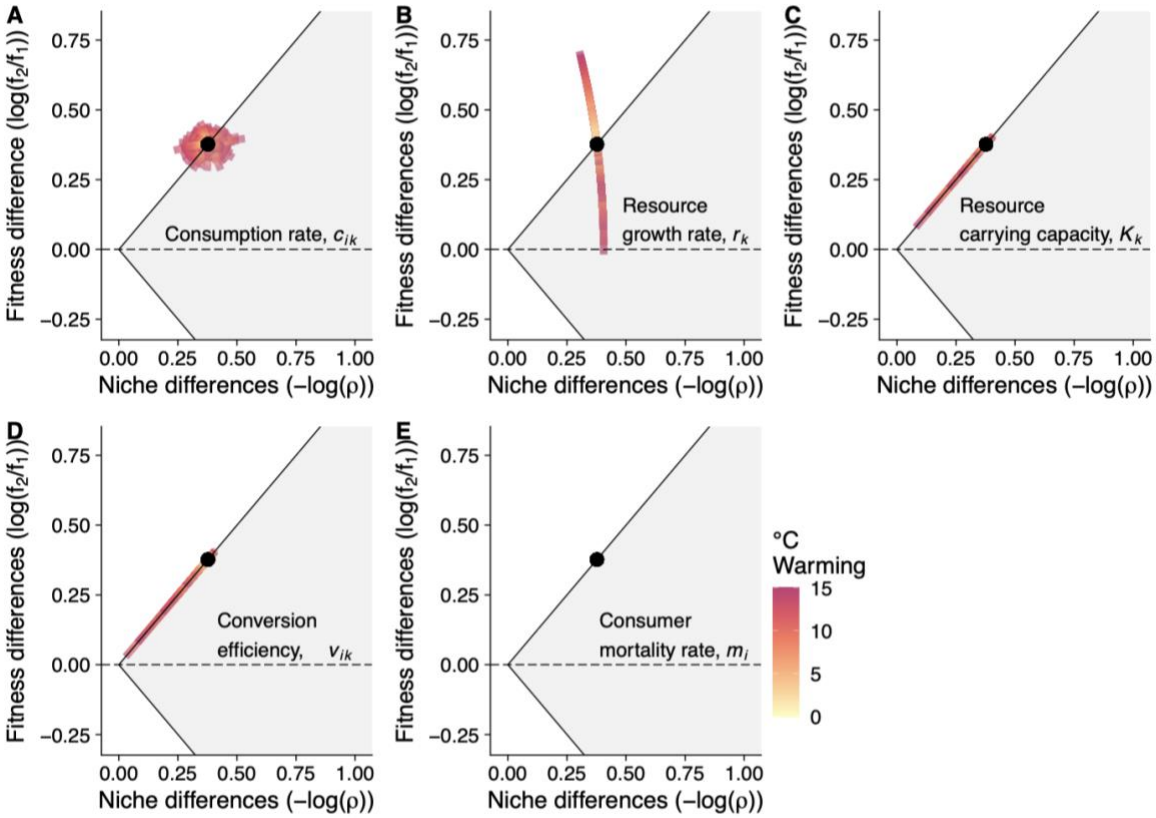
A
B
C
D
E
Fitness difference (log(f2/f1))
Fitness differences (log(f2/f1))
Niche differences (−log(ρ))
0.75
0.50
0.25
0.00
−0.25
0.00 0.25 0.50 0.75 1.00
Consumption rate, cik
Resource growth rate, rk
Resource carrying capacity, Kk
Conversion efficiency, vik
Consumer mortality rate, mi
°C Warming
15
10
5
0

Figure 4

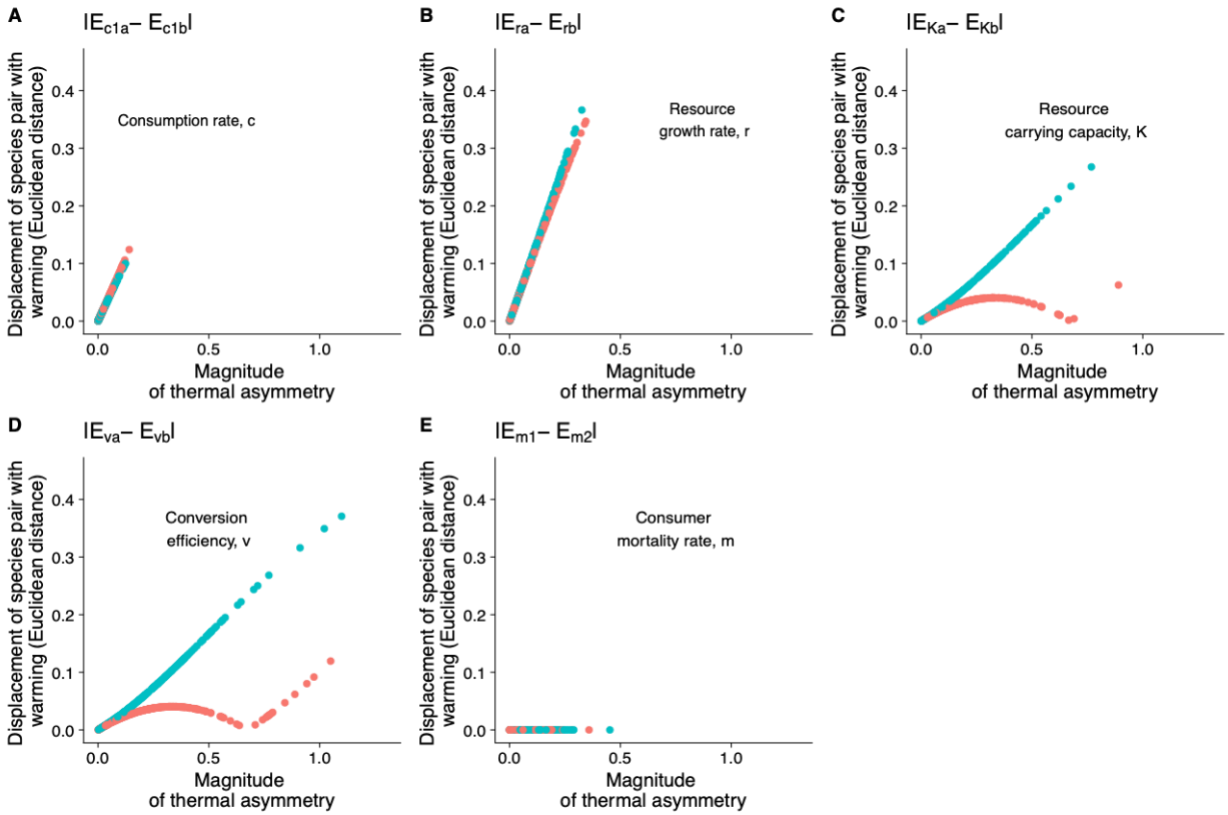
A
|Ec1a– Ec1b|
Consumption rate, c
B
|Era– Erb|
Resource growth rate, r
C
|EKa– EKb|
Resource carrying capacity, K
D
|Eva– Evb|
Conversion efficiency, v
E
|Em1– Em2|
Consumer mortality rate, m
Displacement of species pair with warming (Euclidean distance)
Magnitude of thermal asymmetry
0.0
0.1
0.2
0.3
0.4
0.5
1.0

Figure 5

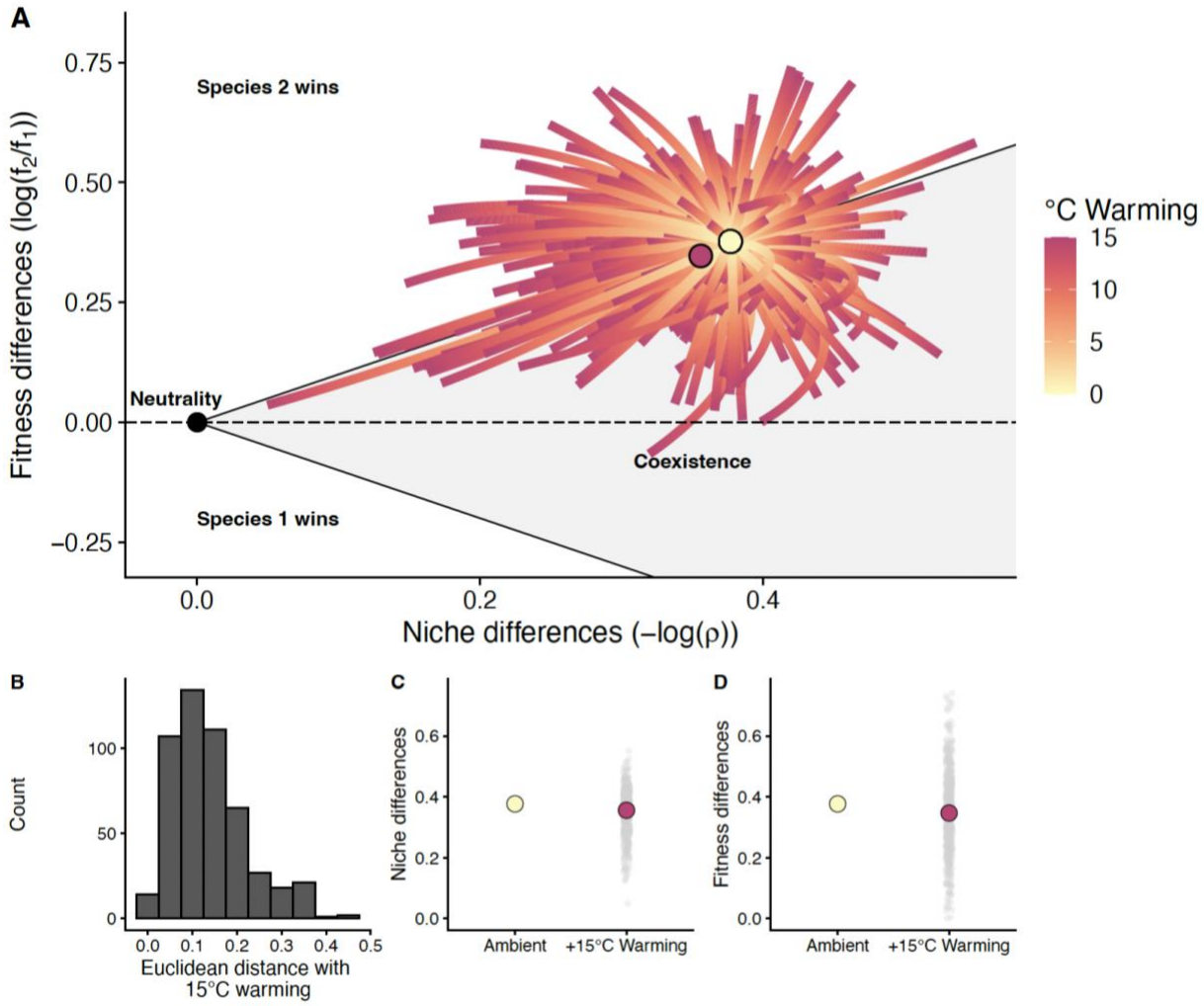
A
Species 2 wins
Neutrality
Coexistence
Species 1 wins
Fitness differences (log(f2/f1))
Niche differences (−log(ρ))
°C Warming
15
10
5
0
B
Count
Euclidean distance with 15°C warming
C
Niche differences
Ambient
+15°C Warming
D
Fitness differences
Ambient
+15°C Warming

Figure Captions

Figure 1. Schematic of a consumer-resource model with temperature dependent processes, yielding inter- and intra-process thermal asymmetries. In panel A, two unique consumers are shown as boxes (N_1 and N_2) and two substitutable resources as circles (R_a and R_b). Arrows show directional energy flow processes and are labeled with the model parameters they represent: m_i is the mortality of consumer i, c_{ik} is consumption rate of resource k by consumer i, and r_k is the intrinsic growth rate of resource k. Parameters K_k, resource carrying capacity, and v_{ik}, conversion efficiency, are not shown, but mediate the abundance of available resource, R_k, and the transfer of energy from R_k to N_i, respectively. Panels B and C show how temperature sensitivity, E, or the increase in the rate of a process with temperature below the thermal inflection point (central panels, grey zone), is incorporated into the model via biological rates of the consumer and resource, and how this can generate two types of thermal asymmetries depending on where in the consumer-resource system a difference in temperature sensitivity occurs (left panels). The thickness of the arrows in the left panels corresponds to the temperature sensitivity depicted in the central panels. The right panels in B and C relate a single observation of temperature sensitivity (dashed line) for a parameter to the broader empirical distribution of temperature sensitivities for that parameter constructed from our data synthesis. In an inter-process thermal asymmetry (Panel B), the two temperature sensitivities come from independent distributions of temperature sensitivity in each parameter, whereas in an intra-process

thermal asymmetry (Panel C), the two temperature sensitivities come from the same distribution of temperature sensitivity.

Figure 2. Posterior distributions for temperature sensitivity of consumer-resource model parameters. Panels A-E show published empirical observations for each parameter in the consumer resource model (Eq. 4) in orange circles and posterior distributions informed by these observations in grey density plots. Red lines indicate the mean of the posterior distribution. Panel F shows the means and 95% credible intervals (CIs) for each parameter.

Figure 3. Effects of temperature sensitivity in each model parameter on competition with warming. In each panel, temperature sensitivities of the focal parameter are drawn randomly from the parameter's empirical distribution (Fig. 2) and then the system is warmed 15°C, while temperature sensitivities for all other parameters are held at 0. This is repeated 500 times and each simulated warming path is plotted. All simulations begin at the same ambient temperature, 10°C (black point). For all parameters except for consumption rate (i.e. panels B-E), the number of temperature sensitivities drawn for each simulation is two -- one for each consumer or resource species (Fig. 1A). This results in perfectly overlain trajectories for each simulation: note different lengths of the temperature gradient path, which ends with a dark red color. For consumption rate, in panel A, there are four temperature sensitivities drawn for each simulation, corresponding to one temperature sensitivity per resource, for each species (Fig. 1A). As a result, warming trajectories do not fall perfectly on top of one another.

The shaded region in the plots shows where species can coexist, i.e., where $ND > |FD|$, and the unshaded regions show where one species competitively excludes the other, i.e., $ND < |FD|$.

Figure 4. Shifts in competition with warming are related to intra-process thermal asymmetries. Thermal asymmetries are given as the absolute value of the difference between two draws of temperature sensitivities (one for each consumer or resource species) in each simulation and displacement is given as the Euclidean distance between a species pair's starting position and its position after 15°C warming. For each panel, only the focal temperature sensitivity parameter was allowed to vary; all other temperature sensitivity parameters were fixed at 0. Data points correspond to the difference in temperature sensitivities drawn for each of 500 simulations, and the color of the points indicates the direction of the thermal asymmetry, i.e. which E_Y value is larger. For consumption rate (panel A), we vary only two of the four possible temperature sensitivities, here species N_1's consumption rate of each resource, to display the effect of this thermal asymmetry most clearly.

Figure 5. Effects of warming on competition. All parameters are drawn from their distributions and then warmed 15°C, and this simulation is repeated 500 times. A) Simulation path for each draw of parameter values from the ambient temperature, 10°C (yellow dot), to 25°C (15°C warming). The median position along both axes after 15°C warming is plotted as a magenta dot. B) Distribution of Euclidean distances between the position at the ambient temperature and after 15°C warming across 500 simulations. C)

Shifts in niche differences with warming. The median niche difference values (magenta dot) and the niche difference values for each simulation (grey dots) after 15°C warming are shown compared to the value at the ambient temperature (yellow dot). D) Shifts in fitness differences with warming, displayed as in panel C.