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# Considering the effects of temperature × nutrient interactions on the thermal response curve of carrying capacity

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*Abstract.* Climate warming will likely destabilize populations or drive consumers locally extinct. These predictions arise from consumer–resource models incorporating temperature-dependent parameters, and the accuracy of these predictions hinges on the validity of temperature scalings for each parameter. Among all parameters, carrying capacity ( $K$ ) is the most ill-defined and the temperature scaling of this parameter has no empirically verified foundation. Most studies assume that  $K$  declines exponentially with warming, but others have assumed a positive or no relationship between  $K$  and temperature. Here, I developed a theoretical foundation for a temperature scaling of  $K$  based on physiological principles of temperature and nutrient limitation of phytoplankton growth. The trade-off between thermodynamics and nutrient uptake yields a unimodal thermal response curve for  $K$ , and this prediction is supported by empirical data on both phytoplankton and insects. Analyses of consumer–resource models demonstrate the primacy of  $K$  in determining predictions of coexistence and stability. Since  $K$  exerts a dominant influence on model predictions, ecologists should carefully consider the temperature scaling of  $K$  for the species and region in question to ensure accurate estimates of population stability and extinction risk.

*Key words:* asymptotic population size; climate change; Lotka–Volterra models; Metabolic Theory of Ecology; nutrients; physiology; predator–prey interactions.

## INTRODUCTION

Consumer–resource interactions between species pairs are the basic unit of food webs and a primary method of species interactions. These interactions form the foundation of many emergent aspects of community structure and function. Community stability and species coexistence, for example, both depend on the number and strength of consumer–resource interactions. Strong species interactions often destabilize food webs unless counterbalanced by numerous weak interactions (McCann et al. 1998). Conversely, weak species interactions promote the coexistence of both predator–prey and competitor–competitor species pairs, increasing long-term diversity (Kokkoris et al. 2002). As a result, any change to consumer–resource interaction strengths can induce changes in ecosystem function (O’Connor et al. 2011, Fussmann et al. 2014), and there is a pressing need to predict how rapid climate change alters fundamental consumer–resource interactions and population dynamics.

The most common model used to predict how climate change affects species interactions and population dynamics is the bioenergetic Lotka–Volterra consumer–resource model (Vasseur and McCann 2005, O’Connor et al. 2011, Fussmann et al. 2014, Gilbert et al. 2014,

Amarasekare 2015, Osmond et al. 2017, Uszko et al. 2017). This model has the form

$$\frac{dR}{dt} = Rb \left( 1 - \frac{R}{K} \right) - f(R)C \quad (1)$$

$$\frac{dC}{dt} = ef(R)C - mC. \quad (2)$$

here,  $R$  is resource abundance,  $b$  is resource intrinsic growth rate,  $K$  is resource asymptotic population size (i.e., carrying capacity),  $C$  is consumer abundance,  $e$  is consumer production efficiency, and  $m$  is consumer mortality rate. The function  $f(R)$  relates consumption rates to resource abundance and is generally assumed to follow a Type II functional response curve (Fussmann et al. 2014, West and Post 2016, but see Uszko et al. 2017):

$$f(R) = \frac{aR}{c + R} \quad (3)$$

where  $a$  is the maximum consumption rate and  $c$  is the half-saturation constant.

This model provides a useful method for integrating community ecology with thermal physiology because most parameters have strong theoretically and empirically supported thermal response curves. Mortality rates ( $m$ ) and carrying capacity ( $K$ ) often increase and decrease exponentially with temperature, respectively (Brown

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et al. 2004, Savage et al. 2004). Production efficiency ( $e$ ) has long been assumed to be constant across temperatures, although recent meta-analyses suggest that it might increase with temperature, depending on trophic level (Lang et al. 2017). In contrast, resource intrinsic growth rates ( $b$ ) and the consumer functional response ( $a$ ,  $c$ ) curve unimodally with temperature across multiple taxonomic groups (Dell et al. 2011) and trophic levels (Englund et al. 2011). The consistency of these thermal response curves has generated repeatable predictions regarding the effects of warming on population dynamics. In a simple one consumer–one resource model, population stability and species coexistence almost always decline at high temperatures (Vasseur and McCann 2005, O'Connor et al. 2011, Fussmann et al. 2014, Gilbert et al. 2014, Amarasekare 2015). However, because these predictions are sensitive to the underlying assumptions regarding the temperature scaling of each parameter, it is critically important that parameter thermal response curves be theoretically sound and empirically verified.

The most important parameters are those describing consumer relative growth and resource biomass accumulation. Consumer relative growth is the ratio of resource assimilation to mortality rates ( $aelm$  for a Type I functional response), and resource biomass accumulation is approximated by resource carrying capacity ( $K$ ). The ratio of these two rates determines biomass accumulation for each species (i.e., the consumer:resource biomass ratio) as well as population stability and the probability of consumer extinction (Gilbert et al. 2014). Thus, the thermal response curves of  $a$ ,  $e$ ,  $m$ , and  $K$  strongly influence model behavior across a temperature range, including predictions of stability and coexistence under climate warming. Although  $a$ ,  $m$ , and to a lesser extent  $e$ , have empirically supported temperature scalings (Gillooly et al. 2001, Savage et al. 2004, Englund et al. 2011, Lang et al. 2017), the temperature dependence of  $K$  is uncertain. Some studies have assumed that  $K$  increases (Osmond et al. 2017), remains constant (Vasseur and McCann 2005, Uszko et al. 2017), or exhibits a U-shaped thermal response curve (Amarasekare 2015), but by far most models assume that  $K$  declines exponentially with warming (Savage et al. 2004, O'Connor et al. 2011, Fussmann et al. 2014, Gilbert et al. 2014). The exponential decline of  $K$  at high temperatures inevitably increases the ratio between consumer relative growth and resource biomass accumulation, thereby inducing unstable population dynamics and generating the repeated prediction that population stability and consumer existence should decline with warming. Given the primacy of  $K$  in model predictions, it is surprising that no study has yet empirically validated the theoretical prediction of a negative exponential thermal response curve for  $K$ .

Here, I briefly revisit the theoretical derivation of the negative exponential form of  $K$  in order to highlight conceptual issues with this prediction. I then demonstrate that  $K$  can decrease, increase, or curve unimodally with temperature, at least for phytoplankton, based on the

physiological principles of thermodynamic vs. nutrient trade-offs in cellular growth rates. These predictions subsequently are tested against empirical data collected for two common resource groups, phytoplankton and insects, demonstrating the primacy of unimodal temperature scaling of  $K$ . Finally, to demonstrate the sensitivity of model predictions to the thermal response curve of  $K$ , I parameterized the consumer–resource model for a *Daphnia*–phytoplankton system and conducted linear stability analysis for three  $K$  thermal response curves: negative, positive, and unimodal. These analyses demonstrate the sensitivity of predictions to resource evolutionary history and local adaptation, and suggest that ecologists must carefully incorporate such information to obtain accurate predictions.

#### A NEW PREDICTION FOR CARRYING CAPACITY

Based on the Metabolic Theory of Ecology, Savage et al. (2004) predicted that warming should drive an exponential decrease in resource equilibrium population size (i.e., carrying capacity). The logic of this prediction is straightforward. Rising temperatures drive an exponential increase in per capita metabolic demand. If a system receives a fixed, temperature-independent supply of energy, higher per capita metabolic demands necessarily yield a lower maximum population size because the available energy supports fewer individuals (Savage et al. 2004). As a result,  $K$  should decline exponentially with warming as the inverse of metabolic scaling. Yet this simple and widely used, but crucial, prediction has never been empirically tested, and it makes the unrealistic assumption that energy limits population sizes.

Instead, population growth rates are often restricted by other essential, inorganic nutrients. Nitrogen (N) and phosphorus (P), for example, limit primary production in marine, freshwater, and terrestrial ecosystems (Elser et al. 2007, Allgeier et al. 2011). Phytoplankton, perhaps the most common resource in thermal consumer–resource models (O'Connor et al. 2011, Gilbert et al. 2014, Osmond et al. 2017, Uszko et al. 2017), experience severe P-limitation (Elser et al. 2007), the strength of which depends upon temperature (Rhee and Gotham 1981, Thomas et al. 2017). At low temperatures, thermodynamic constraints reduce both cellular division (via increased activation energy of biological rates) and nutrient uptake rates (via low diffusion rates) (Rhee and Gotham 1981, Aksnes and Egge 1991). Warming initially increases cellular division and nutrient uptake, while simultaneously reducing cellular nutrient demand, thus facilitating phytoplankton growth on a fixed resource amount (Goldman 1977, Rhee and Gotham 1981, Hesse et al. 2017). At exceedingly high temperatures, both photosynthetic efficiency and nutrient uptake decline (Geider 1987). The decline in nutrient uptake at high temperatures occurs because warming reduces cell size (Chen et al. 2011); smaller cells possess less surface area and therefore experience slower diffusive nutrient uptake

despite increased molecular activity (Aksnes and Egge 1991, Edwards et al. 2012). Such temperature  $\times$  nutrient interactions likely regulate the population size of most species, but we still lack a theoretical framework for understanding these interactions and how they influence consumer–resource dynamics (Cross et al. 2015).

To explore the effects of nutrient acquisition on the thermal response curve for  $K$ , I parameterized a common physiological model of phytoplankton growth rates. Phytoplankton are the most common resource in bioenergetic consumer–resource models for which the physiological constraints on growth have been mathematically well-defined (Droop 1973, Goldman 1977, Rhee and Gotham 1981). Specifically, I used a simplified version of the Droop equations (Droop 1973) to describe phytoplankton growth as a function of external and internal cellular nutrient dynamics while holding resource supply ( $P_0$ ) constant. This model is particularly useful because it does not rely on the abstract parameter  $K$  and instead treats asymptotic population size as the equilibrium balance between nutrient uptake and nutrient expenditures.

The modified Droop equations consist of three coupled differential equations describing phytoplankton growth in a chemostat:

$$\frac{dP}{dt} = V(P_0 - P) - \rho \left( \frac{P}{K_P + P} \right) X \quad (4)$$

$$\frac{dQ_P}{dt} = \rho \left( \frac{P}{K_P + P} \right) - \mu(Q_P - q_0) \quad (5)$$

$$\frac{dX}{dt} = X\mu \left( 1 - \frac{q_0}{Q_P} \right) - dX. \quad (6)$$

The first equation describes the change in background nutrient concentrations ( $P$ ) as a function of constant, temperature-invariant nutrient supply ( $VP_0$ ), loss due to outflow ( $VP$ ), and loss due to cellular nutrient uptake. The second equation describes the change in internal cellular nutrient pools ( $Q_P$ ). Cellular nutrient concentra-

Importantly, this model does not rely on the abstract term  $K$ , but instead represents asymptotic population size as the equilibrium point where  $dP/dt = dQ_P/dt = dX/dt = 0$ . The internal equilibrium point, i.e., steady-state biomass ( $X^* \equiv K$ ), depends on the physiological parameters  $\mu$ ,  $d$ ,  $q_0$ ,  $K_P$ , and  $\rho$ :

$$X^* = - \frac{V(d - \mu)(K_P d \mu q_0 + P_0 d \mu q_0 + P_0 d \rho - P_0 \mu \rho)}{d \mu q_0 (d \mu q_0 + d \rho - \mu \rho)}. \quad (7)$$

As a result, the thermal response curve of  $K$  emerges from interactions among the individual thermal response curves of  $\mu$ ,  $d$ ,  $q_0$ ,  $K_P$ , and  $\rho$ . Across 1,022 experiments,  $\mu$  curved unimodally with temperature in almost every case ( $\approx 94\%$ ), whereas  $q_0$  decreases exponentially with warming (Appendix S1, see also Tilman et al. 1981). Mortality rates often increase exponentially with temperature (Savage et al. 2004), resulting in the following thermal response curves:

$$\begin{aligned} \mu &= \mu_0 \exp \left[ - \frac{(T - T_{\text{opt}_\mu})^2}{2T_{\sigma_\mu}^2} \right] \\ q_0 &= \exp [Q_0 - Q_1 T] \quad d = \exp [D_0 + D_1 T] \end{aligned} \quad (8)$$

where  $T_{\text{opt}_\mu}$  and  $T_{\sigma_\mu}$  are the thermal optimum and thermal tolerance of phytoplankton growth, respectively. The thermal response curve for  $K_P$  and  $\rho$  are less certain;  $K_P$  often does not change with temperature and so was held constant (Goldman 1977) while  $\rho$  curves unimodally with temperature (Rhee and Gotham 1981). Because nutrient uptake and growth are likely correlated, I assigned  $\rho$  the same thermal response curve as  $\mu$ :

$$\rho = \rho_0 \exp \left[ - \frac{(T - T_{\text{opt}_\mu})^2}{2T_{\sigma_\mu}^2} \right]. \quad (9)$$

Inserting Eq. 8 into Eq. 7 yields the temperature-dependent equilibrium

$$X^*(T) = - \frac{V(\mu_0 M - e^{D_0 + D_1 T})(\mu_0 K_P e^{D_0 + D_1 T + Q_0 - Q_1 T} - \mu_0 M P_0 \rho_0 + \mu_0 P_0 e^{D_0 + D_1 T + Q_0 - Q_1 T} + P_0 \rho_0 e^{D_0 + D_1 T}) e^{-D_0 - D_1 T - Q_0 + Q_1 T}}{\mu_0 M (\mu_0 M \rho_0 - \mu_0 e^{D_0} e^{Q_0} e^{D_1 T} e^{-Q_1 T} - \rho_0 e^{D_0} e^{D_1 T})} \quad (10)$$

tions increase as a saturating Monod function with a maximum nutrient uptake rate ( $\rho$ ) and a half-saturation constant ( $K_P$ ). Internal nutrient concentrations decrease with nutrient expenditure on growth ( $\mu$ ), which increases proportionally as internal nutrient concentrations exceed the minimum nutrient quota for cellular maintenance ( $q_0$ ). Finally, cellular biomass ( $X$ ) increases as a logistic function of  $Q_P$  where growth is absent when  $Q_P = q_0$  and approaches its maximum as  $Q_P \gg q_0$ . The loss term  $d$  is either washout or mortality, and here I consider it to be mortality for consistency with other bioenergetic consumer–resource models.

where

$$M = e^{-\frac{(T - T_{\text{opt}_\mu})^2}{2T_{\sigma_\mu}^2}}. \quad (11)$$

To qualitatively evaluate how the shape of the thermal response curve for  $K$  emerges from individual parameters, I took the partial derivative of  $X^*$  with respect to temperature  $\partial X^*/\partial T$ . I then evaluated  $\partial X^*/\partial T$  across a 40°C temperature gradient (0–40°C) for different combinations of  $T_{\text{opt}_\mu}$ ,  $T_{\sigma_\mu}$ , and  $D_1$ . Parameter combinations were chosen to reflect the different potential thermal adaptations of phytoplankton. Phytoplankton were allowed to range from cool-

adapted growth ( $T_{opt_\mu} = 0^\circ\text{C}$ ) to warm-adapted growth ( $T_{opt_\mu} = 40^\circ\text{C}$ ). Baseline phytoplankton mortality rates were 0.01 at  $0^\circ\text{C}$ , and the thermal response of mortality varied from temperature insensitive ( $D_1 = 0.01$ , mortality rate = 0.015 at  $40^\circ\text{C}$ ) to highly temperature sensitive ( $D_1 = 0.11$ , mortality rate = 0.82 at  $40^\circ\text{C}$ ). Finally, all potential combinations of growth and mortality were evaluated for thermal specialists ( $T_\sigma = 5$ ), modest thermal generalists ( $T_\sigma = 10$ ), and broad thermal generalists ( $T_\sigma = 15$ ).

After evaluating  $\partial X^*/\partial T$  for all parameter combinations, I recorded the output as follows: positive thermal response curve if  $\partial X^*/\partial T > 0$  for all  $T$ , negative thermal response curve if  $\partial X^*/\partial T < 0$  for all  $T$ , and unimodal if  $\partial X^*/\partial T$  exhibited a positive-negative sign change (there were no instances of concave-up, negative-positive sign changes; see Appendix S1 for details). Two main points arise from the model results: (1) a negative relationship between temperature and carrying capacity was rare, occurring only at exceedingly high mortality rates ( $D_1$ ), and (2) a unimodal thermal response curve of  $K$  is the most likely result (Fig. 1). Positive thermal response curves occurred only at low  $D_1$  and high  $T_{opt_\mu}$ , suggesting that positive thermal response curves are simply unimodal curves truncated below  $T_{opt_\mu}$  (Fig. 1). Although increased  $T_{\sigma_\mu}$  substantially increased the probability of positive thermal response curves, unimodality remained a common and likely outcome under all  $T_{\sigma_\mu}$  values (Fig. 1). It is important to note that  $K$  does not always exhibit a bell-shaped curve with temperature since it depends on three underlying and independent thermal response curves. Indeed, the thermal response curve of  $K$  is often left skewed, as with most biological rates (Appendix S1: Figs. S1–S3).

### VERIFYING THE TEMPERATURE SCALING OF CARRYING CAPACITY

The thermal Droop equations predict that positive or unimodal thermal response curves for  $K$  should be

prevalent. To verify this prediction, I searched the literature for studies reporting steady-state population size as a function of temperature. Although the Droop equations only model phytoplankton, I also searched for insect studies because insects also experience strong temperature  $\times$  nutrient interactions (Lemoine and Shantz 2016) and because they are perhaps the second-most common resource in bioenergetic consumer–resource models (Vasseur and McCann 2005, Rall et al. 2010). I searched Google Scholar using the terms (*\*group\* temperature carrying capacity*) and (*\*group\* temperature steady state*). The term *\*group\** was set as *phytoplankton*, *algae*, or *insect* for each search. To ensure I had thoroughly sampled the insect literature, I searched the journals *Ecological Entomology* and *Environmental Entomology* using the same search terms. Studies were only included if they (1) reported steady-state population sizes, (2) used more than two temperatures to capture potential unimodality, (3) were controlled laboratory experiments free of competitors and consumers (i.e., no herbivores in phytoplankton studies, no predators in insect studies), and (4) consistently replaced resources (e.g., using a chemostat) to prevent resource depletion. In all, I identified 15 studies containing 39 experiments (23 phytoplankton, 16 insect) reporting steady-state population size as a function of three or more temperatures. Although data are limited, 39 experiments is sufficient to determine if  $K$  exhibits consistent temperature scaling, or at least to determine if temperature scaling departs from a negative exponential (data available in Data S1). For each experiment, I fit the log-linear equation

$$\log K(T) = \log \beta_0 + \beta_1 T + \beta_2 T^2 \quad (12)$$

where  $K(T)$  is the steady-state population size at each temperature ( $T$ ) and converted the parameters into carrying capacity thermal optimum ( $T_{opt_K}$ ) and thermal tolerance ( $T_{\sigma_K}$ ) as described in Appendix S2.

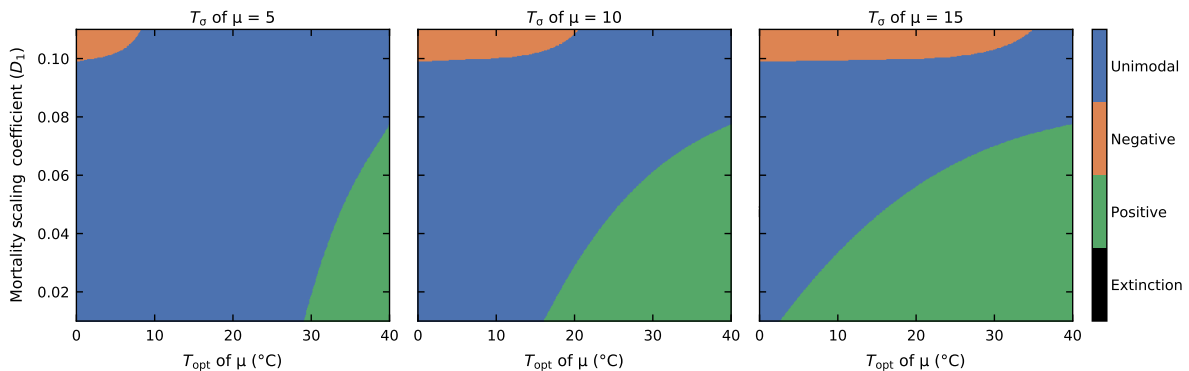


FIG. 1. This figure shows how the shape of the thermal response curve of  $X^* \equiv K$  varies with  $T_{opt}$ ,  $T_\sigma$ , and the scaling coefficient  $D_1$ . The orange area defines parameter combinations for which carrying capacity decreased across the entire temperature range. The green area outlines the region for which carrying capacity increased with temperature throughout the temperature range. The blue area denotes the parameter combinations for which carrying capacity was unimodal. For this analysis, I set  $P_0 = 1$ ,  $Q_0 = -2.1$ ,  $Q_1 = 0.1$ ,  $D_0 = -4.6$ , and  $\mu_0 = 1$ . See Appendix S1 for further details.  $\mu$  is phytoplankton intrinsic growth rate;  $T\alpha$  is the thermal tolerance of phytoplankton growth rate;  $T_{opt}$  is the thermal optimum of phytoplankton growth rate; and  $D_1$  is the temperature scaling of phytoplankton mortality rates.

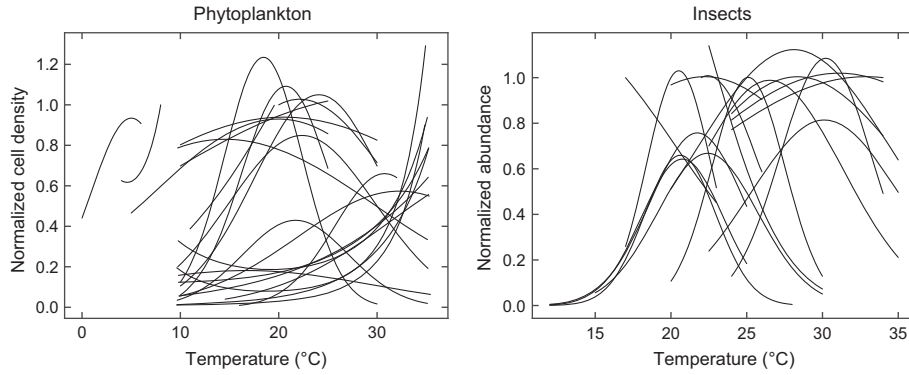


FIG. 2. Best-fit curves describing the relationship between temperature and  $K$  for phytoplankton and insects. Prior to analysis,  $K$  (phytoplankton cell densities; insects population size) was normalized within each study by dividing each observation by the within-study maximum. This placed all observations on the 0–1 scale, where normalized  $K$  is the proportion of maximum observed population size.

The thermal response curve of  $K$  varied considerably among species and experiments for both phytoplankton and insects, but data support predictions of the Droop equations that  $K$  should either increase or curve unimodally with temperature. Over one-half (57%) of phytoplankton experiments exhibited strong or weak unimodal curvature of  $K$ , whereas 43% of experiments reported an exponential increase in  $K$  with warming (Fig. 2). These patterns match the theoretical prediction that  $K$  should generally curve or increase exponentially with rising temperatures (Fig. 1). In addition, 88% of insect experiments also exhibited unimodal relationships between temperature and  $K$ , further suggesting that this is a general trend across multiple taxonomic groups (Fig. 2). Instances where  $K$  declined exponentially with warming throughout the temperature range, as predicted by the Metabolic Theory of Ecology (Savage et al. 2004), were rare and occurred in only 12% of insect experiments, just as predicted by the Droop model. Given the prevalence of unimodal curves, it is highly likely that both exponential increases and decreases occur in studies with incomplete temperature ranges that excluded  $T_{opt_K}$ , which is determined by evolutionary history and local adaptation (Thomas et al. 2012). Phytoplankton also demonstrated considerably higher variability than insects in both  $T_{opt_K}$  (phytoplankton  $31.4 \pm 7.8$ , insects  $24.3 \pm 1.3$ ) and  $T_{\sigma_K}$  (phytoplankton  $11.8 \pm 2.0$ , insects  $5.2 \pm 0.7$ ), but this could be due to the limited number of insect studies.

THE INFLUENCE OF CARRYING CAPACITY ON PERSISTENCE AND STABILITY

Since  $K$  is one of the predominant parameters dictating coexistence and population stability, predictions of consumer–resource dynamics across a temperature gradient likely depend, at least in part, on the thermal response curve of  $K$ . I explored how the thermal

response curve of  $K$  influences predictions of population dynamics across a temperature gradient by parameterizing the Lotka-Volterra consumer–resource model (Eqs. 1, 2) for a *Daphnia*–phytoplankton system. I chose the Lotka-Volterra model instead of the Droop

TABLE 1. The temperature dependencies used in analysis of the bioenergetic Lotka-Volterra model.

Parameter	Temperature scaling
$b$	$b(T) = b_0 \exp(-0.5[T - T_{opt_b}]^2/[T_{\sigma_b}^2])$ , $b_0 = 1.5, T_{opt_b} = 25, T_{\sigma_b} = 8$
$a$	$a(T) = a_0 \exp(-0.5[T - T_{opt_a}]^2/[T_{\sigma_a}^2])$ , $a_0 = 1.6, T_{opt_a} = 21.9, T_{\sigma_a} = 8.5$
$c$	$c = 0.8$
$e$	$e = 0.8$
$m$	$m(T) = M_0 \exp(M_1 T), M_0 = 0.03, M_1 = 0.08$
$K$	
Constant	$K(T) = K, K \in [0.00, 1.00]$
Positive exponential	$K(T) = K_0 \exp(K_1 T), K_0 = 0.2, K_1 \in [0.00, 0.05]$
Negative exponential	$K(T) = K_0 \exp(-K_1 T), K_0 = 1.0, K_1 \in [0.00, 0.20]$
Unimodal	$K(T) = (-0.5[T - T_{opt_K}]^2/[T_{\sigma_K}^2]), T_{opt_K} \in [0, 30], T_{\sigma_K} \in [5, 10, 15]$

Notes: Parameters were derived from literature sources (Appendix S3). The parameter values below each thermal response curve of  $K$  denote the range of parameter values for which consumer persistence and population stability were evaluated.  $T$ , temperature (degrees C);  $b$ , resource intrinsic growth rate;  $T_{opt_b}$ , the thermal optimum of  $b$ ;  $T_{\sigma_b}$ , the thermal tolerance of  $b$ ;  $a$ , consumer attack rate;  $T_{opt_a}$ , the thermal optimum of consumer attack rates;  $c$ , the half-saturation constant for the consumer Type II functional response;  $e$  is consumer assimilation efficiency;  $m$ , consumer mortality rate;  $M_1$ , the temperature scaling of consumer mortality;  $K$ , resource carrying capacity;  $K_1$ , the temperature scaling of carrying capacity for positive and negative exponential models.  $T_{opt_K}$  and  $T_{\sigma_K}$  are the thermal optimum and tolerance, respectively, of carrying capacity in the unimodal model. All parameters with subscript 0 refer to the baseline rate at  $T = 0^\circ\text{C}$ .

equations so that results of this study can be directly compared to previous work on temperature-dependent population dynamics (O'Connor et al. 2011, Fussmann et al. 2014, Gilbert et al. 2014, Amarasekare 2015, Osmond et al. 2017, among others) and to generalize theory beyond algal resources since many resources (e.g., insects) exhibit unimodal curvature in  $K$  (Fig. 2; Rall et al. 2010).

Temperature dependencies for all parameters were derived from literature sources (Table 1; Appendix S3), while the thermal response curve of  $K$  varied among four possible forms: the negative exponential form predicted by Savage et al. (2004), the Gaussian form predicted by the Droop equations and verified empirically (Figs. 1, 2), the positive exponential form also predicted by the Droop equations and present in many experiments (Figs. 1, 2), and constant (e.g., Osmond et al. 2017). For each thermal response of  $K$ , I varied the temperature-scaling parameters to identify how they affect consumer persistence and population stability (Table 1). Persistence was defined as parameter combinations where the equilibrium consumer population size was positive. I assessed consumer population stability via linear stability analysis of the Jacobian matrix, which categorized population dynamics around the equilibrium point (e.g., stable/unstable, oscillations/direct) and also quantified the strength of stability (i.e., speed of recovery to equilibrium following perturbation). All other parameters were

initially held constant across analyses to isolate the effects of  $K$  on model outcomes. See Appendix S3 for full analytical details.

The effect of temperature on consumer persistence and population stability depended on the thermal response curve of  $K$ . A negative exponential response curve yielded similar predictions to prior studies; warming negated the ability of consumers to persist in the system, and stronger declines in  $K$  with warming caused consumer extinction at cooler temperatures (Fig. 3). When consumers persisted, populations always exhibited damped oscillations toward a stable equilibrium, the magnitude of which decreased with warming (Fig. 3). In contrast, rising temperatures facilitated consumer persistence and enhanced population stability under a positive exponential thermal response curve (Fig. 3). More rapid increases in  $K$  with temperature further enhanced consumer population stability at high temperatures (Fig. 3). The same was generally true for temperature-invariant  $K$ , which exhibited the same trends as a positive thermal response curve except with a wider temperature range that promoted persistence (Fig. 3).

The unimodal thermal response curve for  $K$  suggests that consumer persistence depends on both the thermal optimum and thermal tolerance of phytoplankton. In general, mismatches between resource  $T_{opt,K}$  and environmental temperature ( $T$ ) led to consumer extinction.

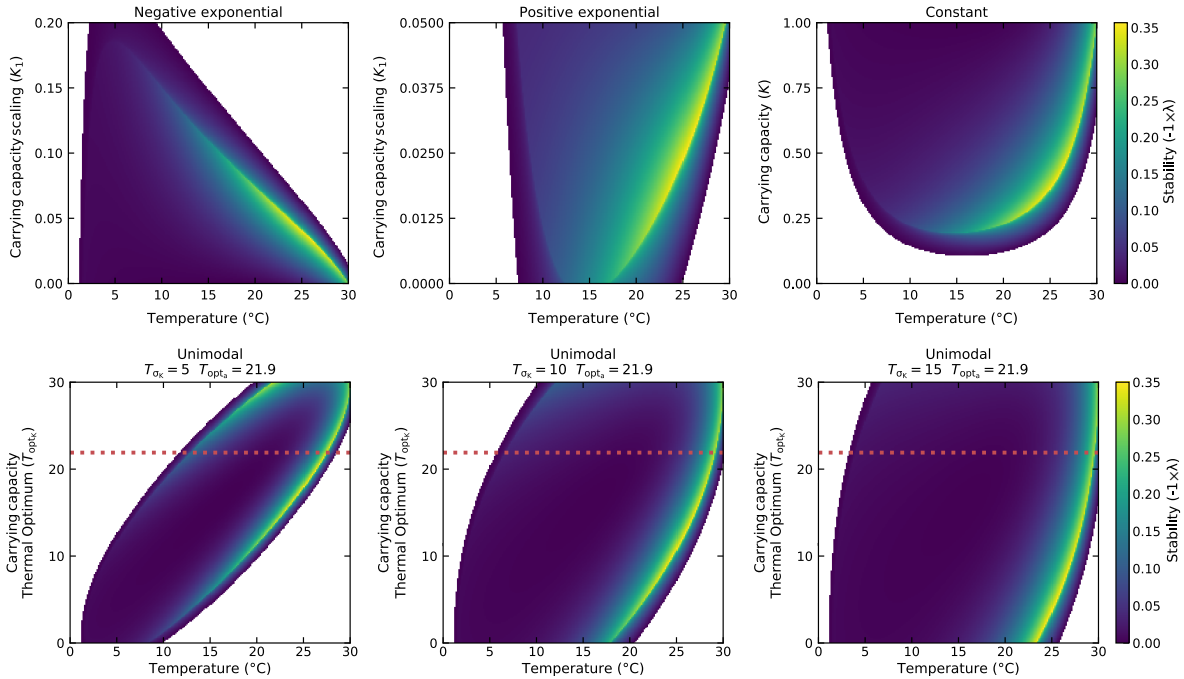


FIG. 3. Results of linear stability analysis for each thermal response curve of  $K$ . The white regions denote areas where consumers could not persist in the system (consumer equilibrium population size  $< 0$ ). The colored region denotes coexistence, which in all cases consisted of damped oscillations toward a stable equilibrium. Stability was quantified as  $-1 \times \lambda$ , where  $\lambda$  was the dominant eigenvalue of the Jacobian matrix evaluated at equilibrium (Gilbert et al. 2014). Larger stability values indicate that the system returns more rapidly to the equilibrium point following perturbation. The red dashed line indicates the thermal optimum of consumer maximum intake rates ( $T_{opt,K}$ , see Table 1).

That is, consumers could only persist at cool temperatures with cool-adapted resources and warm temperatures with warm-adapted resources (Fig. 3). Increasing resource thermal tolerance via larger  $T_{\sigma_K}$  expanded the degree to which mismatches between  $T$  and  $T_{opt_K}$  enabled consumer persistence, such that thermal generalist resources could support a stable consumer population across a broad temperature gradient (Fig. 3). These results suggest that resource local adaptation and evolutionary history (manifested here in  $T_{opt_K}$  and  $T_{\sigma_K}$ ) impact not only resource population dynamics under climate warming, but also determine how warming influences population stability and the persistence of higher trophic levels.

Although the thermal response curve of  $K$  exerts a large influence on model predictions, population dynamics ultimately derive from the ratio of biomass accumulation rates for both resources ( $K$ ) and consumers ( $aelm$ ; Gilbert et al. 2014). Since both  $a$  and  $K$  curve unimodally with temperature (Table 1, Fig. 2; Englund et al. 2011), any mismatch between the ideal temperatures for resource growth ( $T_{opt_K}$ ) and consumer growth ( $T_{opt_c}$ ) alters the consumer:resource biomass accumulation ratio and, as a result, population dynamics. To assess the sensitivity of population dynamics to  $T_{opt_c}$ , I repeated linear stability analyses for both cool-

and warm-adapted consumers ( $T_{opt_c} = 10^\circ\text{C}$  and  $T_{opt_c} = 30^\circ\text{C}$ , respectively). With cool-adapted consumers, populations exhibited unstable oscillations (spiraling outward away from an equilibrium) when  $T_{opt_K} \approx T$  at cool temperatures (Fig. 4). Stable consumer populations only existed when  $T$  substantially exceeded  $T_{opt_K}$  or vice versa, although exceedingly high mismatches between  $T$  or  $T_{opt_K}$  caused consumer extinction. Indeed, consumer extinction was assured above  $20^\circ\text{C}$  as  $a$  fell below sustainable levels for cool-adapted individuals. Warm-adapted consumers exhibited nearly the exact opposite pattern; persistence only occurred a narrow, high-temperature window where  $T_{opt_K} \approx T$ , and exceedingly high mismatches between environmental temperature and resource thermal adaptation resulted in consumer extinction (Fig. 4). Increasing resource thermal tolerance ( $T_{\sigma_K}$ ) had the same effect as in previous analyses; thermal generalist resources increased the degree of mismatch between  $T_{opt_K}$  and  $T$  that permitted both consumer persistence and population stability (Fig. 4).

### DISCUSSION

Early thermal consumer–resource models derived their parameter estimates from the predictions of the

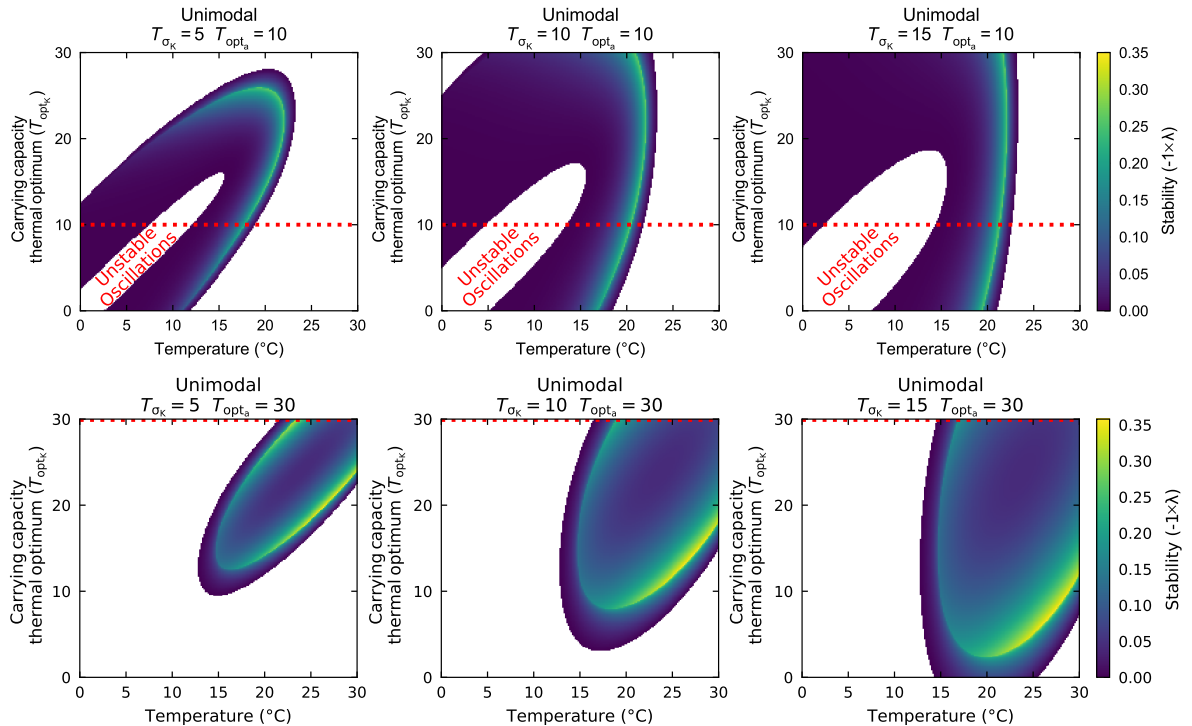


FIG. 4. Results of linear stability analysis for a unimodal response curve for  $K$ , while varying the thermal response curve for maximum consumer intake rate ( $T_{opt_c}$ ). The white regions denote areas where consumers could not persist in the system (consumer equilibrium population size  $<0$ ), unless labeled otherwise. The colored region denotes coexistence, which in all cases consisted of damped oscillations toward a stable equilibrium. Stability was quantified as  $-1 \times \lambda$ , where  $\lambda$  was the dominant eigenvalue of the Jacobian matrix evaluated at equilibrium (Gilbert et al. 2014). Larger stability values indicate that the system returns more rapidly to the equilibrium point following perturbation. The red dashed line indicates the thermal optimum of consumer maximum intake rates ( $T_{opt_c}$ ).



Metabolic Theory of Ecology (Vasseur and McCann 2005, O'Connor et al. 2011). However, these predictions are often incorrect in natural settings or at high temperatures relevant to climate change (Dell et al. 2011, Lemoine and Burkepile 2012). To rectify these shortcomings, ecologists have been steadily improving model predictions by incorporating more realistic temperature effects based on empirical evidence, laboratory experiments, or new theory. Metabolic Theory, for example, predicted that attack rates increase exponentially with warming (Brown et al. 2004), but meta-analyses conclusively demonstrated that attack rates curve unimodally with temperature (Englund et al. 2011). The unimodal thermal response curve of attack rates is now commonplace in bioenergetic models (Fussmann et al. 2014, Osmond et al. 2017, Uszko et al. 2017). More recently, Uszko et al. (2017) expanded consumer–resource models to incorporate nutrient enrichment and a Type III consumer functional response, and Osmond et al. (2017) accounted for the negative effects of warming on consumer body size. Both modeling efforts suggest that unstable population dynamics and consumer extinction are not inevitable consequences of warming. Likewise, my results show that using the more accurate, unimodal curve for  $K$  can drastically alter model outcomes, and the effects of warming on population dynamics depend on the evolutionary history and local adaptation of both resources and consumers. Continual refinements to bioenergetic models will undoubtedly improve our ability to accurately predict the consequences of warming on communities and represent an important avenue of future research.

Theoretical and empirical results presented here demonstrate that carrying capacity often curves unimodally with temperature for multiple resource types. For primary producers, including both phytoplankton and vascular plants, a unimodal thermal response of  $K$  likely arises from unimodal thermal responses of both intrinsic growth rates ( $\mu$ ) and nutrient uptake rates ( $\rho$ ) (Rhee and Gotham 1981, Cumbus and Nye 1985, Aksnes and Egge 1991, BassiriRad et al. 1991). Thermodynamic constraints at cool temperatures limit both cellular division and nutrient uptake (Rhee and Gotham 1981). As temperatures approach  $T_{opt_{\mu}}$ , cellular division and nutrient uptake rates increase while the minimum cell nutrient quota declines (Rhee and Gotham 1981, Aksnes and Egge 1991, BassiriRad et al. 1991). Beyond the thermal optimum, cellular growth rates slow as photosynthetic efficiency collapses (Geider 1987) and respiration increases (BassiriRad et al. 1991). Less generally, warming also reduces phytoplankton cell size (Chen et al. 2011), potentially limiting nutrient uptake rates as cells become too small to effectively absorb nutrients (Edwards et al. 2012). The combination of more rapid growth, more efficient nutrient uptake, and lower per capita nutrient demand suggests that a fixed supply of nutrients should support more individuals at  $T_{opt_{\mu}}$ . Indeed, experimental studies of nutrient demand have

repeatedly demonstrated a U-shaped thermal response of nutrient demand ( $R^*$ , Tilman et al. 1981, Tilman 2004, Shatwell et al. 2013), implying that the number of primary producers supported by a fixed nutrient supply should curve unimodally with temperature as predicted by the Droop equations.

The data presented here also show that  $K$  curves unimodally for other taxonomic groups and higher trophic levels (e.g., insects). Although the Droop equations explicitly describe phytoplankton population dynamics, experimental evidence suggests that similar temperature  $\times$  nutrient interactions are a plausible mechanism for the unimodal relationship between insect population size and temperature documented here. Similar to primary producers, many consumers experience temperature-limited growth at cool temperatures, and warming rapidly induces nutrient-limited growth (Wojewodzic et al. 2011, Lemoine and Shantz 2016). *Daphnia*, for example, suffer reduced growth rates and lower production efficiencies when fed phytoplankton of insufficient P content, such as those grown under high temperatures (Sternner et al. 1998). Warming might induce consumer nutrient limitation in three ways. First, primary producer nutrient content declines as producer biomass increases due to stronger nutrient competition among individuals (Loladze et al. 2000). Second, per capita producer nutrient content declines at high temperatures because individual, P-rich ribosomes become more efficient and total ribosomal concentrations decline (Hessen et al. 2017). Third, warming might directly affect consumer nutrient acquisition. Gut passage time of herbivorous caterpillars declines at higher temperatures, thereby decreasing nutrient absorption efficiency and inducing nutrient-limited growth (Lemoine and Shantz 2016). Any of these mechanisms result in reduced consumer production efficiency at high temperatures that might stabilize population dynamics with warming. Incorporating consumer nutrient limitation into bioenergetic models is a promising avenue of future research because temperature  $\times$  nutrient interactions appear to be ubiquitous in nature and we are only just beginning to understand how they alter the expected consequences of warming (Cross et al. 2015).

Since carrying capacity curves unimodally with temperature, and  $T_{opt_K}$  and  $T_{\sigma_K}$  both result from evolutionary history, my results suggest that the consequences of warming strongly depend on the evolutionary history and local adaptation of both resources and consumers. Thermal specialists are generally considered to be more susceptible to warming than thermal generalists due to the narrow temperature range that allows for population growth (Huey et al. 2012). Tropical species, for example, evolved in constant thermal environments and possess narrower thermal tolerances than temperate or polar species (Janzen 1967). As a result, tropical species are more vulnerable to climate warming because even small increases in temperature push most species' beyond their thermal optima (Dillon et al. 2010, Thomas et al. 2012, but see Walters et al.

2012). Thermal specialization of consumers, and the potential mismatch between consumer and resource thermal optima, also influences the impact of warming on consumer population stability and persistence (Amarasekare 2015). Yet most work has focused on the link between thermal specialization, population dynamics, and extinction risk of a single taxonomic group or trophic level. My results expand on previous work by suggesting that thermal specialization of resources dictates not only the resource's probability of extinction, but also the probability of extinction for higher trophic levels. Thus, predicting extinction risk under warming requires focusing on the thermal physiology of both consumers and resource and how their interactions are shaped by changing temperatures (Gilman et al. 2010).

Consumer–resource models generally predict that species coexistence, consumer persistence, and community stability all decline with warming (O'Connor et al. 2011, Fussmann et al. 2014, Amarasekare 2015). These predictions rightly raise concerns about the effects of climate change on higher trophic levels and food web stability (Petchey et al. 2010). Yet the accuracy of these predictions necessitates valid temperature scalings for each parameter. Most parameters have consistent, empirically supported temperature scalings (Kingsolver 2009, Dell et al. 2011, Englund et al. 2011), but the temperature scaling of  $K$  relies on an unverified prediction from the Metabolic Theory of Ecology (Savage et al. 2004). As a result of this uncertainty, studies have assumed a variety of thermal response curves for  $K$ , including a negative exponential (Savage et al. 2004, O'Connor et al. 2011, Fussmann et al. 2014, Gilbert et al. 2014), positive exponential (Osmond et al. 2017), or null (Vasseur and McCann 2005) relationship. Here, I resolve this uncertainty by theoretically and empirically demonstrating that carrying capacity curves unimodally with temperature for both phytoplankton and insects, although the exact temperature scaling of  $K$  depends on species specific evolutionary histories and the temperature range in question. Given that  $K$  exerts an incredibly strong influence on model predictions, ecologists should carefully consider the temperature scaling of  $K$  for the species and region in question. Continual improvements to the underlying theory of population growth and nutrient uptake will undoubtedly improve model predictions and help ecologists determine stability and extinction risk in the future.

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