Warming-Induced Changes to Body Size Stabilize Consumer-Resource Dynamics

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ABSTRACT: Both body size and temperature directly influence consumer-resource dynamics. There is also widespread empirical evidence for the temperature-size rule (TSR), which creates a negative relationship between temperature and body size. However, it is not known how the TSR affects community dynamics. Here we integrate temperature- and size-dependent models to include indirect effects of warming, through changes in body size, to answer the question, How does the TSR affect the predicted response of consumer-resource systems to warming? We find that the TSR is expected to maintain consumer-resource biomass ratios and buffer the community from extinctions under warming. While our results are limited to conditions where organisms are below their thermal optimum, they hold under a range of realistic temperature-size responses and are robust to the type of functional response. Our analyses suggest that the widely observed TSR may reduce the impacts of warming on consumer-resource systems.

Keywords: metabolic scaling theory, predator-prey, plant-herbivore, functional response, mathematical model, temperature-size rule.

Introduction

Consumer-resource interactions are a fundamental aspect of ecological communities. The strength and stability of these interactions generate patterns in the structure and functioning of ecosystems, dictating the flow of energy between trophic levels. Because of the temperature dependence of metabolism (Gillooly et al. 2001), rates of birth, death, and consumption vary with temperature (Savage et al. 2004; Gilbert et al. 2014). Thus, the flow of energy from resource to consumer often changes under warming, and even small changes in temperature that are not neces-

sarily physiologically stressful can affect stability and coexistence, producing predictable effects of warming on simple food webs (Vasseur and McCann 2005; Rall et al. 2010; O'Connor et al. 2011; Gilbert et al. 2014).

Warming also causes predictable changes in body size. For example, adult body size tends to decline with temperature during ontogeny (the temperature-size rule [TSR]; reviewed in Atkinson 1994), and mean body size often declines toward the equator, both between and within species (Bergmann's rule; reviewed in Blackburn et al. 1999). Although the mechanism varies (e.g., phenotypic plasticity in the case of the TSR, selection for smaller individuals and species turnover in the case of Bergmann's rule), the pattern is similar, and declining body size with warming is considered a universal response to warming (Daufresne et al. 2009; Gardner et al. 2011). Here we focus on the TSR, where plastic changes in body size occur rapidly relative to population dynamics.

Because body size (Yodzis and Innes 1992; DeLong et al. 2015) and body size ratios (Kalinkat et al. 2013) affect demographic rates and hence consumer-resource dynamics, such a systematic pattern of changing body sizes with temperature could alter predictions for how temperature affects stability and coexistence in consumer-resource systems. To formally explore this possibility, we integrated the TSR into a general framework for temperature-dependent consumer-resource interactions to answer the question, How does the TSR affect the predicted response of consumer-resource interaction strength, equilibrium consumer : resource biomass ratios, and community stability to warming? We then explored the effect of the magnitude of body size–temperature scaling, under both a type I and a type II functional response, including cases where the scaling differs between consumers and their resources. Because body size changes may also affect the overall functional response (e.g., changes from type II to type III; Kalinkat et al. 2013), we also explored (in the

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supplementary material, available online) whether changes in temperature might induce a change in functional response through body size–temperature responses, as described by the TSR.

Methods and Results

The Underlying Consumer-Resource Dynamics

We begin, like Gilbert et al. (2014), with a general consumer-resource model

$$\frac{dR}{dt} = rR\left(1 - \frac{R}{K}\right) - f(R)RC,$$

$$\frac{dC}{dt} = ef(R)RC - mC, \tag{1}$$

which describes the rates of change in total resource ($R \in [0, K]$) and consumer ($C \geq 0$) biomass with time t.

In the absence of consumers, $C = 0$ and the resource grows logistically, with intrinsic growth rate $r \geq 0$ and carrying capacity $K > 0$. The intrinsic growth rate describes the rate at which resource biomass increases (per unit biomass) in the absence of consumers when the resource is rare, $R \approx 0$. The carrying capacity is the equilibrium biomass of the resource without consumers.

Resource biomass is consumed by consumers at a rate $f(R)RC$, where $f(R)R \geq 0$ is called the functional response. Of the biomass consumed, the unitless conversion efficiency parameter $e \in [0, 1]$ determines the proportion of resource biomass that is directly converted into consumer biomass. Consumer biomass dies at a constant per unit biomass mortality rate $m \geq 0$.

An equilibrium is reached when the two rates of change in equation (1) are 0, and solving the system at this point gives equilibrium resource ($\hat{R}$) and consumer ($\hat{C}$) biomass. At the coexistence equilibrium (i.e., where both $\hat{C}$ and $\hat{R}$ are >0), one can calculate the ratio of consumer to resource biomass, $\hat{C}:\hat{R}$, and also perform a linear stability analysis to derive the dominant (largest in absolute value) eigenvalue,

λ, which determines whether (and how readily) the system, when perturbed a small amount, will return to it (see supplementary material for derivation). Together, these two measures tell us how biomass is partitioned across trophic levels and how stable this partitioning is.

As explained in Gilbert et al. (2014), two parameters well describe the dynamics of this system. The first is K, the equilibrium biomass of the resource in the absence of consumers. The second is $m(ef(\hat{R}))^{-1}$, the equilibrium biomass of the resource in the presence of consumers. Dividing the former by the latter thus describes the degree to which a consumer suppresses resource biomass, which gives a measure of interaction strength,

$$B_{CR} = \frac{ef(\hat{R})K}{m}. \tag{2}$$

In what follows, we examine how our three measures, B_{CR}, $\hat{C}:\hat{R}$, and stability ($-\lambda$), change with temperature. We start by assuming a type I functional response, $f(R)R = aR$, where attack rate a describes the rate of resource consumption per resource biomass. We also explore the effect of a type II functional response (below) and the potential for the functional response to change with changes in temperature (supplementary material).

Adding Temperature Dependence

Gilbert et al. (2014) discuss what is known about the temperature dependencies of the population dynamic parameters r, K, a, m, and e. In our analyses we use both their equations and their parameter estimates; see table 1 here and table 1 in Gilbert et al. (2014) for a summary (note that in the main text we use $E_B = 0.32$ for comparison with fig. 3 in Gilbert et al. 2014). Briefly, resource growth rate r is expected to scale with metabolism as a Boltzmann-Arrhenius factor,

$$r(T) = r_0 \exp\left(-\frac{E_B}{kT}\right),$$

Table 1: Summary of population dynamic parameters, the form of temperature T and mass M dependency, and the empirical values used to generate the plots in figure 1

Parameter	Temperature dependence	Mass dependence	Values used
r	$\exp(-E_B/(kT))$	M_R^ρ	$E_B = .32, \rho = -.81$
K	$\exp(-(E_S - E_B)/(kT))$	M_R^κ	$E_S = .9, \kappa = -.81$
m	$\exp(-E_m/(kT))$	M_R^μ	$E_m = .65, \mu = -.29$
a	$(\Sigma_i [\nu_{0,i} \exp(-E_{\nu,i}/(kT))]^2)^{1/2}$	M_C^α	$E_{\nu,i} = .46, \nu_{0,i} = 1, \alpha = 1$
e	None	M_C^ε	$\varepsilon = -.5$
b	$\exp(-E_b/(kT))$	$M_R^{b_R} M_C^{b_C}$	$E_b = .65, b_R = 1/3, b_C = 1/4 + 2/3$
h	$\exp(-E_h/(kT))$	$M_R^{h_R} M_C^{h_C}$	$E_h = -.65, h_R = .5, h_C = -2/3$

Note: Equations and estimated empirical values come from Rall et al. (2012), Gilbert et al. (2014), and DeLong et al. (2015); we refer interested readers to those papers for details. Activation energies (E_i) have units eV, and Boltzmann's constant is $k = 8.62 \times 10^{-5}$ eV/Kelvin.

where E_B is the activation energy of metabolism B (in units of eV), k is Boltzmann's constant ($\approx 8.62 \times 10^{-5}$ eV/Kelvin), and T is the temperature (in Kelvin).

Resource carrying capacity, K, is determined by the ratio of the supply rate of nutrients into the system, S, and the rate of uptake of nutrients by the resource, r. With supply rate also scaling as a Boltzmann-Arrhenius factor with activation energy E_S, the prediction for carrying capacity becomes

$$K(T) = K_0 \exp\left(-\frac{E_S - E_B}{kT}\right).$$

Thus, whether carrying capacity increases or decreases with temperature depends on whether supply rate increases faster than metabolism with temperature, $E_S \gtrless E_B$. In the main text, we assume $E_S > E_B$, such that carrying capacity increases with temperature (DeLong and Hanson 2011; Gilbert et al. 2014). The response of carrying capacity to temperature is, however, uncertain because of the temperature response of limiting abiotic resources (Savage et al. 2004; O'Connor et al. 2011; Gilbert et al. 2014), and so we explore $E_S \leq E_B$ in the supplementary material.

Attack rate, a, depends on the temperature dependence of the body velocities, ν, in both species, both of which scale as Boltzmann-Arrhenius factors with activation energies $E_{\nu,i}$, for $i = \{R, C\}$. When individuals move randomly before detection, the attack rate is

$$a(T) = a_0 \sqrt{\sum_i \left[\nu_{0,i} \exp\left(-\frac{E_{\nu,i}}{kT}\right)\right]^2}$$

(Dell et al. 2014), where $\nu_{0,i}$ are rate constants. Consumer mortality is also expected to scale as a Boltzmann-Arrhenius factor,

$$m(T) = m_0 \exp\left(-\frac{E_m}{kT}\right).$$

Conversion efficiency is assumed to be independent of temperature, such that $e(T) = e_0$.

With the above dependencies, we can make predictions for how consumer-resource dynamics will change with temperature. First, warming increases attack rate and carrying capacity, which causes a greater flow of biomass from resource to consumer (B_{CR}; gray curve in fig. 1*A*, obscured by black curve). Second, warming increases consumer mortality, which causes a decline in the relative biomass of the consumer at equilibrium ($\hat{C}:\hat{R}$; gray curve in fig. 1*B*). And finally, the warming-induced increases in attack rate and carrying capacity also cause the system to become less stable (gray curve in fig. 1*C*).

Adding Mass Dependence and the Temperature-Size Rule

We next allow the population dynamic parameters to depend on the body sizes of the interacting species. Following DeLong et al. (2015), each parameter can be written as a power-law function of the body mass of the resource, M_R, or of the consumer, M_C. Here we combine DeLong et al. (2015) and Gilbert et al. (2014) by letting the constants depend on mass: $r_0 = r_0^* M_R^\rho$, $K_0 = K_0^* M_R^\kappa$, $a_0 = a_0^* M_C^\alpha$, $e_0 = e_0^* M_C^\varepsilon$, and $m_0 = m_0^* M_C^\mu$.

If mass does not change with temperature, then adding these mass dependencies does not change the response of the consumer-resource dynamics to changes in temperature. However, as stated above, mass is expected to change with temperature, according to the TSR (Atkinson 1994; Gardner et al. 2011; Forster et al. 2012). We incorporate a simple form of the TSR here for illustrative purposes. In particular, we assume that the body masses of both resource and consumer decline linearly with temperature,

$$M_i(T) = M_i(T_{ref})[1 - \beta_i(T - T_{ref})],$$

where $i = \{R, C\}$, β_i is the fraction by which mass is reduced as temperature is increased by 1°C, and T_{ref} is a reference temperature, which we arbitrarily set to 15°C throughout. This linear decline best approximates the response of organisms with a dry mass of less than 10^{-3} mg (i.e., unicellular consumer and resource; e.g., DeLong 2012). Larger organisms exhibit nonlinear temperature-size responses (Forster et al. 2012; Horne et al. 2015), which could easily be incorporated but are ignored here for simplicity. Our linear approximation still works well for large organisms when the change in temperature is small.

Adding mass dependencies and the TSR modifies our prediction of how consumer-resource dynamics will respond to changes in temperature (black curves in fig. 1*A*–1*C*). While there is little change in B_{CR} (at least with symmetric temperature-size responses in consumer and resource), the equilibrium consumer-to-resource biomass ratio, $\hat{C}:\hat{R}$, is no longer expected to decline with increasing temperature, and stability is now expected to increase. These changes are brought about by the indirect effects of temperature, through body mass, on the population dynamic parameters. In particular, the lack of decline in $\hat{C}:\hat{R}$ with a temperature-size response, relative to the case without it, is primarily driven by changes in consumer conversion efficiency and the intrinsic growth rate of the resource. Both of these rates increase with declining body mass, supporting a relatively larger consumer biomass at higher temperatures. The increase in stability at higher temperatures with a temperature-size response is caused by the increase in the resource's intrinsic growth rate, along with a decrease in attack rate with decreasing consumer body size (see supplementary material
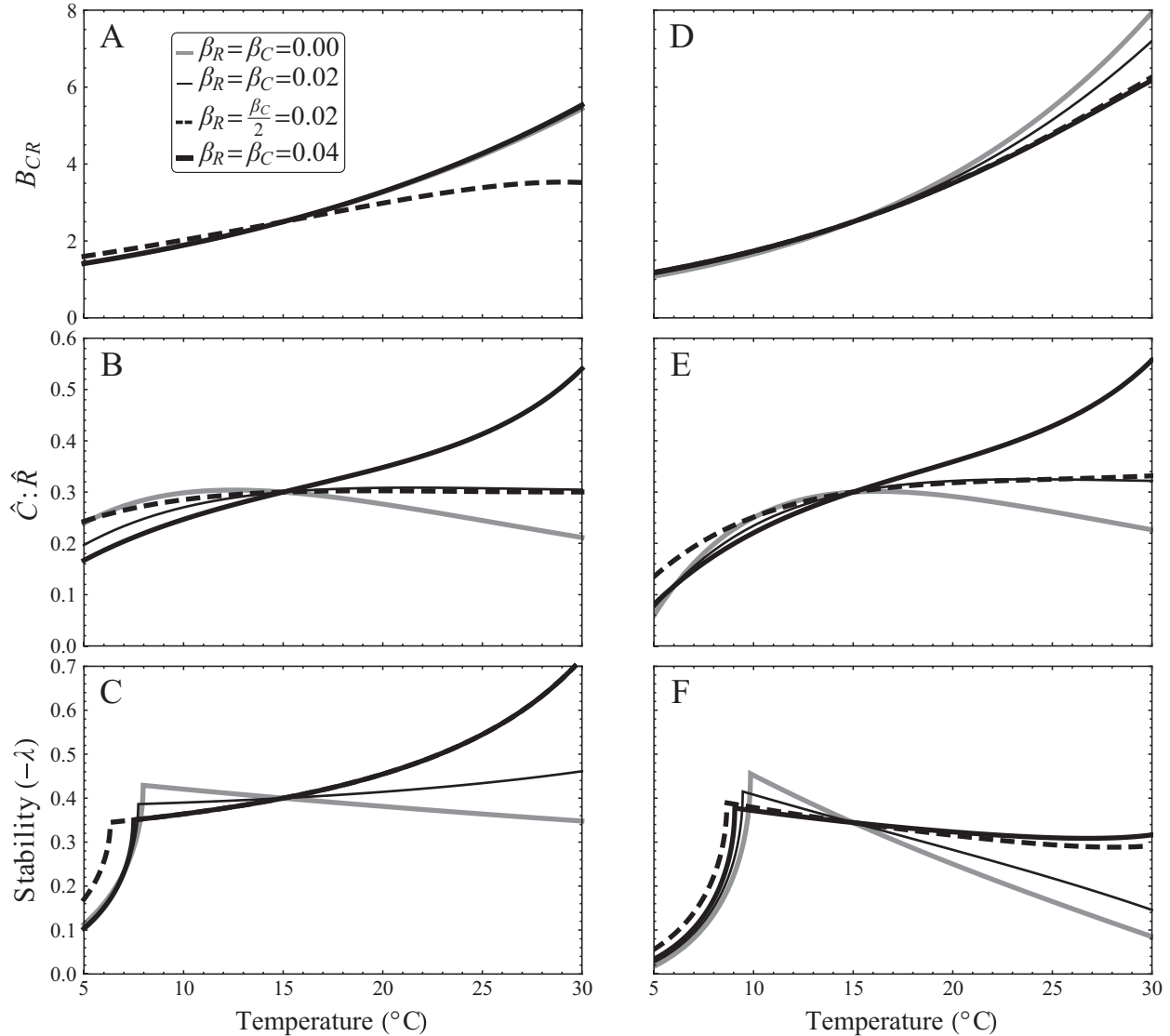
Figure 1: B_{CR}, equilibrium consumer-to-resource biomass ratio $\hat{C}:\hat{R}$, and stability of the coexistence equilibrium as functions of temperature *T*. Shown are results with a type I functional response (*A–C*) and a type II functional response (*D–F*), with (black curves) and without (gray curves) the temperature-size rule (TSR). Three TSR scenarios are shown: weak symmetric temperature-size responses (thin black curves), asymmetric temperature-size responses (dashed black curves), and strong symmetric temperature-size responses (thick black curves). Rate constants (r_0^*, K_0^*, a_0^*, b_0^*, m_0^*, and e_0^*) were chosen to make $r = 2$, $K = 100$, $f(R) = 0.1$, $m = 0.6$, and $e = 0.15$ at 15°C (as in fig. 3 of Gilbert et al. 2014). In *D–F*, we used $h_0^* = 10^{-13}$, so that the coexistence equilibrium was stable over the range of temperatures shown. Other parameters given in table 1.

for details). So we see that in the case of stability, the indirect effect of temperature is stabilizing, and its effect is strong enough to override the direct, destabilizing effect of temperature, producing a qualitatively different prediction for how consumer-resource systems will respond to warming.

Note that our model predicts that the equilibrium biomass ratio, $\hat{C}:\hat{R}$, and stability will not decrease with warming whenever body mass declines at least 2%/°C ($\beta_C = \beta_R =$

$\beta \geq 0.02$; thin black curves in fig. 1*B*, 1*C*), a realistic response for many aquatic species (Forster et al. 2012; Horne et al. 2015). In addition, our model predicts that $\hat{C}:\hat{R}$ will increase with temperature when $\beta \geq 0.03$ (thick black curve in fig. 1*B*). Larger temperature-size responses are predicted to cause faster increases in the biomass ratio and stability with temperature (see supplementary material for details).

Asymmetric Temperature-Size Responses

Larger aquatic organisms often experience larger proportional declines in body size with temperature (Forster et al. 2012; Horne et al. 2015). To explore this asymmetric effect of temperature on body size (while still assuming linear declines, for simplicity), we let consumer body size decline twice as fast as the resource body size, $2\beta_R = \beta_C$ (dashed curves in fig. 1). The main effect of the asymmetric temperature-size response is that B_{CR} now asymptotes at warm temperatures (compare dashed and solid black curves in fig. 1*A*). This is primarily driven by the now larger relative decline in attack rate with warming-induced body size reductions.

Type II Functional Response

Thus far we have considered a simple type I functional response. The consumption of resources in some systems may be better described by a type II functional response,

$$f(R)R = \frac{bR}{1 + bhR},$$

where b is sometimes called the capture rate (the per resource biomass per consumer biomass rate of resource biomass consumption) and h the handling time. This collapses to a type I functional response at low resource biomass, $f(R)R \approx bR$ for $R \ll 1/(bh)$. At high resource biomass, a type II functional response implies that the rate of resource consumption per consumer biomass asymptotes at $\lim_{R\to\infty} f(R)R = 1/h$, describing a limit in the consumption rate of the consumer.

Both capture rate and handling time are known to depend on temperature and body mass. In particular, Rall et al. (2012) argue that capture rate scales as

$$b(T, M_R, M_C) = b_0^* M_R^{b_R} M_C^{b_C} \exp\left(-\frac{E_b}{kT}\right)$$

and handling time as

$$h(T, M_R, M_C) = h_0^* M_R^{h_R} M_C^{h_C} \exp\left(-\frac{E_h}{kT}\right).$$

With these temperature and mass scalings, the type II functional response increases faster with temperature than the type I functional response. Much of the difference in the reactions of the functional responses to temperature is due to the differing temperature and mass dependencies of attack rate, a, and capture rate, b, and is not due to the form of the functional responses (i.e., setting $h = 0$ has little effect on the response of the type II functional response to temperature). When capture rate has the same temperature and mass dependencies as attack rate (as given in Gilbert et al. 2014), both the type I and type II functional re-

sponses respond similarly to temperature (see supplementary material for details).

With the parameter values given in Rall et al. (2012), we can plot B_{CR}, $\hat{C}:\hat{R}$, and stability as functions of temperature when there is a type II functional response (fig. 1*D*–1*F*). We find that including body size scaling with temperature according to the TSR induces similar changes with both type II and type I functional responses: under warming, body size scaling (1) induces minor changes to the rate at which B_{CR} increases, (2) prevents equilibrium consumer-to-resource biomass ratio from decreasing, and (3) increases stability in the consumer-resource system. However, with a type II functional response, a relatively strong temperature-size response ($>5\%/°C$) is required for stability to increase with temperature.

In this analysis, we chose b_0^* such that $f(R) = 0.1$ at 15°C, to remain consistent with Gilbert et al. (2014). This leaves h_0^* as a free parameter, which does not affect B_{CR} and $\hat{C}:\hat{R}$ but does influence stability. We find that increasing h_0^* lowers stability at the reference temperature and causes stability to decrease faster under warming. The faster declines in stability with temperature when h_0^* is larger are caused by greater lags in the numerical response of the consumer to changes in resource biomass (Murdoch et al. 2003).

Finally, Rall et al. (2012) compiled a large database on capture rates and handling times and compared the data to their theoretical predictions. They found that capture rate and handling time responded less strongly to temperature than expected (see their fig. 2*a*, 2*d*). Interestingly, we find that including the temperature-size rule reduces the sensitivity of both capture rate and handling time to temperature (see supplementary material) and hence may help explain the discrepancies between the data (in which body size may have changed) and the theoretical predictions.

Discussion

Here we have demonstrated that warming-induced changes in body size may have important dynamical consequences for food webs in changing thermal environments. In our temperature- and mass-dependent consumer-resource model, with empirically derived parameter estimates (compiled in Rall et al. 2012; Gilbert et al. 2014; DeLong et al. 2015), including the temperature-size rule (TSR) qualitatively alters the predicted outcome of consumer-resource dynamics in response to temperature. When body sizes decline with warming at rates consistent with empirical observations (Forster et al. 2012; Horne et al. 2015), consumer-resource biomass ratios remain stable or increase under warming, which differs from the expected declines when body sizes do not change with temperature (fig. 1*B*, 1*E*). Furthermore, with sufficiently strong body size responses, inclusion of the TSR can facilitate an increase in system stability with warming, differing from

the predicted decrease in stability when body sizes are constant across temperatures (fig. 1*C*, 1*F*).

That the TSR enhanced stability is our most striking result. This enhancement occurred even though warming caused a monotonic increase in the flow of biomass from resource to consumer, B_{CR}, and an equal or greater consumer-resource biomass ratio, $\hat{C} : \hat{R}$. This apparently surprising result makes sense in light of general theory on consumer-resource interactions. In particular, any biological mechanism that increases the strength of intraspecific interactions relative to the strength of interspecific interactions acts to enhance the stability of consumer-resource dynamics (Chesson and Kunag 2008; McCann 2011). When body sizes change with temperature, warming results in a larger increase in intrinsic growth rate, r, relative to the increase in carrying capacity, K. Increasing r relative to K enhances the strength of intraspecific competition in the resource, stabilizing the dynamics. Meanwhile, greater increases in the conversion efficiency, e, and resource carrying capacity, K, when body sizes decrease with temperature result in stronger interspecific interactions at warmer temperatures (eq. [2]), which is destabilizing. Therefore, the enhanced stability conferred by the TSR appears to be due to intraspecific competition in the resource increasing relatively faster than the consumer-resource interaction strength with warming. It is important to note, however, that the stabilizing effect of increasing r is contingent on the assumption of a stable (nonoscillating) consumer-resource equilibrium (May 1976; McCann 2011; Nilsson and McCann 2016). If, on the other hand, the consumer-resource equilibrium was, for example, oscillating in a limit cycle with a type II functional response, then increasing r would destabilize the system further (see supplementary material).

The magnitude of body size declines used here was drawn from a comprehensive synthesis of experimentally observed temperature–body size responses in organisms ranging from fish to microbes (Forster et al. 2012). Our theoretical results thus show that temperature-size responses of realistic strengths can have large effects on system composition and stability. However, rates of body size decline vary considerably across studies (e.g., ranging from 6% to -2%/°C in unicellular organisms; Forster et al. 2012), and methodological details may contribute to this variability. For example, most studies do not hold resource biomass constant across temperature treatments, so slopes of body size decline with temperature likely confound physiological effects with resource-supply effects (DeLong 2012). In his experimental system, DeLong (2012) found that when resources were kept constant, the physiological size response to temperature was closer to -15%/°C. While both effects of temperature are likely important and may result in a roughly -2%/°C scaling rate, articulating the physiological metabolic effects separately from those driven by resource-supply changes could substantially improve estimates of the strength of

temperature-size responses. In our model, larger temperature-size responses have yet larger consequences on consumer-resource dynamics, although the same qualitative results ($\hat{C} : \hat{R}$ does not decline under warming, and stability increases with temperature) are reached whenever body mass declines at least 2%/°C. Another cause of variability in the temperature-size response is mean adult body size before warming (Forster et al. 2012; Horne et al. 2015): larger species generally exhibit larger proportional declines with temperature. In our model, when the consumer exhibits a larger temperature-size response than the resource, the strength of the interaction, B_{CR}, becomes less sensitive to temperature (dashed curve in fig. 1*A*), and vice versa when the resource has the larger temperature-size response (see supplementary material). Meanwhile, we found that the biomass ratio, $\hat{C} : \hat{R}$, depends primarily on the temperature-size response of the resource, while stability depends primarily on the temperature-size response of the consumer. Thus, our model prediction that temperature-size scaling reduces the sensitivity of consumer and resource biomasses to temperature is robust to variation in the form of the TSR.

Our conclusions are based on a number of simplifying assumptions. For example, we have used the Arrhenius equation with constant activation energies to describe the response of population-level parameters to temperature. Although many biological rates exhibit a unimodal temperature response (Angilletta 2009; Dell et al. 2011), there is good reason to expect current temperatures to fall within the rising portion of their temperature-response curves (Martin and Huey 2008), and the Arrhenius equation with constant activation energy is the best fit for the majority of existing data (Pawar et al. 2016). We have also used a simple consumer-resource model with one set of (empirically justified) parameters. However, we have shown that the qualitative results are robust against some deviations in model structure (e.g., functional response) and parameter values (e.g., strength and asymmetry of the temperature-size response). Other deviations change the result; for example, when the activation energy of the supply rate is less than that of metabolism, $E_S < E_B$, the temperature-size response has little effect on stability (see supplementary material). Thus, while we have shown that the temperature-size response will likely stabilize many consumer-resource systems under warming, the temperature-size response may not affect or destabilize other systems. We hope that this initial demonstration stimulates future work that relaxes assumptions and generalizes across larger regions of parameter space.

The simplified approach we have taken could be expanded in several other interesting ways. For instance, we consider only two interacting species. Additional resources, among which the consumer could switch, or multiple consumers competing for a single resource could produce complex dynamics under warming if the various resources

and consumers responded differently to temperature. Likewise, it would be interesting to incorporate additional trophic levels to evaluate how including the TSR affects the strength of mass- and temperature-dependent trophic cascades (DeLong et al. 2015). Another interesting extension would be to add size structure and let the consumer-resource interaction impose selection on body size (Abrams and Rowe 1996). Size structure itself can produce complex dynamics (Ohlberger et al. 2011), and incorporating life-history evolution is thus likely to produce yet more unexpected results.

Our results create a number of new, testable predictions for how warming might affect outcomes in experimental consumer-resource systems that exhibit a temperature-size response. The two most straightforward are (1) the equilibrium consumer-to-resource biomass ratio is expected to increase with temperature when there is a sufficiently strong temperature-size response but is expected to decrease without it and (2) consumer and resource biomasses are expected to become more resilient to perturbation at warm temperatures when there is a sufficiently strong temperature-size response but are expected to become less resilient without it. Testing these predictions may be achieved through experimental manipulation of body sizes within systems to affect the strength or asymmetry of body size scaling with temperature (e.g., artificial selection for similar body sizes) or through comparative analysis across systems in which the coefficient of temperature-size scaling naturally varies (e.g., aquatic vs. terrestrial; Forster et al. 2012; Horne et al. 2015). Given the importance of the TSR for the outcome of community interactions in the face of warming, experimental tests of the effects of temperature on body size are needed in multitrophic systems.

Acknowledgments

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The temperature-size response is expected to stabilize consumer-resource systems under warming, meaning that plastic changes in predators like this backswimmer (*Notonecta glauca*) may improve their chance of persistence. Photo credit: Michelle Tseng.