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A Mechanistic Approach for Modeling Temperature-Dependent Consumer-Resource Dynamics

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ABSTRACT: Paramount to our ability to manage and protect biological communities from impending changes in the environment is an understanding of how communities will respond. General mathematical models of community dynamics are often too simplistic to accurately describe this response, partly to retain mathematical tractability and partly for the lack of biologically pleasing functions representing the model/environment interface. We address these problems of tractability and plausibility in community/environment models by incorporating the Boltzmann factor (temperature dependence) in a bioenergetic consumer-resource framework. Our analysis leads to three predictions for the response of consumer-resource systems to increasing mean temperature (warming). First, mathematical extinctions do not occur with warming; however, stable systems may transition into an unstable (cycling) state. Second, there is a decrease in the biomass density of resources with warming. The biomass density of consumers may increase or decrease depending on their proximity to the feasibility (extinction) boundary. Third, consumer biomass density is more sensitive to warming than resource biomass density (with some exceptions). These predictions are in line with many current observations and experiments. The model presented and analyzed here provides an advancement in the testing framework for global change scenarios and hypotheses of latitudinal and elevational species distributions.

Keywords: predator-prey, allometry, global change, environmental variability, temperature, mathematical model.

Many of the characteristics that researchers use to describe biological populations and communities, such as their density, distribution, diversity, and dynamics, rely on environmental temperature. Recent climate projections suggest that unprecedented warming will occur in many of the earth's environments during the current century (Houghton et al. 2001) with uncertain impacts on biological populations and communities. Predictive models often consider that populations persist within a range of climatic conditions known as their climate envelope. Current climate projections indicate that envelopes and their inhabitant populations will move to higher latitudes in response to changing conditions because of local speciation and extinction events at the range extrema or changes in migratory routes (Parmesan et al. 1999). Although evidence for such shifts in nature is accumulating (Parmesan et al. 1999; Humphries et al. 2002; Root et al. 2003), they may not occur as predicted by the population envelope approach since the envelopes of interacting species may not change symmetrically (Davis et al. 1998), the temporal associations of species may become disrupted (Harrington et al. 1999), and, for populations with fixed ranges, the strength of the interactions themselves may vary with temperature (Post et al. 1999; Jiang and Morin 2004). This suggests we should invest in models treating communities rather than populations as the basic unit with which to assess the importance of environmental change (e.g., Ives 1995; Ripa et al. 1998; Ripa and Ives 2003).

Known physiological constraints and responses of organismal and within organism processes have been paramount in formulating predictions for population processes. Such approaches use a bioenergetic framework to estimate the flux in measurable individual and population parameters associated with changes in body size (e.g., Peters 1983) and temperature (e.g., Brown et al. 2004). These relationships have then been used to explain variability in metabolic rate (Gillooly et al. 2001), developmental rate (Gillooly et al. 2002), population growth rate (Savage et al. 2004), and global trends in species density (Enquist and Niklas 2001); to predict temperature-induced changes in population ranges (Humphries et al. 2002) and energy

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usage (Ernest et al. 2003); and to describe gradients of global biodiversity (Allen et al. 2002). The extension of bioenergetic models to the community level has been limited to the analysis of body size in consumer-resource dynamics (Yodzis and Innes 1992). Extending this bioenergetic framework to include community-based temperature dependence will arguably provide a useful tool for the description and prediction of communities in changing environments.

Although more realistic, community models require additional parameter and function specification often coming at the cost of generality, and when the interactions among populations are themselves dependent on environmental conditions, scaling up models to the level of communities and ecosystems leads to an explosion in the number of required parameters. Researchers are left with a trade-off between model simplicity, which allows mathematical tractability but sacrifices model comprehensiveness. We address this problem with a general but biologically plausible model for temperature dependence in consumer-resource systems. We combine the bioenergetic-allometric framework provided by Yodzis and Innes (1992) with a recent advancement in temperature scaling theory (Gillooly et al. 2001; Brown et al. 2004) to scale the per unit time parameters of a consumer-resource model. We show that the mathematical analysis of this system remains tractable while incorporating environmental dependence in a biologically pleasing manner. We make three main predictions for the dynamics of consumer-resource systems undergoing long-term temperature change and show that this framework has great potential for future analyses of global change scenarios and ecological species gradients.

The Model

Yodzis and Innes (1992) provided the following framework for a system of consumers and resources based on the model first proposed by Rosenzweig and MacArthur (1963):

$$\frac{dR}{dt} = rR\left(1 - \frac{R}{K}\right) - \frac{JC}{f_e}\left(\frac{R}{R + R_0}\right),$$

$$\frac{dC}{dt} = C\left[-M + (1 - \delta)J\left(\frac{R}{R + R_0}\right)\right], \tag{1}$$

where the state variables R and C describe the amount of energy in the resource and consumer populations in units of biomass density (mass per unit area). In the absence of consumers ($C = 0$), resources increase according to the Verhulst equation, which is described by the production/biomass ratio r and the population carrying capacity K. Consumers ingest resources according to a Monod function defined by the maximum ingestion rate J and the resource density required to achieve half-saturation of this rate, R_0 (Yodzis and Innes [1992] used a more general form of the functional response capable of producing a sigmoidal saturation function). The parameter δ is the fraction of biomass lost during ingestion and digestion, and f_e is the fraction of biomass removed from the resource population that is actually ingested by the consumer. The parameter M represents the amount of energy lost to consumer metabolism. This basic model structure can be easily iterated to include more diverse trophic structures and levels, although particular attention must be paid to the implementation of multispecies functional responses (Koen Alonso and Yodzis, forthcoming). All parameters used in the model are nonnegative.

Yodzis and Innes (1992) recognized the need to reduce the number of parameters in this model in order to obtain a general theory for the dynamics of consumer-resource systems. They suggested that the per unit time rates r could be scaled with resource body mass (m_R) and J and M with consumer body mass (m_C) according to empirically derived power laws and assuming a scaling exponent of 0.75. The "true" value of such scaling exponents remains a contentious point, but Brown et al. (2000) present strong derivations for quarter-power scaling laws in biology. Standardizing these relationships by body mass generates a mass-specific scaling exponent -0.25, which can then be incorporated in the energetic model framework using power functions.

Our argument for the inclusion of temperature as a parameter in consumer-resource models originates from its ability to explain variability in rates of growth, ingestion, and metabolism in the empirical literature; second to body mass, temperature explains the largest amount of residual variation in biological rates (Peters 1983). The wide range of temperature experienced by many species influences their rates of growth, foraging, reproduction, and metabolism (among others) via a direct influence on enzyme kinetics. This influence is often described using the empirically derived coefficient Q_{10} as the change in rate associated with a 10° change in temperature. This constant has been measured for a suite of biological and ecological rates across a broad taxonomic scale (e.g., Peters 1983). However, recent advances in metabolic theory have shown that scaling biological rates in this manner can lead to as much as 15% error over the range of biologically plausible temperatures from 0° to 40°C since the Q_{10} is itself dependent on temperature (Gillooly et al. 2001). Rather, it is more precise to scale rates according to the Boltzmann factor $e^{-E/kT}$, where T is temperature in Kelvin, E is the activation energy, and k is Boltzmann's constant (Gillooly et al. 2001). This factor originates from first principles;

Table 1: Empirically derived intercepts (a_i) of the allometric relationships from Yodzis and Innes (1992) in kg (kg year)$^{-1}$ kg$^{0.25}$

Parameter	$a_i(T_0)$	Details	Source
Metabolism a_M (T_0):			
Vertebrate ectotherms	2.3[a]	Average field metabolic rate for iguanid lizards and active metabolic rate in salmon	Brett and Glass 1973; Nagy 1982
Invertebrates	.51 (20)	Average oxygen consumption for 77 species of marine zooplankton	Ikeda 1977
Ingestion a_J (T_0):			
Vertebrate ectotherms	6.4[b]	Derived from maximal O_2 consumption in lizards and in feeding experiments in salmon	Brett 1971; Bennett and Dawson 1976
Invertebrates	9.7 (20)	Average feeding rates of eight marine planktonic copepods	Ikeda 1977
Production a_r (T_0):			
Unicells	.386 (20)	Average maximal division rate in 14 species of salt marsh pennate diatoms	Williams 1964

Note: We have added information on the temperatures at which the allometric intercepts were measured, T_0.

[a] Field metabolic rate for iguanid lizards was measured during the active season, which excludes hot, dry periods and cold periods (Nagy 1982). Brett and Glass (1973) measured active metabolic rates at 5°, 15°, and 20°C. We take 20°C as the intercept for this coefficient.

[b] Bennet and Dawson (1976) supplied a summary of $\dot{V}o_{2\max}$ during activity by reptiles at 30°C. Brett (1971) measured food intake at 15°C. Our corrected coefficient for vertebrate ectotherm ingestion at 20°C is 6.4 kg (kg year)$^{-1}$ kg$^{0.25}$ (assuming $E_J = 0.7$ eV).

higher kinetic energy leads to a larger fraction of molecular collisions with enough energy to activate a reaction. We write the biological rate functions including body mass and temperature scaling:

$$\begin{aligned} r &= f_r a_r(T_0) m_R^{-0.25} e^{E_r(T-T_0)/kTT_0}, \\ (1-\delta)J &= f_J a_J(T_0) m_C^{-0.25} e^{E_J(T-T_0)/kTT_0}, \qquad (2) \\ M &= a_M(T_0) m_C^{-0.25} e^{E_M(T-T_0)/kTT_0}, \end{aligned}$$

where the E_i are the rate-specific activation energies. The intercepts of the allometric relationships ($a_i(T_0)$) are empirically derived constants representing the maximum sustainable rates (physiological maxima) measured at temperature T_0, and the f_i are the fractions of those rates realized in nature. The intercepts (a_i) are conservative within each of four metabolic classifications: unicellular poikilotherms, invertebrate poikilotherms, vertebrate ectotherms, and vertebrate endotherms (Robinson et al. 1983). However, the accuracy of these relationships is diminished when the average body masses (m_C, m_R) represent a large, skewed, and/or platy- or leptokurtic distribution of body mass (Savage 2004).

Incorporating temperature dependence into a consumer-resource energetic model not only introduces mathematical complexity but also complicates the assumptions of the model; the methods by which certain metabolic classes cope with heat loss to a cooler ambient environment or heat gain from a warmer ambient environment become an important consideration. For poikilotherms, ambient temperature is closely tracked by body temperature, and thus the expressions in equations (2) should well describe the dependence of community processes on ambient temperature. For ectotherms, the correlation between ambient and body temperature can be weaker because of behavioral thermoregulation; however, ambient temperature still largely determines body temperature for these organisms. For endotherms, maintenance of a constant body temperature invokes complicated rate sensitivities to temperature, requiring model extensions outside the limits of our general framework (e.g., Humphries et al. 2002, 2004).

In a survey of published literature, Yodzis and Innes (1992) provide a set of allometric intercepts for scaling the three biological rates *r*, *J*, and *M* to consumer and resource body mass. We incorporate their intercepts in the size and temperature scaling functions (eqq. [2]) by resolving the temperatures at which they were measured, T_0 (table 1). In addition, we sought studies in the literature describing the effect of temperature on the rates *r*, *J*, and *M*. Gillooly et al. (2001) suggest that the range of activation energies for population rates ought to be within the range of experimentally derived activation energies for all chemical reactions (0.2–1.2 eV), and they provide activation energies for metabolic rates of a variety of functional groups. More commonly, temperature effects have been quantified using Q_{10} coefficients rather than activation energies. Provided that the range of temperatures used to estimate the Q_{10} is known, an approximation of the activation energy (E) can be determined using the relationship

$$E = 0.1(kT_0^2)\ln Q_{10}, \qquad (3)$$

where T_0 is the median of the range over which Q_{10} was measured and k is Boltzmann's constant (Dixon and Webb 1964; Gillooly et al. 2001). It is important to consider that our model formulation precludes the need for estimates of M and J for populations of unicellular organisms since they are herein always assigned to the resource level. Populations of heterotrophic organisms, which may under normal circumstances occupy a "consumer" role, can be incorporated into the model as a "resource" given that their production per unit biomass (r) is some fraction (f_r) of their maximum capacity for ingestion less metabolic costs:

$$r = f_r[(1 - \delta)J - M] \tag{4}$$

(from Yodzis and Innes 1992). As we show later in this article, choice of the function representing maximal production and the realized fraction of this amount has no effect on the qualitative behavior of the system.

We present a short survey of experimentally and empirically derived values of the Q_{10} coefficients and corresponding activation energies for each model parameter and metabolic classification in table 2. While data for metabolism/temperature relationships abound, there has been relatively little work describing the temperature dependence of ingestion and production. We sought to include those studies reviewing a large range of taxonomy to provide "average" values for each metabolic functional group. In one of the larger summaries, Robinson et al. (1983) described the body size and temperature dependence of metabolic rate in 109 species of active fish and reptiles (vertebrate ectotherms) and 729 species of invertebrate poikilotherms, obtaining Q_{10} coefficients of 1.44 and 1.7 for these groups, respectively. These coefficients are smaller than those reported by many studies; however, Clarke and Johnston (1999) noted that Q_{10} coefficients for diverse taxonomic assemblages tended to be smaller than those of single-species groups. They found Q_{10} coefficients of 1.83 for 69 species of teleost fish, while within species, Q_{10} coefficients averaged 2.40. This suggests that some form of functional compensation occurs in response to temperature in the diverse assemblage, highlighting the need for parameter specificity when formulating system-specific predictions. Hansen et al. (1997) provide Q_{10} coefficients for respiration and ingestion rates across a variety of zooplankton functional groups, with coefficients averaging 2.51 and 2.97, respectively. The Q_{10} coefficients for the ingestion rates of vertebrate ectotherms have been measured for juvenile cod using digestion velocity (3.41; Knut-

Table 2: Empirically derived Q_{10} temperature coefficients and their corresponding activation energies

Parameter	Q_{10}	E_i (eV)	Details	Source
Metabolism (E_M):				
Vertebrate ectotherms		.433	Fish	Gillooly et al. 2001
		.500	Amphibians	Gillooly et al. 2001
		.757	Reptiles	Gillooly et al. 2001
	1.44 (5°–40°C)	.274	Standard metabolism of 109 species of active fish and reptiles	Robinson et al. 1983
	1.83 (0°–30°C)	.432	Standard metabolism of 69 species of teleost fish	Clarke and Johnston 1999
Invertebrates		.790	Multicellular invertebrates	Gillooly et al. 2001
	1.7 (0°–40°C)	.393	Respiration rates of 729 species of poikilotherms	Robinson et al. 1983
	2.51 ± .61	.652 ± .061	Respiration rates of seven functional groups including ciliates, meroplankton larvae, and copepods	Hansen et al. 1997
Ingestion (E_J):				
Vertebrate ectotherms	3.41 (6°–13°C)	.671	Digestion velocity in juvenile cod (*Gadus morhua*)	Knutsen and Salvanes 1999
	3.0 (1°–15°C)	.748	Gastric evacuation rate in cod (*G. morhua*)	Temming and Herrmann 2003
Invertebrates	2.97 ± .16	.772 ± .045	Maximal ingestion rates of 11 functional groups including flagellates, ciliates, meroplankton larvae, and copepods	Hansen et al. 1997
	1.9 (10°–22°C)	.462	Flow velocity through the burrow of the filter feeding *Urechis caupo*	Julian et al. 2001
Production (E_r):				
Unicells	1.88 (0°–40°C)	.467	Maximum expected growth rate for marine and freshwater photoautotrophic algae	Eppley 1972
	2.8 (20°–30°C)	.788	Net photosynthesis in lake cyanobacteria mats	Wieland and Kühl 2000

Note: The Boltzmann constant $k = 8.618 \times 10^{-5}$ eV K^{-1}.

sen and Salvanes 1999) and gut evacuation rate (3.0; Temming and Herrmann 2003). Eppley (1972) summarized data for phytoplankton growth in marine and freshwater environments and found that growth rates fell between 0 and μ doublings per day, where $\log_{10}\mu = 0.0275T - 0.070$ and T is measured in degrees Celsius. This relationship gives a $Q_{10} = 1.88$ for the rate of maximal primary production in unicellular organisms. The inefficiency of C3 photosynthesis at high temperatures due to photorespiration may explain the relatively weaker dependence of primary production on temperature when compared with heterotrophic metabolism (Ricklefs and Miller 2000). Last, the assimilation efficiency $(1 - \delta)$, which is independent of both body size and temperature (Peters 1983), is related to the food type: 0.45 for herbivorous consumers and 0.85 for carnivorous consumers (see Yodzis and Innes 1992).

Model Analysis

In the analysis of differential equation models, it is useful to define both the qualitative and quantitative response of the model to changes in parameter values. Here we focus on the model's response to temperature. We refer to the changes in the stability of the equilibrium (stable/unstable) and the character of the equilibrium (node, focus, limit cycle) as qualitative changes. The response of the equilibrium densities and their resilience are herein described as quantitative changes. For simplicity, we describe our results only in response to increasing temperature (herein called warming) since the effect of decreasing temperature is easily inferred.

Qualitative Response to Temperature Change

For the purpose of determining the qualitative behavior of the model equilibrium, it is useful to define the nondimensionalized model (see app. A for derivation):

$$\frac{dR}{dt} = R\left(1 - \frac{R}{K}\right) - \frac{xy}{(1-\delta)f_{\mathrm{e}}}\left(\frac{RC}{R+R_0}\right),$$

$$\frac{dC}{dt} = xC\left[-1 + y\left(\frac{R}{R+R_0}\right)\right], \tag{5}$$

where the units of time have been chosen such that $r = 1$. Correcting all allometric relationships such that the a_i define the rate at $T_0 = 20°\mathrm{C}$ (293 K), we can represent the new parameters x and y as

$$x = \frac{M}{r} = \frac{a_M m_C^{-0.25}}{f_r a_r m_R^{-0.25}} \times e^{-(E_r - E_M)(T-T_0)/kTT_0}, \tag{6}$$

$$y = \frac{(1-\delta)J}{M} = \frac{f_J a_J}{a_M} \times e^{(E_J - E_M)(T-T_0)/kTT_0}. \tag{7}$$

Parameter x describes the rate of consumer metabolism normalized to the production biomass ratio of the resource population, and parameter y is the consumer's realized rate of ingestion per unit metabolism (Yodzis and Innes 1992). The two parameters x and y contain the temperature dependence of the model, and these quantities are in turn governed by the activation energy differences $E_r - E_M$ and $E_J - E_M$. The difference $E_r - E_M$ represents the potential thermal efficiency (PTE) of the consumer-resource system. For positive values of PTE, the system has an increasing potential to retain energy with warming; increases in production at the resource level outpace increases in energy metabolism at the consumer level. This change in system energy is a potential change, since the amount of energy lost to trophic transfer can change disproportionately. The impact of the consumer on its resources is determined by the parameter y, whose response to temperature is determined by the difference $E_J - E_M$. For positive values, warming-induced increases in the maximum ingestion rate outpace metabolic demands, leading to a larger impact (per unit mass) on the resource population. We call this difference the consumer thermal impact (CTI).

Yodzis and Innes (1992) analyzed the qualitative changes in the equilibrium in response to changes in y and, in doing so, cataloged all possible outcomes for variation in the parameters influencing y. We reiterate their derivations in order to clearly describe how temperature (T) and the activation energies (E_i) influence the model inside this range of previously cataloged behavior.

The model has three possible equilibrium states, and we categorize them according to the existence or nonexistence of each species:

$$\begin{aligned} &\mathrm{Eq}_1: \text{ trivial, } R_{\mathrm{e}}, C_{\mathrm{e}} = 0; \\ &\mathrm{Eq}_2: \text{ resource only, } R_{\mathrm{e}} = K, C_{\mathrm{e}} = 0; \\ &\mathrm{Eq}_3: \text{ coexistence, } R_{\mathrm{e}} = \frac{R_0}{y-1}, C_{\mathrm{e}} = \left(1 - \frac{R_{\mathrm{e}}}{K}\right)\left[\frac{(1-\delta)f_{\mathrm{e}}}{x}\right]R_{\mathrm{e}}. \end{aligned} \tag{8}$$

For plausible parameter combinations, Eq_1 is always unstable, while one of Eq_2 or Eq_3 can be stable depending on parameter values. To determine the response of the qualitative behavior of the model to changes in temperature, it is useful to employ a bifurcation analysis, which tracks equilibria and their inherent characteristics across a range of parameter space. Points in parameter space where equilibria undergo qualitative changes in stability are called bifurcation points.

The exchange of stability between Eq_2 to Eq_3 denotes a transcritical bifurcation, which we herein refer to as the "feasibility boundary" for the system. A feasible two-species equilibrium (Eq_3) exists when $0 < R_e < K$, and therefore $K(y-1) > R_0$ defines the feasibility boundary (transcritical bifurcation) for the two-species system. In the feasible parameter space of Eq_3, the equilibrium has two stable states: a stable node, whereby communities at nonequilibrium densities approach the equilibrium monotonically, and a stable focus, whereby the approach is characterized by decaying oscillations around the equilibrium point. The location of the focus/node boundary is dependent on both model parameters x and y, and its proximity to the feasibility boundary is controlled mainly by the body mass ratio m_C/m_R and PTE (for a full description, see Yodzis and Innes 1992). Also in the feasible parameter space, the equilibrium Eq_3 can be an unstable focus. In this case, it is surrounded by a stable limit cycle, which is approached from outside (inside) by decaying (expanding) oscillations. The Hopf bifurcation denotes the change in stability of Eq_3 from a stable focus to an unstable focus and marks the emergence of a stable limit cycle. The state Eq_3 is locally stable when (see app. A)

$$\frac{K(y-1)}{R_0(y+1)} < 1, \tag{9}$$

and it is locally unstable, but surrounded by a limit cycle, when condition (9) is not satisfied.

From the above equations, it is apparent that the qualitative behavior of the model is completely determined by the parameters R_0, K, and y. To further reduce the dimensionality of the analysis, Yodzis and Innes (1992) defined the ratio R_0/K as an inverse measure of resource abundance as perceived by the consumer population; as R_0 decreases (K increases), consumers perceive a higher density (or enriched) resource supply, resulting in a larger flux of biomass from the resource to the consumer population. We make the assumption that this "inverse enrichment ratio" is independent of temperature, and we discuss the full implications of this assumption later in this article.

We analyze changes in the loci of the feasibility boundary and Hopf bifurcation across a range of biologically plausible temperatures ($0°C < T < 40°C$) and across a range (± 1) in the CTI ($E_J - E_M$). This encompasses a satisfactory range in CTI given that measured activation energies of chemical reactions range from 0.2 to 1.2 eV (Gillooly et al. 2001). Since the value of the parameter y depends only on the consumer population, it is sufficient to perform two bifurcation analyses corresponding to the two possible metabolic classifications for the consumer population considered here. Figure 1 shows the Hopf bifurcation surface for (a) an invertebrate poikilotherm consumer and (b) a vertebrate ectotherm consumer. When $CTI > 0$, the Hopf bifurcation locus increases with warming, reaching an asymptotic value of 1 in the R_0/K plane. This leads to a larger incidence of limit cycles in R_0/K parameter space since limit cycles occur below the Hopf bifurcation. Alternatively, where $CTI < 0$, the Hopf bifurcation locus decreases with warming, and the incidence of limit cycles in R_0/K parameter space lessens. When $CTI = 0$, the Hopf bifurcation is independent of tem-

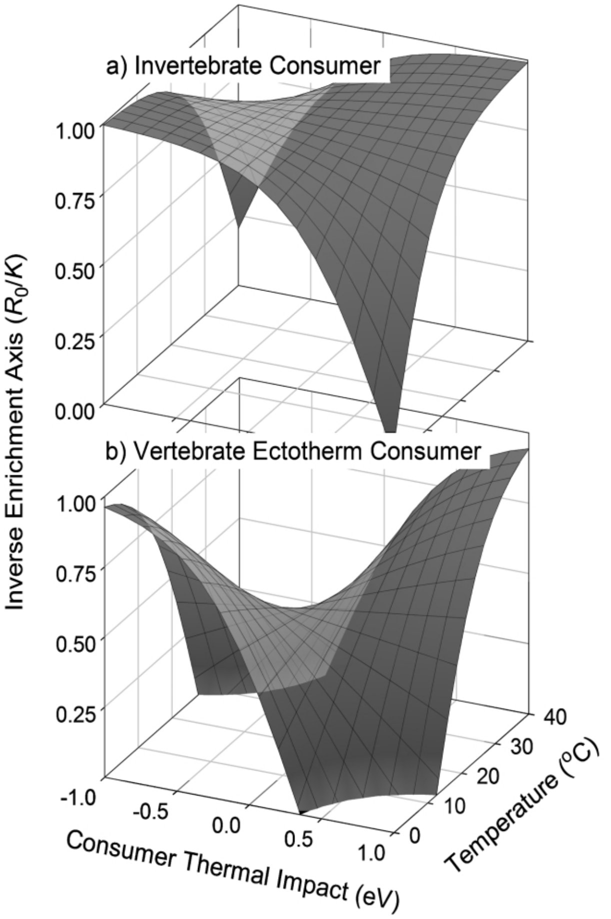

Figure 1: Hopf bifurcation surface across the independent parameters temperature and CTI for (a) an invertebrate consumer ($a_J/a_M = 19$) and (b) a vertebrate ectotherm consumer ($a_J/a_M = 2.8$). Above the Hopf bifurcation, the equilibrium is stable, and below the Hopf bifurcation, the equilibrium is unstable. Along the two independent axes, the Hopf bifurcation surface approaches $R_0/K = 1$ according to a Monod function. The two axes of invariance occur at $CTI = 0$ eV, where temperature change has no effect on the Hopf bifurcation, and at $T = 20°C$, where the intercepts of the temperature-dependent functions are defined.

perature. In both panels, the response of the Hopf bifurcation is similar in nature, but saturation of the curve to $R_0/K = 1$ occurs much quicker for invertebrate consumers (*a*) because of the relative differences in the ratio of the intercepts a_J/a_M (see table 1).

Similar results are observed for the feasibility boundary of invertebrate consumers and vertebrate ectotherm consumers (fig. 2), with the exception that the feasibility boundary is not a saturating function, but rather it grows/decays exponentially with warming. When CTI > 0, the locus of the feasibility boundary grows exponentially with warming, and while CTI < 0, the locus of the feasibility boundary decays exponentially with warming. Below the feasibility boundary, the system is persistent, and where the curve crosses the $R_0/K = 0$ plane, the consumer cannot persist regardless of its capacity to ingest resources.

Empirical estimates of the activation energies influencing the bifurcation loci E_i (table 2) suggest that the CTI for invertebrate consumers falls in the range 0.1–0.38 and for vertebrate ectotherm consumers 0.24–0.47. Figure 3 shows the two-dimensional slices from figures 1 and 2 corresponding to empirical estimates of the CTI from table 2. In both examples, there is an increase in the parameter space occupied by unstable equilibria (limit cycles) with warming (although very slight for invertebrate consumers). However, the proportion of unstable parameter space within the domain of feasible solutions decreases with warming, since the feasibility boundary increases in R_0/K. This leads to two predictions for the qualitative stability of consumer-resource systems in response to warming. First, warming may lead to qualitative instability; for any value of $R_0/K < 1$, a stable system may cross the Hopf bifurcation, resulting in an unstable (cycling) state. Second, warming does not lead to mathematical extinctions (where mathematical extinction corresponds to crossing the feasibility boundary) but rather may facilitate the persistence of consumer-resource systems because of the increase in feasible R_0/K parameter space.

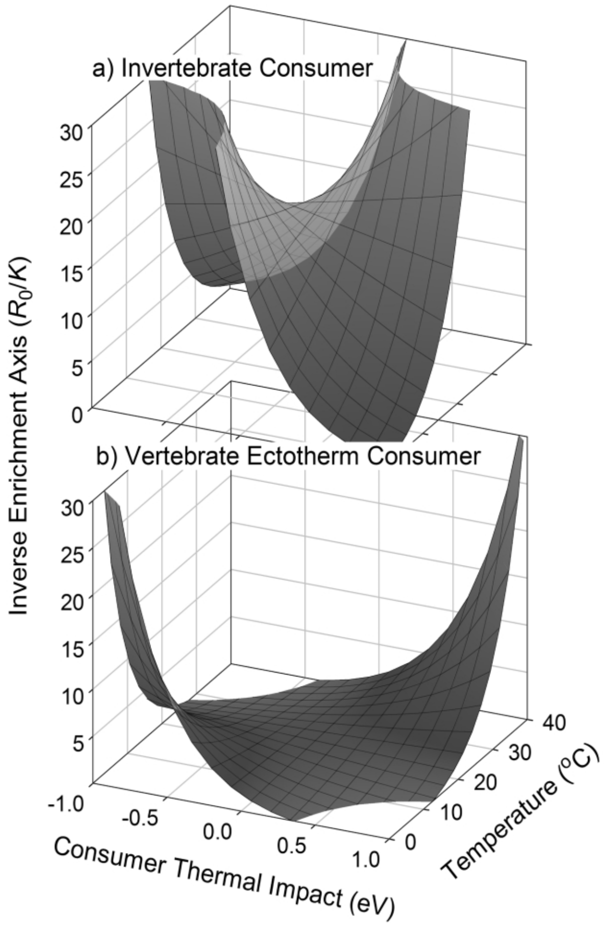

Figure 2: Locus of the feasibility boundary (transcritical bifurcation) across the independent parameters temperature and CTI for (*a*) an invertebrate consumer ($a_J/a_M = 19$) and (*b*) a vertebrate ectotherm consumer ($a_J/a_M = 2.8$). Above the feasibility boundary, the consumer cannot persist. Below the feasibility boundary, both the resource and consumer persist, and in this region, the system stability is determined by the Hopf bifurcation (fig. 1). In both *a* and *b*, the feasibility boundary varies exponentially along the two independent axes. The two axes of invariance occur at CTI = 0 eV, where temperature change has no effect on the feasibility boundary, and at $T = 20°\text{C}$, where the intercepts of the temperature-dependent functions are defined.

Quantitative Response to Temperature

It is useful to determine the quantitative behavior of Eq_3 in response to warming since the density of resource and consumer populations can be highly variable within any particular region of qualitatively similar parameter space. We determine the response of R_e and C_e to temperature using the derivates dR_e/dT and dC_e/dT and using a parameterized example.

The derivative of equilibrium resource density R_e with respect to ambient temperature is a dampened exponential function whose sign is completely determined by the CTI:

$$\frac{dR_e}{dT} = \frac{-R_0 y(E_J - E_M)}{(y-1)^2 kT^2}. \tag{10}$$

This generates a rather simple relationship governing the directional response of equilibrium resource density to temperature change; where the CTI > 0, resource density decreases with warming. Alternatively, if the CTI < 0, resource density increases with warming. Where the CTI $= 0$, resource density is constant across temperature.

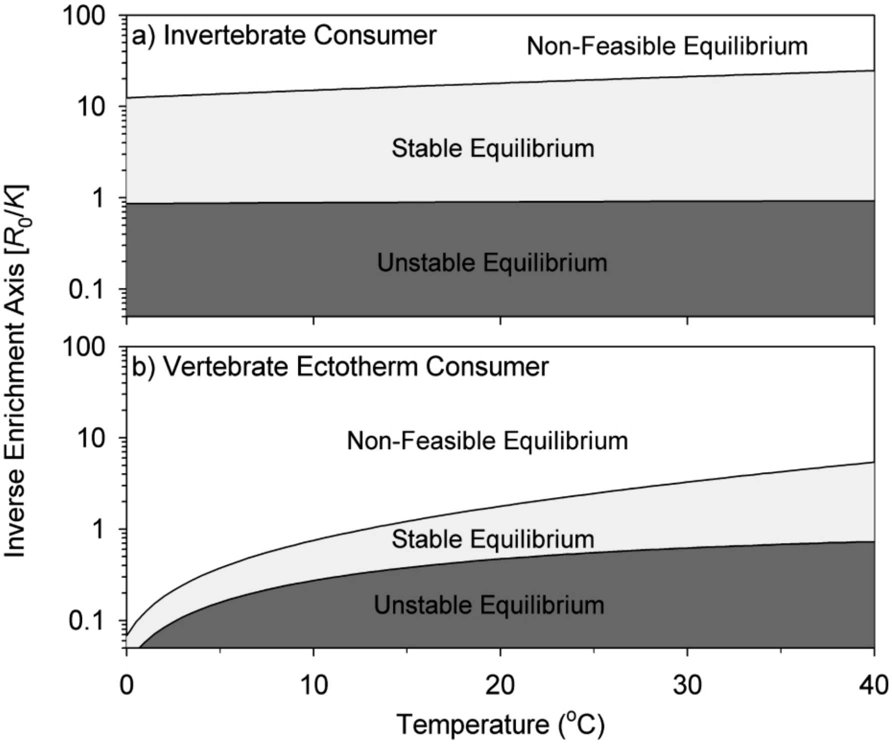

Figure 3: Two-dimensional slices of the bifurcation loci given the CTI values estimated from table 2. For invertebrate consumers (*a*), we estimated CTI from the coefficients $E_J = 0.77$ and $E_M = 0.65$ measured by Hansen et al. (1997). For vertebrate ectotherm consumers (*b*), we estimated CTI from the average values of $E_J = 0.71$ and $E_M = 0.38$ for fish (excluding reptiles and amphibians).

Empirical estimates in table 2 suggest that, for the majority of systems, CTI should be >0 and thus that $dR_e/dT < 0$.

The consumer population displays a more complex response to temperature:

$$\frac{dC_e}{dT} = \frac{(1-\delta)f_e}{x}\left[\frac{(E_r - E_M)(1 - R_e/K)R_e}{kT^2} + \frac{dR_e}{dT}\left(1 - \frac{2R_e}{K}\right)\right], \tag{11}$$

where the sign of dC_e/dT relies on the PTE, the relative equilibrium resource density R_e/K, and the response of equilibrium resource density to temperature (dR_e/dT). With the potential for two real roots, the consumer density may reach local extrema in response to varying temperature; however, these local extrema can lie outside the range of biologically relevant conditions. The analysis of equation (11) proceeds more easily under the assumption that $dR_e/dT < 0$, and the results below adhere to this assumption. Near the feasibility boundary, R_e is only slightly less than K, and thus $dC_e/dT > 0$. This is a rather obvious conclusion given that $C_e = 0$ at the feasibility boundary and increases to positive density with warming. When PTE < 0, dC_e/dT reaches a local maximum in the range $K/2 < R_e < K$ (recall that R_e is decreasing with warming) and is always negative beyond $R_e \leq K/2$. Alternatively, when PTE > 0, dC_e/dT is positive in the range $K/2 \leq R_e < K$ and reaches a local maximum when $R_e < K/2$. It is important to consider that these relationships describe the quantitative behavior of equilibrium resource density in the range of stable parameter space; however, they do not provide any information about the response of equilibrium densities to temperature within unstable (cyclic) parameter space. In this region, it is more informative to perform numerical simulation to obtain the attributes of the limit cycle (see parameterized example below). We therefore proceed in our analysis of the quantitative behavior of the system using numerical simulation of an exemplary consumer-resource system.

Using the coefficients E_M and E_J derived from Hansen et al. (1997), E_r derived from Eppley (1972), and the intercepts listed in table 1, we parameterize a model representing the interaction between a herbivorous invertebrate consumer and a unicellular resource (PTE = −0.19 and CTI = 0.12). Figure 4 shows the equilibrium response of this system to warming given three values of the enrichment

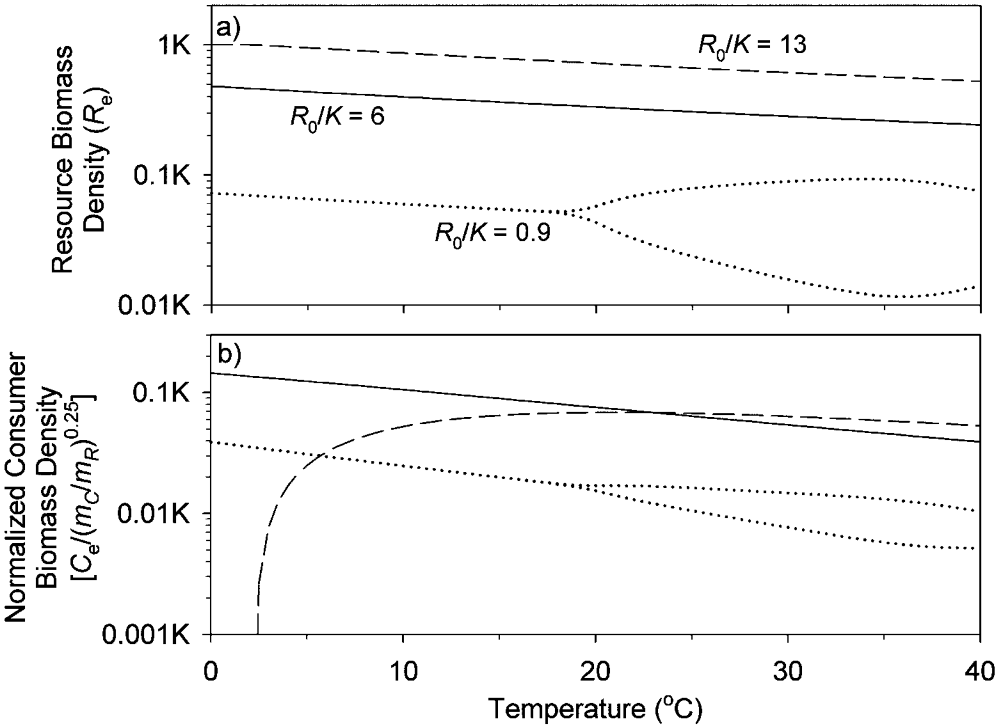

Figure 4: Equilibrium densities of resources (*a*) and consumers (*b*) across a gradient of temperature parameterized to represent the interaction between an invertebrate consumer and a unicellular resource. Resource biomass density is normalized by the carrying capacity *K*; consumer biomass is normalized by the resource carrying capacity *K* and by the body mass ratio $(m_C/m_R)^{0.25}$. Three ratios of the inverse enrichment ratio R_0/K are shown to highlight three potential behaviors: $R_0/K = 13$ (*dashed line*) shows the equilibrium response near the feasibility boundary, $R_0/K = 6$ (*solid line*) shows the equilibrium response in the stable region, and $R_0/K = 0.9$ (*dotted line*) shows the equilibrium response as it crosses the Hopf bifurcation into unstable (cyclic) space. Coefficients a_i are from table 1, $E_r = 0.467$ (table 2; Eppley 1972), $E_{J,M} = 0.772$ and 0.652, respectively (table 2; Hansen et al. 1997), $f_r, f_J, f_e = 1$, and $(1 - \delta) = 0.45$.

ratio R_0/K: a low-enrichment community that crosses the feasibility boundary ($R_0/K = 13$), a medium-enrichment community that remains in the stable state space ($R_0/K = 6$), and a high-enrichment community that crosses the Hopf bifurcation ($R_0/K = 0.9$). Resource density is a decreasing function of temperature for all values of the enrichment ratio within the range of stable state space (fig. 4). In the cyclic domain, the amplitude of cycles generally increases with warming, and the lower bound of the cycle drops to low densities. This occurs in concordance with the "paradox of enrichment," which suggests that consumer-resource systems become unstable and often nonpersistent because of large amplitude cycles after crossing the Hopf bifurcation (Rosenzweig 1971). The response of consumer density is more complicated because of the potential for a local maximum within the range of biologically relevant temperatures. In the low-enrichment community, the consumer density increases with warming as it crosses the feasibility boundary and reaches a local maximum thereafter. The curves for medium and high enrichment are decreasing functions for the range of temperatures shown, since $R_e < K/2$ over the entire range. On the logarithmic scale of figure 4, it is evident that the equilibrium consumer density is more sensitive than the equilibrium resource density given their relative slopes at medium- and high-enrichment levels ($R_0/K = 6$, 0.9; excluding $R_0/K = 13$ since it is proximate to the feasibility boundary). We have factored out the body mass ratio $(m_C/m_R)^{0.25}$ from figure 4*b* to show the characteristic response of consumer biomass density.

Given the coefficients listed in table 2, we expect CTI to be >0 for the majority of systems. This leads to a robust prediction for the response of equilibrium resource biomass density: in the domain of stable solutions, equilibrium resource density declines with warming because of the increasing capacity for ingestion in the consumer population. Similarly, the median density of resources in the unstable domain decreases with warming, with a tendency for high-amplitude cycles at high temperatures. For the consumer population, the response of equilibrium density to warming relies also on the PTE. In our example, PTE is <0, resulting in a decreasing equilibrium consumer density in response to warming when the system is sufficiently far from the feasibility boundary. Systems that are proximate to the feasibility boundary will initially increase with warming and reach a local maximum. For invertebrate consumers, the influence of the feasibility boundary is limited to a small range of the stable parameter space. However, for vertebrate ectotherm consumers whose feasibility boundary is potentially crossed for nearly all feasible values of R_0/K, this effect will be more prominent (see fig. 3).

In addition to changes in the density, it is important to consider changes in the "attractiveness" or resilience of the system. Resilience of the system can be defined as the rate at which population density returns to equilibrium after a perturbation (Pimm 1991), and the negative reciprocal of the dominant eigenvalue of the Jacobian matrix provides a quantitative measure of the amount of time required for the system to reach e^{-1} (or approximately 37%) of the initial perturbation displacement. This measure is an asymptotically unbiased estimate of the actual value; error in the estimate increases with the perturbation displacement. It is important to note that the eigenvalues determined in appendix A are those of the nondimensional system and require back transformation to properly estimate the return time.

Figure 5 shows the dependence of return time on temperature for each of the three low-, medium-, and high-enrichment communities from figure 4. Since the return time is estimated from the dominant eigenvalue of the Jacobian matrix, the effects of consumer and resource body mass cannot be scaled out. We chose body sizes representative of the interaction between zooplankton and unicellular algae that fit the activation energies used in figure 4 (1×10^{-7} kg and 6×10^{-12} kg, respectively). For the low-enrichment community, the feasibility boundary produces a vertical asymptote at low temperatures where the dominant eigenvalue passes through the origin. Similarly, for the high-enrichment community, there is a vertical asymptote at the Hopf bifurcation where the system becomes unstable (at both bifurcation points, the real portion of the dominant eigenvalue is equal to 0, and the return time is thus infinite). For each of the low- and medium-enrichment communities, return time decreases with warming since they are bounded well away from the Hopf bifurcation. The decrease in return time results from a larger throughput of energy at warmer temperatures, which allows the system to equilibrate more quickly following perturbation (see DeAngelis 1992). It is important to consider that larger body sizes of both resources and consumers increase the return time of the system because of their slower per unit mass rates of growth, ingestion, and metabolism but do not qualitatively affect the results.

Discussion

In response to an increase in mean temperature, three general predictions emerge from the analysis of our temperature-dependent model, given the empirical parameter estimates in table 1. First, mathematical extinctions do not occur with warming; however, stable systems may transition into an unstable (cyclic) state. Vertebrate ectotherm consumers are likelier than invertebrate consum-

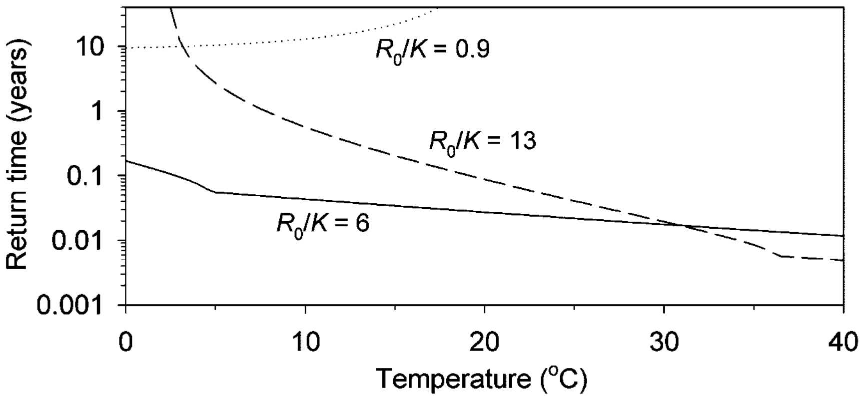

Figure 5: Return times of the consumer-resource system parameterized to represent the interaction between an invertebrate consumer and a unicellular resource at the low-, medium-, and high-enrichment levels shown in figure 4. Return times are estimated as the reciprocal of the dominant eigenvalue of the Jacobian matrix; they represent the time required for the system to reach e^{-1} (or approximately 37%) of the initial perturbation displacement. The abrupt change in the low- and medium-enrichment curves is caused by the qualitative change in stability from stable node to stable focus.

ers to drive the system into an unstable state because of their relatively larger metabolic requirement per unit mass. Second, the biomass density of resources always decreases, and the biomass density of consumers will decrease with warming provided that their existence is not proximate to the feasibility boundary (e.g., consumers are not on the verge of extinction because of an inability to acquire adequate resources). Practical extinctions may occur with warming, given that both resources and consumers can reach low densities. Third, given our exemplary parameters, consumer biomass density is more sensitive to warming than resource biomass density. This prediction depends on the proximity to the feasibility boundary and on the relative magnitudes of CTI and PTE. In the cyclic state, the median biomass density of consumers is more sensitive than that of resources. However, the change in cyclic amplitude is larger for resource biomass density, and since the majority of the cycle period can be spent at low densities, the mean biomass density of resources may show increased sensitivity. This distinction may be important when considering the sensitivity of cyclic systems in nature.

Our predictions for the response of population biomass densities, sensitivities, and community stability and resilience rely on empirical estimates of the intercepts and parameters that govern the scaling functions. The intercepts for production and ingestion provided by Yodzis and Innes (1992; table 1) represent the physiological maxima that can be attained under ideal conditions. Realized rates of these maxima may be only small fractions when species are "ecologically limited" (f_r, $f_J \ll 1$) rather than "physiologically limited" (f_r, $f_J \approx 1$). Our examples for invertebrate and vertebrate ectotherm consumers represent the behavior of the model at the physiologically limited extent. For ecologically limited consumers, the loci of the feasibility boundary and Hopf bifurcations are more sensitive to temperature (e.g., they show more curvature); for example, an ecologically limited invertebrate consumer may have bifurcation curves similar to those of a physiologically limited vertebrate ectotherm consumer. Additionally, the equilibrium densities depend on the extent to which consumers and resources are ecologically or physiologically limited. Despite these dependencies, the trends describing the response of equilibrium densities to warming are independent of the extent of ecological or physiological limitation; ecologically limited species are more prone to undergo the qualitative changes of the first prediction and more likely to behave as systems proximate to the feasibility boundary when at low temperatures for the second and third predictions.

Although our model does not suggest mathematical extinctions will occur at warmer temperatures (mathematical extinction corresponds to crossing the feasibility boundary), biomass densities of both consumers and resources are predicted to decline with warming, increasing their susceptibility to extinction through demographic stochasticity, genetic bottlenecks, and Allee effects. In addition, we predict that systems may destabilize with warming, leading to limit cycles with relatively low minimum densities of both resources and consumers. Short of the present date, climate change has only been implicated in one species-level extinction (Pounds et al. 1999), although some studies predict high rates of extinction in the near future (Thomas et al. 2004). In a study of population densities of trees and terrestrial ectotherms (amphibians, reptiles, and invertebrates) the biomass density of both groups decreased at warmer temperatures (Allen et al. 2002). Petchey et al. (1999) found that 30%–40% of species of aquatic microbes in a microcosm were extinct after 7 weeks of a $+2°\mathrm{C}\ \mathrm{week}^{-1}$ change in temperature (approximately 0.1°–0.2°C per generation). In their experiment, producer (resource) biomass increased with warming while consumer biomass decreased, and only consumers showed increased rates of extinction. Our model mimics the observed increase in resource biomass only when $\mathrm{CTI} < 0$, suggesting that despite our empirical estimates for CTI (which are >0), there may be instances where the capacity for ingestion by consumers increases more slowly with warming than metabolism or where the capacity for ingestion decreases with warming. There is evidence supporting the existence of thermal optima for ingestion in a variety of species and similarly for critical thermal limits in production and metabolism, which could account for discrepancies between our model and empirical data. Like any scaling relationship based on diverse assemblages, our model is best suited to explain large-scale patterns since species-specific responses to temperature are obscured within the general scaling framework.

Voigt et al. (2003) compiled plant, herbivore, and carnivore abundances from two grassland communities to determine whether the climate sensitivity of functional groups differed between trophic levels. Their analysis showed that the temporal variance in abundance, attributable to climatic variability, increased with trophic level. Similarly, Allen et al. (2002) show that the density of terrestrial ectotherms is more sensitive than the density of plants to temperature. Pianka (1981) suggested that differences in the metabolic requirements of carnivores, herbivores, and autotrophs could account for differences in their climatic sensitivity. However, the response of autotrophs additionally causes the resource availability to vary for herbivores and can lead to amplified sensitivity at higher trophic levels (Voigt et al. 2003). In our example system (fig. 4), both mechanisms account for the increased sensitivity of higher trophic levels: consumers ingest more energy per unit mass at higher temperatures, causing resource density to decline. Fewer resources combined with an increased consumer ingestion rate lead to a relatively larger decline in consumer density. The generality of this property and mechanism for a broader class of consumer-resource systems remains to be determined.

Our amalgamation of the Boltzmann factor into the Yodzis and Innes (1992) consumer-resource model provides a general framework for temperature-dependent models of interacting populations. General theories for the inclusion of further environmental variables in allometric models may be limited, since body mass and temperature tend to be the only variables accounting for significant amounts of variability in broadscale regressions (e.g., Peters 1983). The framework used to model consumer-resource dynamics in this study neglects to include the direct effects of consumer mortality in the model. The relationship between mortality, temperature, and body size follows the same relationship as metabolism (Savage et al. 2004), and evidence suggests that the two are governed by the same scaling parameters (E_i for fish mortality is 0.45 eV [Savage et al. 2004] and 0.43 eV for fish metabolism [table 2]). If, indeed, the scaling parameters are conservative, then directly including consumer mortality in the model would further limit any consumer from existing at its physiologically limited extent (see app. B in the online edition of the *American Naturalist*). There is still much to be learned about the influence of temperature on alternative model formulations, structures, and, with direct impact for our results, the potential temperature dependence of the per unit area parameters R_0 and K.

The temperature dependence of carrying capacity K has received surprisingly little attention in the literature (Savage et al. 2004). In Verhulst population models, K defines the maximum attainable density of a population, and under steady state conditions, it is the equilibrium density. Verhulst growth is included in our model framework to define density-dependent growth of resources and assumes that factors such as nutrients and light are static. Population models that account for the metabolic costs offsetting growth but neglect community interactions suggest that where resource supply is constant, K must decrease with temperature to balance the effects of increasing metabolic costs (Savage et al. 2004). Savage et al. (2004) argue that the findings of Allen et al. (2002; decreased ectotherm density with temperature) support a negative relationship between temperature and carrying capacity. However, our model framework similarly explains the decline in ectotherm density using a community framework, scaling only the per unit time elements of the model. Our model differs from that of Savage et al. (2004) in that resource density is not influenced by temperature in the absence of predators (since K is temperature invariant). Populations that exist truly in the absence of predators are rare, but tree biomass density, which is arguably limited by competition rather than consumer grazing, provides a reasonable example for which data are available. Enquist and Niklas (2001) show that tree biomass density is constant across latitudes ranging from −40° to 60°, which is at least suggestive that carrying capacity may be independent of temperature. Much work remains to determine the scaling of carrying capacity with temperature and, as importantly, to determine whether its implicit scaling in population models is analogous to the results produced by our community approach.

The half-saturation density of the functional response R_0, in unison with the maximum capacity for ingestion J, controls the realized rate at which resources are consumed. The effects of temperature on the half-saturation density itself are not well documented. However, there has been some research on the temperature dependence of the attack rate in the traditional Holling Type II functional response model (Holling 1965). This model defines the functional response as $f(R) = \alpha RC/(1 + \alpha t_h R)$, where α is the attack rate, t_h is the amount of time required to handle a prey item, and R and C are resource and consumer densities. The parameters of our Monod model can be expressed as those of the Holling Type II, where the maximum capacity for ingestion $J \equiv 1/t_h$ and the half-saturation density $R_0 \equiv 1/\alpha t_h$. In our study, we assume R_0 is independent of temperature, and given that handling timescales as $1/J$ (where $1/J \propto e^{E_J/kT}$), this requires that the Holling attack rate (α) scales according to $\alpha \propto e^{-E_J/kT}$. Holling (1965) considers attack rate to be a function of the reactive distance of the predator, speeds of movement of the predator and prey, and their capture success. Thompson (1978) showed that the attack coefficient of damselfly larvae increased with temperature according to a sigmoidal function over the range 5°–27.5°C. However, inspection of Thompson's curve suggests that exponential growth well explains the changes in the attack rate below approximately 20°C. Marchand et al. (2002) observed a positive and nonlinear relationship between the attack rate of juvenile brook charr and temperature below their upper avoidance temperature of 22°C. The existence of an upper threshold for this relationship is not surprising, given that species-specific thermal tolerances are often well bounded within our range of "biologically plausible" temperatures. These results are at least suggestive of a positive exponential relationship among attack rate and temperature, and they thus indicate that temperature invariance of R_0 may indeed be a reasonable suggestion. In practice, any scaling relationship that exists between R_0 and temperature will most likely be influenced by environmental correlates of temperature that alter the efficiency of consumers. For example, an increase in the density of emergent macrophytes in an aquatic system may reduce the effectiveness of sensory cues in zooplanktivorous fish.

Our results suggest that long term-changes in temperature can influence the equilibrium dynamics of species in predictable ways, given the dependence of their rates of growth, ingestion, and metabolism on temperature. Further work addressing short-term periodic variability, such as seasonal and El Niño oscillations, and stochastic variability will provide additional insight into the influence of environmental conditions on short-term, nonequilibrium (equilibrium transient) dynamics. For those communities whose range is limited by the spatial extent of their habitat (e.g., lake communities), we expect that our model provides a testable and applicable framework for formulating predictions. For communities whose range is flexible, integrating this bioenergetic community approach into climate-envelope predictions will provide a stronger basis for the ecological consequences of global change scenarios.

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APPENDIX A

Bifurcation and Sensitivity Analysis of the Model System

Starting with the model (eqq. [1]) from Yodzis and Innes (1992), we define the nondimensionalized model by selecting units of time such that $r = 1$. Normalizing the remaining rates in the model by r gives

$$\frac{dR}{dt} = R\left(1 - \frac{R}{K}\right) - \frac{JC}{rf_e}\left(\frac{R}{R + R_0}\right),$$

$$\frac{dC}{dt} = C\left[-\frac{M}{r} + \frac{(1-\delta)J}{r}\left(\frac{R}{R + R_0}\right)\right], \tag{A1}$$

and given that $x = M/r$ and $y = (1 - \delta)J/M$, the model reduces to

$$\frac{dR}{dt} = R\left(1 - \frac{R}{K}\right) - \frac{xy}{(1-\delta)f_e}\left(\frac{RC}{R + R_0}\right),$$

$$\frac{dC}{dt} = xC\left[-1 + y\left(\frac{R}{R + R_0}\right)\right]. \tag{A2}$$

Solving for $dR/dt = dC/dt = 0$, we obtain the nontrivial equilibrium conditions:

$$C_e = \left(1 - \frac{R_e}{K}\right)\left[\frac{(1-\delta)f_e}{x}\right]R_e,$$

$$R_e = \frac{R_0}{y - 1}. \tag{A3}$$

Since all model parameters are nonnegative and $C_e > 0$ for all $0 < R_e < K$, we derive $R_0/K < (y - 1)$ as the upper limit for feasibility (transcritical bifurcation). Since R_0/K is always positive, the ratio $(1 - \delta)J/M$ must be >1 for a two-species equilibrium to exist. This provides a derivation of the energetic constraints of the model; energy ingestion must be greater than energy metabolism in order to sustain consumers in the model.

To determine the stability of the equilibrium densities (eqq. [A3]), we define the Jacobian matrix at the nontrivial equilibrium point Eq_3,

$$\mathrm{Jac}\Big|_{\mathrm{Eq}_3} = \begin{bmatrix} \dfrac{\partial R}{\partial R} & \dfrac{\partial R}{\partial C} \\[2ex] \dfrac{\partial C}{\partial R} & \dfrac{\partial C}{\partial C} \end{bmatrix}_{\mathrm{Eq}_3}$$

$$= \begin{bmatrix} \dfrac{Ky - R_0y - K - R_0}{y(y-1)K} & \dfrac{-x}{(1-\delta)f_e} \\[2ex] \dfrac{f_e(1-\delta)(Ky - K - R_0)}{yK} & 0 \end{bmatrix}, \tag{A4}$$

and the solution of its eigenvalues,

$$\lambda_{1,2} = \frac{\partial R/\partial R \pm \sqrt{(\partial R/\partial R)^2 - 4(-\partial R/\partial C \times \partial C/\partial R)}}{2}. \tag{A5}$$

The model equilibrium (A3) is globally stable when both eigenvalues have negative real parts, and since $\partial R/\partial C \times \partial C/\partial R < 0$ for all $R_0/K < y - 1$, the discriminant in equation (A5) will always be less than $\partial R/\partial R$. Therefore, we must satisfy only the condition $\partial R/\partial R < 0$. This condition is satisfied when

$$\frac{R_0}{K} > \frac{y - 1}{y + 1}. \tag{A6}$$

The condition (A6) defines the Hopf bifurcation locus in the R_0/K plane. Below this stability threshold, the equilibrium becomes locally unstable but is surrounded by a stable limit cycle. Within the realm of locally stable equilibria, the approach to equilibrium can be monotonic (node) or damped oscillations (focus). The limit between nodes and foci occurs when $\lambda_{1,2}$ transition from real to complex numbers (for a full description, see Yodzis and Innes 1992).

Literature Cited

Allen, A. P., J. H. Brown, and J. F. Gillooly. 2002. Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. Nature 297:1545–1548.

Bennett, A. F., and W. R. Dawson. 1976. Metabolism. Pages 127–224 *in* C. Gans and W. R. Dawson, eds. Biology of the reptilia. Vol. 5. Academic Press, London.

Brett, J. R. 1971. Satiation time, appetite, and maximum food intake of sockeye salmon (*Oncorhynchus nerka*). Journal of the Fisheries Research Board of Canada 28:409–415.

Brett, J. R., and N. R. Glass. 1973. Metabolic rates and critical swimming speeds of sockeye salmon (*Oncorhynchus nerka*) in relation to size and temperature. Journal of the Fisheries Research Board of Canada 30:379–387.

Brown, J. H., G. B. West, and B. J. Enquist. 2000. Scaling in biology: patterns and processes, causes and consequences. Pages 1–24 *in* J. H. Brown and G. B. West, eds. Scaling in biology. Oxford University Press, Oxford.

Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. Ecology 85:1771–1789.

Clarke, A., and N. M. Johnston. 1999. Scaling of metabolic rate with body mass and temperature in teleost fish. Journal of Animal Ecology 68:893–905.

Davis, A. J., L. S. Jenkinson, J. H. Lawton, B. Shorrocks, and S. Wood. 1998. Making mistakes when predicting shifts in species range in response to global warming. Nature 391:783–786.

DeAngelis, D. L. 1992. Dynamics of nutrient cycling and food webs. Chapman & Hall, New York.

Dixon, M., and E. C. Webb. 1964. Enzymes. 2nd ed. Academic Press, New York.

Enquist, B. J., and K. L. Niklas. 2001. Invariant scaling relations across tree-dominated communities. Nature 410:655–660.

Eppley, R. W. 1972. Temperature and phytoplankton growth in the sea. Fishery Bulletin 70:1063–1085.

Ernest, S. K. M., B. J. Enquist, J. H. Brown, E. L. Charnov, J. F. Gillooly, V. M. Savage, E. P. White, et al. 2003. Thermodynamic and metabolic effects on the scaling of production and population energy use. Ecology Letters 6:990–995.

Gillooly, J. F., J. H. Brown, G. B. West, V. M. Savage, and E. L. Charnov. 2001. Effects of size and temperature on metabolic rate. Science 293:2248–2251.

Gillooly, J. F., E. L. Charnov, G. B. West, V. M. Savage, and J. H. Brown. 2002. Effects of size and temperature on developmental time. Nature 417:70-73.

Hansen, P. J., P. K. Bjørnsen, and B. W. Hansen. 1997. Zooplankton grazing and growth: scaling within the 2–2,000-μm body size range. Limnology and Oceanography 42:687–704.

Harrington, R., I. Woiwod, and T. Sparks. 1999. Climate change and trophic interactions. Trends in Ecology & Evolution 14:146–150.

Holling, C. S. 1965. The functional response of predators to prey density and its role in mimicry and population regulation. Memoirs of the Entomological Society of Canada 45:3–60.

Houghton, J. T., Y. Ding, D. J. Griggs, M. Noguer, P. J. van der Linden, X. Dai, K. Maskell, and C. A. Johnson, eds. 2001. Climate change 2001: the scientific basis. Cambridge University Press, Cambridge.

Humphries, M. M., D. W. Thomas, and D. L. Kramer. 2002. Climate-mediated energetic constraints on the distribution of hibernating mammals. Nature 418:313–316.

Humphries, M. M., J. Umbanhowar, and K. S. McCann. 2004. Bioenergetic prediction of climate change impacts on northern mammals. Integrative and Comparative Biology 44:152–162.

Ikeda, T. 1977. Feeding rates of planktonic copepods from a tropical sea. Journal of Experimental Marine Biology and Ecology 29:263–277.

Ives, A. R. 1995. Predicting the response of populations to environmental change. Ecology 76:926–941.

Jiang, L., and P. J. Morin. 2004. Temperature-dependent interactions explain unexpected responses to environmental warming in communities of competitors. Journal of Animal Ecology 73:569–576.

Julian, D., M. L. Chang, J. R. Judd, and A. J. Arp. 2001. Influence of environmental factors on burrow irrigation and oxygen consumption in the mudflat invertebrate *Urechis caupo*. Marine Biology 139:163–173.

Knutsen, I., and A. G. V. Salvanes. 1999. Temperature-dependent digestion handling time in juvenile cod and possible consequences for prey choice. Marine Ecology Progress Series 181:61–79.

Koen Alonso, M., and P. Yodzis. Forthcoming. Multispecies modeling of some components of the northern and central Patagonia marine community, Argentina. Canadian Journal of Fisheries and Aquatic Sciences.

Marchand, F., P. Magnan, and D. Boisclair. 2002. Water temperature, light intensity, and zooplankton density and the feeding activity of juvenile brook charr (*Salvelinus fontinalis*). Freshwater Biology 47:2153–2162.

Nagy, K. A. 1982. Energy requirements of free-living iguanid lizards. Pages 49–59 *in* G. M. Gurghardt and A. S. Rand, eds. Iguanas of the world: their behavior, ecology, and conservation. Noyes, Park Ridge, NJ.

Parmesan, C., N. Ryrholm, C. Stafanescu, J. K. Hill, C. D. Thomas, H. Descimon, B. Huntley, et al. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. Nature 399:579–583.

Petchey, O. L., P. T. McPhearson, T. M. Casey, and P. J. Morin. 1999. Environmental warming alters food-web structure and ecosystem function. Nature 305:69–72.

Peters, R. H. 1983. The ecological implications of body size. Cambridge University Press, New York.

Pianka, E. R. 1981. Resource acquisition and allocation among animals. Pages 300–314 *in* C. Townsend and P. Calow, eds. Physiological ecology: an evolutionary approach to resource use. Blackwell, Oxford.

Pimm, S. L. 1991. The balance of nature? University of Chicago Press, Chicago.

Post, E., R. O. Peterson, N. C. Stenseth, and B. E. McLaren. 1999. Ecosystem consequences of wolf behavioural response to climate. Nature 401:905–907.

Pounds, J. A., M. P. L. Fogden, and J. H. Campbell. 1999. Biological response to climate change on a tropical mountain. Nature 398: 611–615.

Ricklefs, R. E., and G. L. Miller. 2000. Ecology. 4th ed. W. H. Freeman, New York.

Ripa, J., and A. R. Ives. 2003. Food web dynamics in correlated and autocorrelated environments. Theoretical Population Biology 64: 369–384.

Ripa, J., P. Lundberg, and V. Kaitala. 1998. A general theory of environmental noise in ecological food webs. American Naturalist 151:256–263.

Robinson, W. R., R. H. Peters, and J. Zimmermann. 1983. The effects of body size and temperature on metabolic rate of organisms. Canadian Journal of Zoology 61:281–288.

Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig, and J. A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. Nature 421:57–60.

Rosenzweig, M. L. 1971. Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. Science 171:385–387.

Rosenzweig, M. L., and R. H. MacArthur. 1963. Graphical representation and stability conditions of predator-prey interactions. American Naturalist 107:209–223.

Savage, V. M. 2004. Improved approximations to scaling relationships for species, populations, and ecosystems across latitudinal and elevational gradients. Journal of Theoretical Biology 227:525–534.

Savage, V. M., J. F. Gillooly, J. H. Brown, G. B. West, and E. L. Charnov. 2004. Effects of body size and temperature on population growth. American Naturalist 163:429–441.

Temming, A., and J. P. Herrmann. 2003. Gastric evacuation in cod: prey-specific evacuation rates for use in North Sea, Baltic Sea and Barents Sea multi-species models. Fisheries Research 63:21–41.

Thomas, C. D., A. Cameron, R. E. Green, M. Bakkenes, L. J. Beaumont, Y. C. Collingham, B. F. N. Erasmus, et al. 2004. Extinction risk from climate change. Nature 427:145–148.

Thompson, D. J. 1978. Towards a realistic predator-prey model: the effect of temperature on the functional response and life history of larvae of the damselfly, *Ischnura elegans*. Journal of Animal Ecology 47:757–767.

Voigt, W., J. Perner, A. J. Davis, T. Eggers, J. Schumacher, R. Bahrmann, B. Fabian, et al. 2003. Trophic levels are differentially sensitive to climate. Ecology 84:2444–2453.

Wieland, A., and M. Kühl. 2000. Irradiance and temperature regulation of oxygenic photosynthesis and O_2 consumption in a hypersaline cyanobacterial mat (Solar Lake, Egypt). Marine Biology 137:71–85.

Williams, R. B. 1964. Division rates of salt marsh diatoms in relation to salinity and cell size. Ecology 45:877–880.

Yodzis, P., and S. Innes. 1992. Body size and consumer-resource dynamics. American Naturalist 139:1151–1175.

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Appendix B from D. A. Vasseur and K. S. McCann, “A Mechanistic Approach for Modeling Temperature-Dependent Consumer-Resource Dynamics”

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Including Consumer Natural Mortality in the Model System

The Yodzis and Innes (1992) bioenergetic-allometric framework for consumer-resource interactions that forms our model system neglects to include the direct effects of a consumer’s natural mortality. In the two trophic level system described and analyzed here, energy escapes the model only through inefficient energy assimilation (the fraction δ of ingested biomass) and through metabolism. For some populations, particularly those inhabiting the uppermost trophic level(s), natural mortality may be a significant energy sink and thus may influence the dynamics of the system. We derive the scaling properties of natural mortality (from Brown et al. 2004) and describe its influence in our model system.

A consumer population (C) will experience a complete turnover of its biomass, due solely to natural mortality, in the period of time corresponding to the average life span of an individual in the population (t_L). Thus, the instantaneous rate of change of consumer biomass density due to natural mortality is $-CN$, where the rate of natural mortality (N) is equal to $1/t_\mathrm{L}$. Like many biological rates, life span scales with body size and temperature according to the relationship $t_\mathrm{L} \propto m^{0.25}e^{E/kT}$, where m is the average individual body mass, E is the activation energy, k is Boltzmann’s constant, and T is temperature in Kelvin (Brown et al. 2004; Savage et al. 2004). Natural mortality then scales as $N \propto m^{-0.25}e^{-E_N/kT}$. Converting this relationship to scale from an intercept value at a known temperature ($a_N(T_0)$; see, e.g., Gillooly et al. 2001), we have

$$N = a_N(T_0)m_C^{-0.25}e^{E_N(T-T_0)/kTT_0}. \tag{B1}$$

This relationship takes the exact form as that for all biological rates in our article (cf. eqq. [2]).

The activation energy E_N, which controls the rate of natural mortality as temperature varies, should be nearly equal to the activation energy for metabolism (E_M) for any given consumer since life span scales inversely with metabolism ($t_\mathrm{L} \propto 1/M$; Savage et al. 2004). For example, Savage et al. (2004) predicted an activation energy for mass-corrected instantaneous mortality in fish of 0.45 eV, which is very close to the activation energy used for fish metabolic rate in our model (0.43 eV; derived in Gillooly et al. 2001). Provided that metabolism and natural mortality indeed scale similarly with mass and temperature, we can rewrite the two scaling functions as a single function, defining the new parameter M_J as the joint effect of metabolism and natural mortality:

$$M_J = [a_M(T_0) + a_N(T_0)]m_C^{-0.25}e^{E_{M_J}(T-T_0)/kTT_0}. \tag{B2}$$

To include natural mortality in our model, we replace metabolism M with the joint effects of metabolism and mortality M_J. The leading effect of this change is an increase in the per unit energy demands of the consumer population, since $M_J > M$ at all temperatures. This transformation manifests as an increase in the parameter x ($x = M/r$) and a decrease in the parameter y ($y = J/M$), ultimately influencing the qualitative and quantitative dynamics of the model. Recalling that the parameters x and y are also the subject of variation in the physiological/ecological extent of limitation through the fractions f_r and f_J (which denote the realized fractions of the biological rates r and J), it is evident that increasing M by adding natural mortality has the same dynamical consequences as reducing the fractions f_r and f_J. Thus, the inclusion of natural mortality is analogous to shifting the originally specified system toward a more ecologically limited state. The consequences for the dynamics of our consumer-resource system under ecological limitation are discussed in the main text. We reiterate here that ecologically limited systems are more prone to undergo bifurcations with temperature change and have reduced densities at all temperatures when compared with their physiologically limited counterparts.

The extent of change in the model owing to this modification is dependent on the relative contributions of metabolism and natural mortality to the overall energy expenditure of the consumer. At any temperature and for any consumer body mass, the fraction of energy expenditure due to metabolism alone (M/M_J) is $a_M(T_0)/[a_M(T_0) + a_N(T_0)]$. We estimated this fraction to be 0.76 for vertebrate ectotherms (fish) using the 20°C intercept value for natural mortality from Savage et al. (2004; 0.73 individuals [individual year]$^{-1}$ kg$^{0.25}$) and metabolism data from table 1 (2.3 kg [kg year]$^{-1}$ kg$^{0.25}$). In practice, the relative contributions of metabolism and natural mortality to overall consumer energy expenditure may depend on a variety of factors. Further research defining the scaling attributes of natural mortality will be vital to determining its importance in modeling exercises.