The University of Chicago

Theoretical Predictions for How Temperature Affects the Dynamics of Interacting Herbivores and Plants

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ABSTRACT: Concern about climate change has spurred experimental tests of how warming affects species' abundance and performance. As this body of research grows, interpretation and extrapolation to other species and systems have been limited by a lack of theory. To address the need for theory for how warming affects species interactions, we used consumer-prey models and the metabolic theory of ecology to develop quantitative predictions for how systematic differences between the temperature dependence of heterotrophic and autotrophic population growth lead to temperature-dependent herbivory. We found that herbivore and plant abundances change with temperature in proportion to the ratio of autotrophic to heterotrophic metabolic temperature dependences. This result is consistent across five different formulations of consumer-prey models and over varying resource supply rates. Two models predict that temperature-dependent herbivory causes primary producer abundance to be independent of temperature. This finding contradicts simpler extensions of metabolic theory to abundance that ignore trophic interactions, and is consistent with patterns in terrestrial ecosystems. When applied to experimental data, the model explained 77% and 66% of the variation in phytoplankton and zooplankton abundances, respectively. We suggest that metabolic theory provides a foundation for understanding the effects of temperature change on multitrophic ecological communities.

Keywords: consumer-resource models, herbivore, primary production, metabolic theory, temperature, mesocosm, plankton.

Introduction

Climate change is driving directional trends in environmental factors including temperature, precipitation, and water chemistry. This abiotic variation can be modeled with growing confidence and precision, but the ecological consequences are far less clear. Projecting ecological effects of climate change requires quantitatively linking environmental variation to the rates and outcomes of ecological processes in a framework that incorporates general mechanisms with specific conditions of particular ecological systems. Such a framework would produce testable hypotheses for how environmental change affects ecological structure and function and would foster an approach to global change science that would be more easily integrated with basic ecological and evolutionary theory.

A promising framework for joining abiotic environmental change and population- and community-structuring processes can be developed by extending general relationships between temperature, metabolism, and demographic rates (Robinson et al. 1983; Gillooly et al. 2001). The acceleration of metabolic rate with increasing temperature has been empirically described for diverse taxonomic groups by simple mathematical functions (Robinson et al. 1983; Pepin 1991; Gillooly et al. 2001; Rose and Caron 2007). General temperature-dependence of growth and reproduction rates suggests potential effects of temperature on population abundance. Direct extensions of temperature-dependent metabolic models to population abundance produce quantitative predictions for how warming should affect populations. Savage et al. (2004) demonstrated that the maximum growth rate ($r_{\max}$) of populations is temperature dependent, and the slope of the temperature effect is consistent with an underlying constraint of temperature on respiratory processes. Allen et al. (2002) used the energetic equivalence rule (Damuth 1987) to predict that mass-corrected population abundance declines with warming in direct proportion to the temperature dependence of heterotrophic metabolism, assuming that the total energy flux of a population per unit area is invariant with respect to body size.

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Vasseur and McCann (2005) considered effects of temperature on consumer and prey abundance and found decreases in abundance with warming. The most straightforward extensions of metabolic theories predict that abundance declines with temperature. However, these extensions typically ignore biotic feedbacks, resource supply rates, and how different temperature dependencies of metabolic rates influence species interactions.

Though general temperature-dependent demographic models can inform expectations for how temperature affects abundance, previous applications have not included a critical difference between primary and secondary producers. Heterotrophs and autotrophs respond differently to nonlethal temperature shifts as a result of differences between metabolic complexes that cause respiration-limited metabolism to be more sensitive to temperature than photosynthesis-limited metabolism (Dewar et al. 1999; Allen et al. 2005; Lopez-Urrutia et al. 2006; Rose and Caron 2007). This systematic difference implies a general temperature dependence of herbivory that could drive predictable responses of multitrophic systems to changes in environmental temperature. For example, general differences in the effects of warming on consumer and plant metabolism may be sufficient to shift food web structure, as has been observed in natural and experimental systems (Thompson et al. 2004; Lopez-Urrutia et al. 2006; Vazquez-Dominguez et al. 2007; O'Connor et al. 2009; Wohlers et al. 2009). However, general predictions for metabolic temperature dependence on the abundance of herbivores and their prey have not been articulated.

We analyzed a set of consumer-prey models that incorporate temperature-dependent rates for heterotrophic and autotrophic processes and resource-based carrying capacities for autotrophs. Our goal was to determine whether temperature-dependent herbivory could produce new and general predictions for the effects of temperature on the abundance of populations in food webs. We used metabolic theory and consumer-prey models to answer three questions: (1) Is there a simple relationship between temperature and abundance, or does trophic context introduce enough complexity to obscure detectable and predictable temperature effects? (2) Can temperature-dependent consumer-prey models relate the short-term effects of temperature typically observed in experiments to longer-term effects that are more relevant to natural impacts of climate change? (3) Do these predictions differ from predictions derived for single trophic level systems? To answer these questions, we evaluate the effects of temperature on model equilibria for herbivore and plant abundance. We show that long-term predictions for herbivores are consistent for all consumer-prey models developed, while predictions for primary producers varied among models. These dynamic models are also well suited to testing short-term

dynamics, and we use the models to relate experimental results to predictions for natural systems. Our approach builds upon well-studied models of consumer-prey dynamics to link the effects of environmental temperature on fundamental metabolic processes to the outcome of species interactions, and it generates quantitative hypotheses for the effects of environmental temperature change in natural environments.

Model Formulation

Choosing Models

We modeled the dynamics of autotrophic primary producers (P) and heterotrophic secondary producers (H), using a general consumer-prey model that relates changes in abundance over time to rates of autotroph growth (g), heterotroph consumption (c), conversion efficiency (ϵ) and heterotroph mortality (h):

$$\frac{dP}{dt} = g(P) - c(P, H),$$

$$\frac{dH}{dt} = \epsilon c(P, H) - h(H). \tag{1}$$

We modeled the temperature dependence of the rates in equation (1). Several formulations for the relationship between temperature and metabolic rate have been repeatedly supported by empirical tests (Robinson et al. 1983; Gillooly et al. 2001). A general formulation that captures two competing relationships can be expressed as

$$I = I_0 e^{E \times t} \tag{2}$$

in which a metabolic rate (I) scales exponentially with temperature (t) according to the factor E. The normalization constant (I_0) captures variation in I due to factors other than temperature. The generic temperature term t can take either the form T (°C or °Kelvin) in a simple exponential model, or it can take the form $-1/kT$ in the Arrhenius relationship. In the Arrhenius formulation of a metabolic model, E is denoted as E_a and represents the activation energy of metabolic processes (Gillooly et al. 2001). In this formulation, a metabolic rate (I) is related to temperature (T in °Kelvin) by the Boltzmann constant (k).

The difference between the temperature dependence as modeled by $e^{E \times T}$ and by $e^{-E_a/kT}$ is subtle over the biological range of temperatures (0°–35°C; Arrhenius 1915; Belehradek 1928), and tests of these models against empirical data often reveal that each model performs well (Robinson et al. 1983; O'Connor et al. 2007). Though either formulation could be used to relate body temperature to rate parameters (intrinsic rate of increase, herbivore attack, and

mortality rates) and carrying capacity (K) in the subsequent analysis, we used the Arrhenius formulation ($e^{-E_a/kT}$) in equation (2). This model has been used by biologists for a century and is a cornerstone of the metabolic theory of ecology (MTE), which provides a useful framework for applying the metabolic effects of temperature to more complex community and ecosystem processes (Gillooly et al. 2001; Brown et al. 2004; Allen et al. 2005). We apply equation (2) assuming that body temperature is known for consumer and prey. For aquatic ectotherms, which represent the vast majority of taxa on Earth (Ruppert and Barnes 1994), body temperature is strongly influenced by environmental (water) temperature. For endotherms, variation in body temperature is highly constrained. For terrestrial and intertidal organisms, body temperatures can be decoupled from environmental temperatures (Helmuth 1998), and these relationships need to be known to relate the metabolic model to environmental temperature.

To test the effect of differential temperature dependence of primary and secondary production on consumer-prey model predictions, we assigned rates of primary producer- and consumer-driven processes the activation energies that reflect specific rates of increase with warming (table 1). To obtain a first-order prediction of how temperature dependent rates affect abundance, we assume that consumption rate is related to the body temperature of the herbivore. This approach is robust to the inclusion of endotherms or any organism with a known relationship between body temperature and consumption rates. Transfer efficiency has repeatedly been shown emprically to be temperature independent (del Giorgio and Cole 1998; Vazquez-Dominguez et al. 2007), so we leave this term independent of temperature. In addition, we used the relationship between constant nutrient supply, autotroph metabolism, and temperature to assign an activation energy to the carrying capacity (K; table 1; Savage et al. 2004).

All of our models implicitly assume that body size distributions remain constant. Although there is evidence that changes in body size may occur with temperature (Daufresne et al. 2010; Atkinson 1994), there is no consistent pattern or theoretical prediction for this phenomenon that facilitates its inclusion in our model. Nonetheless, body size could easily be included in this framework by developing size classes that are scaled at $mass^{3/4}$, where $mass$ is the average body mass for a given size class.

Our goal was to determine whether, taking into account differences between heterotrophs and autotrophs, a general temperature dependence of metabolism leads to general effects on abundance when considered in a context of trophic interactions. An alternative hypothesis is that different trophic dynamics interact with metabolic temperature dependence to create numerous possible outcomes that are difficult to anticipate or interpret without substantial information about a particular system. We therefore considered five different common versions of the consumer-prey model (eq. [1]). The simplest model is one with primary producers only, and we modeled maximum growth (r) and carrying capacity (K) in a logistic growth model to capture effects of resource limitation (model 1, table 2). To this model, we added an herbivore population with constant per capita mortality and a nonsaturating (type I) feeding response (model 2), or a saturating feeding response (type II, modeled using a Monod function, model 3). We also considered a version of model 2 with density-dependent herbivore mortality, which could reflect density-dependent predation or disease (model 4). Finally, we considered a model with exponential primary producer growth, a nonsaturating herbivore response, and density-dependent herbivore mortality (model 5). This last model, while unrealistic in the absence of herbivores, represents a scenario where autotrophs grow at maximum rates under the range of conditions they encounter. Other combinations of these basic functional forms do not produce stable

Table 1: Model parameters and their average temperature dependence as characterized by activation energies (E_a) in eV, according to the general predictions of metabolic theory using the Arrhenius formulation in equation (2) and empirical data

Parameter	Variable	E_a	Reference
Primary producer growth rate (based on primary productivity rate)	r	.32	Allen et al. 2005; Lopez-Urrutia et al. 2006; Rose and Caron 2007
Primary producer carrying capacity	K	−.32	Savage et al. 2004
Herbivore attack rate (inclusive of capture and ingestion rates and handling time)	α	.65	Gillooly et al. 2001
Herbivore mortality rate	m	.65	Gillooly et al. 2001; Savage et al. 2004
Transfer efficiency	ε	0	del Giorgio and Cole 1998; Vazquez-Dominguez et al. 2007
Half saturation constant for herbivore feeding response	b	0	

Table 2: Equilibrium conditions for five consumer-resource models

Model	$g(P)$	$c(H, P)$	$h(H)$	Equilibria	Temperature-dependent equilibria
1	$rP\left(1 - \frac{P}{K}\right)$	...	...	$\hat{P} = K$	$\ln(\hat{P}) = \frac{E_P}{kT} + \ln(K_0)$
2	$rP\left(1 - \frac{P}{K}\right)$	αPH	mH	$\hat{P} = K,$ $\hat{H} = 0;$	$\ln(\hat{P}) = \frac{E_P}{kT} + \ln(K_0)$
				$\hat{P} = \frac{m}{\varepsilon\alpha},$	$\ln(\hat{P}) = \ln\left(\frac{m_0}{\varepsilon\alpha_0}\right)$
				$\hat{H} = \frac{r}{\alpha}\left(1 - \frac{m}{\varepsilon\alpha K}\right)$	$\ln(\hat{H}) = \frac{E_H - E_P}{kT} + \ln\left[\frac{r_0}{\alpha_0}\left(1 - \frac{m_0 e^{-E_P/kT}}{\alpha_0 \varepsilon K_0}\right)\right]$
3	$rP\left(1 - \frac{P}{K}\right)$	$\alpha H\left(\frac{P}{P+b}\right)$	mH	$\hat{P} = K,$ $\hat{H} = 0;$	$\ln(\hat{P}) = \frac{E_P}{kT} + \ln(K_0)$
				$\hat{P} = \frac{mb}{\varepsilon\alpha - m},$	$\ln(\hat{P}) = \ln\left(\frac{m_0 b}{\varepsilon\alpha_0 - m_0}\right)$
				$\hat{H} = \frac{\varepsilon rb(K\varepsilon\alpha - Km - mb)}{K(\varepsilon\alpha - m)^2}$	$\ln(\hat{H}) = \frac{E_H - E_P}{kT} + \ln\left\{\frac{b\varepsilon r_0[K_0(\varepsilon\alpha_0 - m_0) - bm_0 e^{-E_P/kT}]}{K_0(\varepsilon\alpha_0 - m_0)^2}\right\}$
4	$rP\left(1 - \frac{P}{K}\right)$	αPH	mH^2	$\hat{P} = K,$ $\hat{H} = 0;$	$\ln(\hat{P}) = \frac{E_P}{kT} + \ln(K_0)$
				$\hat{P} = \frac{Krm}{\varepsilon K\alpha^2 + rm},$	$\ln(\hat{P}) = \frac{E_H - E_P}{kT} + \ln\left(\frac{K_0 r_0 m_0}{\varepsilon K_0 \alpha_0^2 + m_0 r_0 e^{(E_H - 2E_P/kT)}}\right)$
				$\hat{H} = \frac{K\varepsilon\alpha r}{\varepsilon K\alpha^2 + rm}$	$\ln(\hat{H}) = \frac{E_H - E_P}{kT} + \ln\left(\frac{K_0 r_0 \alpha_0 \varepsilon}{\varepsilon K_0 \alpha_0^2 + m_0 r_0 e^{(E_H - 2E_P/kT)}}\right)$
5	rP	αPH	mH^2	$\hat{P} = \left(\frac{mr}{\varepsilon\alpha^2}\right)$	$\ln(\hat{P}) = \frac{E_H - E_P}{kT} + \ln\left(\frac{m_0 r_0}{\varepsilon\alpha_0^2}\right)$
				$\hat{H} = \left(\frac{r}{\alpha}\right)$	$\ln(\hat{H}) = \frac{E_H - E_P}{kT} + \ln\left(\frac{r_0}{\alpha_0}\right)$

Note: Models use different functions to relate abundance (P, H) to primary producer growth $f(P)$, herbivore consumption $h(H)$, and mortality $h(H)$. The temperature dependence of these rates is modeled with an Arrhenius function using equation (2). General, stable equilibrium conditions (eq. [1]) are given and are restated with temperature-dependence terms for autotrophic (E_P) or heterotrophic (E_H) processes to give general formulations for the temperature dependence of equilibrium abundance. These temperature-dependent equilibria are presented in the form of equation (3a), $\ln(\hat{N}) = (-E_{ab}/kT) + \ln(B)$, in which the first term includes the predominant temperature dependence and the second term (B) captures all other model terms.

equilibrium solutions under any conditions or they have equilibria that are too complex to be interpreted biologically, and we therefore did not consider them in this analysis.

Modeling the Effect of Temperature on Abundance

To compare effects of temperature on abundance among models and determine whether a general temperature-dependent equilibrium solution is possible, we express solutions for equilibrium abundance N as a function of temperature using the Arrhenius relationship:

$$\ln(\hat{N}) = \frac{-E_{ab}}{kT} + \ln(B), \qquad (3a)$$

where temperature is expressed as $-1/kT$, B captures all

other drivers of variation in abundance other than temperature including growth, consumption, and mortality rate parameters (r, α, m) and carrying capacity (K). The term E_{ab} represents the slope of the effect of temperature on the abundance N. When used to model abundance rather than a metabolic process, E_{ab} is a calculation based on the activation energies that determine the net effect of metabolic temperature dependence on abundance of herbivores (E_H) and primary producers (E_P). Equation (3a) models a change in abundance N with a change in temperature. To compare abundance at two specific temperatures (T_1, T_2), we solved for the ratio of abundances:

$$\ln\left(\frac{\hat{N}_{T2}}{\hat{N}_{T1}}\right) = \frac{-E_{ab}(T_2 - T_1)}{kT_1 T_2} + \ln\left(\frac{B_{T2}}{B_{T1}}\right). \qquad (3b)$$

By combining equation (3a) for two different temperatures and simplifying algebraically, equation (3b) predicts abundance at T_2 (N_{T2}) based only on a known pair of temperatures (T_1, T_2), abundance at T_1 (N_{T1}) and E_{ab}. Importantly, this solution does not require additional parameters comprising B for a wide range of conditions (appendix, available online) because the main effects of temperature have been moved algebraically to the first term.

Modeling Effects of Changes in Resource Supply

In natural systems, temperature often changes in conjunction with resource supply rates. To determine how changes in resource supply could modify the effects of temperature change, we modeled K as a linear function of resource supply, R, so that

$$\frac{K_{0(R2)}}{K_{0(R1)}} \propto \frac{R_2}{R_1} = \dot{R}. \tag{4}$$

A change in K with temperature could affect either the slope or intercept of a temperature-dependent abundance solution expressed as in equation (3a) or (3b). When K appears in the second term but is not multiplied by T, a change in K affects the intercept only. In other words, change in abundance with concurrent changes in temperature and resource supply could be considered as a change in the slope (due to temperature) and the intercept (due to resource supply). In contrast, for solutions where K is multiplied by T in the second term of equation (3a), a change in resource supply would also affect the slope of abundance against temperature. To explore the potential importance of changing K in modifying the slope from a temperature-only prediction, we added the term $\dot{R}$ to equilibrium solutions expressed as in equation (3b) to capture a change in resource supply correlated with a change in temperature from T_1 to T_2 (appendix). To test the conditions under which increasing resources changed the ratio of abundances, we ran a sensitivity analysis that was similar to that run for the change in abundance with temperature (appendix), except that it included changes in resources from 1 (no change) upward to 50 times the base level and downward to 0.1 times the base level. In particular, we tested the conditions under which a change in $\dot{R}$ caused the slope of the line of log change in abundance versus $\Delta T/(1 + \Delta T/T_1)$ to differ by more than 1% from model predictions. Because the effect of $\dot{R}$ on the slope decreases with larger changes in temperature, we tested a small change in temperature, from 4° to 7°C. Simulations with larger changes in temperature (from 15° to 25°C) produced qualitatively similar results.

Analytical Methods

For each model, equilibrium conditions were identified and tested for stability using Routh-Hurwitz conditions for equilibria that included both herbivores and plants (Otto and Day 2007; appendix). The Routh-Hurwitz conditions specify when equilibria are locally stable, without requiring explicit solving of the eigenvalues of the stability matrix, and are therefore useful for complicated stability matrices. We determined the conditions for stability and invasibility (the ability of each trophic level to establish in the community when one or both trophic levels were initially absent), and also determined whether periodic fluctuations occurred over any parameter values (following Otto and Day 2007). For each consumer-prey model, we analyzed the effect of temperature on the equilibrium abundance of herbivores and plants.

To visualize the model results and to test model predictions, we chose specific parameter values based on the temperature dependences of photosynthesis and respiration ($E_P = 0.32$ eV and $E_H = 0.65$ eV, respectively; Allen et al. 2005; Lopez-Urrutia et al. 2006; Lopez-Urrutia 2008; table 1). These values have been empirically estimated in several independent investigations using very large sample sizes (Gillooly et al. 2001; Lopez-Urrutia et al. 2006, 2008). It is important to note that the values used for E_P and E_H do not influence the general result that abundance is a predictable function of temperature. Rather than a particular value for E in equation (2), the models simply require that a general scaling relationship be estimated by a value of E. For example, the effect of a steeper slope for heterotrophs, as found by Frazier et al. (2006) for insect r_{max}, could be solved for by substituting their value of $E_H = 0.97$ into the appropriate equations.

To determine the utility of the activation energy of metabolism for predicting how temperature affects abundance, we explored the sensitivity of the model outputs to a wide range of consumer-prey parameter values (appendix). In particular, we determined the range of parameter values under which the first half of equation (3a) was sufficient to determine the effect of temperature change on abundance. Using a similar sensitivity analysis as for changes in temperature, we tested the range of resource changes and parameter values that caused model predictions to deviate from the first half of equation (3a) (appendix).

Relating Short- and Long-Term Effects of Temperature

The dynamical models that we developed are equally useful for exploring short-term dynamics as they are for long-term equilibria. We explored the utility of our modeling approach for explaining short-term dynamics by testing

model predictions against abundance data from an experiment measuring the response of phyto- and zooplankton abundance to factorial manipulations of temperature (four levels at 2°C intervals) and nutrient supplies (control and addition of nitrogen and phosphorus; O'Connor et al. 2009). At the end of the 8-day experiment, the density of multispecies assemblages of zooplankton and phytoplankton had responded to warming and nutrient addition: phytoplankton abundance declined despite increased primary productivity (C^{14} uptake), and zooplankton abundance increased.

We identified a priori the model formulation that was most appropriate for the experimental system. In particular, we assumed that zooplankton feeding rates were best modeled with a saturating (type II) functional response, that nutrient supply rates determined phytoplankton carrying capacity and that zooplankton mortality was not strongly density dependent over the range of densities found within the experiment. This model is commonly related to the dynamics of spatially and temporally confined experimental conditions (Norberg and DeAngelis 1997). Because the phytoplankton and zooplankton showed no change in size distribution, we fitted our model 3 (table 2) after incorporating equation (4) with two resource supply rates (full model in appendix).

We used a differential equation solver (fitOdeModel, Simecol library, R 2.8.1) to fit the model to the data. We set the initial phytoplankton and zooplankton abundance to the starting conditions in the experiment and then determined the maximum likelihood estimates for parameters by fitting modeled abundance after 8 days to experimental results. The basal rates of parameters were held constant across all temperatures but the rate of resource supply (and therefore the carrying capacity) varied between resource treatments. Realized rates of temperature-dependent parameters varied according to equation (2) (using activation energy values chosen a priori; table 1).

Although the model that we fit to the short-term dynamics was constrained by our a priori choices for temperature dependencies (table 1), we used maximum likelihood to solve for other model parameters (α_0, r_0, b, K_0, m_0, ε). To assess the sensitivity of the model results, we used a cross-validation analysis. In particular, we fit the model using all but one data point (i.e., results from one replicate mesocosm), and then used the model to predict the abundances of zooplankton and phytoplankton in the removed mesocosm. This procedure was then repeated for each mesocosm, so that the predicted values were always determined without the focal mesocosm used in the model fit. We then compared the predicted fit to the observed data.

Results

A Simple Relationship between Temperature and Abundance

We found that the effect of temperature on herbivore and plant abundance can be represented by one or two model parameters (E_P, E_H), regardless of the trophic dynamics in the model. More specifically, in all models the log of herbivore abundance responds to temperature according to $E_{ab} = E_H - E_P$ when expressed as equation (3a) (table 2; see table A1, available online, for solutions expressed as eq. [3b]). This result is not intuitive based on simple conceptual extensions of temperature-dependent demographic models, because each consumer-prey model solution differs markedly in the term B (eq. [3a]), which in some cases even includes a temperature-dependent parameter (table 2). However, numerical analyses of these equilibrium solutions indicate that the B term has virtually no influence on the overall slope of the relationship, and the temperature dependence of the log of herbivore abundance can therefore be accurately represented simply by $E_H - E_P$ (appendix).

In the absence of herbivores, primary producer abundance declined directly in proportion to the temperature-dependence of the carrying capacity (fig. 1; table 2). In all models, herbivores declined in abundance with warming. In the presence of herbivores, primary producer abundance declined at a rate identical to herbivore abundance when herbivore mortality was dependent on density (fig. 1D, 1E). In contrast, primary producer abundance was independent of temperature when per capita herbivore mortality was not density dependent (fig. 1B, 1C).

In addition to the decline in equilibrium herbivore abundance predicted by the consumer-prey models (fig. 1), models 2 and 3 predict that warming can cause herbivore populations to become dynamically unstable and become extinct (1F; table A2). For herbivores to invade and persist in these models, the carrying capacity must be above a threshold determined by the parameter values and equilibrium conditions. Specifically, for model 2, $m/\varepsilon\alpha < K$, and for model 3, $mb/(\varepsilon\alpha - m) < K$ is necessary for viable equilibria and invasion of H into the systems. For model 3, additional criteria for K determine whether equilibria are stable points or oscillations (1F). A change in temperature can affect model stability because K decreases with temperature (tables 1 and 2), but the stability conditions remain constant (e.g., $K > m/\varepsilon\alpha$ for model 2; table A2). Thus, if the carrying capacity is close to the threshold herbivores require for persistence, warming could cause herbivore extinction. Similarly, model 3 may stop cycling and move to a stable point equilibrium with an increase in temperature (1F). This pattern could appear as a stabilizing effect of warming.
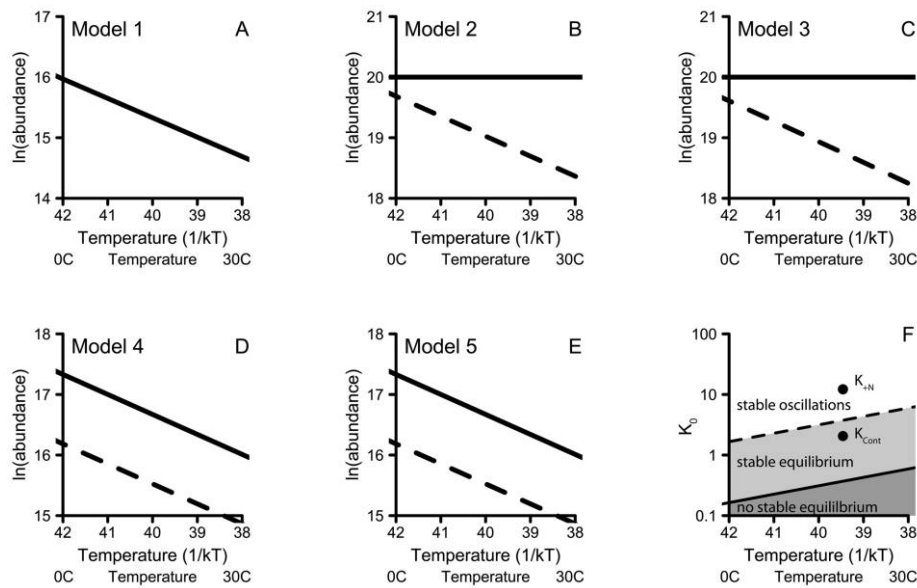
Figure 1: Predicted temperature dependence of herbivore and primary producer equilibrium abundance (N) for different model structures, plotted against temperature expressed as $1/kT$ (T in °Kelvin, °C also shown; both axes present increasing T from left to right). *A–E*, Herbivore abundance (dashed lines) declines with increasing temperature in most cases, while primary producer abundance (solid lines) either declines or does not change. Slopes are determined by net activation energy in the temperature-dependent equilibrium formulas in table 2. *F* illustrates how a change in temperature can change the range of possible stable values for carrying capacity K_0 for model 3. Viable equilibria and invasion of H requires $mb/(\varepsilon\alpha - m) < K$ (dark gray region). Stable equilbria with H and P occur when $mb/(\varepsilon\alpha - m) < K < b(\varepsilon\alpha + m)/(\varepsilon\alpha - m)$ (light gray region), and stable periodic cycles occur when $b(\varepsilon\alpha + m)/(\varepsilon\alpha - m) < K$ (white region). Parameter values are those fit to emprical data, except for K_0 (fig. 3). For comparison, estimated K_0 for experimental nutrient addition (K_{+N}) and nutrient control (K_{Cont}) are shown.

The effect of a change in temperature on the log of abundance can be captured by a simple term ($E_H - E_P$), despite consumer-prey dynamics, when no change in resource supply is assumed. Adding a change in resource supply to the model changes the carrying capacity and, in turn, herbivore and primary producer abundance. The largest effects of changing K occur in the intercept. However, in models 2–4, the second term in the equilibrium solution (B in eq. [3b]), includes K multiplied by T (table 2), indicating an effect of K on the relationship between T and abundance (table A2). A sensitivity analysis showed that when controlling for temperature, changes in resource supply had a nonlinear effect on abundance. A resource-driven change in abundance per unit change in resource was greatest with small changes in resources, and additional change was less influential (fig. A1). As a result, decreases in resource supply, rather than increases, have the greatest effect on abundance (fig. 2). Increases in resource supply and warming have opposite effects on abundance.

Relating Short- and Long-Term Dynamics

The consumer-prey model that we chose a priori to model mesocosm dynamics (model 3 with eq. [4] incorporated) was highly consistent with the observed effects of warming and nutrient addition on plankton abundance (fig. 3). The model accurately simulated the decline in phytoplankton abundance and the increase in zooplankton abundance with warming at high resource levels and captured the highly constrained temperature effects at low resource levels ($r^2 = 0.77$ for phytoplankton and $r^2 = 0.66$ for zooplankton, both $P < .001$; fig. 3). These results were robust when tested with cross-validation analysis: when plankton abundances were fit to replicates that were not included in the model-fitting analysis, r^2 values for phytoplankton and zooplankton remained high (0.74 and 0.62, respectively). As predicted from our model, the decline in phytoplankton abundance occurred even though primary productivity increased with temperature (O'Connor et al. 2009).
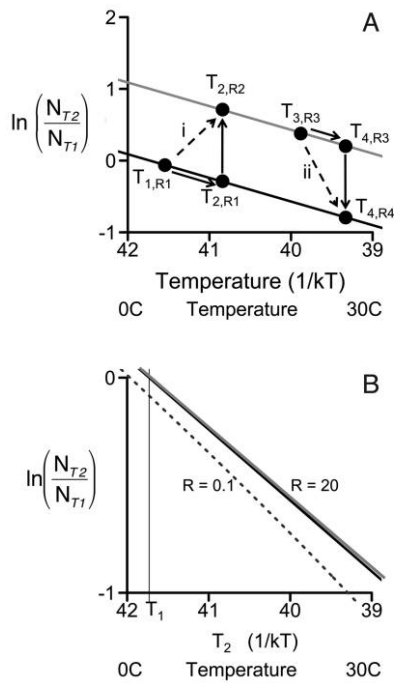
Figure 2: Changes in the primary producer carrying capacity *K* can interact with temperature to affect herbivore and plant abundance. *A*, A change in *K* can alter the intercept of a modeled change in log abundance with temperature if *K* appears in the solution for equilibrium abundance but is not multiplied by *T* (e.g., models 1 and 2, table 2). In this case, the effect of a concurrent warming ($T_2 > T_1$) and increase in resources ($R2 > R1$; eq. [4]) on population trajectories (solid lines, as in fig. 1) would lead to an increase in abundance (arrow i). In contrast, a decline in resource supply with warming leads to a more severe decline in abundance than expected from temperature alone (arrow ii). *B*, A change in *K* can also change the slope of log abundance with temperature, when the equilibrium solution contains *K* multiplied by *T* (as in models 2–5, table 2). The relative abundance of herbivores at temperature T_2 along the *X*-axis and relative to $T_1 = 5°C$ (vertical line) is shown (model 3, table A3, available online). Resources have the maximum effect at parameter values near the boundary for stable equilibrium (appendix, available online), so for these values (e.g., $m_0 = 0.1$, $\varepsilon = 0.1$, $\alpha = 2$, $b = 100$, and $K = 5,680$), changes in resource supply of a 10-, 20- or 200-fold increase ($\dot{R} = 10$, $\dot{R} = 20$, $\dot{R} = 200$, respectively; solid gray lines overlap and appear as one line) do not have a large effect relative to no change ($\dot{R} = 1$, black line) or a 10-fold decrease in resource supply ($\dot{R} = 0.1$, dashed line).

Discussion

Consumer-prey models that incorporated general temperature-dependence functions for heterotrophs and autotrophs produced a small set of testable predictions for the effects of temperature on the abundances of interacting herbivores and primary producers. Across five different model formulations and a wide range of parameter values, slopes of the log of abundance as a function of temperature

converge on a single difference of temperature-dependence terms for herbivore abundance, and three possible slopes for primary producer abundance (table 2; fig. 1). The finding that trophic dynamics can cause primary producer population abundance to be independent of temperature is new and highlights the importance of considering population dynamics in the context of trophic interactions. These models that relate temperature to abundance via growth, consumption, and mortality rates can inform broader hypotheses about effects of environmental change.

General Predictions

Despite the complexity of consumer-prey models, model predictions for effects of temperature on abundance are surprisingly simple and general across different formulations. Each consumer-prey model produced a unique general solution (table 2), yet these models predict virtually identical temperature dependences of herbivore and plant abundances. These solutions suggest negative or null effects of temperature on abundance, despite positive effects of temperature on growth and consumption rates. Further, the ability to characterize the temperature dependence of abundance simply as the temperature dependence (E_a) of primary productivity or as the difference in E_a between primary and secondary productivity means that the solutions are inclusive of taxa for which the values of E_H and E_P deviate from those given in table 1 (Kerkhoff et al. 2005; de Castro and Gaedke 2008). Deviations may occur because E_a is an average of observed temperature dependencies for relevant rates, and for particular cases, E_a may deviate from the mean. In other cases, acclimation or changes in species composition of metabolism may modify the relationship between photosynthesis and net primary production (Enquist et al. 2007). The E_a may not capture the relationship between environmental temperature and metabolic rates, as for endotherms.

In addition to gradual declines in abundance with temperature, temperature-dependent consumer-prey models can explain sudden shifts in food web dynamics. Warming can destabilize some models, or drive a transition from periodic cycling to a stable point equilibrium (fig. 1). Thus, despite the continuous scaling of metabolic rates with temperature, changes in relative rates within certain model formulations can alter the stability of their equilibria, manifesting in sudden changes to dynamics that can lead to extinction of herbivores (Murdoch and McCauley 1985; Beisner et al. 1997; Vasseur and McCann 2005) or, alternatively, lead to more steady conditions. In an emprical study, Beisner et al. (1997) found that warming caused a closed planktonic system to transition into unstable conditions that led to herbivore extinction, as is predicted by
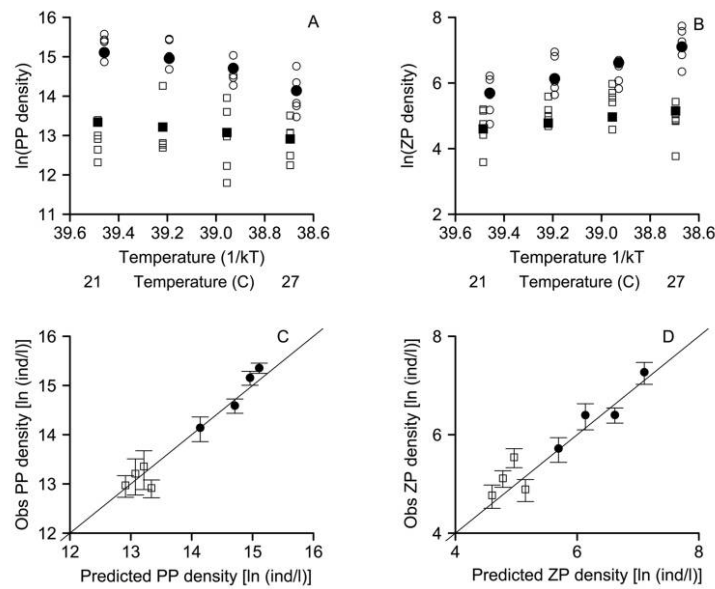
Figure 3: Comparison of model predictions for consumer and prey abundance as a function of general constraints on metabolism and known initial conditions (eq. [1]) with experimental data (O'Connor et al. 2009). Final abundance (open symbols) of phytoplankton (PP, *A*) and zooplankton (ZP, *B*) are plotted along with simulated abundance after 8 days (filled circles), given dynamics in model 3, parameter values fit to the data, and temperature dependence according to the metabolic theory of ecology (eq. [2]; table 1). Experimental treatments for increased resource (N, P) supply (circles) and resource limitation (squares) are plotted. Observed means (SE) are plotted against predictions for phytoplankton (*C*) and zooplankton (*D*), and the line indicates the 1 : 1 relationship. Parameter values are $\alpha = 10^{3.08}$, $r = 0.62$, $K = 10^{6.62}$, $b = 10^{6.00}$, $m = 0.05$, $\varepsilon = 10^{-3.42}$, and $\dot{R} = 5.90$ at 21°C.

our models when primary producer carrying capacity is initially low (fig. 1*F*).

Like changes in stability conditions, changes in resource supply to autotrophs can occur simultaneously with warming and potentially obscure a gradual scaling of abundance with temperature (fig. 2). Relationships between temperature change and supply of resources can be complicated in nature. In pelagic systems, warmer surface waters are typically more stratified and nutrient-poor than colder waters. For this kind of situation, our models would predict a severe effect of nutrient limitation to autotrophs that would reduce the carrying capacity of the system beyond the temperature-driven reductions alone. A prediction based only on how warming affects abundance might be that phytoplankton abundance does not change consumer abundance declines (fig. 1*B* or 1*C*), but when resources are taken into account, the revised prediction should include declines in phytoplankton abundance (fig. 2). Indeed, this pattern is consistent with trends in oceanic systems (Roemmich and McGowan 1995; McGowan et al. 1998). Resource supply does not always change with temperature, however. Light is an important resource for autotrophs, and while environmental temperature may

change with climate change, light availability generally should not.

The temperature dependence of herbivore and plant dynamics that we present is an important first step in modeling the overall impacts of temperature change. In nature, realized temperature effects on abundance could deviate from these predictions for numerous reasons, such as temperature-dependent changes in resource supply that are not driven by metabolic rates (appendix), evolutionary change and changes in body size distributions. We and others have shown how some of these variations can be built into this modeling framework (e.g., Savage et al. 2004; Vasseur and McCann 2005; Lopez-Urrutia et al. 2006; Arim et al. 2007; de Castro and Gaedke 2008). For example, several authors have included body size in MTE demographic predictions (Vasseur and McCann 2005; Arim et al. 2007), but unless there is a known, causal relationship between body size and temperature, such modeling does not facilitate predictions about the effects of changing temperature. Although there are several examples of reductions in body size with environmental warming, general quantitative predictions for this trend are lacking (Atkinson 1994; Daufresne et al. 2010; Moran

et al. 2010). Similarly, exceptions occur when herbivores are endotherms or exist in complex thermal environments (Helmuth et al. 2006), in which case models would require additional terms (Kearney and Porter 2009).

Relating the Model to Empirical Data and Long-Term Studies

Relating simple theory to field data is a challenge, in part because the information needed to rigorously test models is often different from the measurements taken by empirical ecologists. We have tested our model against empirical data from a short-term experiment, and the model successfully captured short-term dynamics in a simple system (figs. 3, 4). These models may also inform predictions for long-term trends in herbivore and primary producer abundance and in doing so may relate short-term experiments to long-term patterns. For example, phyto- and zooplankton abundance has generally declined with environmental warming (Roemmich and McGowan 1995; Richardson and Schoeman 2004), and such trends might be interpreted as contradictory to short-term increases in abundance with temperature observed in experiments. Our analysis shows that exactly the same underlying consumer-prey dynamics and temperature dependencies can explain both patterns, suggesting that short-term trends could actually be compatible with long-term declines (fig. 4). Though the consistency of mesocosm results and theory do not imply that temperature-dependent abundance alone explains long-term patterns, their congruence does suggest that the underlying mechanisms should not be ignored.

The model predictions presented in table 2 are straightforward to test in systems where equilbrium dynamics can be assumed. Effects of temperature on equilibrium abundance might be meaningful when demographic rates are very slow or very fast relative to temperature change. For example, for long-lived primary producers, the average growing season temperature may be representative of the effect of temperature on productivity. Alternatively, for fast-growing plankton systems in aseasonal (tropical ocean) environments, equilibrium dynamics might be adequate to capture effects of changing ocean temperature on plankton abundance. Fortunately, the models can also be tested in systems not at equilibrium (figs. 3, 4). Developing and testing model predictions for nonequilibrium dynamics is essential to understanding climate change impacts in natural systems. For example, seasonal planktonic systems in temperate lakes and oceans likely never reach equilibrium and instead are governed by bloom dynamics that are characterized by a brief period of ideal growth conditions followed by resource limitation (Lopez-Urrutia et al. 2006; Rose and Caron 2007).
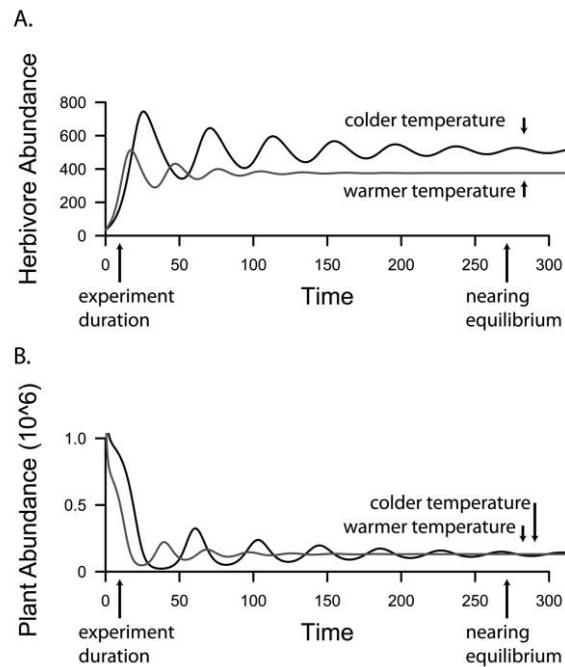

Figure 4: Dynamics of model 3 over time at two temperatures. Temperatures are reflected in parameter values. The "cold" parameters (black lines) are those fit to the experimental data in figure 3 for 21°C, except K was adjusted to $K = 10^{6.00}$ to meet conditions for a stable point equilibrium rather than stable periodic cycles (fig. 1*F*). The "warm" parameters (gray lines) are predicted parameters using model 3 (fig. 1*C*) for 27°C. Transient dynamics can explain an increased herbivore abundance (*A*) concurrent with a decline in primary producer abundance (*B*) in the short-term and long-term declines in herbivore abundance but no change in primary producer abundance (fig. 1*C*).

Our analyses have shown that estimates of mortality, consumption, and so forth are not required for testing model predictions against data (table 2) as long as the temperature dependence or independence of these parameters is understood. Nonetheless, tests do require data on the abundance of herbivores and their prey, any systematic body size shifts, and concurrent changes in resource supply, and this full set of data is rarely reported. Additional data sets should be collected with theoretical predictions in mind. Testing the models in table 2 require data on abundance, temperature, changes in resource supply, and model specifications such as herbivore functional response and whether mortality is density dependent.

Implications for Biogeographic Patterns and Climate Change Responses

Analysis of temperature-dependent consumer-prey models produced new insights about how temperature might af-

fect populations. Effects of tempreature on the demographic and consumption rates of interacting species can lead to predictable changes in abundance. Our finding that primary producer abundance can be independent of temperature even when primary productivity is temperature dependent contradicts previous models (Allen et al. 2002; Vasseur and McCann 2005). Temperature-dependent herbivory has the greatest influence on primary production, causing it to be independent of temperature, in systems where herbivory is strong (herbivores are food limited; models 2 and 3) and can reduce plant abundance (e.g., aquatic systems). In contrast, in systems where the impact of herbivory is controlled by predation or other factors, warming is likely to have a negative effect on the abundance of primary producers (fig. 1; models 4 and 5). In the absence of herbivory, warming causes a decline in plant abundance inversely proportional to the temperature dependence of primary productivity.

The result that temperature-dependent herbivory can cause temperature-independent primary producer abundance may have important implications for understanding latitudinal gradients in terrestrial plant communities. In terrestrial systems, direct extensions of the metabolic temperature dependence models to whole system productivity (Kerkhoff et al. 2005) find that the simplest models are wrong. Biomass accumulation in terrestrial plants does not vary with temperature, despite instantaneous effects of temperature on photosynthesis (Kerkhoff et al. 2005; Enquist et al. 2007). In fact, the observed relationship between temperature and net primary productivity is consistent with our model of temperature-dependent herbivory (models 2 and 3; fig. 1), though so far this hypothesis has not been considered, despite evidence that up to 30% of terrestrial primary production is consumed by herbivores annually in many systems (Cyr and Pace 1993; Cebrian 1999). Thus our model predictions suggest that temperature-dependent herbivory could explain patterns in nature.

Temperature-dependent herbivory is also relevant to ecosystem models of global change impacts. Numerous assessments of global fisheries productivity have used simple models to relate consumer biomass to environmental conditions including temperature (Chassot et al. 2010; Cheung et al. 2010), and some have incorporated metabolic theory (Jennings et al. 2008). However, none have included a temperature-dependent ratio of secondary to primary productivity. Our models indicate that this difference in rates can have large and unexpected outcomes on herbivore and plant abundances. For example, warming of 3°C is projected in many regions with climate change in the coming century, and it could cause on the order of a 10% decline in herbivore abundance due to metabolic scaling alone, which could imply a reduction in abundance at higher trophic levels that would be of great concern in marine food webs (Arim et al. 2007). Such a decline in secondary producer abundance due to temperature-induced changes in trophic dynamics is not currently considered in global models. Rather, these models scale consumer productivity directly to changes in primary productivity. Thus, our incorporation of metabolic theory into simple food webs identifies further hypotheses for the impacts of temperature that need to be tested.

In summary and in conclusion, our results show that incorporating temperature-dependent rates into trophic models alters predictions from direct effects of a temperature change on population abundance. Five common consumer-prey models that vary in their complexity and assumptions converge on a small set of predictions for the effects of temperature on equilibrium abundance of consumers and primary producers. These models also predict effects of changes in resource supply and short-term effects of temperature, thus potentially relating diverse observations of the effects of temperature change in different places or times. This provides a mechanistic framework for developing quantitative predictions of how global change affects species interactions and food web structure. The advantages of this approach include its basis in theory that does not require detailed information on the species involved to generate predictions about the effects of temperature. Thoughtful application of general metabolic temperature-dependence models to more complex models can provide more informative tests of metabolic theory and possibly yield new insights about the effects of temperature on ecological processes.

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