

METABOLIC CONSTRAINTS AND CURRENCIES IN ANIMAL ECOLOGY

A metabolic perspective on competition and body size reductions with warmingDaniel C. Reuman^{1,2*}, Robert D. Holt³ and Gabriel Yvon-Durocher^{4,5}¹Division of Ecology and Evolution, Imperial College London, Silwood Park Campus, Ascot, SL5 7PY, UK;²Laboratory of Populations, Rockefeller University, 1230 York Ave, New York, NY, 10065, USA; ³Department of Biology, University of Florida, 223 Bartram Hall, PO Box 118525, Gainesville, FL, 32611-8525, USA; ⁴School of Biological and Chemical Sciences, Queen Mary University of London, London, E1 4NS, UK; and ⁵Environment and Sustainability Institute, University of Exeter, Penryn, Cornwall, TR10 9EZ, UK**Summary**

1. Temperature is a key driver of ecological processes and patterns. The ramifications of temperature for ecological communities include not only its direct effects on the physiology of individuals, but also how these effects play out in the context of other processes such as competition.

2. Apparently idiosyncratic or difficult to predict effects of temperature on competitive outcomes are well represented in the literature. General theoretical understanding of how physiological influences of temperature filter through community dynamics to determine outcomes is limited.

3. We present a theoretical framework for predicting the effects of temperature on competition among species, based on understanding the effects of temperature on the physiological and population parameters of the species. The approach helps unify formal resource competition theory with metabolic and physiological ecology.

4. Phytoplankton and many other ectotherms are smaller at higher temperatures. This has been observed experimentally, across geographical gradients, and as change accompanying climate warming, but it has not been explained in terms of competition. As a case study, we apply our theoretical framework to competition for nutrients among differently sized phytoplankton.

5. Based on this analysis, we hypothesize that the prevalence of smaller phytoplankton at higher temperatures is at least partly due to an accentuated competitive advantage of smaller cells at higher temperatures with respect to nutrient uptake and growth. We examine the scope for extending the approach to understand resource competition, generally, among ectotherms of different sizes.

Key-words: body size, climate change, competition, metabolism, phytoplankton, R^* theory

Introduction and review

Temperature is a key abiotic driver of ecological systems and a fundamental dimension of the metabolic theory of ecology (Gillooly *et al.* 2001; Brown *et al.* 2004). Yet, the effects of temperature are complex: organism performance, the distribution and abundance of species and the structure of ecological communities do not depend just on the direct impacts of temperature on physiology, but also on how these direct effects play out in the context of other processes. Ever since Darwin, it has been recognized

that the distribution of species along environmental temperature gradients reflects interactions among species, not just direct effects. For instance, climate can impose species range limits directly, through increased mortality or decreased reproduction (e.g. Gaston 2003), but also indirectly, through geographically varying competitor abundance and modified interactions with competitors (Gross & Price 2000; Price & Kirkpatrick 2009). Southern range margins of northern-hemisphere species are believed often to be set by competition, with northern limits set by physiological tolerances (MacArthur 1972; Gaston 2003).

Many examples have been documented of temperature affecting competitive outcomes. For instance, classic

*Correspondence author. E-mail: d.reuman@imperial.ac.uk

experiments showed that temperature can influence competition in *Tribolium* beetles (Park 1954). When grown on their own, both *Tribolium confusum* and *T. castaneum* persisted across the entire range of temperatures tested. When placed together, competitive exclusion was observed. At 34°C and high humidity, *T. castaneum* always won. At 24°C, *T. confusum* prevailed about 70% of the time.

In a conceptually important example, Tilman *et al.* (1981) studied competition for silicates between two freshwater diatoms: *Asterionella formosa* and *Synedra ulna*. Silicates were provided regularly in laboratory cultures. *A. formosa* displaced *S. ulna* at temperatures below 20°C, whereas the reverse occurred above 20°C. Crucially, the equilibrium concentration to which each species in isolation was able to reduce environmental silicate (the so-called R^*) was lower for *A. formosa* below 20°C, whereas it was lower for *S. ulna* above 20°C. Thus, R^* values determined from single-species experiments were predictors of competitive outcomes in two-species experiments (Tilman 1982).

Dunson & Travis (1991) provided a broad overview of abiotic influences on community organization, and in their Table 1 list several other examples (including plants, flatworms, barnacles, fruit flies and fish) of experimental demonstrations that competition can be strongly influenced by temperature. A recent review of 688 studies found ubiquitous evidence that climate change affects several types of species interaction, including competition (Tylianakis *et al.* 2008). Woodward *et al.* (2010), Gilman *et al.* (2010) and Kordas *et al.* (2011) provided useful recent overviews of the potential impact of climate change on interspecific interactions. Amarasekare (2007, 2008) provide examples exploring the effects of a temperature-based temporal refuge on intraguild predation.

The above examples are informative, but they and other studies of competition lack at least one of two important features: either the physiological mechanisms are not understood by which environmental conditions (e.g. temperature) influence survival, fecundity and other vital rates, or the population-dynamic mechanisms are not understood by which changes in vital rates lead to differences in competitive outcomes, or both. For instance, Park (1954) realized that temperature and humidity affect devel-

opmental and physiological processes in *Tribolium*, but he had no precise description of these effects, nor did he know how they influence population dynamics. Excellent population-dynamic models of *T. castaneum* and *T. confusum* now exist (Benoit *et al.* 1998; Dennis *et al.* 2001; Reuman *et al.* 2008), but to our knowledge, parameters of the models have not been related to environmental conditions. Tilman *et al.* (1981) considered a population-dynamic model and parameterized it experimentally for each of his two species at each temperature he considered. However, the physiological link between environmental conditions and species parameters was not explicitly described, making it hard to generalize findings. Buckley *et al.* (2014) have described the link between environmental temperatures and aspects of physiology in grasshopper populations on an altitude gradient, but have not yet linked physiology to population dynamics and competition.

The aim should be to describe thermal dependence quantitatively, without having to measure parameters species by species. We assume that parameters are not entirely idiosyncratic among species and can be inferred from species traits. Understanding and predicting the ecological effects of climate change has become a major goal of ecology. But this goal is hampered by the lack of generality that characterizes most studies of competition and that arises from the two shortcomings in mechanistic understanding described above.

If one has an explicit model of competition, a protocol for examining how temperature (or another factor) might influence competition is to make the parameters of the model functions of temperature. This basic approach was suggested by Gilman *et al.* (2010). Lafferty & Holt (2003) provide a comparable host–pathogen example, Vasseur & McCann (2005) developed a predator–prey example and Ohlberger *et al.* (2011) explore an example that examines intraspecific competition. A general model sheds light on the proposed approach. Consider the Lotka–Volterra model of competition, where we have abstractly expressed the model parameters as functions of temperature, T :

$$\frac{dN_i}{dt} = r_i(T) - a_{ii}(T)N_i - a_{ij}(T)N_j, \quad \text{eqn 1}$$

where $i \neq j$ and $i, j = 1, 2$ (Baskett 2012). Here, N_i is the density of competitor i , a_{ii} measures the strength of intraspecific competition, and a_{ij} measures the strength of interspecific competition. If a species is alone in an environment with a constant temperature, it reaches an equilibrium population density $N_i^* = r_i(T)/a_{ii}(T)$, and it should persist, provided its intrinsic growth rate is positive (and ignoring demographic stochasticity). If we assume temperature is constant, then we can in the usual way write down conditions for coexistence (so that each species can increase when it is rare and its competitor is at its equilibrium density): $a_{22}(T)/a_{12}(T) > r_2(T)/r_1(T) > a_{21}(T)/a_{11}(T)$. If intraspecific and interspecific density dependence are equivalent, so the two outer ratios are unity, then coexistence is impossible; the species with the higher carrying capacity,

Table 1. Summary of model parameters. Parameters are defined in eqns 8 and 9. $T_0 = 293.15\text{K}$ and $k = 8.6173324 \times 10^{-5}\text{eV K}^{-1}$. Here $E_{\mu_{\max}}$ has units eV, $k_{\mu_{\max}}$ has units $\text{d}^{-1} \mu\text{m}^{-3}e_{\mu_{\max}}$, and $e_{\mu_{\max}}$ and $e_{H_{\text{gro}}}$ are dimensionless

Parameter	Estimate	SE	Sources
$e_{\mu_{\max}}$	-0.28	0.018	Edwards <i>et al.</i> (2012)
$\log_{10}(k_{\mu_{\max}})$	0.65	0.059	Edwards <i>et al.</i> (2012)
$E_{\mu_{\max}}$	0.474	0.036	Eppley (1972); Bissinger <i>et al.</i> (2008)
$e_{H_{\text{gro}}}$	0.29	0.091	Edwards <i>et al.</i> (2012), this paper

which is also the species with the higher intrinsic growth rate, will win. Growth rate is a measure of species competitive performance for this scenario. Both temperature and body size have a strong effect on growth rate (Savage *et al.* 2004; Amarasekare & Savage 2012), so will influence competitive dominance.

Species performance as a function of temperature typically is unimodal, albeit often with sharper declines at high temperatures than low temperatures (Angilletta 2009; Dell *et al.* 2011; Amarasekare & Savage 2012). Along an environmental temperature gradient, one might observe patterns of species replacement, with local dominance by whichever species has the higher local growth rate. This can happen in two different ways. First, two species may have similar performance curves, but with different optima (Fig. 1a). Second, one species may be more tolerant of a broader range of conditions, without there being any difference in optima (Fig. 1b). In case one, both species are equally generalized, but to different temperatures. In the latter case, one species is more specialized. In both cases, species 1 dominates below the points x on Fig. 1 and is supplanted at temperatures above x . So different biological interpretations can underlie a given pattern of species replacement along a temperature gradient. More complex scenarios can also occur, where the strengths of density dependence are not equal and vary as a function of temperature. A species may be an inferior competitor not because it has low carrying capacity, but because it is particularly sensitive in a given thermal regime to the per capita effects of the competing species. This simple model (eqn 1), while informative about possibilities, is clearly not mechanistic enough to fully explore the consequences of temperature change; models with truly mechanistic formulations of physiology–temperature relationships and more realistic depictions of dynamics are needed. In the simple case considered, if no crossing point, x , exists, then

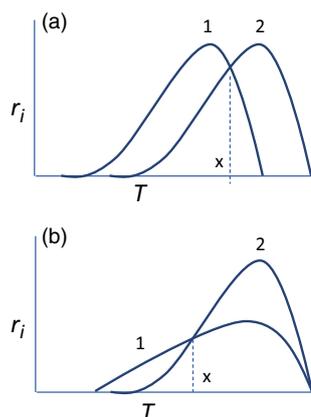


Fig. 1. Competition at different temperatures according to the simple general model of the Introduction, eqn 1. (a) Two species with similar performance curves as a function of temperature, T , but with different optima. (b) Two species with the same optimum temperature, but one is more cold tolerant. More details are in the Introduction. Kordas *et al.* (2011) produced a similar figure.

one species is strictly inferior and can only exist if the superior competitor has not dispersed to its range.

Reduced body size of ectotherms has been called a universal ecological response to global warming (Daufresne *et al.* 2009), and warming-related size reductions have been documented in many species (Millien *et al.* 2006; Daufresne *et al.* 2009; Sheridan & Bickford 2011). Geographical variation in body size along a temperature gradient, with smaller sizes in warmer areas, is long studied (Bergmann 1847). Phytoplankton, specifically, are smaller in warmer regions of the ocean or in response to experimental temperature manipulation (Figs 2 and 3 and Winder *et al.* 2009; Daufresne *et al.* 2009; Morán *et al.* 2010; Yvon-Durocher *et al.* 2011 for examples). Shrinking phytoplankton may be practically important because fisheries are based mainly on phytoplankton production, and marine consumer–resource relationships are size-structured (Barnes *et al.* 2010b). Also, carbon export to the deep ocean proceeds by sinking plankton (Smetacek 1985, 1999), and differently sized plankton sink at different rates (Miklasz & Denny 2010).

Various explanations have been advanced for smaller size in ectotherms at warmer temperatures (Sheridan & Bickford 2011). Perhaps the best known explanation relates to metabolism: if the total metabolic rate of a trophic level increases with increasing population abundance, temperature and body size, and if nutrient inputs to the trophic level remain fixed, then increased metabolic demand due to warmer temperatures can be compensated for through reduced abundance or reduced body size, or

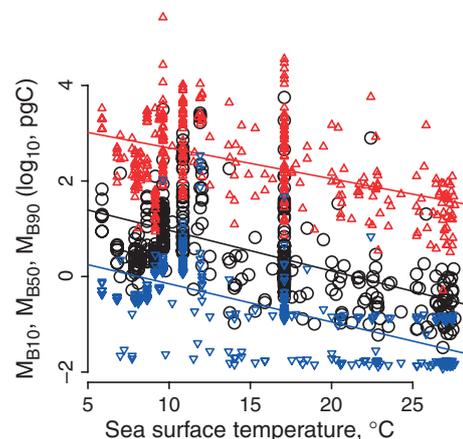


Fig. 2. An empirical example of smaller phytoplankton at warmer temperatures, from the marine environment. The figure presents similar information to Barnes *et al.* (2010a) in adapted format, using their data; it shows size distributions of phytoplankton in 361 water samples collected in the North Atlantic, South Atlantic, Benguela upwelling, Bergen fjord, Irminger Sea, Long Island Sound, North Sea, Norwegian Sea, and Oregon upwelling. M_{B10} , M_{B50} and M_{B90} refer to the cell sizes below which 10%, 50% and 90% of the biomass of the sample was represented, depicted with blue downward triangles, black open circles and red upward triangles, respectively. Lines show ordinary least-squares regressions through the three point types.

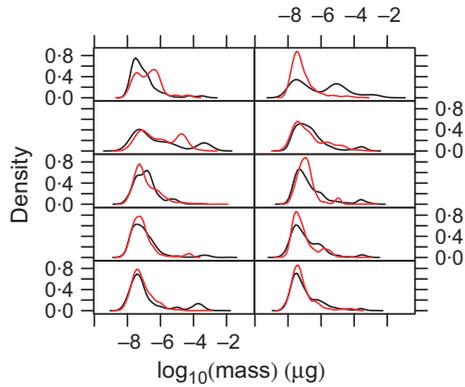


Fig. 3. An empirical example of smaller phytoplankton at warmer temperatures, from a freshwater mesocosm. The figure presents similar information to Yvon-Durocher *et al.* (2011) in adapted format, and uses their data; it shows distributions of \log_{10} cell size of phytoplankton in 10 freshwater pond mesocosms that experienced ambient temperatures in Dorset, UK (black lines), along with distributions of \log_{10} cell sizes in 10 mesocosms that were heated by 3 to 5 °C above ambient. Red peaks at small sizes on most panels indicate small cells have become relatively more common in the warmed mesocosms. Mean mass in the ambient-temperature ponds was $3.72 \times 10^{-5} \mu\text{g}$ (SE 2.95×10^{-6}), whereas in the warmed ponds, it was $3.71 \times 10^{-6} \mu\text{g}$ (SE 5.33×10^{-7}), an order of magnitude smaller.

a combination (Sheridan & Bickford 2011). Competition is not mentioned explicitly in this explanation, nor in any of the other common explanations (Sheridan & Bickford 2011), though it seems likely to play a role. The important question of how competition among differently sized ectotherms causes observed size reductions will serve as a focal point for our proposed approach.

This study has three main goals. We will (i) examine whether changes in the competitive abilities of differently sized plankton may be responsible for observed reductions in size under warming, using a model of phytoplankton nutrient uptake, growth and competition for nutrients. Phytoplankton are a good place to start, because of the extensive information that is available on their resource requirements, cell size dependencies and basic population dynamics. We write model parameters in terms of cell size and temperature. We explore how R^* and invasion fitness are expected to vary with cell size at different temperatures. In so doing, we will (ii) illustrate our proposed theoretical framework and advocate its broader application. We will also (iii) examine a general model of resource exploitation using the same approach to assess possibilities for inferences about ectotherms generally.

Phytoplankton

MODEL

We model phytoplankton growth and competition for nutrients using a system of ordinary differential equations with parameters that reflect cell physiology. System state variables, where i is a species index, are as follows: popu-

lation density, N_i (cells L^{-1}); internal cellular nutrient quota, Q_i ($\mu\text{mol nutrient cell}^{-1}$); and external concentration of the nutrient R ($\mu\text{mol nutrient L}^{-1}$). Growth rate depends on internal nutrient quota following the model of Droop (1973), with minimum cellular nutrient concentration $Q_{\min,i}$ ($\mu\text{mol nutrient cell}^{-1}$) and growth rate at theoretical infinite cellular nutrient concentration $\mu_{\infty,i}$ (day^{-1}). Nutrient uptake depends on external nutrients via Michaelis–Menten kinetics, with an uptake half-saturation constant of $H_{\text{up},i}$ ($\mu\text{mol nutrient L}^{-1}$; Aksnes & Egge 1991). It also depends on internal nutrient concentration, with maximal uptake rate $V_{\max,i}$ ($\mu\text{mol nutrient cell}^{-1}\text{day}^{-1}$) occurring when external nutrients are abundant and $Q_i = Q_{\min,i}$. The quantity $Q_{\max,i}$ ($\mu\text{mol nutrient cell}^{-1}$) is a theoretical maximal cellular nutrient concentration at which uptake is 0. Cellular mortality rate is m_i (day^{-1}), which could be caused by multiple factors. R_0 is input nutrient concentration ($\mu\text{mol nutrient L}^{-1}$), and d is nutrient supply rate (day^{-1}). Equations are as follows:

$$\frac{dN_i}{dt} = N_i \left(\mu_{\infty,i} \left(1 - \frac{Q_{\min,i}}{Q_i} \right) - m_i \right) \quad \text{eqn 2}$$

$$\frac{dQ_i}{dt} = V_{\max,i} \left(\frac{Q_{\max,i} - Q_i}{Q_{\max,i} - Q_{\min,i}} \right) \frac{R}{R + H_{\text{up},i}} - \mu_{\infty,i} \left(1 - \frac{Q_{\min,i}}{Q_i} \right) Q_i \quad \text{eqn 3}$$

$$\frac{dR}{dt} = d(R_0 - R) - \sum_i V_{\max,i} \left(\frac{Q_{\max,i} - Q_i}{Q_{\max,i} - Q_{\min,i}} \right) \frac{R}{R + H_{\text{up},i} N_i} \quad \text{eqn 4}$$

The term $d(R - R_0)$ is supply rate times the difference between inflow and outflow nutrient concentrations because inflow and outflow volumes are equal. Variant models of this form are common (Morel 1987; Grover 1991; Klausmeier *et al.* 2004; Litchman *et al.* 2009; Verdy *et al.* 2009). The model can be considered with one, two or many species present. For brevity, species subscripts are sometimes not displayed.

According to resource competition theory (e.g. Tilman 1982), the species that, when considered in isolation, drives the external resource concentration R to the lowest equilibrium level, R^* , will exclude other species. R^* was computed following Verdy *et al.* (2009):

$$R^* = \frac{m H_{\text{gro}}}{\mu_{\max} - m}; \quad \text{eqn 5}$$

$$H_{\text{gro}} = \frac{H_{\text{up}} Q_{\min} \mu_{\max}}{V_{\max}}; \quad \text{eqn 6a}$$

$$\mu_{\max} = \frac{\mu_{\infty} V_{\max} \Delta Q}{V_{\max} Q_{\max} + \mu_{\infty} Q_{\min} \Delta Q}; \quad \text{eqn 6b}$$

$$\Delta Q = Q_{\max} - Q_{\min}. \quad \text{eqn 6c}$$

Verdy *et al.* show that a positive equilibrium exists as long as $\mu_{\max} > m$ and $R_0 > R^*$; otherwise, extinction occurs. μ_{\max} is the maximum observable growth rate when

internal nutrient concentration is at equilibrium. H_{gro} is a half-saturation parameter with respect to external nutrient for growth at equilibrium internal nutrient (Monod 1949). The growth rate of a species j introduced at low density into a monoculture of i , called the invasion fitness of j into i , was also computed following Verdy *et al.* (2009):

$$G_{i,j} = \mu_{max,j} \frac{R_i^*}{R_i^* + H_{gro,j}} - m_j. \quad \text{eqn 7}$$

$G_{i,j}$ is positive when $R_i^* > R_j^*$ and negative when $R_i^* < R_j^*$. $G_{i,j}$ provides information beyond R_i^* and R_j^* because it indicates the rate of invasion (or extirpation of the putative invader), whereas R_i^* and R_j^* give the final outcome of competition.

If s is cell size (μm^3), and s_{re} and s_{in} are sizes of the resident (i) and invader (j), our strategy is to establish the dependencies of R^* on s and T and of G on s_{re} , s_{in} and T . The derivative $\partial G(s_{in}, s_{re})/\partial T$, when positive, indicates that invasion fitness is accentuated by warmer temperatures; and when negative, invasion fitness is decreased by warming. The ratio $G(s_{in}, s_{re}, T_1)/G(s_{in}, s_{re}, T_2)$, for $T_1 > T_2$, represents how a specific amount of warming affects invasions. When this ratio is >1 , warmer temperatures mean successful invasions happen faster and unsuccessful ones fail faster. When between 0 and 1, warming means successful invasions happen slower and unsuccessful ones fail slower. When negative, an invasion that would have failed at one temperature succeeds at the other.

PARAMETERIZATION

The dependencies of μ_{max} and H_{gro} on cell size and temperature need to be quantified. Edwards *et al.* (2012) found that $\log_{10}(\mu_{max})$ depends linearly on $\log_{10}(s)$ with slope -0.28 (SE 0.018) and intercept 0.65 (SE 0.059), using data from over 200 species. The same study found that the \log_{10} of 'scaled assimilation affinity', $V_{max}/(H_{up}Q_{min})$, depends linearly on $\log_{10}(s)$ with slope -0.57 (SE 0.089). Combining these results and using the expression for H_{gro} (eqn 6a) shows H_{gro} depends on s via a power law with exponent 0.29 (SE 0.091). Edwards *et al.* (2012) used data from studies carried out at or close to 20 °C.

Prior work (Eppley 1972; Raven & Geider 1988; Bissinger *et al.* 2008) supports Arrhenius dependence of μ_{max} on temperature:

$$\mu_{max} = k_{\mu_{max}} \exp\left(\frac{E_{\mu_{max}}(T - T_0)}{kTT_0}\right) s^{e_{\mu_{max}}}. \quad \text{eqn 8}$$

The results of Edwards *et al.* (2012) give $e_{\mu_{max}} = -0.28$ and $k_{\mu_{max}} = 10^{0.65}$ if we set $T_0 = 293.13\text{K}$ (equal to the 20 °C at which the data of Edwards *et al.* were measured). Here and in all Arrhenius dependencies, T is in K and $k = 8.6173324 \times 10^{-5} \text{eV K}^{-1}$ is Boltzmann's constant. This functional form for μ_{max} is also consistent with the results of Savage *et al.* (2004). Eppley (1972) reported a

Q_{10} of 1.88 between about 5 and 40 °C for μ_{max} , which is very nearly an Arrhenius dependence with $E_{\mu_{max}} = 0.474\text{eV}$. In an analysis using 1500 data points, Bissinger *et al.* (2008) reported an exponential dependence of μ_{max} on temperature that is very nearly an Arrhenius dependence with $E_{\mu_{max}} = 0.474$ (SE 0.036), agreeing with Eppley (1972) to three decimal places. We use $E_{\mu_{max}} = 0.474$ (SE 0.036).

Data on the temperature dependence of H_{gro} are scarce (Edwards *et al.* 2012), but fortunately we can use an arbitrary dependence,

$$H_{gro} = f_{H_{gro}}(T) s^{e_{H_{gro}}}, \quad \text{eqn 9}$$

where $e_{H_{gro}} = 0.29$ is from the study by Edwards *et al.* (2012); we will see below that results will not depend on $f_{H_{gro}}(T)$. Parameterizations are summarized in Table 1. Additional details are in Appendix S1. Because parameterizations use data on N competition (Appendix S1), results correspond chiefly to competition under N-limited conditions, thought to be common in the sea (Litchman *et al.* 2009). Allometric relationships for P competition are similar (Edwards *et al.* 2012). Theoretical and empirical arguments exist supporting a particular form for $f_{H_{gro}}(T)$, but are in Appendix S2 because they are not needed for our main results.

We assume initially that m is independent of temperature. This can be true in chemostats, in which mortality is the washout rate, d , which can be set independently of temperature. Mass and temperature dependence of m in natural environments depends on ecological circumstances such as the zooplankton community. Our goal is to understand how temperature affects aspects of competition that relate to nutrient uptake and growth, so it makes sense initially to neglect other factors such as predation. We also consider two cases for which m depends on temperature. Sinking of cells below the thermocline causes mortality. Sinking-induced mortality is proportional to sinking rate (Litchman *et al.* 2009). In physiologically competent cells, sinking rate is independent of cell size; for inactivated cells, it depends on cell size to a power between about 1.2 and 1.6 (Waite *et al.* 1997; Miklasz & Denny 2010). Sinking rate has also been shown to be described by Stokes' Law (Miklasz & Denny 2010), which implies that sinking rate is proportional to the inverse of the dynamic viscosity of the medium. Inverse dynamic viscosity of seawater depends on temperature via an Arrhenius form with activation energy 0.1781eV (SE 0.001; Appendix S1). Therefore,

$$m = g_m(s) \exp(E_m(T - T_0)/(kTT_0)) \quad \text{eqn 10}$$

is the general form we use for m , with either (i) g_m arbitrary and $E_m = 0$ (chemostat); or (ii) $g_m(s) = k_m$ a constant and $E_m = 0.1781$ (cell-size-independent sinking); or (iii) $g_m(s) = k_m s^{1.4}$ and $E_m = 0.1781$ (cell-size-dependent sinking). We use 1.4 for the s exponent in (iii) because it is between 1.2 and 1.6, the range reported by Miklasz & Denny (2010).

MODEL ANALYSIS AND RESULTS

Our principal result is that smaller cells have accentuated competitive advantage in warmer waters. We consider the case $m = g_m(s)$ first (chemostat case). Substituting eqns 8, 9 and 10 (with $E_m = 0$) into eqns 5 and 7 and simplifying gives

$$G = \frac{\mu_{\max}(s_{\text{in}}, T)g_m(s_{\text{re}})s_{\text{re}}^{e_{H_{\text{gro}}}}}{g_m(s_{\text{re}})s_{\text{re}}^{e_{H_{\text{gro}}}} + s_{\text{in}}^{e_{H_{\text{gro}}}}(\mu_{\max}(s_{\text{re}}, T) - g_m(s_{\text{re}}))} - g_m(s_{\text{in}}), \quad \text{eqn 11}$$

which does not depend on $f_{H_{\text{gro}}}(T)$. It is straightforward to compute the derivative $\partial G(s_{\text{in}}, s_{\text{re}})/\partial T$ and to show that it is greater than 0 for $s_{\text{re}} > s_{\text{in}}$ and less than 0 for $s_{\text{re}} < s_{\text{in}}$ (Appendix S3). Hence, smaller cells are more likely to invade communities of larger cells or to do so faster in warmer waters than in colder waters. Also, attempted invasions by larger cells into communities of smaller cells are more likely to fail, or they will do so faster. Effects of temperature can be substantial (Fig. 4a–d), with invasion of small cells into communities of large cells happening up to almost 100% faster in 20 °C compared with 10 °C (Fig. 4e), and up to about 20% faster at 23 °C compared with 20 °C (Fig. 4f). Here, 3 °C was used as a benchmark for climate change (IPCC 2007). Results are insensitive to errors in parameter estimation (section ‘Phytoplankton: Parameterization’) because they rely only on having $e_{H_{\text{gro}}} > 0$ (Appendix S3), which we know with great confidence (Table 1).

If $m = g_m(s) = k_m s^{e_m}$, then an evolutionarily stable size (ESS) is possible, and it is smaller under warmer temperatures. This is a special case of the prior paragraph, because m still depends only on s , now as a power law. By resource competition theory (Tilman 1982; Verdy *et al.* 2009), the ESS occurs where R^* is minimal. Substituting eqns 8 and 9 and $m = k_m s^{e_m}$ into eqn 5 gives

$$R^* = \frac{k_m f_{H_{\text{gro}}}(T) s^{e_{H_{\text{gro}}} + e_m}}{k_{\mu_{\max}} \exp\left(\frac{E_{\mu_{\max}}(T - T_0)}{kTT_0}\right) s^{e_{\mu_{\max}}} - k_m s^{e_m}}. \quad \text{eqn 12}$$

This has a minimum if and only if $e_{\mu_{\max}} - e_{H_{\text{gro}}} < e_m < e_{\mu_{\max}}$ ($-0.57 < e_m < -0.28$; Table 1), and in that case the minimum is at

$$s_{\text{ESS}} = \left(\frac{e_{H_{\text{gro}}} k_m}{(e_m + e_{H_{\text{gro}}} - e_{\mu_{\max}}) k_{\mu_{\max}} \exp\left(\frac{E_{\mu_{\max}}(T - T_0)}{kTT_0}\right)} \right)^{\frac{1}{e_{\mu_{\max}} - e_m}} \quad \text{eqn 13}$$

(Appendix S4). As $k_{\mu_{\max}} \exp\left(\frac{E_{\mu_{\max}}(T - T_0)}{kTT_0}\right)$ increases as T increases, this implies the ESS decreases with warming. See Fig. 5 for an example. The condition $e_{\mu_{\max}} - e_{H_{\text{gro}}} < e_m < e_{\mu_{\max}}$ is the same as $0 < e_{\mu_{\max}} - e_m < e_{H_{\text{gro}}}$, that is, the ratio of maximum growth to mortality must increase with cell size, but must do so slower than does the half-saturation constant for growth. The result here is insensitive to errors in the estimation of parameters because it relies only

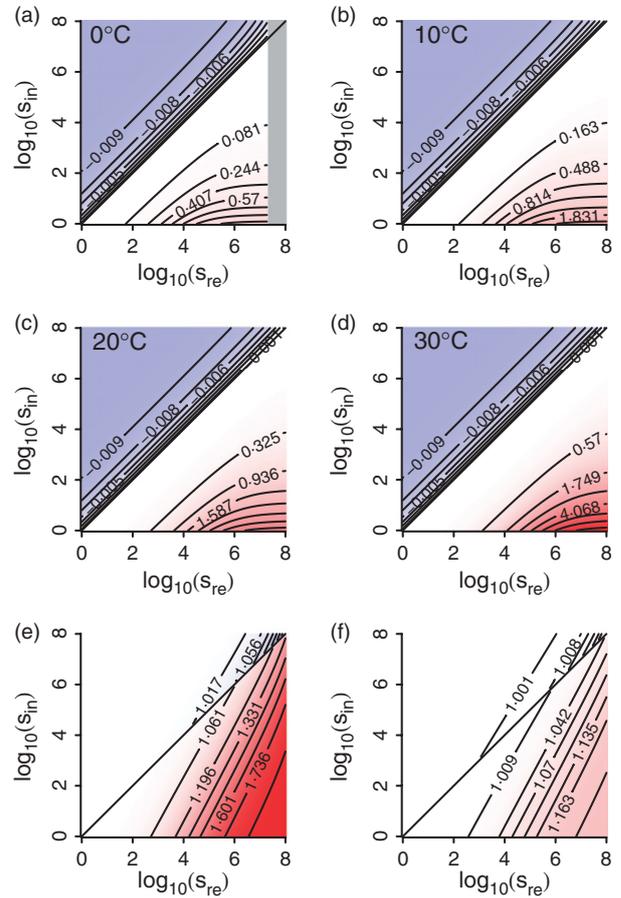


Fig. 4. (a–d) Pairwise invasibility plots, $G(s_{\text{in}}, s_{\text{re}})$, at different temperatures for $m = 0.01 \text{ day}^{-1}$; s_{in} and s_{re} are the cell sizes of the invading and resident species, respectively, and m is a mortality rate. Invasion fitness, G , was always positive for $s_{\text{in}} < s_{\text{re}}$, indicating smaller sizes are always more competitive, but the competitive advantage of smaller sizes is accentuated at warmer temperatures. Red corresponds to positive G and blue to negative G . The red (respectively, blue) colour scales are the same across these four panels. Black lines are contour lines and the line $s_{\text{in}} = s_{\text{re}}$. The grey area on (a) indicates resident cells that were not viable on their own. (e–f) Ratios of pairwise invasibilities at different temperatures, for the same m as a–d. Plots show $G(s_{\text{in}}, s_{\text{re}}, T_1)/G(s_{\text{in}}, s_{\text{re}}, T_2)$ for $T_1 = 20$ °C and $T_2 = 10$ °C (e) and for $T_1 = 23$ °C and $T_2 = 20$ °C (f). See sections ‘Phytoplankton: Model’ and ‘Phytoplankton: Model analysis and results’ for interpretation of this ratio. The red (respectively, blue) colour scales are the same across these two panels. The same result of accentuated invasion fitness of smaller invaders at warmer temperatures was also true for $m = 0.0001, 0.001, \text{ and } 0.02$; m in this range have been used in earlier studies (e.g. Litchman *et al.* 2009). For larger m , many of the resident sizes were not viable on their own.

on having $E_{\mu_{\max}} > 0$, which we know with great confidence (Table 1).

Using $m = k_m \exp(E_m(T - T_0)/(kTT_0))$ (cell-size-independent sinking) or using $m = k_m s^{1.4} \exp(E_m(T - T_0)/(kTT_0))$ (cell-size-dependent sinking), similar results held to the constant- m case of Fig. 4: smaller cells were always able to invade larger cells, with rates accentuated in warmer temperatures (e.g. Fig. S2). The R^* and invasion-

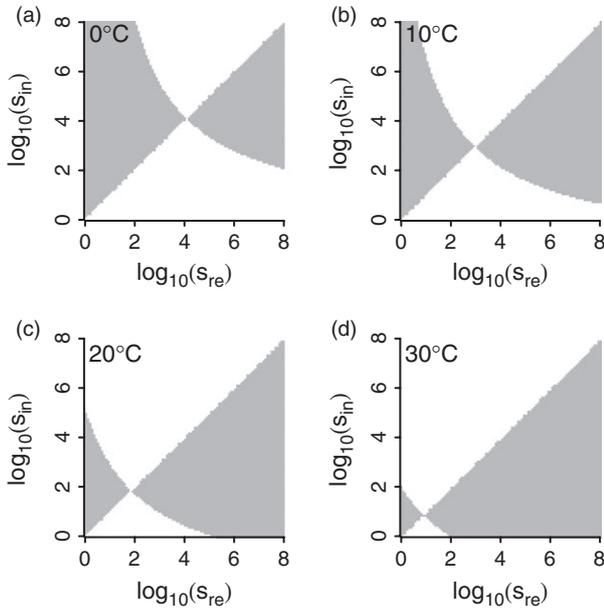


Fig. 5. Signs of pairwise invasibility plots, $G(s_{in}, s_{re})$, at different temperatures for $m = s^{-0.55}$; s_{in} and s_{re} are the cell sizes of the invading and resident species, respectively, and m is a mortality rate. Grey indicates positive G and white indicates negative G . Positive (respectively, negative) G means invasion is possible (respectively, impossible). The evolutionarily stable size (ESS) is the value of s_{re} for which $G(s_{in}, s_{re}) < 0$ for all s_{in} . The ESS is smaller at warmer temperatures.

fitness considerations of this section assume that model equilibria are stable. This was true for wide ranges of parameters encompassing biologically reasonable values (Appendix S5).

Discussion of possibilities beyond phytoplankton

Can our approach be applied to gain insight about the effects of temperature on competition for ectotherms generally? We explored possibilities with the Rosenzweig–MacArthur model, often used as a general model (Rosenzweig & MacArthur 1963; Dell *et al.* 2014; DeLong *et al.* 2014).

MODEL

If R is biomass density of a resource and N_i is biomass density of consumer i , the model is

$$\frac{dN_i}{dt} = N_i \left(-m_i + \mu_{max,i} \left(\frac{R}{R + H_{con,i}} \right) \right) \quad \text{eqn 14}$$

$$\frac{dR}{dt} = rR \left(1 - \frac{R}{K} \right) - \sum_i \frac{\mu_{max,i}}{e} N_i \left(\frac{R}{R + H_{con,i}} \right). \quad \text{eqn 15}$$

Here, m_i is the mortality or respiration rate for i ; $\mu_{max,i}$ is the maximum growth rate, related to the maximum rate by which i removes biomass from the resource via the

efficiency e ; $H_{con,i}$ is the half-saturation for consumption; and r and K are the growth rate and carrying capacity of R . H_{con} is related to the attack rate, α , and handling time, t_h , in a Holling type II functional response (Holling 1965) via $H_{con} = \frac{s_R}{\alpha t_h}$, where s_R is the body mass of R (Vasseur & McCann 2005).

It is known (Vasseur & McCann 2005) that when the one-species model has a stable equilibrium, it is globally stable, and the equilibrium value for R is

$$R^* = \frac{m H_{con}}{\mu_{max} - m}. \quad \text{eqn 16}$$

If the model has a stable equilibrium for i , then the invasion fitness for j invading i is

$$G_{i,j} = \frac{\mu_{max,j} m_i H_{con,i}}{m_i H_{con,i} + H_{con,j} (\mu_{max,i} - m_i)} - m_j. \quad \text{eqn 17}$$

These expressions have parallel structure to eqns 5 and 11: the only variables are m , μ_{max} and H_{con} , which are analogous to m , μ_{max} and H_{gro} . If m , μ_{max} and H_{con} can be written as functions of temperature and consumer body size, s , then we can get insight into the effect of temperature on competition among differently sized consumers of R .

PROSPECTS FOR PARAMETERIZATION

Is it currently possible to parameterize m , μ_{max} and $H_{con} = \frac{s_R}{\alpha t_h}$ in terms of s and T ? For μ_{max} and m , metabolic theory applies and data are available. Vasseur & McCann (2005) have already provided parameterizations. Those authors used different parameterizations for different ‘metabolic categories’ of consumer (e.g. vertebrate ectotherms, invertebrates).

Because handling time, t_h , should be inversely related to maximum consumption rate, which is related to metabolic rate, metabolic theory predicts $t_h \propto s^{e_{t_h}} \exp\left(\frac{E_{t_h}(T-T_0)}{kTT_0}\right)$ for ectotherm consumers of a resource of mass s_R , where $e_{t_h}, E_{t_h} < 0$ (Brown *et al.* 2004; Vasseur & McCann 2005). Handling time is therefore predicted to decrease with increasing temperature or consumer size. The metabolic categories used by Vasseur & McCann (2005) should again affect proportionality constants. Power-law dependence of t_h on s was supported by Vucic-Pestic *et al.* (2010), who reported $e_{t_h} = -0.94$ (SE 0.09). Earlier studies supported the qualitative conclusion that t_h decreases with increasing s (e.g. Thompson 1975; Hassell *et al.* 1976; Aljetlawi *et al.* 2004; Vucic-Pestic *et al.* 2010 cited more). Good support for the temperature dependence of handling time was provided by Vucic-Pestic *et al.* (2011), who obtained $E_{t_h} = -0.23$ (SE 0.07) for a sedentary prey species and $E_{t_h} = -0.24$ (SE 0.1) for a mobile prey species. Earlier work also generally supports a similar temperature dependence of t_h (e.g. Thompson 1978; Song & Heong 1997; García-Martín *et al.* 2008; Vucic-Pestic *et al.* 2011 cited more). However, recent meta-studies have

argued for hump-shaped dependencies in some contexts and heterogeneity of scaling exponents across taxonomic and metabolic groups and habitat types (Englund *et al.* 2011; Rall *et al.* 2012).

The body mass and temperature dependence of α are complex. Brose *et al.* (2008) and Vucic-Pestic *et al.* (2010, 2011) described a hump-shaped dependence of α on the consumer–resource body mass ratio s/s_R , supporting prior research (e.g. Hassell *et al.* 1976; Wahlström *et al.* 2000; Vonesh & Bolker 2005). If s_R is fixed, this is a hump-shaped dependence of α on s . Vucic-Pestic *et al.* (2011) provided support for the idea that α is independent of T for sedentary prey and has Arrhenius dependence on T for mobile prey. The regressions of Vucic-Pestic *et al.* (2011) were based on only 18 data points, and their statistical power and confidence levels were modest, but nevertheless T dependence of α seems likely to depend on the nature of the foraging interaction; this idea is also supported by Dell *et al.* (2014), although those authors do not support temperature independence of α for sedentary prey in all cases. Vucic-Pestic *et al.* (2011) cited earlier studies that reported heterogeneous dependencies of α on T , including linear, power-law, hyperbolic and dome-shaped functions (e.g. Thompson 1978; Dreisig 1981; Cave & Gaylor 1989; Song & Heong 1997; Gilioli *et al.* 2005; García-Martin *et al.* 2008). Englund *et al.* (2011) and Rall *et al.* (2012) again argue for hump-shaped dependencies for some contexts and heterogeneity of scaling across taxonomic and metabolic groups. In addition to distinctions among metabolic categories (Vasseur & McCann 2005) and among predation strategies (e.g. sit-and-wait, active capture; Vucic-Pestic *et al.* 2011; Dell *et al.* 2014) in the effects of body mass and temperature on parameters of eqns 14 and 15, it has also recently been argued that dimensionality of interaction space is important (Pawar *et al.* 2012; Dell *et al.* 2014).

Thus, writing eqns 16 and 17 in terms of s and T is a promising avenue of research that can be guided by burgeoning results on the s and T dependence of attack rates and handling times. A general approach may not be possible if heterogeneous dependencies of α and t_h on s and T are true features of the data (Rall *et al.* 2012). Which contexts and taxa correspond to what functional forms is not completely understood, but metabolic categories, predation strategies and dimensionality of search space seem likely to be important and jointly may provide categories within which relationships are uniform. A main benefit of the discussion here is to indicate that the major task remaining for understanding the effects of temperature on competition among differently sized ectotherms, generally, may be in parameterizing t_h and α in terms of s , T and appropriate categories.

The R^* and invasion-fitness approach as described here is valid only when equilibria are stable. In contrast to the phytoplankton model (Appendix S5), an equilibrium of the Rosenzweig–MacArthur model need not be stable. This difficulty can be overcome with an analysis that is

technically but not conceptually more sophisticated (Appendix S6). DeLong *et al.* (2014) have discovered that metabolic rate depends on population density as well as body size and temperature. As parameters of eqns 16 and 17 depend on metabolic rate, dynamics may need to be modified from the classic Rosenzweig–MacArthur model, and this may affect predictions about the effects of temperature on competition among sizes. Additional complexities will also need to be addressed to develop a metabolic theory of both interference and resource competition; Arditi & Ginzburg (2012) have compiled evidence that consumers directly interfere with each other via the functional response.

Further discussion

Our modelling results indicate that smaller sizes in phytoplankton at higher temperatures can be explained partly by accentuated competitive advantage of smaller phytoplankton cells with regard to nutrient uptake and growth. Metabolism played a key role through the temperature dependence of μ_{\max} , the maximum growth rate. Our framework can be applied much more broadly as research continues to clarify the body size and temperature dependence of parameters such as attack rates and handling times in the Rosenzweig–MacArthur model.

Perhaps the best known prior ‘explanation’ of reduced ectotherm sizes at higher temperatures is that warmer temperatures will raise metabolic rates; so assuming a fixed resource supply, unless population numbers decline to compensate, body sizes must decrease. This truism is not really an explanation at all, because it does not explain why body sizes decrease instead of population numbers. If smaller sizes are competitively inferior, increased demand for the same resource supply seems unlikely to produce selective pressures towards smaller sizes. What seems important is the relative magnitudes of reductions in metabolic demand through smaller sizes and associated possible reductions in competitive ability to sequester resources. We have demonstrated for phytoplankton that smaller cells are better competitors for nutrients and that this advantage is accentuated at higher temperatures, hence providing mechanistic support for the general ‘explanation’ described above.

COMPARISON WITH OTHER MECHANISMS FOR SMALLER SIZE

It has also been suggested that nutrient pulse rates and ocean acidification are related to smaller phytoplankton sizes. Litchman *et al.* (2009) used a dynamical model similar to the one used here, parameterized by species’ cell sizes but not temperature, and incorporating a pulsed nutrient supply representing periodic thermocline disruptions. They found that infrequent pulsing selects for small species, whereas more frequent pulsing, with period around 5–30 days depending on thermocline depth, selects

for larger species. Larger cells gain an advantage here because of their better nutrient storage. As warmer waters tend to be more stratified, this effect may also partly explain the observation in the ocean that warmer waters have smaller cells. Acidification, which is concomitant with global warming, has also been linked to slower growth of some phytoplankton (Shi *et al.* 2010; Sheridan & Bickford 2011). However, neither pulse rates nor acidification can be the whole story because experimental mesocosms are also dominated by smaller phytoplankton when artificially warmed (Fig. 3; Daufresne *et al.* 2009; Yvon-Durocher *et al.* 2011; see also Morán *et al.* 2010). The relative importance of these three effects is unknown. Possible interactions have also not been explored. These topics could be investigated using our modelling paradigm if the parameters of a model can be written in terms of pH as well as temperature and cell size.

Our model was formulated as a model of competition between species; it could also be viewed as a model of competition between size classes within a species, although we did not take this approach. These viewpoints are complementary. The index i in eqns 2–4 was defined as a species index. Species were seen to have fixed body mass and nutrient uptake and growth parameters. The index i could also have been a size class index with no major change in the theoretical development or conclusions; here, size classes include all lineages of any species in a size range, and it is assumed that lineages remain in a size class. The model can also be formulated as a model of competition between size classes within a species, if i is taken to be an index of such a size class, size variation within a species is due principally to inter-lineage differences as opposed to ontogenetic growth or phenotypic plasticity, and sizes within a lineage are again fixed. We did not follow this intraspecific approach because data for model parameterization are typically at the species level (e.g. our main data reference, Edwards *et al.* 2012). It may be interesting to determine whether intraspecific scaling relationships of nutrient uptake and growth rates vs. body size are heterogeneous among species, if data can be gathered. The potential for differences between inter- and intraspecific scaling suggests the intriguing possibility that warming may favour smaller species in interspecific competition, while simultaneously favouring larger individuals in intraspecific competition within some species. Description of the parameters of the Rosenzweig–MacArthur model in terms of body sizes and temperature and study of heterogeneity in these parameters among species may be facilitated by theoretical efforts to reduce some model parameters to commonly measured quantities (Amarasekare & Savage 2012).

An existing body of work explores physiological, non-competitive reasons why warming causes smaller sizes within a species, yet another complementary approach. Direct, physiological impacts of warming are common in ectotherms. Studies rearing individuals in isolation or in environments where competition is unlikely (e.g. frogs, Walsh *et al.* 2008; *Caenorhabditis elegans*, Kammenga

et al. 2007; beetles, Ernsting & Isaaks 1997; and salamanders, Licht & Bogart 1989) are part of a larger body of work showing that purely physiological responses typically result in smaller body sizes in warmer temperatures. The relative importance of interspecific, intraspecific and physiological effects of warming on body size is unknown.

COEXISTENCE

Our phytoplankton model predicts competitive exclusion. Yet natural phytoplankton communities are diverse in taxonomic and cell size composition (Hutchinson 1961). Many mechanisms have been proposed to explain diversity in spite of a tendency towards exclusion. These mechanisms will prevent complete competitive exclusion, so that our result of accentuated competitive ability of smaller cells at higher temperatures should translate into abundance-vs.-cell size distributions that are more biased towards small sizes, as has been observed (Daufresne *et al.* 2009; Winder *et al.* 2009; Barnes *et al.* 2010a; Morán *et al.* 2010; Yvon-Durocher *et al.* 2011). Possible coexistence mechanisms for phytoplankton include limitation by multiple resources (Tilman 1982), spatial or temporal fluctuations in nutrients and other environmental factors (Tilman *et al.* 1981; Sommer 1984; Litchman *et al.* 2009), and intrinsic instability emerging from competition for multiple resources (Huisman & Weissing 2002; see Chesson 2000 for a general review of mechanisms).

FUTURE PROSPECTS AND RECOMMENDATIONS

The hypothesis that smaller plankton species have an accentuated competitive advantage at higher temperatures could be directly experimentally assessed with competition experiments measuring time until competitive exclusion or initial speed of invasion. Tilman *et al.* (1981) carried out this general type of experiment, but in silicate-limited conditions. We suggest experiments in Si-, N-, P- and Fe-limited conditions, as well as extension of the modelling done here, if possible, to Si-, P- and Fe-limited contexts. The experiments of Tilman *et al.* (1981) also used only two species; robust laboratory tests of the effects of temperature on competition among differently sized cells will require a range of sizes.

Predicting future impacts of climate change on ecological systems requires an understanding of system dynamics and extrapolation beyond current environmental conditions. The experiment of Tilman *et al.* (1981) and R^* theory generally suggest a paradigm: that shifts in competitive outcomes across a temperature gradient can be predicted without doing actual competition experiments, by doing single-species experiments. But the challenge posed by climate change is too great for this approach, because we cannot do single-species R^* experiments for all relevant species across any temperature gradient. What is needed instead is generality via a trait-based approach: to predict the value of R^* and its depen-

dence on temperature from organism traits such as body size. We demonstrated that this is possible. The use of R^* is not essential. Invasion fitnesses or models permitting coexistence can be used instead. Large data compilations that describe model parameters in terms of organism traits and environmental factors (e.g. Bissinger *et al.* 2008; Dell *et al.* 2011; Englund *et al.* 2011; Edwards *et al.* 2012; Rall *et al.* 2012) are crucial for this approach and are in short supply. Because studies of this kind may be the biggest factor limiting our ability to understand and predict the effects of climate change on populations and communities, we recommend that future research prioritize them. We suggest that future data compilations report not only species average parameters and body sizes, but also specific values from individual experiments, so that both inter- and intraspecific scaling can be examined.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. *s* and *T* dependence of parameters

Appendix S2. A specific *T* dependence of H_{gro}

Appendix S3. Derivative of *G* with respect to *T*

Appendix S4. R^* for the case $m = k_{ms}e^{em}$

Appendix S5. The equilibrium assumption

Appendix S6. Non-equilibrium dynamics