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Does universal temperature dependence apply to communities? An experimental test using natural marine plankton assemblages

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The metabolic theory of ecology (MTE) is an intriguing but controversial theory that tries to explain ecological patterns at all scales on the basis of first principles. Temperature plays a pivotal role in this theory. According to MTE, the Arrhenius relationship that describes the effect of temperature on biochemical reactions extends to a 'universal temperature dependence' that encompasses all kinds of processes and scales up to the cellular, the organismal, and the community level. In this study we test the prediction that community growth rate is temperature dependent in an Arrhenius-like way. First, we performed a literature review of the scanty data on the temperature dependence of the rates of metabolism, photosynthesis and growth of communities. In contrast to the predictions of MTE, the community activation energies did not cluster around 0.32 eV, the activation energy of photosynthesis and primary production or around 0.65 eV, the activation energy of metabolism. However, in none of the published studies the conditions were sufficiently controlled to allow firm conclusions. We therefore also performed replicated and controlled experiments using natural assemblages of marine plankton. As predicted by MTE, the maximal growth rates of community biomass increased linearly in an Arrhenius plot, with a slope close to 0.32 eV. However, a diversity of other models for the temperature dependence of community growth rates fit our data equally well. Hence, our results are at best a weak confirmation of MTE.

Virtually all aspects of life are influenced by temperature. Based on the laws of thermodynamics, we have a fairly good understanding of how the reaction rates of enzymes are affected by temperature. In contrast, it is still largely debated how temperature influences vital rates at higher levels of organization, such as the growth rates of individuals, populations or communities. The authors of the metabolic theory of ecology (MTE) claim that the thermodynamical principles governing simple biochemical reactions can be extrapolated in a straightforward manner to individual metabolism, and from there to all kinds of biological rates at all levels of organisation (Gillooly et al. 2001, Brown et al. 2004). Accordingly, MTE makes the strong prediction that the temperature dependence of virtually any biological rate r can be described by an Arrhenius relationship of the form:

$$r(T) = r_0 \times e^{-\frac{E}{k \times T}} \quad (1)$$

Here T is temperature in Kelvin, r_0 is a normalization constant, $k = 8.618 \times 10^{-5}$ eV K^{-1} is Boltzmann's constant, and E is the so-called activation energy in electron volts (Gillooly et al. 2001, Brown et al. 2004). Equivalently, MTE predicts that in an Arrhenius-plot, where the natural logarithm of r is plotted against the inverse of temperature 1/kT, a linear relationship results with slope $-E$ and intercept $\ln(r_0)$:

$$\ln(r(T)) = \ln(r_0) - E \times (1/kT) \quad (2)$$

In addition, MTE makes the more specific prediction that the 'activation energy' E of metabolism is generally close to 0.65 eV (Gillooly et al. 2001). However, it has been argued that activation energies corresponding to photosynthesis and primary production should be lower and close to 0.32 eV (Allen et al. 2005, López-Urrutia et al. 2006).

MTE is an intriguing theory, for at least two reasons. First, proponents of the theory argue that it can be used to explain all kinds of thermal trends, including the temperature dependence of resource consumption (Enquist et al. 2003), the maximum per capita growth rate (Savage et al. 2004), the rates of predation and parasitism (Brown et al. 2004), the rate of biomass turnover and energy flux of ecosystems (Enquist et al. 2003), and even global carbon flux (Allen et al. 2005). Second, the theory makes

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quantitative a priori predictions that can be tested both in the lab and in the field.

Not surprisingly, an all-encompassing theory like MTE has attracted a lot of criticism, both concerning its theoretical foundation and its empirical support. On the theoretical side, it is not at all clear whether, and to what extent, the thermal properties of single biochemical reactions are reflected in the temperature dependence of individual metabolism (Precht et al. 1973, Clarke 2004, Clarke and Fraser 2004). Even if individual metabolism were related to temperature in an Arrhenius-like fashion, the extrapolation to higher levels of organization is far from straightforward (Cottingham and Zens 2004, Marquet et al. 2004, O'Connor et al 2007), since additional factors like resource limitation or temperature acclimation are undoubtedly of major importance for the temperature response of an organism (Rhee and Gotham 1981, Vasseur and McCann 2005, Clarke 2006, López-Urrutia and Morán 2007, Terblanche et al. 2007). On the empirical side, it is important to realize that so far virtually all evidence is either based on field studies or on data compiled from the literature. The mechanisms supposedly underlying the thermal properties of biological rates have thus far not been exposed to thorough experimental testing (Brown et al. 2004, Cottingham and Zens 2004, Cyr and Walker 2004, Marquet et al. 2004, Van der Meer 2006). Still, the Arrhenius relationship seems to provide a good phenomenological description, at least at the individual and the population level. This holds, for example, for the temperature dependence of individual metabolism (Gillooly et al. 2001, Brown et al. 2004) and population growth rates (Savage et al. 2004). It has not yet been investigated whether this is also the case at the community level. We therefore screened the literature for empirical studies and meta-analyses on the effect of temperature on community rates of metabolism, growth, and photosynthesis. In addition, we performed replicated and temperature-controlled experiments on natural assemblages of marine plankton. In both cases the aim was to test whether 1) the temperature dependence of community growth rate is indeed described by an Arrhenius relationship, and 2) whether the corresponding activation energy is close to the predicted values of either 0.32 or 0.65 eV.

Literature data

We systematically searched the literature for quantitative studies on the dependence of community metabolism, photosynthesis and/or growth rate on temperature. We focused on studies that either reported the results in terms of activation energies (e.g. in terms of an Arrhenius relationship) or in terms of Q_{10}-values (Raven and Geider 1988), since the latter can be translated into activation energies (Vasseur and McCann 2005). Surprisingly, not a single controlled experiment could be found where a community had been exposed to a series of previously defined temperatures (Table 1). All studies encountered refer to some kind of a field experiment where measurements were done either directly in the field or by taking natural samples and simulating the natural conditions. A few of these studies actively controlled for either thermal acclimation or limitation by a certain resource, but most studies did apparently not consider these and other potentially confounding factors. To standardize the results we transformed all reported values for temperature dependence into activation energies in electron volts (eV). In cases where the activation energy was directly estimated in a given study, the corresponding R^2-value (when available) gives an indication of the goodness-of-fit with the Arrhenius relationship. In cases where Q_{10}-values were reported, the R^2-values are given in brackets in Table 1, since the goodness-of-fit refers to an exponential relationship with temperature rather than an Arrhenius relationship. From Table 1 we conclude that based on published studies little can be said about whether and to what extent the natural logarithm of community rates is linearly related to the inverse of temperature. The studies in Table 1 do certainly not support the more specific prediction that activation energies should cluster around either 0.32 eV or 0.65 eV. However, it is questionable whether far-reaching conclusions on the applicability of MTE to the community level can be drawn from such a compilation of data. As indicated above, none of the studies refers to controlled experiments that were specifically set up to test the thermal predictions of MTE. We therefore performed such a controlled and replicated study ourselves.

Controlled experiments: material and methods

Experimental setup

The idea underlying the experimental study was to let natural marine phytoplankton-dominated communities grow for a certain time period to quantify the temperature dependence of the maximum community growth rate. Factors like thermal acclimation and light limitation should be prevented as far as possible.

A large sample of surface water was taken on 15 February 2006 from the Dutch Wadden Sea (53°33′547N, 6°39′671E; water temperature 2.1°C) and immediately portioned out to smaller bottles yielding 15 one-litre subsamples. In the lab the 15 communities were randomly assigned to five subsets with three replicates each. Each subset was brought to the experimental temperatures of 6, 9, 12, 16 or 20°C overnight. During the warming phase the communities were stored in darkness. Subsequently we kept them under constant temperature and continuous light (approximately 200 µmol photons cm^{-2} s^{-1}) for eight days. Before the start of the experiment, at the beginning of the warming phase, we added nutrients and vitamins in high amounts to yield concentrations of f2-sea water (Andersen 2005). This was done to ensure resource saturation and to create conditions for exponential growth. Once a day we diluted the communities with 230 ml fresh f2-medium. This semi-continuous dilution started at day two for the higher temperatures and at day three for the 6 and 9°C-treatment. The daily removed volume was used for subsequent biomass and nutrient analyses. In total the sampling procedure of the 15 cultures, i.e. the 15 nutrient enriched communities, resulted in six 6-days biomass time series for the lower

Table 1. Compilation of literature date on the temperature dependence of rates of metabolism, photosynthesis and/or growth of planktonic, soil microbial, or forest communities. Temperature dependence is quantified by activation energy E in electron volts (eV), which according to MTE is predicted to be close to 0.65 eV for metabolism and close to 0.32 eV for photosynthesis and primary production. Original estimates in terms of Q_{10}-values were translated into activation energies. All studies either present field or in situ measurements or a meta-analysis of field data. If not stated differently in column six, the systems studied were probably affected by long-term acclimation to ambient temperature and by some sort of resource limitation. R^2-values in brackets refer to goodness-of-fit to an exponential model, i.e., to a model differing from an Arrhenius relationship. [a]Q_{10}-values were converted to activation energies by $E(eV) = 0.1 \times (k T_0^2) \times \ln(Q_{10})$, where T_0 is the median temperature (in K) of the temperature range from which $Q_{10}$was calculated (Vasseur and McCann 2005); [b]activation energies converted from KJ/mol by $E(eV) = 1.037 \times 10^{-2}$ E(kJ mol^{-1}); [c]activation energies converted by multiplying original estimates (corresponding to E/k) with Boltzmann's constant; [d]no long-term acclimation but medium-term acclimation during 60 and 110 days.

Rate	Community	E(eV)	Q_{10}	R^2	Control for acclimation/ resource limitation	Reference
Metabolism	soil bacteria	0.31	–	0.99	acclimation	Pietikäinen 2005
		[a]0.65	2.42	(0.83)	–	Yan et al. 2006
		[a]0.64	2.39	(0.88)	–	
		[a]0.60	2.28	(0.83)	–	
		[a]0.23	1.35	–	[d]acclimation	Niklinska and Klimek 2007
		[a]0.53	2.22	–	–	
		[a]0.77	2.93	–	–	
		[b]0.93	–	0.82	–	Gaumont-Guay et al. 2006
		[a]0.41	1.8	(0.7)	[d]acclimation	Yuste et al. 2007
		[a]0.77	3.1	(0.8)	water limitation	
	marine bacterioplankton	0.75	–	0.66	–	Apple et al. 2006
		[b]0.52	–	–	acclimation	Hancke 2004
		[b]0.35	–	–	–	
		[b]0.58	–	–	–	
		0.59	–	0.20	–	López-Urrutia and Morán 2007
	marine autotrophic plankton	0.33	–	0.97	–	López-Urrutia et al. 2006
	marine heterotrophic plankton	0.56	–	0.85	–	López-Urrutia et al. 2006
	freshwater phytoplankton	0.06	–	0.53	–	De Castro and Gaedke 2008
	freshwater zooplankton	0.32	–	0.82	–	De Castro and Gaedke 2008
	different microbial communities	[b]1.14	–	–	–	Price 2004
	forests	[c]0.61	–	0.48	–	Enquist et al. 2003
		[c]1.02	–	0.61	–	
		[c]0.62	–	0.32	–	
		[c]0.75	–	0.23	–	
		[c]0.67	–	0.43	–	
		[c]0.68	–	0.23	–	
Photosynthesis	microphytobenthos	[b]0.24	–	–	acclimation	Hancke 2004
		[b]0.52	–	–	light limitation	
		[b]0.32	–	–	–	
Growth	marine bacterioplankton	[a]0.42	1.9	–	–	Kirchman et al. 2005
		[a]0.74	3.1	–	–	

temperatures, 6 and 9°C, and in nine 7-days biomass time series for the higher temperatures.

Sample analysis

In order to determine biomass we measured the amounts of organic carbon (C_{org}), organic nitrogen (N_{org}) and chlorophyll-a (chl-a). For the analysis of C_{org} and N_{org} samples we used 100 ml of culture concentrated on GF/F filters (Whatman). C_{org} and N_{org} were measured with the help of the CN-element analyser. To determine chl-a concentrations 100 ml of culture were concentrated on a GF/F filter. The filter was then put into 4 ml of 90% acetone. After an extraction time of 48 h we determined the concentration of chl-a with a fluorometer at excitation- and emission wavelength of 436 and 668 nm. Fluorescence readings occurred before ('R_b') and 10 min after ('R_a') sample acidification with 150 µl of 10% HCl. We calculated chl-a in µg/l as $\text{chl-a} = \frac{R_b - R_a}{0.77} \times \frac{V_e}{V_f} \times 3.74$ (V_e is extraction volume, V_f is filtered volume). Multiplication factors stem from spectrophotometric calibration using a chl-a standard (Lorenzen 1967).

Estimation of maximum growth rates

For any given temperature, T, we assume that the community was growing exponentially at a rate $r = r(T)$. Let B_t denote the biomass at day t before a fraction D of the culture was removed and replaced by fresh medium. Then the biomass at the following day is given by $B_{t+1} = (1 - D) \times B_t \times e^y$. In our case $1 - D = 0.77 \approx e^{-0.26}$. As a consequence biomass growth was assumed to be governed by $B(t) = B_0 \times e^{(r-0.26)t}$ or, on a logarithmic scale $\ln(B(t)) = \ln(B_0) + (r - 0.26) \times t$.

Hence, r could be estimated by linear regression of ln(B(t)) against time and adding 0.26 to the regression coefficient.

In the experiment the replicate communities developed in a highly consistent way throughout the growth period at all temperatures, showing remarkably little variation even towards the end. For each measurement we therefore pooled the three replicates by taking their average. These averages form the basis for all further calculations. Subsequently, we estimated community growth rate r by means of linear regression of the ln-transformed biomass data as described above. The activation energy of community growth rate, E, was calculated as the slope of the linear regression of ln(r) against the inverse of temperature 1/kT.

Throughout, R^2-values are used for judging the goodness-of-fit between our data and various models. These were calculated from the residual sum of squares obtained from non-linear curve fitting on non-transformed data using Newton's method. All statistics were done using R ver. 2.5.0.

Controlled experiments: results

Biomass dynamics

The natural logarithms of the absolute amounts of C_{org}, N_{org} and chl-a increased linearly over time, indicating that the communities were indeed growing exponentially (Fig. 1). A preliminary comparison of the biomass dynamics between temperatures also indicates that the rate of increase was positively related to temperature. Interestingly, the C_{org} and N_{org} data provide parallel lines while the slope of the chl-a data is steeper. Note that at 16°C and 20°C the logarithms of the three measured variables do not seem to increase linearly over the whole time-period, indicating some growth-limiting effects at these temperatures.

Temperature-dependence of community growth rate

As predicted by MTE, the community growth rates show a roughly linear relationship when plotted against the inverse of temperature, indicating an Arrhenius-like relationship (Fig. 2). Since the samples contained not only phytoplankton but also zooplankton and bacteria, we consider the estimation of r based on the C_{org} data as the most relevant indicator of community biomass, although phytoplankton was the most dominant fraction. Nevertheless, we also present estimations of r based on N_{org} and chl-a, since these quantities are often used as proxies for biomass. For C_{org}, the community activation energy (which corresponds to the slope of the regression line in the Arrhenius plot) equals 0.33 eV (95% CI: (0.22 eV, 0.44 eV), $p < 0.005$, $R^2 = 0.93$). This estimation of E is remarkably close to the predicted value of 0.32 eV for photosynthesis and primary production (Allen et al. 2005). N_{org} data exhibited an activation energy

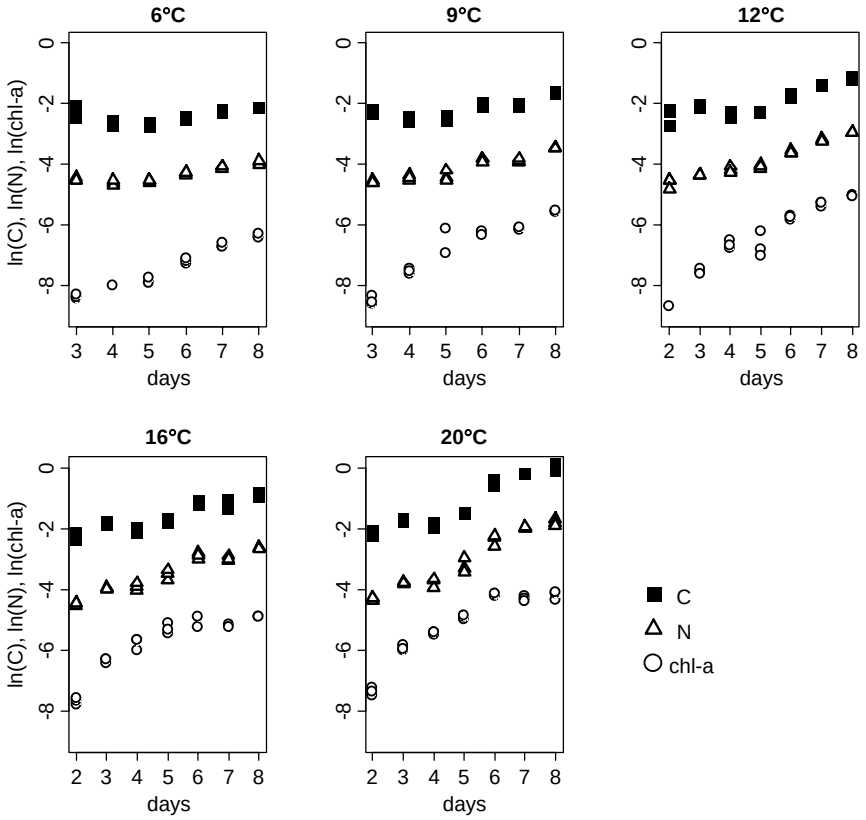

Figure 1. Log-linear plots of the time-series of biomass ('C_{org}', squares), organic nitrogen ('N_{org}', triangles) and chlorophyll-a ('chl-a', circles) [mg] of natural plankton communities grown at 6, 9, 12, 16 and 20°C in the lab. Plankton samples were taken from the field in February 2006 one day before the start of the experiment and grew for a week in semi-continuous cultures. Nutrient concentrations and irradiance were non-limiting in order to achieve maximum growth conditions.

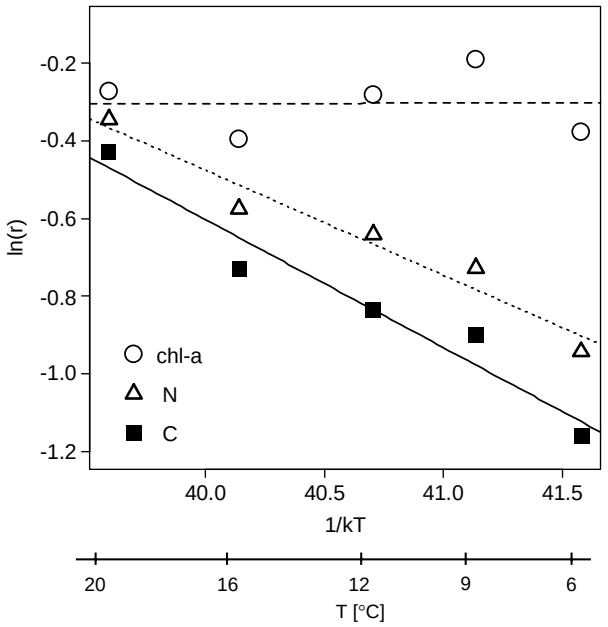

Figure 2. Arrhenius-plots of community growth rate r [day^{-1}], where ln(r) is plotted against the inverse of temperature 1/kT. r was estimated by the slope of the regression lines of the log-linear plots for C_{org} (squares), N_{org} (triangles), or chl-a (circles) in Fig. 1. The temperature dependence of community growth rate, estimated on the basis of C_{org}, corresponds to a linear relationship in the Arrhenius-plot with activation energy 0.33 eV. N_{org} data show a similar trend, with a slightly lower activation energy of 0.27 eV. chl-a data indicated higher absolute values of community growth rate, which appear to be temperature-independent (E = 0.001 eV).

of 0.27 eV (95% confidence interval: (0.01 eV, 0.53 eV), $p < 0.05$, $R^2 = 0.93$), which is quite similar. In contrast to this, community growth based on chl-a data seems to be temperature independent (E = 0.001 eV, 95% CI: (−0.27 eV, 0.26 eV), $R^2 < 0.001$).

Alternative temperature relationships

Obtaining a good fit between data and a model does not necessarily mean that the model is correct, since alternative models might fit the data as well. To check this, we fitted our data not only to the Arrhenius-relationship but also to three other temperature models that are frequently used (Ahlgren 1987). The models and their R^2-values are listed in Table 2. The linear relationship serves as a null model, the Arrhenius-relationship and the Berthelot-relationship reflect different biochemical principles, and the Belehradek-relationship is derived from physical considerations. Intriguingly, all four models fit the temperature relationship equally well for all the three measurements C_{org}, N_{org} and chl-a. In other words, the Arrhenius relationship does not provide a better description of our data than the other three models.

Discussion

There is consensus that in order to judge the validity of the predictions of the metabolic theory of ecology (MTE) controlled and replicated experiments are urgently needed

Table 2. Comparison of the R^2-values for the fit of the experimental C_{org}, N_{org}, and chl-a data to four different models of temperature dependence (Ahlgren 1987). Temperature T is measured in Kelvin. All models have two parameters a and b. Optimal fits were based on the non-transformed growth rate data and obtained by minimizing residual sum of squares resulting from non-linear curve fittings using Newton's method. The R^2-values for the growth rates of carbon and nitrogen are above 0.90 for all models, but close to zero for chl-a growth rates.

Model	R^2		
	C_{org}	N_{org}	chl-a
linear: $r(T) = a + b \times (T - 273)$	0.93	0.95	0.0005
Arrhenius: $r(T) = a \times e^{-b(1/T)}$	0.95	0.95	0.0004
Belehradek: $r(T) = a \times (T - 273)^b$	0.91	0.94	0.001
Berthelot: $r(T) = a \times b^{T-273}$	0.95	0.95	0.0005

(Brown et al. 2004, Cottingham and Zens 2004, Cyr and Walker 2004, Marquet et al. 2004, Van der Meer 2006). Our study is a step in this direction. At first glance the results seem to confirm the prediction of MTE on temperature dependence: the growth rate of community biomass (C_{org}) does indeed show an Arrhenius-type relationship (as indicated by the straight line in the Arrhenius plot of Fig. 2), and the slope of this relationship closely reflects the activation energy of photosynthesis and primary production (i.e. 0.32 eV). A similar agreement with the thermal predictions of MTE was obtained when using intracellular nitrogen (N_{org}) as a proxy for biomass. In this sense our results support the view of MTE that the behaviour of complex systems can to a remarkable degree be explained on the basis of quite simple fundamental principles. In contrast to C_{org} and N_{org}, our chl-a data did not exhibit temperature dependence. One might have expected that just these data, which represent the autotrophic part of the community only, should have a slope of about 0.32 eV in the Arrhenius plot, whereas the overall community should have a slope between 0.32 eV and 0.65 eV, However, chl-a is generally considered a less reliable measure of biomass, since intracellular chl-a concentrations are often not constant (de Jonge 1980). It is conceivable that the more rapid growth of phytoplankton at higher temperatures is associated with a decrease in intracellular chl-a levels. Alternatively, higher temperatures might induce a shift in community composition (from autotrophs to heterotrophs). Both factors might mask the increase in community growth rate with temperature that is predicted by MTE.

We are aware of the fact that our study will not be the final word on the applicability of MTE to whole communities. In fact, our study exemplifies some of the limitations encountered when testing the seemingly straightforward thermal prediction. For instance it turned out to be very difficult to obtain a reliable estimate of maximum growth rates. Apparently, growth at maximal rate only occurred during a rather short initial period. At a later stage, community growth was apparently already limited. Moreover, the size distribution of individuals might have changed during our experiments in a temperature-dependent way. MTE predicts that metabolic rate (and other biological rates) does not only depend on temperature but also on body mass, implying that a reliable estimate of

activation energy E requires a correction for changes in body mass (Gillooly et al. 2001). For natural communities like ours such a correction seems a forbidding task, since one would have to consider size changes in many different organisms, ranging from bacteria to zooplankton (Enquist et al. 2003, de Castro and Gaedke 2008). At best, one might hope to arrive at better estimates of E by simple rules of thumb, such as the empirical finding of Atkinson et al. (2003) that each additional °C rise in temperature leads to a size reduction in protists by about 2.5%. Applying this rule of thumb to our data would raise the community activation energies to 0.49 eV for C_{org}, 0.43 eV for N_{org}, and 0.16 eV for chl-a.

Our results illustrate that a linear relationship of a biological rate with temperature in an Arrhenius plot is by far not sufficient as a 'proof' that the Arrhenius relationship can be upscaled from simple biochemical reactions to higher levels of organisation. There are many reasons why biological rates should increase with temperature, each leading to a different model for temperature dependence. As our study shows (Table 2), the same set of data can be fitted equally well to a variety of quite different models, some of which also having a plausible mechanistic underpinning. Hence, focussing on just a single model may give rise to misleading conclusions, since the observed trends might be even better 'explained' by an alternative model.

There are at least two possibilities to discriminate between the different models for temperature dependence. An obvious approach would be to aim for more data with a better resolution. Yet, we doubt that an extension of this study would really help to distinguish between the alternatives. In our opinion, controlled experiments targeted at unravelling the mechanism behind temperature dependence and the upscaling from lower to higher levels are required to really challenge the metabolic theory of ecology.

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