

# Effects of directional environmental change on extinction dynamics in experimental microbial communities are predicted by a simple model

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Global temperatures are expected to rise between 1.1 and 6.4°C over the next 100 years, although the exact rate will depend on future greenhouse emissions, and will vary spatially. Temperature can alter an individual's metabolic rate, and consequently birth and death rates. In declining populations, these alterations may manifest as changes in the rate of that population's decline, and subsequently the timing of extinction events. Predicting such events could therefore be of considerable use. We use a small-scale experimental system to investigate how the rate of temperature change can alter a population's time to extinction, and whether it is possible to predict this event using a simple phenomenological model that incorporates information about population dynamics at a constant temperature, published scaling of metabolic rates, and temperature. In addition, we examine 1) the relative importance of the direct effects of temperature on metabolic rate, and the indirect effects (via temperature driven changes in body size), on predictive accuracy (defined as the proximity of the predicted date of extinction to the mean observed date of extinction), 2) the combinations of model parameters that maximise accuracy of predictions, and 3) whether substituting temperature change through time with mean temperature produces accurate predictions. We find that extinction occurs earlier in environments that warm faster, and this can be accurately predicted ( $R^2 > 0.84$ ). Increasing the number of parameters that were temperature-dependent increased the model's accuracy, as did scaling these temperature-dependent parameters with either the direct effects of temperature alone, or with the direct and indirect effects. Using mean temperature through time instead of actual temperature produces less accurate predictions of extinction. These results suggest that simple phenomenological models, incorporating metabolic theory, may be useful in understanding how environmental change can alter a population's rate of extinction.

## Synthesis

Understanding how populations will respond to future climatic change is a key goal in ecology, however the exact rate of future warming will vary both spatially and temporally. Consequently, mathematical models must be used to understand the potential range of future population dynamics under various warming scenarios. We use a combination of experimentation and modelling to show that the effects of varying rates of environmental change on population dynamics can be predicted by a simple model. However, the accuracy of these predictions depends upon, amongst other things, a detailed knowledge of how temperature will change over time, rather than approximating this change to mean temperature.

Global climate change is forecast to alter environmental conditions significantly over the next 100 years (IPCC 2007). Current predictions suggest that global temperatures will rise between 1.1 and 6.4°C over this time period, although the exact magnitude, and therefore rate, of temperature change will depend both on location and future greenhouse gas emissions (IPCC 2007). This heterogeneity in the rate of temperature change means that some areas (e.g. the polar regions) are expected to experience rates of warming up to twice the global average (Koenigk et al. 2007), with potentially profound impacts on the species

that reside there (Thomas et al. 2004). Temperature can have complex effects at the individual level – for example increasing temperatures increase metabolic rate, meaning that an individual will use resources at a faster rate, senesce faster, and ultimately die sooner (Van Voorhies and Ward 1999, Brown et al. 2004) – with potential consequences for the persistence of populations. Understanding how varying rates of temperature change may alter a population's dynamics is therefore essential.

Recent developments in theory have produced an apparently accurate, and convenient, way of incorporat-

ing the effects of temperature change into mathematical models (Brown et al. 2004). An organism's metabolic rate, and dependent functions such as growth and mortality rates, have been shown to scale with its body size and temperature, via the Arrhenius equation (Gillooly et al. 2001, Brown et al. 2004). Thus, the metabolic rate of an individual ( $I$ ) scales with temperature ( $T$ , in Kelvin) and body size ( $M$ ), as

$$I = i_0 M^{\frac{3}{4}} e^{-\frac{E}{kT}} \quad (1)$$

where  $i_0$  is the normalization constant, independent of body size and temperature,  $E$  is the activation energy (Ernest et al. 2003) and  $k$  is the Boltzmann constant (Boltzmann 1872). Such scaling relationships hold over a large number of taxa, life histories, and trophic positions (Brown et al. 2004), and this has led to this method's widespread application (Berlow et al. 2009, Reich et al. 2006, Woodward et al. 2005), though there is also evidence suggesting that there is significant variation in the rate of this scaling (i.e. the activation energy) both within and across species (Chown et al. 2007, Glazier 2010, White et al. 2007). Furthermore, temperature has been shown to alter an individual's body size (Atkinson 1994, Atkinson et al. 2003), meaning temperature can both directly alter metabolic rate, and indirectly alter it through the temperature dependence of body size.

From this scaling of metabolic rate (Eq. 1), the subsequent change in birth, growth, feeding, and mortality rates, as well as other metabolic dependent functions, can similarly be scaled via the same power function (Brown et al. 2004). Thus a parameter,  $P$ , at temperature  $t_2$  is scaled from the parameter at  $t_1$  as

$$P_{t_2} = i_0 P_{t_1} M^{\frac{3}{4}} e^{-\frac{E}{kT_1}} \quad (2)$$

Temperature influences a wide range of biological processes, but it may be possible to simplify this complexity by incorporating the effects of temperature change into phenomenological models. For many species phenomenological models, such as the Lotka–Volterra equations (Lotka 1920, Volterra 1928), provide a way of describing a population's dynamics through time. Their advantage lies in their simplicity, and consequently the relatively small amount of information required parameterising them. Knowing whether it is possible to use such simplistic models to accurately predict how a changing environment may alter population dynamics, instead of requiring more complex mechanistic models (that as a result of their inherent complexity require far more information to parameterise), is of some importance.

Ideally, one would tackle such a question using data produced by manipulating natural communities. However, the complexity of such systems, where populations interact within a network of other species, in heterogeneous habitats, means collecting data and isolating replicate populations, whilst eliminating confounding factors, is often unfeasible (Griffen and Drake 2008). Progress can be made, however, by utilising small-scale experimental systems, which by their

nature are highly tractable, and allow abiotic factors such as temperature to be precisely manipulated (Griffen and Drake 2008). Whilst such experiments are clearly simplifications of real world systems (and have their critics, e.g. Carpenter 1996), the ability to replicate extinction events (which are often undesirable in wild populations) has meant that such an experimental approach has often been used as a proving ground for theory (Lawler 1998). Furthermore, if one cannot understand dynamics in such simple systems, then one is unlikely to be able to do so in highly complex natural ones. One of the simplifications often involved in such experimental communities is that they are closed, i.e. there is no immigration or emigration, and/or no inflow or outflow of resources (Godoy and Costa 2005, Drake and Griffen 2010). Whilst such closed systems may appear unrealistic, naturally occurring populations range from being quite closed to very open (Polisini et al. 1970, Hanski and Singer 2001, Mora and Sale 2002), and indeed it is often the scale of study that determines how open or closed a system is (Camus and de Ciencias 2002). Experiments with closed systems are obviously relevant for more closed populations, such as those on isolated islands, isolated habitat patches, or isolated lakes. However, understanding closed system dynamics can provide important information on within patch dynamics required to understand and model populations experiencing immigration, emigration, and resource flows (Hanski 1998, Logue et al. 2011).

We use closed experimental microcosms to investigate the empirical effect of the rate of temperature change on a protozoan population's time of extinction, and whether these extinction events can be predicted using a simple phenomenological model that incorporates metabolic theory. To address this we fitted a phenomenological model that included intrinsic growth ( $r$ ), carrying capacity ( $K$ ), and an exponential decay in the population size ( $\lambda$ ) to the dynamics of an experimental population where temperature remained constant. Then, using information on rates of temperature change through time, we scaled the model parameters to predict when a population would go extinct in the treatments where temperature had been manipulated. Using this method, we then addressed the following objectives: 1) to accurately (defined as the proximity of the predicted date of extinction to the observed date of extinction) predict extinction events where temperature change through time had occurred, 2) to examine if predictions were more accurate if the actual temperature change over time was modelled, rather than the mean temperature, 3) to examine the relative importance, on the predictive accuracy of the model, of scaling parameters either directly, or indirectly (via published temperature driven changes in body size), with temperature.

## Material and methods

### Experimental setup

Experimental microcosms consisted of lidded petri dishes (diameter 100 mm, height 25 mm) containing 50 ml of medium. Medium consisted of Chalkley's solution (Thompson et al. 1988), which provided essential salts, and 0.05 g l<sup>-1</sup> of protist pellet which provided organic nutrients.

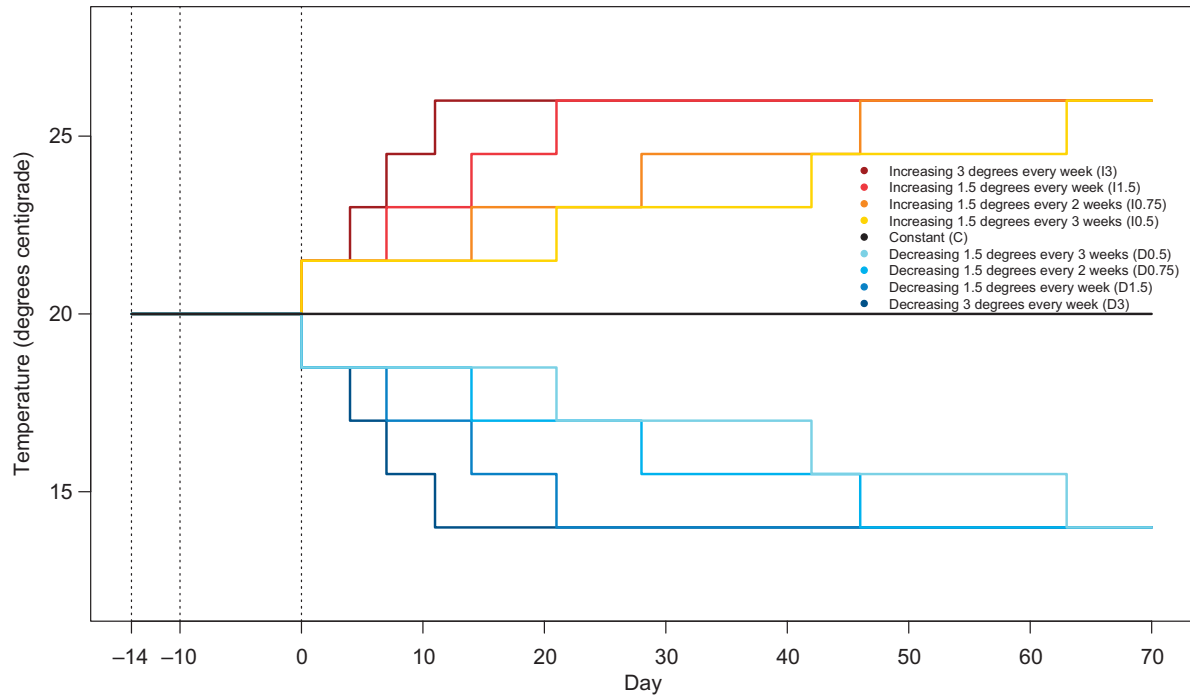


Figure 1. Microcosms were heated or cooled at varying rates by moving them between incubators of different temperatures, giving a series of treatments where the rate of temperature change varied. All media was initially incubated at 20°C before, where the two bacteria species, *Serratia marcescens* and *Bacillus cereus*, were added at day -14, *Loxoecephallus* sp. added at day -10, and the media split into microcosms at day 0.

The medium was inoculated on day -14 with the bacteria *Bacillus cereus* and *Serratia marcescens* and incubated at 20°C. On day -10, 200 individuals of the bacterivorous protist *Loxoecephallus* sp. (a long-term laboratory culture, originally obtained from the Culture Collection of Algae and Protozoa) were added to each litre of medium, incubated at 20°C, and left to reach high densities. On day 0, the first day of the experiment, the medium was homogenised and 50 ml added to each of 27 petri-dishes (three replicate populations of nine temperature treatments).

The nine treatments comprised of one (termed treatment C) that was incubated at 20°C for the duration of the experiment (70 days) and eight treatments that were either heated or cooled. All heated treatments started at 20°C and finished at 26°C, and all cooled treatments started at 20°C and finished at 14°C, however the rate at which microcosms reached these final temperatures differed between treatments (Fig. 1). This was achieved by moving the treatments between nine incubators set at 1.5°C increments from 14°C to 26°C. Thus, the eight rates of cooling and heating were: 1) increasing by 3°C per week (I3), 2) decreasing 3°C per week (D3), 3) increasing 1.5°C per week (I1.5), 4) decreasing 1.5°C per week (D1.5), 5) increasing 1.5°C every two weeks (I0.75), 6) decreasing 1.5°C every two weeks (D0.75), 7) increasing 1.5°C every three weeks (I0.5), 8) decreasing 1.5°C every three weeks (D0.5) (Fig. 1).

### Sampling to estimate abundance

Sampling to estimate population abundances was based on that of Lawler and Morin (1993) and was the same as

that of Clements et al. (2013). Population abundances were estimated twice a week for 70 days. To estimate population abundances the microcosm medium was mixed by repeat pipetting, and a known volume extracted using a Gilson pipette. The individuals of *Loxoecephalus* sp. in this known volume were then counted using a stereoscopic microscope, and from this the total population size in the microcosms estimated. Medium was replaced into the microcosms after counting. When populations became very low, individuals were counted in the whole microcosm under the microscope. A species was recorded as extinct when no individuals were observed after 5 min of searching on two consecutive sampling days. Evaporative loss was replaced with distilled water prior to each sampling event.

### Phenomenological model

To the mean population abundances of treatment C (incubated at a constant 20°C) we fitted, using a maximum likelihood approach, a deterministic, four-parameter phenomenological model that incorporates logistic growth followed by exponential decay. This model was chosen because it requires relatively little information to parameterise (only the population size through time, and not, for example, resource abundances). Mean abundances for each treatment were used, as individual replicate populations were highly variable and either produced inappropriate parameter estimates or failed to find a set of parameters that produced a maximum likelihood for the model. Thus we attempt to predict extinction of the 'best case scenario', where there is little population variability. Initial population growth was modelled as

$$\frac{dn}{dt} = r \times n \left(1 - \frac{n}{K}\right) \quad (3)$$

Where  $r$  is the intrinsic growth rate and  $K$  is the carrying capacity. After initial logistic growth an exponential decay in the carrying capacity,  $K$ , caused a decline in abundance that drives model populations to extinction. This decline in the model carrying capacity mirrored the observed decline in carrying capacity within the experimental microcosms, which was driven by a decline in the availability of the protist resource (bacteria), in response to the closed and nutrient limited nature of the microcosms. The time at which exponential decay occurred was determined by the parameter alpha, such that when  $n \geq \alpha \times K$  the growth model became

$$\frac{dn}{dt} = r \times n \left(1 - \frac{n}{-\lambda K}\right) \quad (4)$$

where  $\lambda$  is the decay constant.

### Scaling parameters with metabolic theory

Estimated parameter values for the constant temperature treatment ( $C$ ) were then scaled with metabolic theory (Eq. 2). Temperature has been shown to alter not only an individual's metabolic rate, but also body size (in protozoa body size decreases linearly with temperature by  $\sim 2.5\%$  per  $1^\circ\text{C}$ , (Atkinson et al. 2003)). We assessed the relative importance of including direct and indirect effects of temperature, by predicting population extinction when parameters were scaled in three ways; 1) with temperature only, 2) with predicted change in body size only, and 3) with both temperature and body size. Thus in the first case model parameters were determined by the direct effects of temperature as

$$P_t = P_c e^{-\frac{E}{kT}} \quad (5)$$

where  $E$  is the activation energy,  $k$  is the Boltzmann constant and  $T$  is the temperature (in Kelvin).

In the second instance we scaled the model parameters with body size, which was determined by temperature, so the magnitude of the parameter at a given temperature ( $P_t$ ) was

$$P_t = P_c M^{\frac{3}{4}} \quad (6)$$

Where  $P_c$  is the parameter in the constant treatment and

$$M = M_{C_t} - ((t - C_t) \times 0.025) \quad (7)$$

where  $t$  is the temperature of the treatment,  $C_t$  is the temperature of treatment  $C$  ( $20^\circ\text{C}$ ) and  $M_{C_t}$  is the mass at the temperature of the constant treatment.

Thirdly we scaled the parameters with both the predicted change in body size and temperature scaling as in Brown et al. (2004).

$$P_t = P_c M^{\frac{3}{4}} e^{-\frac{E}{kT}} \quad (8)$$

We assume the parameters  $r$  (the intrinsic growth rate), lambda (the decay constant) and  $K$  (the carrying capacity) will increase with increasing temperature, due to an increase in the protist's bacterial prey at higher temperatures, and a subsequent increase in the rate of consumption of organic nutrients (Membré et al. 2005, Vasseur and McCann 2005). Thus as temperature increases the growth rate of the protists will increase, as will the carrying capacity and the speed at which these populations decline after the growth period. We assume that alpha, the fraction of the carrying capacity at which exponential decay occurred, decreased with temperature as higher bacterial densities used the available chemical energy at a faster rate, and thus populations will begin to decline

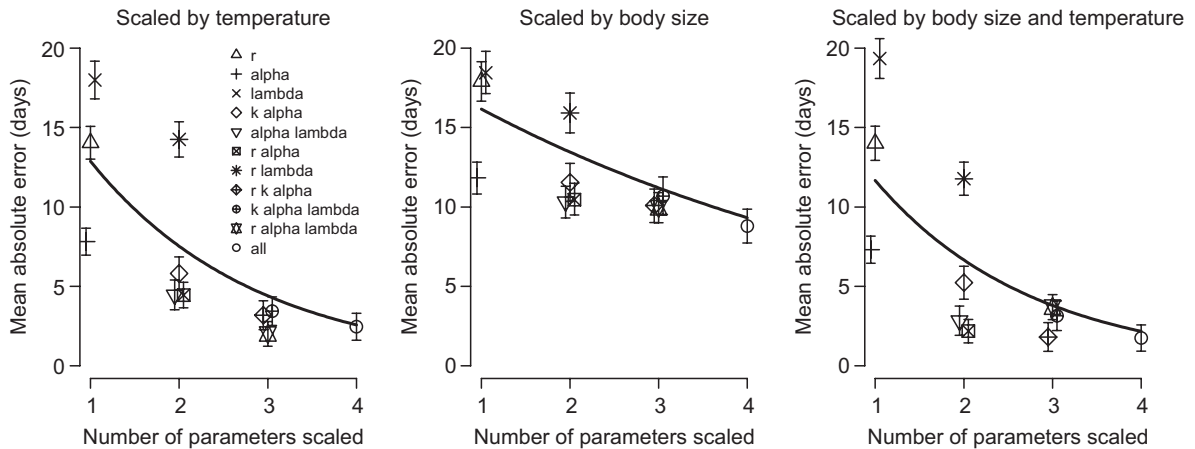


Figure 2. Mean error of predictions ( $\pm 1$  SE) was calculated as the absolute difference (in days) between the predicted date of extinction given by the model and the mean extinction date observed in the experiment, for a random subset of 500 predictions. Data were only included where predictions of extinction were made for all of the seven experimental treatments where extinction was observed (I3, I1.5, I0.75, I0.5, C, D0.5, D0.75). Increasing the number of parameters scaled in general decreased the error associated with extinction predictions. The lowest error was found where all four model parameters were scaled with both body size and temperature.

earlier at higher temperatures. Across species, body size is predicted to negatively correlate with  $r$  (Blueweiss et al. 1978) and  $K$  (Damuth 1981). We assumed that this pattern held between treatments, and that increased body size would decrease  $\lambda$ , as individuals senesce more slowly (Van Voorhies and Ward 1999), but increase  $\alpha$ , as larger individuals require more nutrients.

We investigated how these three scaling methods (1-temperature only, 2-body size only, 3-both temperature and body size) affected prediction accuracy when they were applied to all possible combinations of parameters. i.e. each model parameter was scaled individually (whilst holding the other three parameters constant), in all possible combinations of pairs (whilst holding the other two parameters constant) and triples (whilst holding the other one constant), and all four simultaneously (Fig. 2).

In order to include uncertainty in the model predictions we drew parameter values from a normal distribution with a mean of the predicted parameter value at the constant treatment, and a standard deviation as the predicted error for each parameter. Then, for every combination of parameters (four individually, six in pairs, four in triplicates and one where all four are scaled simultaneously, 15 in total for each scaling method) we ran the simulations 200 times, for 140 time steps (equivalent to 140 days), to produce predicted dates of population extinction for each temperature, each combination of parameters, and each scaling method. Preliminary testing (not reported) showed that 200 simulations were sufficient to produce robust estimates of the mean error of predictions, with no change in the mean error if simulations were run more than 200 times. In addition, we draw the activation energy ( $E$ ) from a normal distribution, with a mean of 0.652 and a standard deviation of 0.061 (Hansen et al. 1997, Vasseur and McCann

2005), as the rate of this scaling varies within species (Brown et al. 2004).

## Assessing the accuracy of predictions

To investigate how well the dynamics produced by the model could match the observed data we compared the output from the model where all four parameters were scaled with both body size and temperature (this represents the most realistic scenario as protists are known to alter body size with temperature, and both body size and temperature are known to alter metabolic rate) to the observed population dynamics. We assessed the fit of the model dynamics using  $r$ -squared values rather than a model comparison method such as AIC, as here we fit a single model to the mean data of one temperature treatment, and then use that model to attempt to predict when the other treatment populations will go extinct.

The error of the model in predicting future extinction events was gauged by comparing the predicted date of extinction to the mean date of extinction of the replicate populations of each temperature treatment, calculated as the first day at which the mean abundance of the replicates fell below one individual. Mean extinction date was used as the model was fitted to the mean abundance of the constant treatment.

Mean error (the difference between the predicted and observed dates of extinction) for each combination of scaled parameters was calculated from 500 randomly selected predictions across all the temperature treatments and only where predictions were made for all experimental treatments where extinction was observed (i.e. I3, I1.5, I0.75, I0.5, C, D0.5, D0.75). A random sub-sample of estimates was used as there was an imbalance in the number of estimates produced by each method.

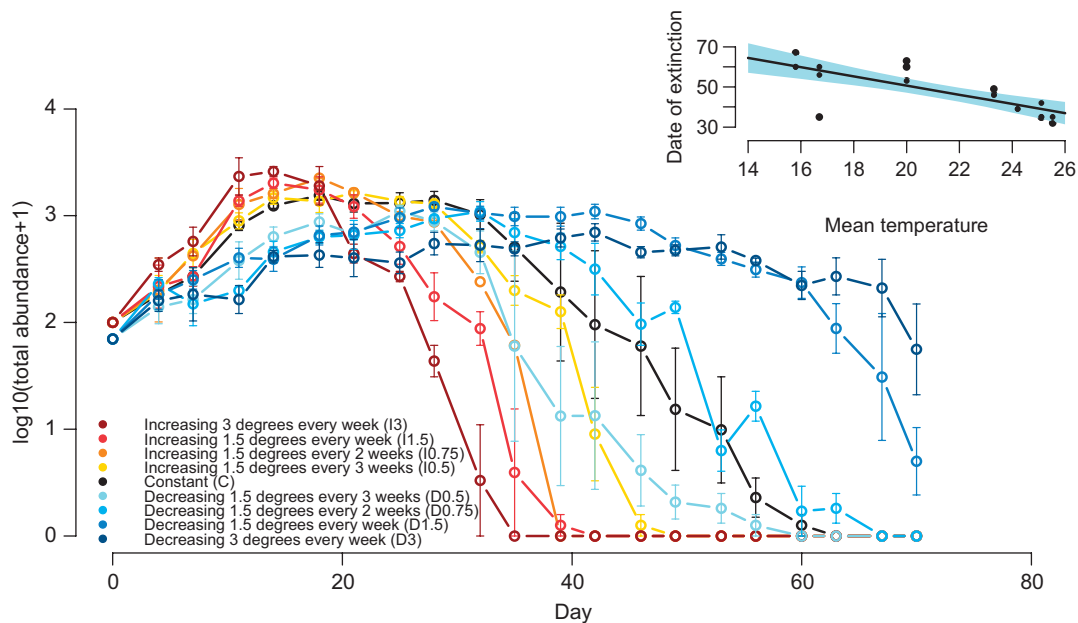


Figure 3. Rate of temperature change altered the speed at which replicate populations of *Loxocephallus* went extinct, and also the rate at which populations grew and the maximum population sizes that they reached. Bars are one SE. Inset, mean temperature negatively correlated with extinction date (linear regression fitted to the extinction dates of all replicate populations where extinction occurred (black dots)). Blue area highlights 95% CI. Mean temperature negatively correlated with extinction date (linear regression,  $\text{coef} = -2.3$ ,  $\text{SE} = 0.46$ ,  $t = 4.93$ ,  $p < 0.001$ ).



## Results

### Experimental results

Extinctions occurred in 19 of 25 populations, and all but two treatments had extinctions in all the replicate populations (all populations of D1.5 and D3 were extant at day 70). One replicate of each of the treatments I0.75 and I3 was contaminated, and so were excluded from the analysis. Where extinctions did occur, mean temperature negatively correlated with extinction date (linear regression,  $\text{coef} = -2.3$ ,  $\text{SE} = 0.46$ ,  $t = 4.93$ ,  $p < 0.001$ , Fig. 3), and the date of extinction differed significantly between treatments (ANOVA,  $\text{DF} = 6$ ,  $F = 7.77$ ,  $p < 0.01$ , Fig. 3).

### Model predictions – scaling parameters with temperature, body size, and both

When model parameters depended on only the direct effect of temperature (i.e. no indirect effects via body size, Eq. 5) there was relatively low mean error (error calculated as the difference, in days, between the predicted and mean observed dates of extinction), although this was highly dependent on which parameters were scaled (Fig. 2). There was a significant negative correlation between the number of parameters scaled with temperature and the mean error of the predicted dates of extinction generated by the model (log linear regression,  $\log\text{-coef} = -0.51$ ,  $\log\text{-SE} = 0.14$ ,  $t = 3.63$ ,  $p < 0.05$ , Fig. 2). The lowest mean error occurred when the parameters  $r$ ,  $\alpha$  and  $\lambda$  were scaled with temperature (mean error of 2.0 days with a standard error of 0.77).

When parameters depended only on indirect effects of temperature via changes in body size (i.e. no direct effects

of temperature, Eq. 6), there was a relatively large error associated with the predicted date of extinction (Fig. 2). Scaling greater numbers of parameters with body size had less of an impact on the mean error, although there was still a significant negative correlation between the number scaled and the mean error (log linear regression,  $\log\text{-coef} = -0.18$ ,  $\log\text{-SE} = 0.05$ ,  $t = 3.57$ ,  $p < 0.01$ , Fig. 2). The lowest mean error was produced when all four model parameters were scaled (mean error 8.80 days with a standard error of 1.07).

When model parameters were dependent on direct and indirect effects of temperature (Eq. 8), prediction error was very similar to when parameters depended on only the direct effect of temperature (Fig. 3). Again, there was strong negative correlation between the number of parameters scaled and the mean error (log linear regression,  $\log\text{-coef} = -0.56$ ,  $\log\text{-SE} = 0.15$ ,  $t = 3.73$ ,  $p < 0.05$ , Fig. 2). As when parameters were scaled with body size only, the lowest mean error was produced when all four parameters were scaled (mean error 1.74 days with a standard error of 0.83). This error was not significantly different in magnitude to the error produced by the combinations  $r$ ,  $K$ ,  $\alpha$  (scaled both directly and indirectly,  $t\text{-test}$ ,  $\text{DF} = 995.1$ ,  $t = 0.63$ ,  $p > 0.05$ ),  $r$ ,  $\alpha$ ,  $\lambda$  (scaled only directly,  $t\text{-test}$ ,  $\text{DF} = 996.5$ ,  $t = 1.22$ ,  $p > 0.05$ ), or when all four parameters were scaled with only the direct effects of temperature ( $t\text{-test}$ ,  $\text{DF} = 996.6$ ,  $t = 1.02$ ,  $p > 0.05$ ).

### Model fits to observed data

The fit of the model was generally good (for all but one of the temperature treatments the  $r$ -squared value was greater than 0.69, with the maximum  $r$ -squared value being 0.98 for the

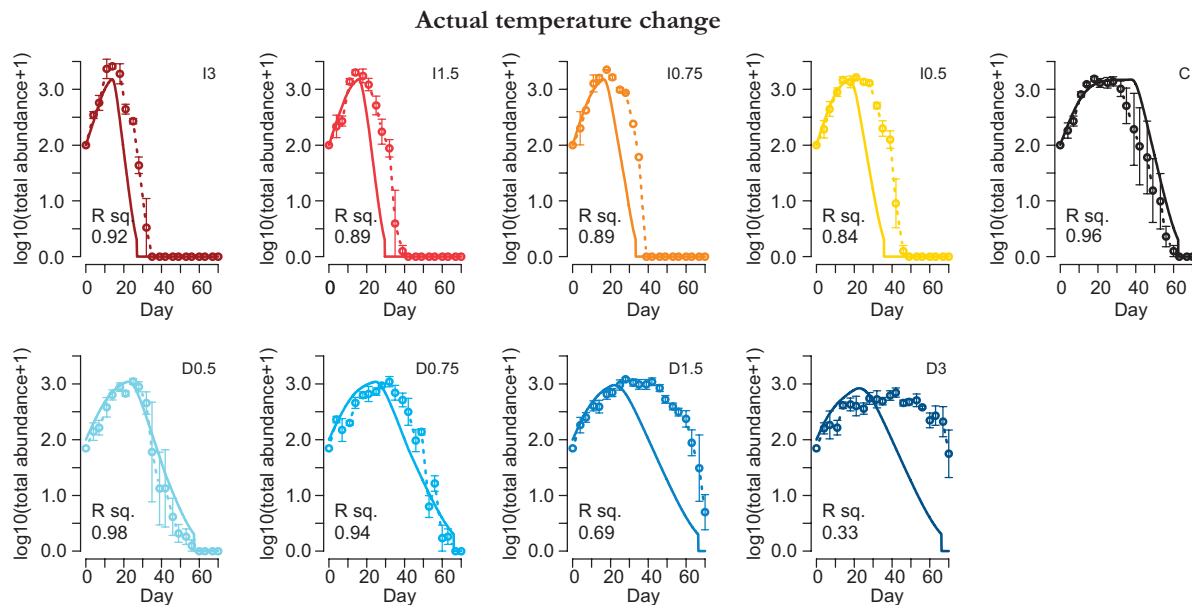


Figure 4. Predicted abundances when all four parameters were scaled with both predicted change in body size and actual temperature (solid lines) are plotted against the experimental data (open circles). The model prediction for treatment 'C' is based on the parameters produced from the maximum likelihood estimation, all other predictions are produced by scaling the model parameters with mean temperature. Model fits were high ( $r^2$ -values 0.69–0.98) for all treatments except D3. The model tended to systematically predict extinction before it had occurred in increasing temperature treatments, and also in the two decreasing treatments where extinction was not observed (D1.5, D3). Bars are one SE.

treatment D0.5, Fig. 4). In general the model predicted the date of extinction to be earlier than the mean extinction date observed in the experimental communities (Fig. 4), but most of the time this error was still within a few days of the mean date of extinction.

In addition to comparing the model fits ( $r^2$ -values) where the parameters were scaled with predicted change in body size and the actual temperature at each time step, we compared the fits of the model where mean temperature within each treatment was used to scale the parameters (Fig. 5). Here every fit is poorer than when temperature at each time step is used (Fig. 4, 5). Predictions for the abundances of the four increasing temperature treatments still followed the patterns observed in the experimental data, and, as with the fits made using actual temperature, predicted date of extinction was earlier than the observed date (Fig. 4, 5). In treatments with decreasing temperatures the model fits were poor, with populations predicted to persist past day 70 (the last day of the experiment).

## Discussion

We show that in a closed, nutrient limited system, the greater the mean temperature (which depends on the rate of temperature change through time), the earlier a population goes extinct. Using a simple phenomenological model, and scaling the parameters with temperature and predicted changes in protist body size, we were able, with reasonable accuracy ( $R^2$ -values in most cases  $> 0.84$ , and mean error of  $< 2$  days), to predict the mean date of extinction of a population in a changing environment,

from information on the population trend in a constant environment. The accuracy of these predictions was dependent not only on which combinations of parameters are scaled, but also the method by which the parameters are scaled and the rate and direction of temperature change, with the most accurate estimates produced when all four parameters are scaled with both the direct and indirect effects of temperature.

The simple four-parameter phenomenological model provides a good fit to the population dynamics of the constant treatment (C) (Fig. 4), and, using metabolic theory, we were able to accurately predict the date of extinction in most temperature treatments (Fig. 4). However, the accuracy of predictions was dependent upon which parameters of the model were scaled with temperature, and what scaling method was used. In general, across all the scaling methods, increasing the number of parameters scaled produced the most accurate estimates of time of extinction (Fig. 2). This is somewhat unsurprising, as temperature is known to alter birth rate, death rate, carrying capacity and the rate at which prey are consumed, all of which are directly or indirectly included within the model presented here, and thus scaling all parameters should include all of the temperature-dependent processes that are occurring within the experimental communities. There is, however, some redundancy in the model, as in some instances scaling only three parameters provided as accurate predictions as scaling all four simultaneously (Fig. 2). Where all four parameters are scaled with by both the direct and indirect effects of temperature the mean error across treatments was around 1.7 days, or approximately two generations of *Loxocephallus* sp. (Clements et al. 2013).

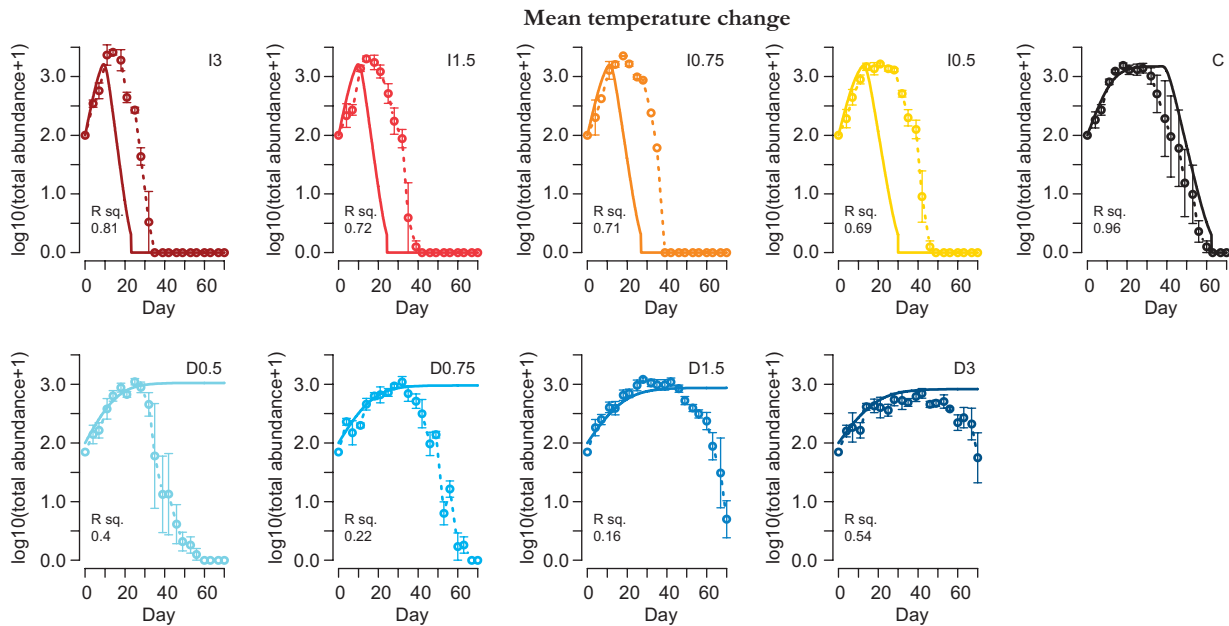


Figure 5. Predicted abundances when all four parameters were scaled with both predicted change in body size and mean temperature of each treatment (solid lines) are plotted against the experimental data (open circles). The model prediction for treatment 'C' is based on the parameters produced from the maximum likelihood estimation, all other predictions are produced by scaling the model parameters with mean temperature. Model fits were high where temperature increased through time (I3–I0.5), but poor where temperature decreased, especially in comparison to predictions made where parameters were scaled with the actual temperature at any given time point. Bars are one SE.

There were large differences in accuracy between the different scaling methods, although to some extent this also depended on the number of parameters being scaled (Fig. 2). When all four parameters were scaled simultaneously with only the predicted change in body size (indirect temperature effects), the error associated with predictions was high (a mean of 8.8 days). Scaling all four parameters with only the direct effects of temperature produced a pattern of errors very similar to that produced when parameters are scaled with both temperature and assumed change in body size (predicted to be  $-2.5\%$  per  $+1^\circ\text{C}$  (Atkinson et al. 2003), body size was not measured in the experiment) (Fig. 2). Indeed, there was no significant difference between the mean error produced when all four parameters were scaled with temperature alone, or with temperature and body size. This implies that when modelling such population declines using metabolic theory, the inclusion of the direct effects of temperature is far more important than any body-size driven indirect effects.

The fit of the model depended on the rate of temperature change, with worst fit in the treatments D1.5 and D3 (Fig. 4). This was due to the simplicity of the model and the method for implementing the decrease in carrying capacity ( $K$ ). The timing of the exponential decline of carrying capacity was controlled by the parameter  $\alpha$ , that is, the fraction of the carrying capacity at which exponential decay of the carrying capacity begins to occur. However other assumptions made in the model, specifically that carrying capacity decreases as temperature decreases, occasionally affect the implementation of this decrease in  $K$ . This was especially problematic with a rapidly decreasing temperature (i.e. D1.5, D3), as carrying capacity also decreases rapidly, and so the exponential decay of  $K$  occurs sooner. While a more mechanistic model might improve this situation, there is a downside; more prior knowledge is required to parameterise such a model. Given

the underlying variation in extinction date inherent within each temperature treatment, and the already relatively high accuracy of the phenomenological model in predicting extinction (where extinction has occurred), it seems unlikely that the benefits of using a more mechanistic model will outweigh the costs, at least within the small-scale closed system presented here.

Whilst mean temperature negatively correlates with mean extinction date, there exists among replicate variation in extinction date (Fig. 6). In most cases this variation is small, but this is not always the case. Where the model was bootstrapped to include the error associated with parameter estimations, all the extinction events fell within the 95% confidence intervals, and in fact the vast majority fell very close to, or exactly on, the mean predicted date of extinction (Fig. 6).

Using metabolic theory to incorporate temperature change into theoretical models has, in part given its convenience and simplicity, been widely applied (Woodward et al. 2005, Reich et al. 2006, Berlow et al. 2009), although variation in the how metabolic rate scales both within and across species suggests that it may not be applicable in all cases (Chown et al. 2007, White et al. 2007, Glazier 2010). We find that when the body size and temperature components of metabolic theory are both used to scale parameters, model fits to observed data are good (Fig. 4), and that in this instance using metabolic theory to scale parameters is therefore reasonable.

The simplicity of the model, and consequently the assumptions made by it, may limit its applicability in real world scenarios. Effectively the model assumes that a species suffers an exponential decline in its population size from carrying capacity until extinction (in this case driven by a closed system with a degrading habitat and limited resources). This assumption may well be valid in some

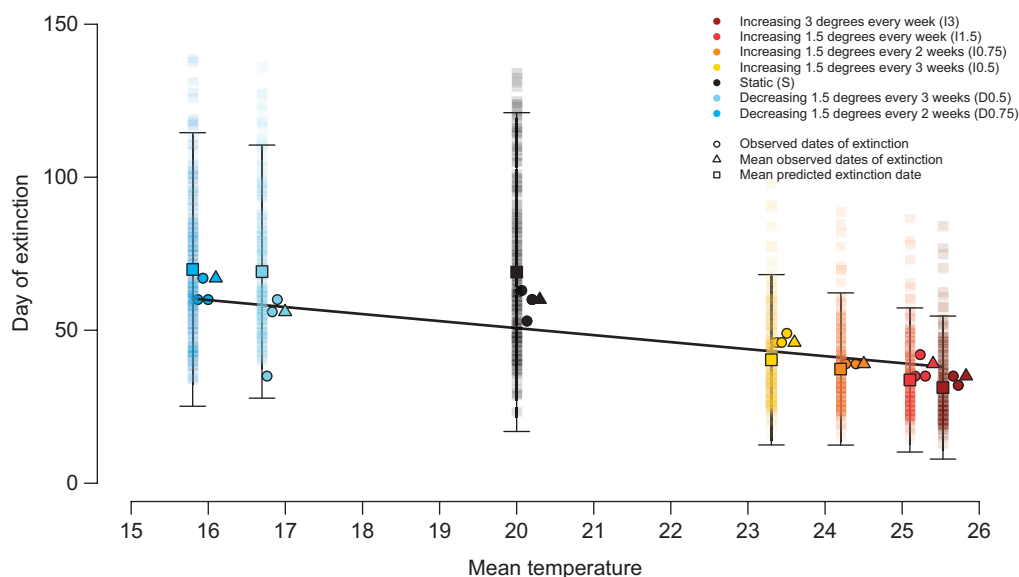


Figure 6. Whilst mean abundance was used to parameterize the phenomenological model, and to gauge the accuracy of model predictions, there was some variance amongst replicates. Mean predicted date of extinction in most cases falls very close to the majority of recorded extinction events. Bars show the 95% confidence intervals of model predictions. All extinction events fell within the 95% CIs, although the confidence intervals were often large (over 100 days for treatment S). Points within a temperature treatment are horizontally displaced for clarity.



circumstances in the natural world (exponential declines in habitat size have previously been observed, and have led to the declines of resident species (Short and Burdick 1996, Hughes et al. 2002)), but caution should be exercised as sudden population crashes (Lande 1993), rescue effects (Brown and Kodric-Brown 1977) or habitat restoration (Waltz and Covington 2004) may invalidate such an assumption. Temperature driven extinction has been proposed through more complex dynamics, such as increased demographic stochasticity, and this may be an additional factor that leads to population loss (Vasseur and McCann 2005), however the data presented here is unsuitable for testing such hypotheses due to the nutrient limitations of the system, and consequent lack of potentially destabilising oscillations.

The work presented here does, however, provide a conceptual starting point for understanding the effects of the rate of temperature change in more complex systems, and adds to a body of work that has previously used simplistic systems as a way of gaining an understanding of complex dynamics, especially those processes that govern the extinction of populations (Griffen and Drake 2008). This work adds to this body of knowledge by showing how simplistic models can be used to forecast extinction in relatively simple systems, and provides a basis for theoretical exploration of these problems in more complex systems. Whilst the closed system we present here may appear unrealistic, in reality resource availability in a habitat can be very low, particularly in declining 'sink' populations, with an insignificant flux of resources (Polis et al. 1970). In such scenarios where the influx of nutrients is much lower than that required to sustain a viable population, extinction will occur. The work presented here suggests that in such a scenario extinction will happen much more rapidly where mean temperature is high, and that it may be possible to infer how such a system would then behave under varying rates of temperature change, using simple phenomenological modelling. Where resource flux is high the use of a more mechanistic model that takes into account the possibility of an increase in the abundances of prey may provide a more helpful starting point. Evaluating the relative merit of phenomenological and mechanistic models to predict extinction in a more open system would provide an interesting next step to the work presented here.

In conclusion, temperature is known to alter many individual and population level processes, including metabolic rate, which in turn alters the rate of senescence and time of death of an individual (Van Voorhies and Ward 1999, Brown et al. 2004). Predicted future changes in temperature could thus alter not only the persistence of individuals, but of populations and potentially of a species. Predicting population declines, in the light of current global change, is necessary, but for many species the detailed knowledge required to parameterise a complex, mechanistic model will be unavailable, or be too costly or take too long to obtain. Fitting a simple model of logistic growth with an exponential decline allows accurate predictions of population extinction under various rates of temperature change in a model system. However, rapid rates of cooling invalidate assumptions made by such a model. Using mean temperature over a given time period (rather than actual temperature) significantly reduces the accuracy of the predictions made by the model, and should be avoided. The results

presented here suggest that using such simplistic models, and incorporating the actual rates of temperature change, to predict the effect of future climatic change has some merit, and that scaling parameters with metabolic theory is, in this instance, appropriate.

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