Nonlinear averaging of thermal experience predicts population growth rates in a thermally variable environment

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Abstract

Incorporating biological effects of environmental variability into predictions of species' performance is a persistent challenge that limits our ability to project across temporal scales in ecology. Here we test the hypothesis that population growth rates in fluctuating thermal environments can be predicted quantitatively from the curvature of thermal performance curves (TPCs) using scale transition theory. Using experimental populations of the green alga *Tetraselmis tetrahele* grown over a range of temperatures in constant and fluctuating thermal regimes, we show that population growth rates in fluctuating thermal regimes can be accurately and quantitatively predicted based on performance in constant thermal regimes. We extrapolate from these results to predict how population growth and critical temperatures for persistence of 89 phytoplankton species assessed in constant conditions would differ in naturally variable thermal environments. Together these results demonstrate a key improvement upon our ability to predict population dynamics in the context of global change.

Introduction

Organisms live in variable environments and their performance reflects their responses to environmental variation over time and space. Demographic rates and outcomes that integrate temporal environmental variation may differ substantially from what might be predicted based on short-term physiological responses to constant, non-varying environments. This difference complicates projections of population performance based on physiological assays under constant conditions (Estay *et al.* 2014), prompting calls for ecologists to explicitly incorporate environmental variation into predictions and models of population and species' performance in

61 the field (Dowd *et al.* 2015). Because environmental variability differs across regions and the
62 lifespans of organisms, an approach that allows quantitative scaling from thermal reaction norms
63 of population growth generated under constant laboratory conditions to population performance
64 in a variable thermal regime may be particularly useful for understanding patterns of abundance
65 and distribution, and species' responses to climate change.
66
67 Biological responses to environmental variation depend on the shape of the relationship between
68 performance and an environmental gradient (Ruel & Ayres 1999; Drake 2005; Lawson *et al.*
69 2015). When performance, P, changes nonlinearly with environmental conditions, mean
70 performance in a variable environment $\overline{P(E)}$ does not necessarily equal performance at the mean
71 environmental condition $P(\bar{E})$. This fact, captured by the well-known mathematical rule Jensen's
72 inequality, leads to clear predictions about how environmental variability should affect
73 performance over time. In the context of temperature, the relationship between organismal or
74 population performance and temperature, called a thermal performance curve (TPC) (Fig. 1A), is
75 almost always nonlinear (Schulte 2015) so the often implicitly assumed linear relationship
76 between environment and population growth in demographic models of environmental
77 variability is inadequate to describe population dynamics over temperature gradients (Lande *et*
78 *al.* 2003). The potential ecological and evolutionary effects of Jensen's inequality have been
79 shown in several recent studies (Martin & Huey 2008; Estay *et al.* 2014; Vasseur *et al.* 2014;
80 Denny 2017). Yet, ecologists struggle to incorporate thermal variability when making
81 predictions about the effects of temperature on growth, abundance, and distributions of species in
82 nature, often assuming that species' thermal experiences are well represented by the mean
83 temperature of their environment.

Principles of non-linear averaging have been formalized in scale transition theory (Chesson *et al.* 2005), which builds on Jensen's inequality, and makes predictions for how non-linear dynamics change over spatial and temporal scales. Scale transition theory is an approach developed for metacommunity models that allows for quantitative predictions for how variation at one scale emerges at another when mediated by a nonlinear relationship such as a TPC. While Jensen's inequality provides qualitative predictions about how the shape of non-linear TPCs will influence the outcome of performance in the face of environmental variation, scale transition theory allows for quantitative predictions of these effects. Here, we use scale transition theory in the context of relating estimated performance over time-averaged scales to performance at short time scales generated under static conditions. Specifically, the expected performance under variable conditions, $\overline{P(T)}$, can be approximated by

$$\overline{P(T)} \approx P(\bar{T}) + \frac{1}{2}P''(\bar{T})\sigma^2{}_T \qquad (1)$$

where $P''(\bar{T})$ is the second derivative of the TPC at an average temperature, $\bar{T}$ and σ_T is the standard deviation of temperature experienced by the organism (Chesson *et al.* 2005; Estay *et al.* 2014; Dowd *et al.* 2015). Equation 1 holds whenever $P(T)$ can be approximated accurately by its second order Taylor expansion, and is likely to be most accurate when σ_T is small relative to the thermal breadth. Equation 1 shows that where the relationship between performance, *P,* and temperature is an accelerating function with a positive second derivative (Fig. 1B), *P* will increase with increasing temporal variance (σ^2) in temperature due to Jensen's inequality. Similarly, *P* will decrease with increasing variance where the TPC is decelerating (i.e. negative

second derivative, Fig. 1B). Where the TPC is linear, temperature variability should have no effect on *P* because the effects at cold temperatures counterbalance the effects of warm temperatures when averaged over time. By quantifying the curvature at a given point on a thermal performance curve, scale transition theory provides a way to mathematically predict the strength and direction of effects of temperature fluctuations around that temperature on performance.

The typical shape of TPCs (Fig. 1A) (Dell *et al.* 2011), with a decelerating phase at higher temperatures within a thermal niche and an accelerating phase at lower temperatures, suggests negative effects of thermal variation at high temperatures and benefits at low temperatures. Current estimates of the consequences of thermal variability for population-level performance such as growth rate have assumed a certain shape to the curve (i.e. a Gaussian rise and a parabolic fall; Vasseur *et al.* 2014) , thus forcing certain outcomes of variability. Yet, new evidence suggests that the shape and skew of the performance curve can vary substantially among species, phenotypes, or contexts (Thomas *et al.* 2012, 2017), and this is likely to have important implications for the effect of environmental variation on performance. Empirical evidence for how variability affects population growth rates to date has been based on tests at only two temperatures (Bozinovic *et al.* 2011). This restricted sampling of the TPC has precluded testing of quantitative predictions based on the curvature of the TPC.

Here we asked: Does population growth in a thermally variable environment reflect the effects of non-linear averaging over the TPC? To answer this question, we experimentally tested whether population growth in thermally variable environments can be predicted by scale transition

130 theory. We experimentally quantified a TPC for population growth of a green alga, *Tetraselmis*
131 *tetrahele*, in a constant thermal regime, and then used this TPC and Equation 1 to predict how
132 population growth differs in a fluctuating temperature regime. Following from Equation 1, we
133 predicted that increased temperature variability over the range of cold temperatures to the left of
134 the inflection point of the TPC (i.e. in the accelerating portion of the curve, where the second
135 derivative of the TPC is positive; Fig. 1B) would lead to higher growth rates relative to constant
136 conditions, and that temperature variability in the range of warm temperatures to the right of the
137 inflection point would be detrimental (i.e. where the second derivative of the TPC is negative;
138 Fig. 2A, dashed curve).
139
140 Then, drawing on a global dataset of empirical TPCs for phytoplankton population growth rates,
141 which vary in shape (skew and position) as well as geographic origin, we use scale transition
142 theory (Equation 1) to estimate *in situ* population growth rates, given levels of *in situ*
143 environmental variation at each species' isolation location. We estimate the extent to which
144 predicted growth rates at each isolation location differ when they are predicted by scale transition
145 theory, as compared to when they are predicted based on mean temperatures only. By including a
146 range of phytoplankton TPC shapes from a global distribution, we explore the consequences of
147 considering thermal variability in projections of population growth rates, with implications for
148 patterns of abundance and distribution.
149
150 **Methods**
151 *Experimental quantification of TPCs in constant and fluctuating environments*

We experimentally quantified TPCs in constant and varying thermal environments for *Tetraselmis tetrahele*, a globally distributed coastal marine phytoplankton species. The cultured strain used here was obtained from the Canadian Centre for the Culture of Microorganisms (UW414), and was originally isolated off the coast of Vancouver Island, British Columbia, Canada. The *T. tetrahele* was maintained in laboratory culture in ESAW medium (Enriched Seawater, Artificial Water, Harrison *et al.* 1980) at 16°C on a 16:8 light:dark cycle under nutrient and light saturated conditions before the start of the experiments.

We initiated twenty replicate experimental populations of *T. tetrahele* in 30 mL glass test tubes containing 20 mL of 10uM nitrate ESAW medium at a density of ~ 700 cells/mL under constant temperature conditions at 0°C, 5°C, 10°C, 15°C, 20°C, 24°C, 27°C, 29°C, and 32°C, and under fluctuating temperature conditions with the same mean temperatures as the constant conditions, but fluctuating ± 5°C; i.e. 0°C – 10°C, 5°C – 15°C, 10°C – 20°C, 15°C – 25°C, 19°C – 29°C and 22°C – 32°C. We created fluctuating temperature treatments by programming temperature-controlled incubators (Panasonic MR 154) to switch between the low and high temperature once per day (i.e. approximately 11.5 hours at the high temperature and approximately 11.5 hours at the low temperature, with 30 minutes of transition time in between each temperature cycle). To avoid experimental artifacts associated with confounding the temperature cycles with daily light cycles, we grew all experimental populations under 24-hour continuous light, at saturating light intensities of 150 umol/m^2/s (see Fig. S1 in Supporting Information). The source population was acclimated to 24-hour continuous light for four months prior to the experiment. We sampled each of the twenty replicate populations, with four replicates sampled destructively at each of five time points over the period corresponding to the exponential growth phase at each

175 temperature. The intervals between sampling periods depended on the temperature, such that for
176 the warmer temperatures (>15°C) sampling time points were condensed (up to 3 samples per
177 day) to capture exponential growth, while at the colder temperatures (<=15°C) sampling
178 intervals were spread out over longer time periods (i.e. one to five days between sampling points
179 at 0°C). Population abundances and cell biovolumes (using area-by-diameter estimation, ABD)
180 were measured from 250 uL samples using a FlowCAM (flow rate = 0.3 ml/min; FlowCAM VS
181 Series, Fluid Imaging Technologies).
182
183 *Statistical estimation of performance curves*
184 We estimated the intrinsic rate of population growth, *r*, during the exponential growth phase as:
185
186 $$N(t) = N(0)e^{rt} \quad (2),$$
187
188 where *N(t)* is the number of individuals at time *t,* using non-linear least squares regression with
189 the *nls* function in R (R Core Team 2017).
190
191 For constant and variable conditions, we fit a thermal performance curve for growth rate
192 (Thomas *et al.* 2012),
193 $$r(T) = ae^{bT}\left[1 - \left(\frac{T - z}{\frac{w}{2}}\right)^2\right] \quad (3)$$
194
195 where growth rate, *r,* is a function of temperature, *T*, *a* and *b* are parameters from the Eppley
196 curve (Eppley 1972) that describe maximum observed population growth rates as a function of

temperature, z determines the location of the maximum of the quadratic portion of the function and w is the range over which the growth rate is positive (i.e. the thermal breadth). We estimated these parameter values using maximum likelihood estimation with the *mle2* function in the *bblme* package (Bolker 2017). Importantly, this TPC equation does not force the curve to take on any particular shape, such that estimated curves can be either fully decelerating throughout the entire range of temperatures over which growth is positive, or can have any combination of accelerating and decelerating portions. We favored this TPC equation over others because of this flexibility, because it is parameterized with biologically meaningful parameters, and because has been used previously in studies of phytoplankton TPCs (Thomas *et al.* 2012, 2016). For comparison, we fitted several other functional forms to the experimental dataset (e.g. a Gaussian x Gompertz function, as in Martin & Huey 2008) but did not find any better fits.

To generate estimates of uncertainty in critical temperatures of the TPC (e.g. T_{opt}), we determined confidence intervals around fitted thermal performance curves using parametric bootstrapping, following the approach outlined in Equation S.3 in (Thomas *et al.* 2012). We then used the TPC fitted under constant conditions and its upper and lower confidence intervals to make predictions under variable conditions. For the thermal performance curve fitted to the nine experimental temperatures under constant conditions, we simulated nine new performance values drawn from a normal distribution such that the mean of the distribution corresponded to the value of Equation 3 at each of the original experiment temperatures, given the estimated parameters and the standard deviation = σ, where σ was calculated by accounting for uncertainty in the estimation of the original maximum likelihood standard deviation, $\hat{\sigma}$, using:

$$\hat{\sigma}^2 = \sigma^2 \sqrt{\frac{n-1}{X}} \quad (4)$$

where n is the number of data points (n = 9), and X is a random number drawn from the chi-squared distribution having (n – 1) degrees of freedom (Gelman & Hill 2007). We then fit Equation 3 to these nine simulated performance estimates using maximum likelihood estimation and repeated this process 10000 times to generate 10000 new thermal performance curves. We calculated 95% confidence intervals as the range between the 2.5th and 97.5th quantiles. We used these 95% confidence intervals to calculate the upper and lower bound of the predicted population growth rate under fluctuating thermal conditions using Equation 1 (Fig. 2A, dashed band). We repeated the same curve fitting and bootstrapping process for the fluctuating temperature regimes, where the TPC (Equation 3) was fit to the mean temperature in each treatment.

We quantified four critical temperatures of the TPC: the optimal temperature for population growth, T_{opt}, the minimum temperature for positive population growth, $T_{r>0,min}$, the maximum temperature for positive population growth, $T_{r>0,max}$, and thermal niche breadth under constant conditions, w. We quantified the analogs of these critical temperatures under fluctuating conditions and refer to them as the minimum mean and maximum mean temperatures for positive population growth under fluctuating conditions, $\overline{T}_{r>0,min}$ and $\overline{T}_{r>0,max}$ respectively, the mean temperature for optimal growth under fluctuating conditions, $\overline{T}_{opt}$, and thermal niche breadth, $\overline{w}$. If the $T_{r>0,min}$ from the estimated curve was below -1.8°C, we set $T_{r>0,min}$ to be -1.8°C because we assumed that *Tetraselmis tetrahele* cannot maintain positive population

growth below the freezing point of seawater. We then calculated the range of temperatures over which population growth rate is positive as the difference between $T_{r>0,min}$ and $T_{r>0,max}$. Following Equation 1, we expected that increased temperature variability should increase and decrease population growth in the accelerating and decelerating portions of the TPC respectively, and that the shift between positive and negative effects of temperature variability should occur at the inflection of the constant-temperature TPC. We predicted that increased variability should push the lower and upper limits of the TPC under variable conditions ($\bar{T}_{r>0,min}$ and $\bar{T}_{r>0,max}$) to lower temperatures than $T_{r>0,min}$ and $T_{r>0,max}$. We expected the maximum growth rate, r_{max}, to decrease under variable temperature conditions relative to constant conditions because T_{opt} is always in a decelerating portion of the constant TPC curve. Finally, we expected the thermal breadth under fluctuating conditions, $\bar{w}$, to also decrease under fluctuating conditions if $T_{r>0,min}$ is close to freezing, thus preventing $\bar{T}_{r>0,min}$ from shifting to lower temperatures to compensate for decreased $\bar{T}_{r>0,max}$.

Applying scale transition theory to estimate in situ *phytoplankton population growth rates*

We used scale transition theory (Equation 1) to estimate population growth rates in thermally variable environments for a set of diverse phytoplankton species. We estimated TPCs for 89 species based on published phytoplankton growth rates (Thomas *et al.* 2016) measured in the lab at arrays of constant temperatures using the fitting approach described in the lab experiment above. We restricted our analysis of the global phytoplankton dataset to marine species that met the following conditions: 1) there were experimental population growth rate estimates from at least five temperatures (n = 89 phytoplankton strains), 2) estimated $T_{r>0,max}$ and $T_{r>0,min}$ were within 5°C of the highest and lowest measurement temperatures respectively, 3) growth rates at

265 two or more temperatures above and below T_{opt} were reported, and 5) fitted curves had an R^2 of
266 at least 0.85, to ensure the estimated parameters describing the shape of the curve accurately
267 captured the curvature of the TPCs. In addition to these curve shape criteria, all the curves in the
268 dataset met the quality control criteria outlined in Thomas *et al.* 2016 (namely that the
269 experimental populations were grown with adequate light and nutrient supply, and non-stressful
270 pH and salinities).
271
272 For each of these 89 species, we used historical reconstructed sea surface temperature data to
273 characterize thermal regimes at isolation locations reported in the original studies. We estimated
274 thermal regimes (mean and variance) for each phytoplankton isolation location (latitude and
275 longitude) reported in Thomas *et al.* 2016. For each species' isolation location, we extracted
276 monthly sea surface temperatures (SST) from NOAA's Extended Reconstructed Sea Surface
277 Temperature dataset, ERSSTv3 (Smith *et al.* 2008). This dataset has a spatial resolution of 0.5-
278 degree (50 km). We calculated the mean and standard deviation of monthly sea surface
279 temperatures from 1986 – 2005. We used monthly temperature data because these data reflect
280 seasonal variation that is central to understanding patterns of long-term population persistence.
281
282 *Statistical estimation of TPCs*
283 We produced two TPCs for each phytoplankton species – one generated assuming temperatures
284 remain constant through time (akin to constant lab conditions), and one that incorporates natural
285 patterns of thermal variability from their habitat. For the 'constant' scenario, we fitted Equation 3
286 to each species' population growth rate dataset using the methods described above, and estimated
287 a growth rate, r, for the species at the isolation location using Equation 3, where T = mean SST at

288 the isolation location. For the 'variable' scenario, we estimated growth rates using the mean and
289 the variance of SST at each isolation location, following Equation 1, using $P(\bar{T})$ equal to the
290 value of Equation 3 fitted to the experimental data, and σ_T as the standard deviation of SST. For
291 each of these two scenarios, we compared three attributes of TPCs: T_{opt}, $T_{r>0,min}$ and $T_{r>0,max}$.
292 Given that differences in TPCs based on constant vs variable thermal environments depend on
293 curve shape and temperature variance (Equation 1), we also explored how the discrepancies in
294 estimated critical temperatures and population growth rates at average *in situ* temperatures
295 depend on the shape of the TPC observed in constant lab conditions. We examined the effects of
296 curve attributes including the skew, using a curve skewness metric developed by Thomas et al.
297 (2016) (Supplementary Equation 5 in Thomas *et al.* 2016), which standardizes the absolute
298 skewness of the curve by the niche width, *w*, using OLS regression. All analyses were conducted
299 in R (version 3.4.1, R Core Team 2017).
300
301 **Results**
302 *1) Does population growth in a thermally variable environment reflect the effects of non-linear*
303 *averaging over the TPC?*
304
305 Population growth in fluctuating conditions differed from that in constant thermal conditions
306 over the thermal gradient, and the differences were predicted quantitatively by scale transition
307 theory (95% CI of the growth rate estimates under fluctuating conditions overlapped with
308 predicted growth rates from Equation 1; points and dashed band in Fig. 2B). Consistent with
309 expectations based on nonlinear averaging of temporal variation in temperature, experimental
310 populations of *T. tetrahele* had higher population growth rates under fluctuating temperature

conditions compared to constant conditions over accelerating portions of the TPC (i.e. at low mean temperatures; 5°C and 10°C), but lower growth rates under fluctuating temperature conditions compared to constant conditions over decelerating portions of the TPC (i.e. at mean temperatures above 10°C, including 15°C, 24°C and 27°C and 29°C) (Fig. 2B). Notably, population growth was lower under fluctuating conditions relative to constant conditions at 24°C, which is close to T_{opt} in this population of *T. tetrahele* (Fig. 2B). Populations had negative growth rates at 32°C. The shift between positive effects of temperature fluctuations on population growth at low temperatures and negative effects of fluctuations at warmer temperatures aligned with the inflection point of the constant-temperature TPC (16.96 °C, 95% CI: 16.71°C, 17.12°C), providing strong empirical support for scale transition theory in predicting population growth in thermally variable environments.

Thermal variation altered estimated parameter values and key features of the thermal performance curve. The maximum exponential growth rate ($\bar{r}_{max}$) was lower under variable conditions than constant conditions, $\bar{r}_{max}$ =1.20 day^{-1} (95% CI: 1.07 day^{-1}, 1.33 day^{-1}) vs r_{max} = 1.62 day^{-1} (95% CI: 1.52 day^{-1}, 1.71 day^{-1}) (Fig. 2A, B). Estimated mean optimal temperatures for growth rate were lower under variable conditions: $\bar{T}_{opt}$ = 21.40°C (95% CI 20.37°C, 22.23°C) vs. T_{opt} = 24.56°C (95% CI: 24.27°C, 24.86°C). Estimated $\bar{r}_{max}$ and $\bar{T}_{opt}$ were quantitatively consistent with theoretical predictions from Equation 1 (i.e. had 95% CI overlapping the predicted values from Equation 1; Fig. 2B). Maximum mean temperatures for positive growth rates were lower under variable conditions $\bar{T}_{r>0,max}$ = 29.96°C (95% CI: 28.59°C, 32.61°C) vs $T_{r>0,max}$ = 31.91°C (95% CI: 31.73°C, 32.11°C). The range of temperatures associated with positive growth rates, accounting for the freezing point of seawater,

i.e. $T_{r>0,max} - T_{r>0,\min}$ was 33.67°C (95% CI: 33.09°C, 33.91°C) under constant conditions and 31.52°C (95% CI: 30.09°C, 33.54°C) under variable conditions. The estimated thermal breadth, *w*, was also lower under variable conditions: $\overline{w}$ = 36.68°C, 95% CI: 13.87°C, 66.29°C, vs *w* = 36.51°C, 95% CI: 32.87°C, 42.51°C). Maximum mean temperatures for positive growth, the range of temperatures associated with positive growth rates and *w* were all lower under variable conditions than constant conditions, but were not statistically distinguishable (i.e. had overlapping 95% CI).

2) How different are predicted TPCs in variable natural environments from predictions based on TPCs generated under constant conditions?

When we estimated the TPCs of the 89 phytoplankton species for constant and varying temperature regimes, we found that for the 90% of species that show negative skew, $\overline{T}_{opt}$ in variable environments is lower than T_{opt} in constant environments (Fig. 3C), while for the remaining 10% of species which show a positive skew, thermal variability is expected to increase $\overline{T}_{opt}$ relative to T_{opt}. The magnitude of the difference between $\overline{T}_{opt}$ and T_{opt} increased with increasing standard deviation of sea surface temperature, and is well explained by curve skew (positive slope = 62.92, 95% CI: 51.72, 74.12) and standard deviation of sea surface temperature (negative slope = -0.22, 95% CI: -0.28, -0.15) (Adjusted R^2 = 0.61, $F_{2,106}$ = 85.85, p < 0.001) (Fig. 3C). Phytoplankton growth rate estimates that include the effects of thermal variability, $\bar{r}$, differ from those that do not account for *in situ* thermal variability, *r*, (Fig. 3D). Generally, predicted growth rates under variable conditions are lower than growth rates under constant conditions (i.e. $\bar{r} - r < 0$, data points below the line y = 0 in Fig. 3D), however for

some species living in regions with thermal regimes typically colder than the species' T_{opt}, growth rates in these environments can exceed those in constant conditions ($\bar{r} > r$); an example of such a species and its TPC is shown in Fig. 3F. Importantly, the differences between $r$and $\bar{r}$ are greatest for species whose isolation locations have mean temperatures that are close to their T_{opt}. Predicted upper thermal limits are almost always lower under variable conditions ($\bar{T}_{r>0,max} < T_{r>0,max}$) (Fig. 3E), and the difference between $\bar{T}_{r>0,max}$ and $T_{r>0,max}$ increases with increasing skewness (positive slope = 38.03, 95% CI: 30.13, 45.92) and standard deviation of SST (negative slope = -0.42, 95% CI: -0.46, -0.37,) (Adjusted R^2 = 0.79, $F_{2,106}$ = 207.8, p < 0.001). Thermal breadth, $\bar{w}$, is consistently estimated to be lower under variable conditions, and the difference between w and $\bar{w}$ increases with SST standard deviation, but not curve skewness (Adjusted R^2 = 0.50, $F_{2,106}$ = 55.53, p < 0.001).

Discussion

Thermal performance curves are widely used to predict patterns of species abundance and distribution (Deutsch *et al.* 2008; Sunday *et al.* 2012; Thomas *et al.* 2012). And yet, these curves are often used with the assumption that performance under constant lab conditions is analogous to performance under naturally variable climate regimes. We have shown experimentally that realized TPCs in variable environments differ from those in constant environments as predicted qualitatively by Jensen's inequality (Ruel & Ayres 1999; Denny 2017) and quantitatively match predictions based on scale transition theory (Chesson *et al.* 2005). Not only do variable vs. constant condition estimated population growth rates differ for any given mean temperature, but so do the key parameters and critical temperatures of the TPC. This result aligns with previous theoretical predictions (Estay *et al.* 2014; Dowd *et al.* 2015) that simply extrapolating critical

380 temperatures from constant condition lab experiments to naturally variable environments is
381 likely to introduce substantial error into projections of population performance, often over-
382 predicting species performance in the field. In the application of scale transition theory to 89
383 species' TPCs and known *in situ* thermal variability, we find that estimated critical temperatures
384 in realistically varying environments deviate substantially from observed critical temperatures
385 under constant conditions. Failing to account for variability can result in greatly over- or
386 underestimating population performance in natural populations. This has important implications
387 for how we use TPCs to make predictions about species distributions under current and future
388 climates.
389
390 Consistent with expectations based on Jensen's inequality and scale transition theory, our
391 experiment showed that temperature fluctuations increased population growth rate relative to
392 constant conditions over the accelerating portions of the TPC, decreased growth rates over the
393 decelerating portions of the curve, and the shift between positive and negative effects of
394 fluctuations matched the inflection point of the constant-temperature TPC (Fig. 1, Fig. 2).
395 Fluctuating thermal conditions changed several aspects of the thermal performance curve,
396 including the mean temperature of optimal population growth ($\bar{T}_{opt}$) and the maximum growth
397 rate attainable ($\bar{r}_{max}$) – effectively shifting the TPC toward lower temperatures and lower
398 population growth rates overall. However, this does not necessarily mean that species'
399 population growth performances are altogether lower in variable environments: for populations
400 living at mean temperatures in the accelerating part of the TPC, our results suggest that they will
401 benefit from environmental variation. Indeed, the *T. tetrahele* isolate used here was collected at a

402 location where temperatures are far colder than its $\bar{T}_{opt}$, in the accelerating portion of the
403 negatively skewed TPC (at mean temperature = 6.92°C, Smith *et al.* 2008).
404
405 When we applied scale transition theory to estimate the growth rates of globally distributed
406 phytoplankton species, we found that the effect of variability on predicted phytoplankton thermal
407 performance depended strongly on the shape and skew of the TPC and the degree of thermal
408 variability in the oceans from which the phytoplankton originated. Previous approaches have, in
409 the absence of more complete datasets, assumed a certain shape to the curve (i.e. a Gaussian rise
410 and a parabolic fall; Vasseur *et al.* 2014), thus forcing certain outcomes of variability. Here we
411 used a model that does not prescribe any particular shape (i.e. allows for fully decelerating
412 curves, or curves with accelerating portions, or any combination of decelerating and accelerating
413 portions), thus enabling a more complete exploration of the potential effects of temperature
414 variability on population performance. Importantly, whether the TPC is positively- or negatively-
415 skewed determined the direction of the shift between T_{opt} and $\bar{T}_{opt}$. The majority of the curves in
416 the dataset were negatively skewed, and in these cases variability shifted $\bar{T}_{opt}$ to colder
417 temperatures. Negatively skewed TPCs are widely observed across ectothermic taxa (Huey &
418 Kingsolver 1989; Dell *et al.* 2011), suggesting that the direction of the effects of thermal
419 variability observed in our experiment may be general across many ectothermic taxa and
420 ecosystems. Because the shape and skew of the TPC determine performance in variable
421 environments, the mechanisms that determine the shape of the thermal performance curve can
422 have an important influence on the outcome of thermal variability on population persistence.
423 More studies of the diversity of TPC shapes among species will elucidate the extent to which

environmental variability increases or decreases performance optima relative to constant lab conditions.

Environmental variation may not always be detrimental for population growth rates, in contrast to what is commonly assumed (Lande *et al.* 2003), and may play an important role in setting species range edges, where populations live close to the margins of their thermal limits. Temperature fluctuations may enhance the probability of population persistence when environmental temperatures fall within the accelerating portion of the TPC. In contrast, temperature fluctuations will decrease performance at the warm end of the TPC. Consistent with the argument that 'suboptimal' is optimal (Martin & Huey 2008), we show both experimentally (Fig. 2B) and theoretically (using empirical TPCs and *in situ* temperatures; Fig. 3D) that population growth rates are often lower under variable thermal conditions relative to constant ones, and this negative effect of temperature variation is greatest for populations living close to their thermal optima.

Importantly, several recent advances in our understanding of species responses to global change have relied on the shapes of TPCs generated under constant conditions to predict species range shifts and other responses to climate change (e.g. Deutsch *et al.* 2008; Thomas *et al.* 2012). Here we show that natural levels of environmental variability can introduce differences in critical mean temperatures for population persistence of up to 3°C, which is on par with the magnitude of predicted temperature changes over the next 100 years (Frölicher & Paynter 2015). Other work has compared acute thermal physiological limits (e.g. CTmax, CTmin) to environmental temperatures at range limits to assess relative sensitivities of range edges to warming (e.g.

447 Sunday *et al.* 2012), yet the underlying nonlinear thermal performance curve expected for these
448 ectotherms suggests that variability at warm range edges will have a stronger effect on
449 population persistence than variability at cold range edges. Specifically, our findings suggest
450 that approaches based on direct applications of lab-determined critical temperatures may under-
451 predict range edges at boundaries defined by cold temperatures, and over-predict range edges at
452 boundaries defined by warm temperatures.
453
454 While here we assumed a normal distribution of temperatures around the temporal average, this
455 is a simplification of real thermal regimes, which likely show more complex patterns variability
456 and temporal autocorrelation, which can further modify the effects of variability on populations
457 (Gonzalez & Holt 2002). Resource supply is also likely to covary with temperature, potentially
458 altering the outcomes of thermal variability on population growth rate. Importantly, organisms
459 may be able to acclimatize or adapt to fluctuating conditions over longer time scales (Angilletta
460 2009), with the potential to alter the shape and limits of the TPC, so the global predictions we
461 make here based on scale transition theory should be viewed as null models which do not
462 incorporate biological responses to environmental variability, and should be tested empirically
463 (Estay *et al.* 2014; Dowd *et al.* 2015). Nevertheless, even in the simplest scenario of
464 environmental variability, we predict significant changes in realized mean TPC critical
465 temperatures.
466
467 Understanding population responses to temperature now and into the future involves
468 understanding biological responses to changes in average temperatures in the context of
469 environmental variation. Omitting the effects of environmental variation from population and

species distribution models may thus limit our ability to predict species' responses to changes in mean temperatures, even if variability patterns remain unchanged. We show that the effects of environmental variation can be predicted based on the shape of the functional relationship between population growth and the environment, adding another tool to the kit for forecasting species' responses to the environment in a changing world.

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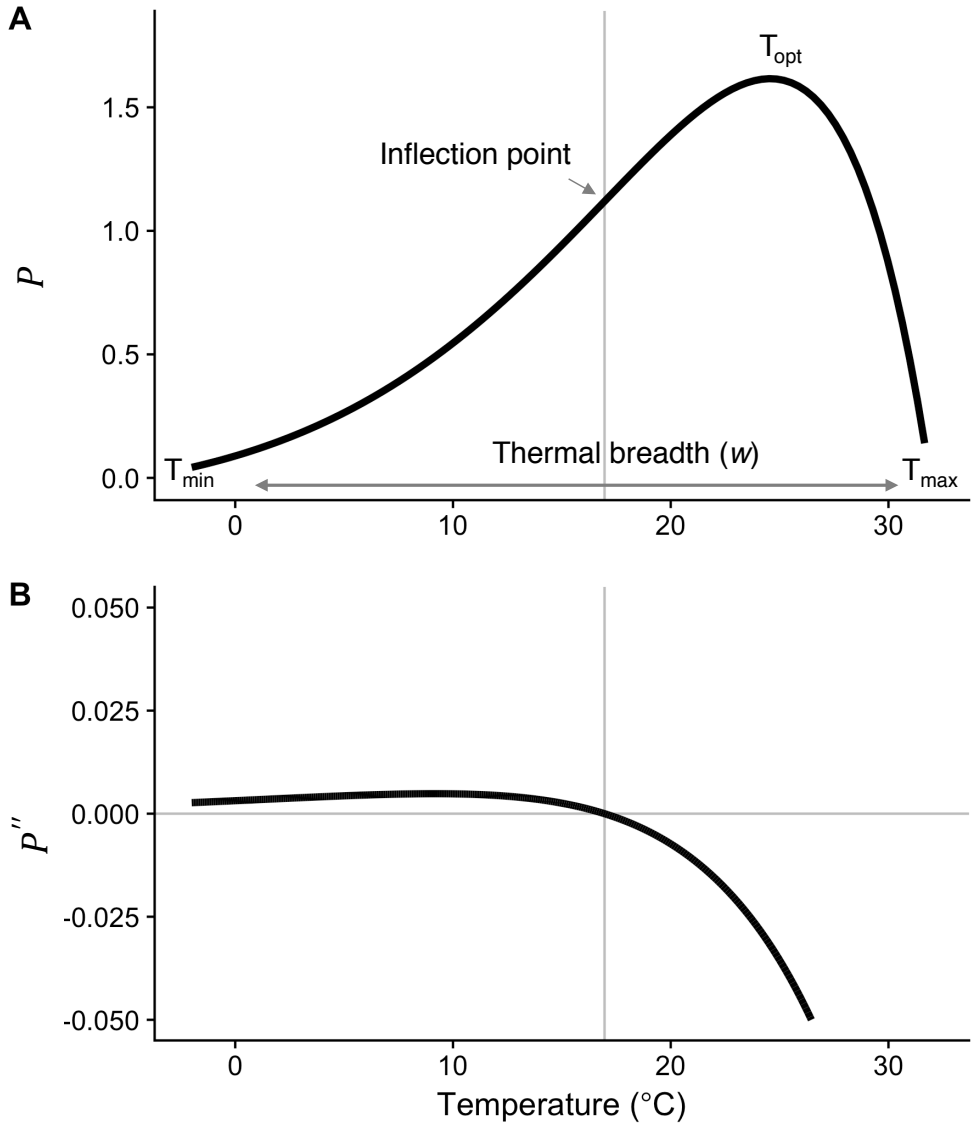
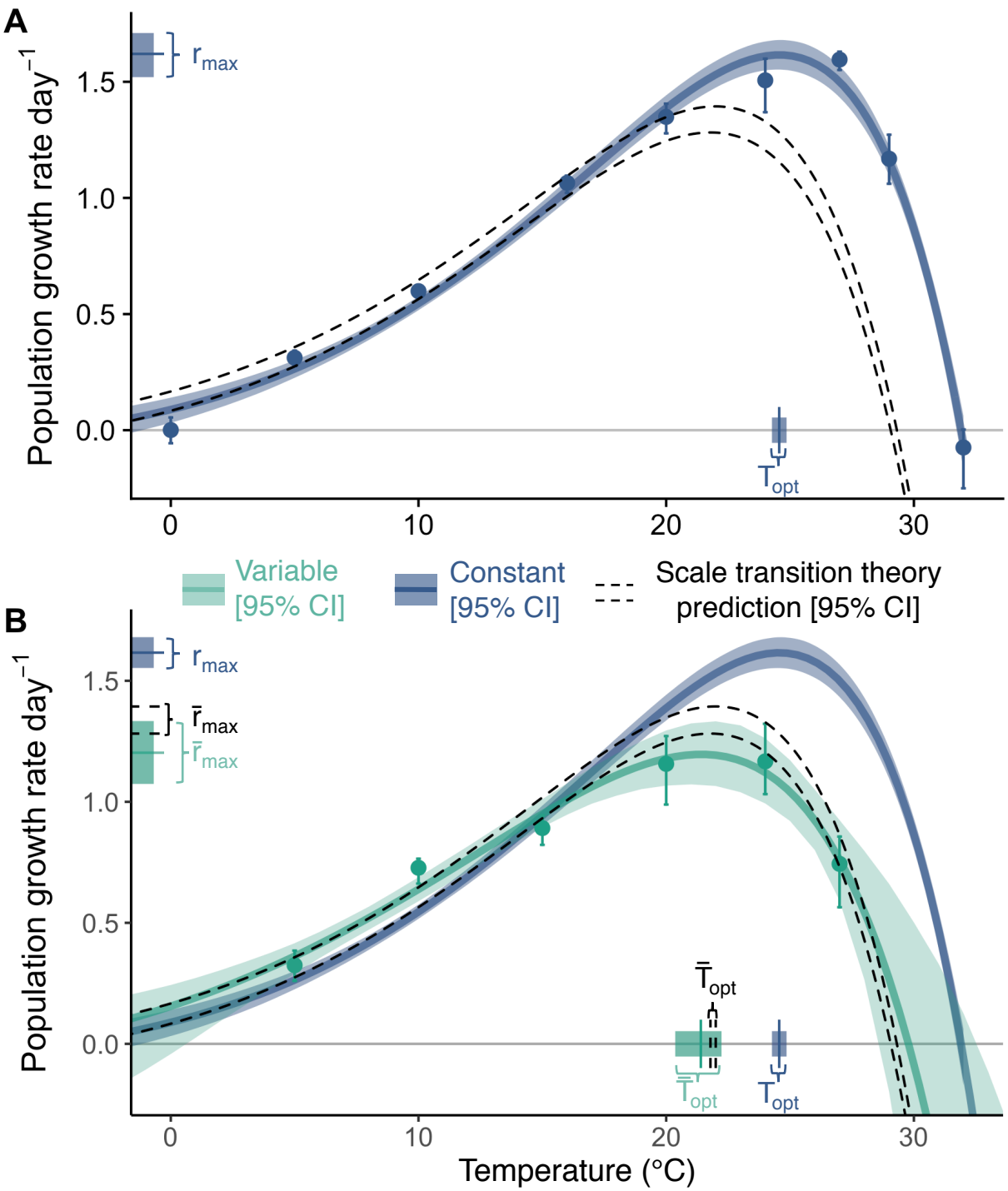
548 **Figures**



549

550 **Figure 1.** A) A thermal performance curve and its key features (T_{min}, T_{max}, T_{opt}, thermal breadth,
551 *w*). This negatively-skewed curve shows an exponential increase typical of processes following
552 an Arrhenius function, with an accelerating region to the left of the inflection point (grey vertical
553 line), followed by a decelerating region to the right of the inflection point. Notice that the
554 accelerating region corresponds to the region with a positive second derivative (panel B). Figure
555 adapted from Dowd *et al.* 2015, but parameterized with *T. tetrahele* data from this study.



556

557

558 **Figure 2.** Thermal performance curves for *T. tetrahele* populations growing under constant and

559 variable temperature conditions. A) Exponential growth rates under constant temperature

conditions; blue line is fitted thermal performance curve and blue shading corresponds to 95% CI generated from parametric bootstrapping. The dashed curve represents predicted growth rate under thermally variable conditions (σ_T = 5°C) based on scale transition theory (Equation 1). Points and error bars are observed mean growth rates and 95% CI. T_{opt} and r_{max} and their 95% CI are shown in blue shaded boxes. B) Exponential growth rates under thermally fluctuating conditions (±5°C); dashed curve is predicted based on panel A and Equation 1, green line is the fitted thermal performance curve, green shading corresponds to 95% CI generated from parametric bootstrapping. Green points and error bars are observed mean growth rates in the fluctuating temperature regime and 95% CI. T_{opt} and r_{max} in constant conditions and their 95% CI are shown in blue shaded boxes, $\bar{r}_{max}$ and $\bar{T}_{opt}$ in variable conditions and their 95% CI are shown in the green shaded boxes. Predictions from Equation 1 and associated 95% CI are shown in black dashed lines.

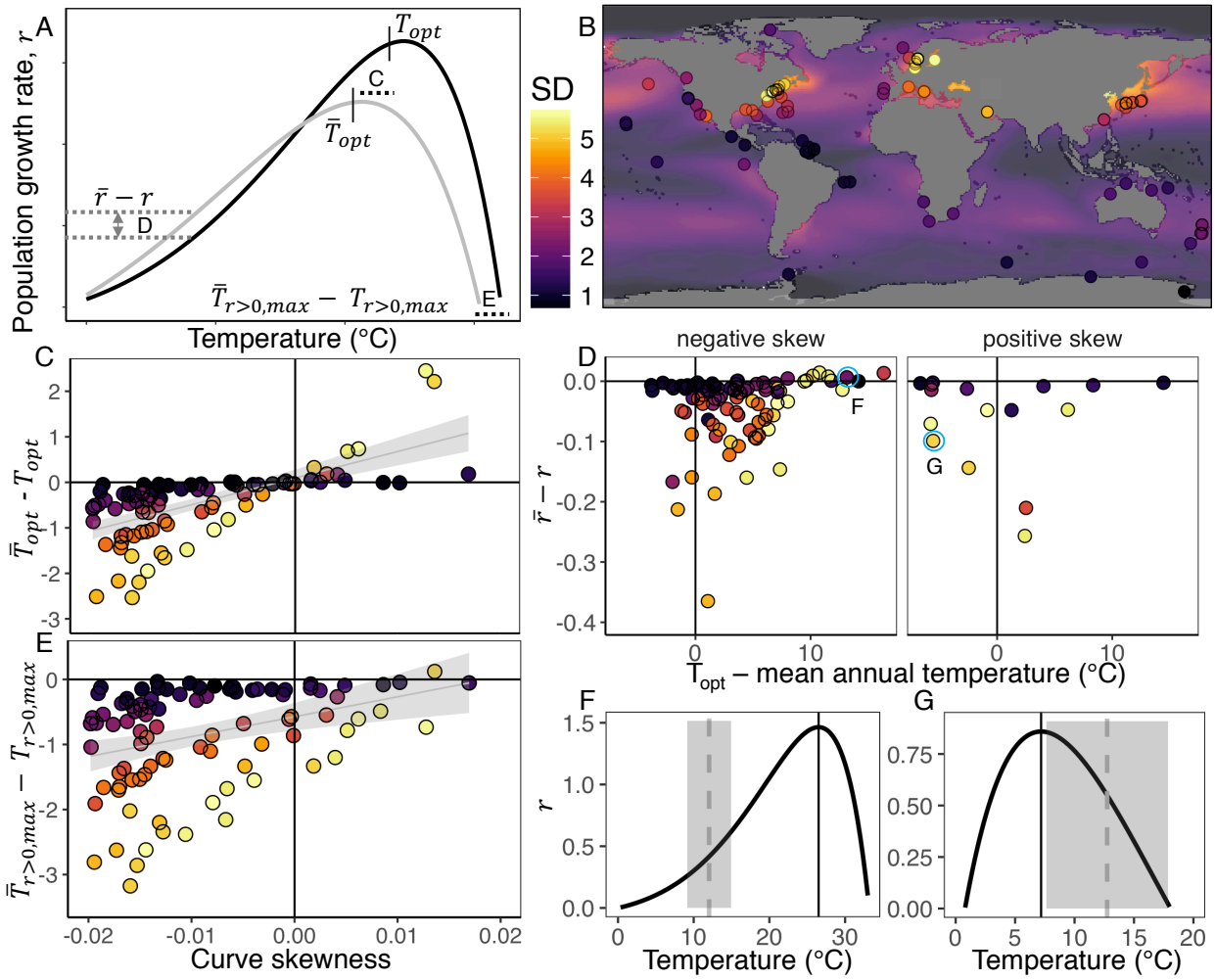


Figure 3. Curve skew and environmental variability predict differences between performance under constant and variable conditions. A) Diagram showing predicted differences in key features of a thermal performance curve under constant (black line) and variable (grey line) environmental conditions. The distance labeled "C", which refers to the difference between $\bar{T}_{opt}$ and T_{opt}, corresponds to the data plotted in panel C of this figure, while the distance labeled "D", i.e. $\bar{r} - r$, refers to the predicted difference between growth rates calculated from a TPC based on constant conditions vs. a TPC based on variable *in situ* conditions, plotted in panel D, and the distance labeled "E" refers to the difference between $\bar{T}_{r>0,max}$ and $T_{r>0,max}$ and

corresponds to the data plotted in panel E of this figure. B) Map of all phytoplankton isolation locations used in the analysis. The color of the ocean and the points corresponds to standard deviation of monthly sea surface temperatures over the time period 1986-2005 (Smith *et al.* 2008). C) The difference between predicted increase $\bar{T}_{opt}$ and T_{opt} generated under constant lab conditions; color coding as in B. D) Predicted differences in phytoplankton growth rates that do not incorporate *in situ* temperature variation (*r*) vs. predicted growth rates based on Equation 1. Blue circles highlight two species shown for illustrative purposes in panels F and G; color coding as in B. E) The difference between $\bar{T}_{r>0,max}$ and $T_{r>0,max}$; color coding as in B. F) Example TPC for *Thalassiosia pseudonana* which shows a negative skew. Mean monthly temperature at the isolation location for this species is shown in the vertical grey dashed line, T_{opt} in the vertical black line, and the monthly SD is shown in the grey shaded region. G) Example TPC for a species with a positive skew TPC, *Detonula confervacea*; vertical lines and shading as in F.