Evolution of thermal performance curves: a meta-analysis of selection experiments

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Abstract

Temperatures are set to increase significantly due to global changes, putting biodiversity at increased risk. Organisms are faced with a limited set of options to cope with this situation: adapt, disperse or die. We here focus on the first possibility, and, more specifically, on evolutionary adaptations to increased temperatures. Organisms are usually characterized by a hump-shaped relationship between fitness and temperature, a non-linear reaction norm that is referred to as the thermal performance curve (TPC). To understand and predict impacts of global change on biodiversity, we need to know whether and how such TPCs evolve.

Therefore, we performed a systematic literature search and a statistical meta-analysis focusing on experimental evolution and artificial selection studies. This focus allows us to quantify relative fitness responses to temperature selection.

Out of 7561 publications screened, we found 47 studies corrsponding to our search criteria representing taxa across the tree of life, from bacteria, to plants and vertebrates. We show that, independently of phylogeny, the studies we found report a clear positive response to temperature selection. Considering entire TPCs, we find that adaptation to higher temperatures trades off with fitness at lower temperatures, leading to niche shifts. By contrast, we do not find statistical support for the often discussed "Hotter is better" hypothesis.

While our meta-analysis provides evidence for adaptive potential of TPCs across a wide range of organisms, our focus on experimental evolution and artificial selection studies highlights that more experimental work is needed, especially for under-represented taxa, such as plants and non-model systems.

Introduction

Human-induced global increases in temperature have been responsible for, and projected to cause, large-scale global extinctions of species (Sinervo *et al.*, 2010), range shifts (Parmesan, 2006; Root *et al.*, 2003), and changes in the composition and dynamics of biological communities (Walther *et al.*, 2002). This situation is likely to get worse in the near future, since, according to the 2021 IPCC report, global temperatures will increase by 4.4 °C until the end of the century (Masson-Delmotte *et al.*, 2021). In order to understand the impacts of such temperature increases on ecological systems and generate appropriate model predictions, both ecological and evolutionary consequences of increased temperatures need to be comprehensively understood.

At a small scale, according to metabolic theory of ecology (MTE; Brown *et al.*, 2004b), temperature directly affects the metabolic rates of organisms. Within a restricted range of temperatures specific to a focal organism, metabolism is thought to scale exponentially with increasing temperature. As a consequence, fitness-relevant components of an organism's life-history, especially rates like fecundity, but also developmental time, to name but two examples, may show similar temperature dependence (Gillooly *et al.*, 2001, 2002). These temperature effects may then cascade across levels of complexity, from individuals to populations and communities, and affect population dynamics, trophic interactions and many other ecological patterns (e.g., Brown *et al.*, 2004a; Uszko *et al.*, 2017).

Such changes in individual performance or fitness as a function of temperature are often referred to as thermal performance curves (TPC) or thermal niches. In general, the niche of an organism, defined as a set of components an organism requires from its environment along with the impact the organism exerts on its environment (Chase & Leibold, 2003), can be used to quantify the fitness response of an organism for a particular environmental requirement. Accordingly, Gvoždík (2018) defines the TPC as the range of body temperatures of ectothermic organisms in which there is positive population growth. The typical shape of the TPC is unimodal, with a gradual increase in fitness as the temperature increases until an optimum is reached beyond which fitness decreases rapidly and reaches the critical thermal limit beyond which growth is not possible (Huey & Kingsolver, 1993). This left skewed response can be explained by the underlying enzyme thermodynamics (Eyring, 1935; Schoolfield *et al.*, 1981; Ratkowsky *et al.*, 2005; DeLong *et al.*, 2017).

While TPCs define how organisms react plastically to temperature, one can imagine that changes in temperature may impact TPCs evolutionarily if TPCs are heritable and enough variation is present for selection to act upon. Indeed, heritability and variation seem to be present as suggested by past research on the evolution of thermal physiology (for an overview see e.g. Angilletta *et al.*, 2010). Based on this existing body of work, evolution in response to increased temperature has been predicted to lead to a

phenomenon termed "Hotter is Better" (Angilletta *et al.*, 2010) which posits that the maximal thermal performance of a genotype increases with temperature. Alternatively, a "Hotter is Wider" pattern has been described (Knies *et al.*, 2009) which implies that genotypes with higher thermal optima may have wider TPCs. In general, the evolution of TPCs may exhibit constraints and trade-offs: as reviewed by Huey & Kingsolver (1993) thermal optima and thermal maxima seem linked but not thermal minima, for example. Other important insights regarding how TPC shapes evolve are discussed in Sexton *et al.* (2017) where the authors argue against the universality of trade-offs and suggest that adaptation can affect TPC width significantly. Most recently, Buckley & Kingsolver (2021) review the evolution of TPCs across a variety of taxa focusing on the importance of realistic environmental variation. The authors highlight that despite clear suggestions of evolutionary potential from experimental studies the evolution of thermal sensitivity seems often constrained which calls for further investigation.

Importantly, a comprehensive understanding of TPCs and their evolution is required for predicting biogeographic responses of species to climate change (Pearman *et al.*, 2008; Banta *et al.*, 2012; Urban *et al.*, 2016; Sinclair *et al.*, 2016). Furthermore, range dynamics and biodiversity maintenance is defined by evolution of TPCs which can significantly interact with other important life-history traits, such as dispersal (Hillaert *et al.*, 2015; Thompson & Fronhofer, 2019). In the context of diseases, the evolution of TPCs of disease vectors critically affects disease prevalence and transmission (Corbin *et al.*, 2017; Cohen *et al.*, 2020; Couper *et al.*, 2021; Hector *et al.*, 2021).

Despite the importance of TPCs and their evolution, past synthesis work has remained narrative which prevents us from having a clear and especially quantitative understanding of thermal adaptation and associated trade-offs or constraints. Therefore, we here carried out a systematic review and meta-analysis of TPC evolution. We focus on experimental studies that report TPCs before and after a selection or experimental evolution experiment. We quantify the relative change in fitness and ask whether there is a consistent evolutionary response to thermal selection across taxa, investigate potential trade-offs and analyse whether aspects such as recombination, the presence of standing genetic variation or number of generations explain evolutionary responses. While our focus on experimental studies restricts the scope of our study somewhat, it allows us to quantify evolutionary changes readily.

In 47 studies retained from a total of 7561 publications screened, reporting experiments on taxa across the tree of life, from bacteria to plants and vertebrates, we show that there is a consistent, positive response to thermal selection. Our analyses show that adaptation to higher temperatures trades off with fitness at lower temperatures, which does not support the "Hotter is wider" hypothesis. Finally, our results do not show a statistically robust signal of "Hotter is better". In addition to this quantitative analysis, we separately discuss work focusing on fluctuating temperature selection, on the interaction between temperature selection and biotic interactions and on thermal evolution in viruses.

Materials and Methods

Systematic literature search

We carried out a systematic literature search using the Web of Science database. We defined a search algorithm that allowed us to find experimental studies that performed selection on TPCs up to and including literature published in 2021 (see Supplementary Material S1 for the search algorithm). We screened the outcome of this search and selected papers that had quantified a TPC of an ancestor or a control, subsequently performed a selection experiment or experimental evolution and finally quantified a TPC after evolution. This allows us to directly compare TPCs before and after evolution. The selected papers had to contain at least one fitness measure like fecundity, population growth rate or another fitness correlate justified by the authors (see Table S1 for an overview of fitness measures used). For simplicity, we did not consider fluctuating temperatures, biotic interactions and viruses in out meta-analysis but report qualitative results. All criteria used for rejecting papers are listed in the Supplementary Material S2 and a flow chart representation of the selection process can be found in the Supplementary Material Fig. S1.

Data extraction

After search, screening and selection we extracted relevant data from the remaining papers, including selection temperatures, assay temperatures and fitness measures. We also recorded the number of generations an experiment lasted, the type of genetic variation used (standing genetic variation vs. de novo variation based on mutations), mode of reproduction (asexual vs. sexual), whether selection was carried out at lower or higher temperatures than the ancestral/ control population and whether the reference was the ancestor or a control treatment. In addition, genus and species of the study organism was recorded, which was used to build a phylogenetic tree with the 'taxize' package version 0.9.99 in R version 4.1.2 and the NCBI database as a reference.

We then extracted the fitness measure as a function of temperature either directly from the papers, their supplementary information, published data associated with the paper, author supplied data or from the graphs. For extracting data from graphs we used the web-based 'WebPlotDigitizer' tool version 4.2 (Drevon *et al.*, 2017; Rohatgi, 2020). An overview of the different methods used for different papers can be found in the Supplementary Material Table S1. This allowed us to broadly classify papers in three categories: First, studies that had selected organisms at a certain temperature and assayed fitness before and after only at this one temperature. Second, studies that include two assay temperature yielding a classical 2-point linear reaction norm. Third, studies that had assayed ancestral/ control populations and evolved populations at more than two temperatures allowing us to study TPC shapes in more detail.

Relative fitness calculation

In order to determine whether and how individual TPCs evolved, we calculated fitness of the derived line relative to the ancestor or control for all assayed temperatures T. Relative fitness was calculated following Chevin (2011). Specifically, for taxa with discrete, non-overlapping generations we calculated relative fitness as $\frac{f_s(T)}{f_a(T)} - 1$ where $f_s(T)$ is fitness of the selected line at temperature T and $f_a(T)$ is the fitness of the ancestor or control line at the same temperature (Eq. 2.5 in Chevin (2011)). For taxa with continuous growth, we calculated relative fitness as $(f_s(T) - f_a(T))\,G$ where G is the generation time (Eq. 3.1 in Chevin (2011); multiplication with generation time allows us to compare studies using different time scales) and for taxa that reproduce by binary fission, we used the approximation $\left(\frac{f_s(T)}{f_a(T)} - 1\right) ln(2)$ (Eq. 3.2 in Chevin (2011)). An overview can be found in the Supplementary Material Table S1.

Relative fitness was calculated using reported means over replicates. In order to take into account the associated uncertainty, we calculated the corresponding standard error (δ) of relative fitness assuming uncorrelated errors which, for non-overlapping generation systems gives $\left(\frac{f_s}{f_a}\right)\sqrt{\left(\frac{\delta_{f_s}}{f_s}\right)^2 + \left(\frac{\delta_{f_a}}{f_a}\right)^2}$. For systems with organisms reproducing by binary fission, the propagated error was calculated in analogy but multiplied with $ln(2)$. For taxa with continuous growth where we did not use the binary fission approximation, the propagated relative fitness error is $\sqrt{\delta_{f_s}^2 + \delta_{f_a}^2}\,G$. If a paper reported standard deviation instead of error we calculated the standard error by dividing the standard deviation with the square-root of the sample size. If confidence intervals were reported we calculated the standard error by dividing the confidence interval with 1.96.

Statistical meta-analysis

The statistical meta-analysis was conducted in R version 4.1.2 using Bayesian linear mixed models that take into account measurement error (for details see Supplementary Material S3). By taking into account measurement error (calculated as described above) we effectively weight the effect sizes (here relative fitness) by study precision (McElreath, 2020, chapter 15). The analyses were performed using the 'rstan' (version 2.21.3) and 'rethinking' (version 2.21) R packages (McElreath, 2020).

We excluded three of the 818 relative fitness measures extracted from a total of 47 selected papers. Two of these three excluded data points were identified as outliers with relative fitness estimates > 20 (overall mean relative fitness: 0.14). The third excluded point had an error estimate of zero and could not be included in the statistical framework used. Of the remaining 815 relative fitness measures, 60 did not report any error measurements and were also excluded.

We conducted four main analyses: First, we asked whether there was an overall direct response to selection by considering fitness assays measured at the same temperature as the selection regime (231

data points). A total of 30 of the 231 TPCs assayed only this condition, whereas the remaining TPCs also tested the evolved organism at different temperatures (two-point and multipoint analysis, see below).

Second, we considered TPCs (122 data points in 61 TPCs) where organisms were assayed at two temperatures before and after selection (Two-point analysis). Here and in the following we will analyse relative fitness as a function of relative assay temperature in order to be able to compare between studies using different selection temperatures. Relative assay temperature is here defined as the difference between assay and selection temperature, positive values indicating an assay temperature above the selection temperature.

Third, we analysed the TPCs (603 data points in 160 TPCs) that contain fitness at three or more assay temperatures before and after selection (Multipoint analysis).

Fourth, for the TPCs that assayed more than three temperature points in the final assay (27 TPCs), we tested the "Hotter is better" hypothesis by taking the maximal fitness value of the selected and control lines to calculate relative fitness.

In all analyses, we analysed the effects of additional explanatory variables identified from the literature that may explain variation in fitness responses. These explanatory variables were: mode of reproduction (asexual vs. sexual), type of genetic variation used (standing genetic variation vs. de novo variation based on mutations) and fitness comparison, that is, whether the reference for relative fitness was the ancestor or a control treatment, as well as the number of generations. Note that not all studies reported the number of generations (or doubling-time periods) an experiment lasted. Therefore, we performed all analyses twice: once with the full data set, not analysing the number of generations and once with a reduced data set including the analysis of the effect of the number of generations.

We compared and ranked all models using the Watanabe-Akaike information criterion (WAIC), a generalised version of the Akaike information criterion (McElreath, 2020). We consistently used a chain length of 30,000 iterations (1,000 warmup iterations) and vaguely informative priors (for details see Supplementary Material S3).

Random effects were 'taxon' (see Fig. 1 and Supplementary Material S1) and 'study ID' in order to take phylogenetic non-independence, as well as within study replication, into account. For the two-point and multipoint analysis we also included 'TPC ID' in order to avoid pooling data from independent TPC measurements.

Finally, publication bias was assessed using funnel plots (see e.g. O'Dea *et al.*, 2021) which indicated no consistent bias (Figs. S2–S5). Detailed statistical methods, including information on priors can be found in the Supplementary Material S3.

Results

From a total of 7561 publications screened, we retained 47 papers which had assayed fitness before and after a thermal selection (see Fig S1). Out of these 47, eight papers had assayed their experimental lines only at the selection temperature, 18 papers examined the evolutionary response at two assay temperatures following a classical, linear reaction norm approach, and 21 papers analysed evolutionary changes in TPC shape in more detail quantifying fitness at three or more temperatures.

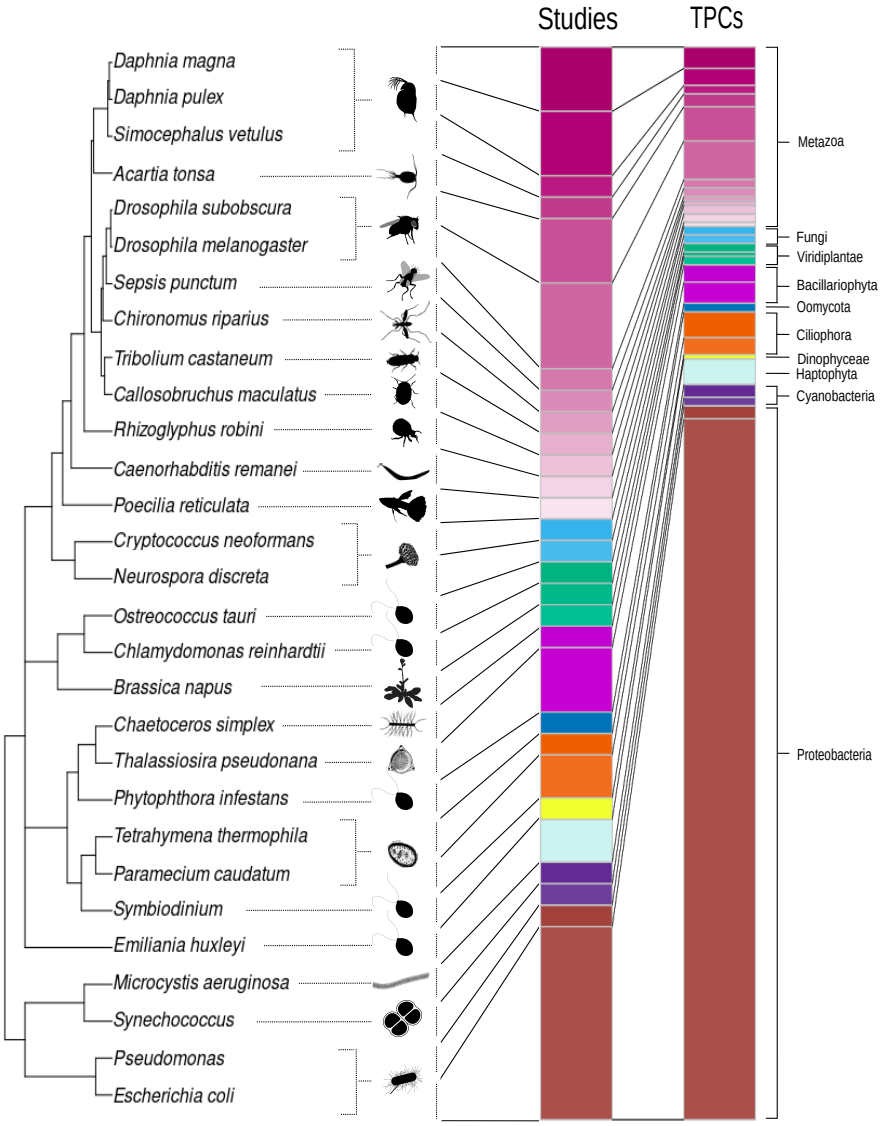

Figure 1: Overview of all the organisms included in the meta-analysis along with taxon as assigned in the statistical analysis represented by different colours. The stacked bars represent the number of studies and the number of TPCs associated with each organism. Quantitative information can be found in Table S2.

Although experiments with established model systems like *Escherichia coli* or *Drosophila* sp. dominated the available literature, we found papers reporting results from species that span the tree of life,

from bacteria to vertebrates (Fig. 1), with a total of 29 species (see Table S2). Note that the total taxonomic breadth was even larger and also included viruses, for example. Studies on viruses, studies including biotic interactions and well as fluctuating temperatures were not included in our meta-analysis, but are discussed qualitatively below.

Fitness response at the selection temperature

In order to evaluate whether there was an overall response to thermal selection, regardless of the taxon and other system-specific details, we analysed the fitness response of populations which were subject to a specific selection temperature at this very same temperature (231 relative fitness estimates; 47 papers). We found an overall positive response to selection across all 10 taxa included in our analysis (Fig. 2A).

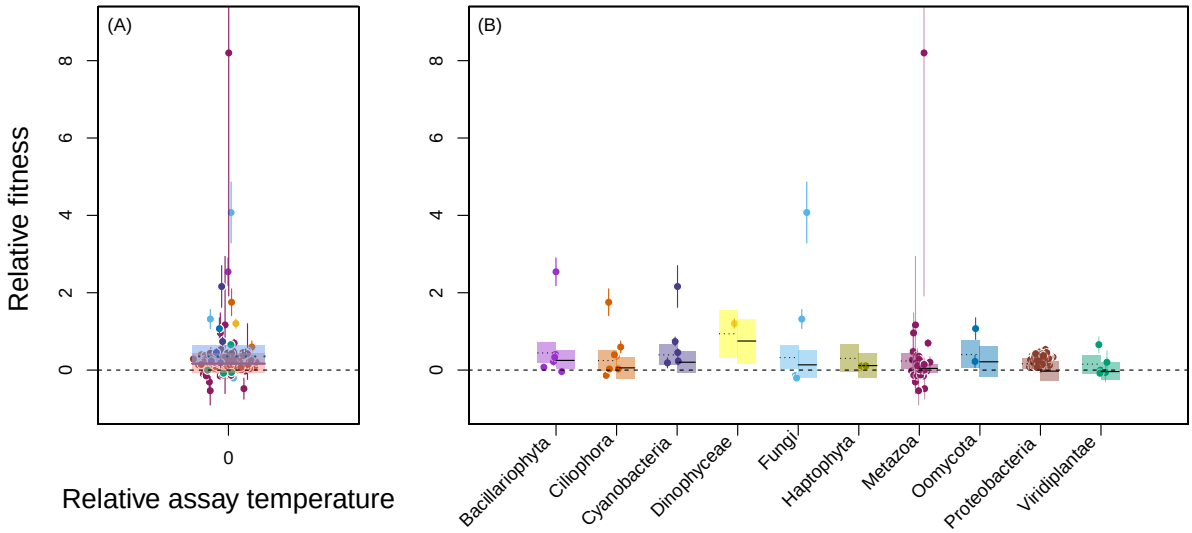

Figure 2: Overall response to thermal selection. (A) Relative fitness, that is, fitness of the selection lines relative to the corresponding control or ancestor assayed at the same temperature as experienced during selection (relative assay temperature of zero). Each point corresponds to one experimental populations (231 experimental units from 47 papers) and the error bars represent the associated standard error. Different colours correspond to different taxa as shown in Fig. 1. Horizontal lines visualize median model predictions and shaded areas are 95% prediction intervals. Here, the best model (Table S7) retains an effect of fitness comparison: relative fitness is higher for studies that compare evolved lines to ancestors (blue) than to controls (red). (B) Visualisation of the 'taxon' random effect, that is, variance explained by the phylogeny. The effect of fitness comparison is shown in the respective left prediction for comparison with an ancestor (dashed line) and in the right prediction for comparison with a control treatment (solid line).

Interestingly, the fitness response was independent of whether selection was for adaptation to increased or decreased temperatures since relative selection temperature (higher, lower or equal to the reference) was not retained (Table S7). Along the same lines, the mode of reproduction (asexual vs. sexual), the type of genetic variation present in the experiment (standing genetic variation vs. de novo variation based on mutations) and the number of generations an experiment lasted were not retained after model

selection (Tables S7 and S8). The best model, however, included an effect of fitness comparison, that is, whether relative fitness was calculated in comparison to an ancestor or to a control treatment (Table S7). Fitness comparisons with an ancestor overall yielded a stronger response to selection than a comparison with a control. These results hold qualitatively across all taxonomic groups considered (Fig. 2B).

Linear thermal reaction norms

Often, thermal selection experiments do not only assay fitness at the same temperature as selection was performed, but also add a different temperature to their assay in order to infer costs of adaptation and trade-offs, for example. Considering these papers (122 data points in 61 TPCs from 18 papers), we did not find any consistent response to selection (Fig. 3, Table S9), in contrast to the results reported in Fig. 2. None of the additional explanatory variables was retained in any of the analyses (Tables S9 and S10).

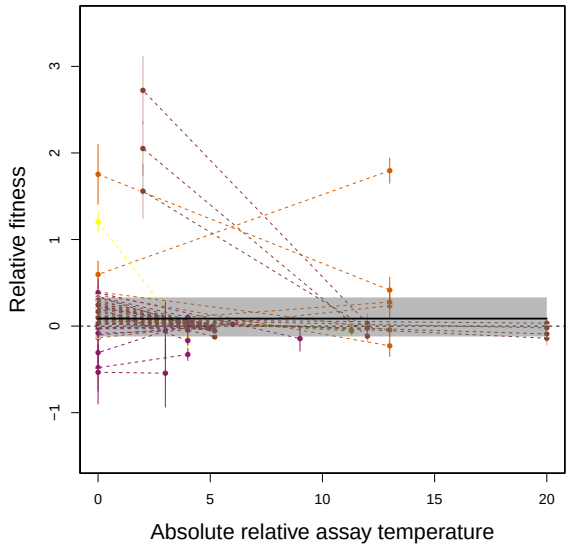

Figure 3: Response to selection in experiments with two assay temperatures. The plot shows relative fitness as a function of absolute relative assay temperature, that is, the absolute difference between selection and assay temperature. Each combination of two points connected by a dashed line corresponds to one TPC (reaction norm; 122 data points in 61 TPCs from 18 papers) and the error bars represent the associated standard error. Different colours correspond to different taxa as shown in Fig. 1. The horizontal lines visualizes the median model prediction and the shaded area is the 95% prediction interval. Here, the best model (Table S9) is the null model and the prediction interval overlaps consistently with 0, indicating no effect of selection.

Evolution of the TPC

Studies that included more than two assay temperatures (603 data points in 160 TPCs from 21 papers) showed a differed picture than their two-point counterparts (Fig. 4). The best fitting model retained a non-linear, cubic relationship between relative fitness and relative assay temperature (Table S11 and S12). While this specific shape should not be interpreted in any mechanistic sense, it allows us to show that while fitness is gained at and beyond the selection temperature (the 95% prediction interval does not overlap the zero line; see inset of Fig. 4), fitness is on average lost below the selection temperature (Fig. 4). In addition, our analysis retained an effect of fitness comparison (ancestor vs. control; Table S12 and S13; interaction between the linear temperature term and fitness comparison) in analogy to the overall fitness response shown in Fig. 2. Fitness gains at and above the selection temperature as well as fitness losses below the selection temperature were larger when fitness of evolved lines was compared to an ancestor vs. to a control treatment (Fig. 4).

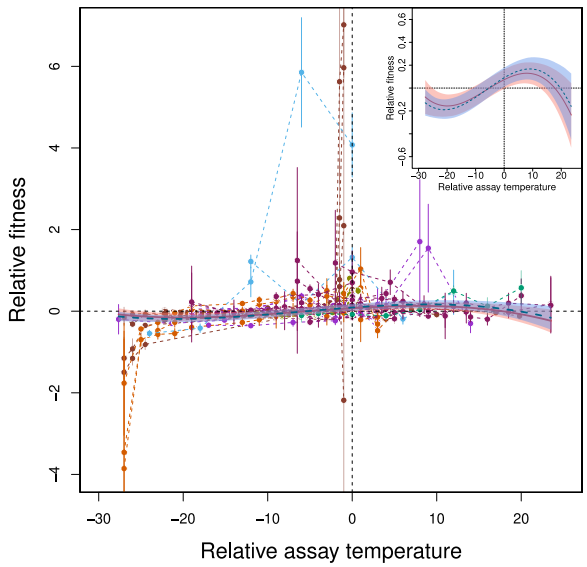

Figure 4: Evolution of the TPC. The plot shows relative fitness as a function of relative assay temperature, that is, the difference between selection and assay temperature, for studies that assayed selected lines at three and more temperatures allowing us to infer changes in TPC shape. Each combination of points connected by a dashed line corresponds to one TPC and the error bars represent the associated standard error (603 data points in 160 TPCs from 21 papers). Different colours correspond to different taxa as shown in Fig. 1. The solid lines visualize the median model predictions and the shaded areas are the 95% prediction interval. Here, the best model (Tables S12 and S13) is a cubic model model that includes an effect of fitness comparison (ancestor vs. control; represented in blue and red, respectively). The inset shows only the statistical model prediction for better visibility of the prediction intervals. Generally, fitness tends to be gained at the selection temperature and slightly above and lost below the selection temperature and for very high temperatures.

Is hotter better?

Finally, for the TPCs that assayed more than three temperature points, we tested the "Hotter is better" hypothesis by taking the maximal fitness value of the selected and ancestor/ control lines to calculate relative fitness (27 data points from 11 papers). If the "Hotter is better" hypothesis is true, relative fitness should be positive when comparing the warm-evolved TPC to the cold-evolved TPC. As visible in Fig. 5, while there is a trend in the right direction, given our dataset, we cannot confirm the "Hotter is better" hypothesis. Other explanatory variables were not retained after model selection (Tables S14 and S15).

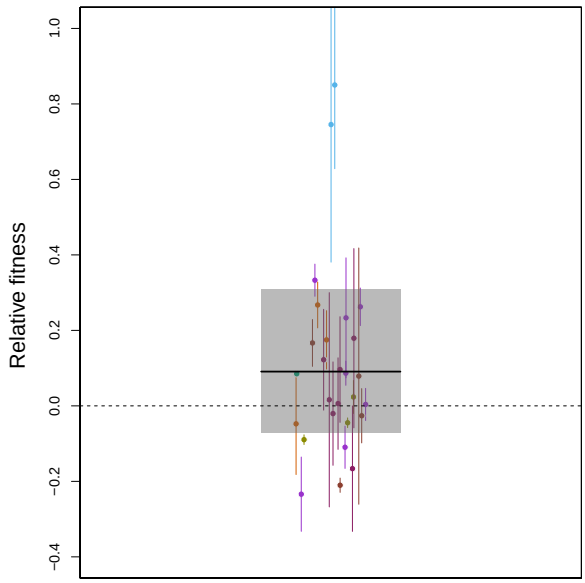

Figure 5: Evaluation of the "Hotter is better" hypothesis. The plot shows relative fitness taking the maximal fitness value of the selected and ancestor/ control lines. Each points corresponds to one comparison and the error bars represent the associated standard error (27 data points from 11 papers). Different colours correspond to different taxa as shown in Fig. 1. The solid line visualizes the median model prediction and the shaded area is the 95% prediction interval.

Discussion

Our systematic literature review yielded a relatively small number of studies (47 in total) that have investigated the evolution of TPCs experimentally. While the studies covered a relatively wide range of organisms, from bacteria to plants and vertebrates (Fig. 1), a large proportion of selection experiments has been carried out on classical model organisms like *E. coli* and *Drosophila* sp. (see also Kellermann & van Heerwaarden, 2019).

Clearly, when interpreting our results one must keep in mind that we here focus on artificial selection

and experimental evolution studies and do not include field-based comparative studies that are much more abundant and have, for instance, very recently been discussed by Buckley & Kingsolver (2021). Of course, our focus on experimental studies allows us to quantify evolutionary changes more readily.

Thermal selection leads to a consistent, positive response across taxa

Quantifying the changes in fitness due to thermal selection overall and specifically at the respective selection temperature applied in each study, we find that, across all taxa, there was a clear and positive response to selection (Fig. 2). While one could envision that the response to selection would be modulated by factors impacting evolutionary potential (for example, number of generations, genetic variation, recombination) none of these factors was retained in our analysis after accounting for phylogeny.

The only retained effect raises a rather technical aspect, that is, whether fitness comparisons were done with an ancestor or with a control. Overall, comparisons with controls showed weaker effects (Fig. 2), which we interpret as a signal that this comparison accounts for standard laboratory selection on growth, for example, due to the specific experimental setup, which is not accounted for when comparing selection outcomes to an ancestor.

These results are encouraging, especially in the light of global changes (Masson-Delmotte *et al.*, 2021), since they indicate that a rather diverse set of species may respond evolutionarily to increased thermal stress. Of course, we here cannot analyse the speed of the evolutionary response which is a central point when populations have to adapt to potentially rapid environmental change. This is important, because evolutionary changes and adaptation to thermal stress may lead to monopolization and actually prevent interacting species from tracking environmental change, resulting in overall loss of biodiversity, as predicted theoretically by Thompson & Fronhofer (2019).

A cautious interpretation of these selection experiments is also warranted because natural systems are obviously more complex than laboratory populations (but see Buckley & Kingsolver, 2021). Specifically, the studies analysed here mainly use fecundity or population growth rate as a measure of fitness (see Table S1) which can be problematic (for a recent discussion, see Kokko, 2021). Fitness is usually multidimensional with different fitness components such as fecundity and viability reacting differently to thermal selection (see e.g., Wadgymar *et al.*, 2017). Under such conditions, where vital rates may trade-off with each other, complex eco-evolutionary feedbacks can be expected under climate change (Cotto *et al.*, 2019).

Caveats of linear reaction norms

Surprisingly, we did not recapture this increase in fitness at the selected temperature when considering studies that had also assay fitness at one additional temperature (Fig. 3). We suggest that this result should not be over-interpreted biologically. Firstly, this part of the meta-analysis has the least power since we only have 61 TPCs from 18 papers with linear reaction norms. Secondly, and most importantly, TPCs are well known to be highly non-linear (discussed in Huey & Kingsolver, 1993, and many others). This suggests that linear reaction norms may not be the most appropriate tool for describing evolutionary responses of a non-linear performance curve. This interpretation gains some weight since we do recapture signals of successful adaptation when analysing data from studies that explore TPC shapes in more detail (Fig. 4).

Thermal adaptation to higher temperatures trades off with fitness at lower temperatures

Analysing responses of better resolved TPCs (here, three and more temperatures assayed; Fig. 4) we recapture very similar results compared to the response to selection at the selection temperature (Fig. 2). We observe a positive response to selection at the selection temperature and the already discussed effect of defining relative fitness in comparison to an ancestor or a control treatment.

While the exact shape of the function we fit here only serves descriptive purposes, it indicates that, overall, after thermal selection, fitness is increased at and beyond the selection temperature. This comes at a fitness cost immediately below the selection temperature and for extreme temperatures. This asymmetry indicates a potential cost of adaptation to higher temperatures that trades off with fitness at lower temperatures. In the context of Huey & Kingsolver (1993), we therefore find evidence for entire TPC shifts rather than changes in TPC width. This findings is in good accordance with recent work by Logan & Cox (2020) who find that species seem to either adapt to shifting means or to variance but not to both. Here, all studies analysed focus on adaptation to constant temperatures. Analogous results of fitness gains at high temperatures associated with losses at low temperatures have also been observed in ants due to urbanisation-related temperature increases (Diamond *et al.*, 2017). The fact that we find adaptation at the selection temperature (Fig. 2) and an increase in performance slightly above (Fig. 4) may hint that TPCs at intermediate temperatures may be more evolvable than suggested by Logan & Cox (2020) who argue that tolerance limits are more readily evolvable based on their review of the literature.

Furthermore, the asymmetry of the response and especially increased fitness beyond the selection temperature (Fig. 4) is in good accordance with Martin & Huey (2008) who argue that due to Jensen's inequality and the asymmetry of the TPC, the maxima of TPCs should be above the experienced tem-

perature.

Limited support for "Hotter is better"

Our data-set also allows us to investigate the "Hotter is Better" hypothesis (Angilletta *et al.*, 2010) by comparing fitness at the respective maxima of TPCs before and after selection (Fig. 5). Overall, we did not obtain any strong response supporting "Hotter is Better" although the data indicate a trend in the right direction. This result should not be over-interpreted as the analysis is rather under-powered with only 27 data points from 11 papers.

Thermal adaptation in plants

In our systematic search, we only found one study on plants (*Brassica napus*). This lack of studies on plants is in line with recent work by Lancaster & Humphreys (2020) who discuss how limited knowledge is available on thermal niches in plants. Lancaster & Humphreys (2020) provide a major database of thermal tolerance in plants and highlight that macrophysiological rules developed in animals seem to also hold in plants.

Of course, this absence of studies may not be very surprising, especially when considering that some vascular plants and trees have long generation times, and, therefore, genetic adaptation may be expected to be slow. Instead, these long-lived organisms may cope with increasing temperatures via phenotypic plasticity. Plasticity allows for rapid responses to the variable environmental conditions experienced by trees during their long lifespan, and will likely represent their first responses to climate changes (Savolainen *et al.*, 2004; Chevin *et al.*, 2013; Franks *et al.*, 2014). However, such responses may not be rapid enough or adaptive for all species (Duputié *et al.*, 2015), and more investigations are clearly needed.

Thermal adaptation in viruses

In the above presented meta-analysis we chose to exclude viruses because of their unique obligate parasitic strategy which hijacks the cellular DNA or RNA replication machinery of the host (Ryu, 2017). Therefore their efficiency of replication would have to be at least partially dependent on the metabolic effects of temperature on the host enzymes along with its own potential adaptations to a given temperature. Nevertheless, researchers have addressed a range of important questions in evolutionary biology, and thermal adaptation more specifically, using viruses as model systems.

Arribas *et al.* (2014), for example, observed convergent evolution across different temperature selection regimes. In fluctuating temperature selection regimes, these authors report that adaptation occurs to the most stressful temperature in the range of selection temperatures. At the same time, Hao *et al.* (2015)

show that fluctuating temperatures may make evolutionary rescue more difficult.

At a more mechanistic level, Betancourt (2009) studied mutations occurring during temperature adaptation and concluded that early emerging mutations had the largest effect on the adaptation to higher temperatures. Poon & Chao (2004) established the increased importance of recombination as populations face genetic drift due to extremely small population sizes when challenged with adaptation to increasing temperature. They used viruses which are able to exchange genetic materials when multiple viruses infect a single host cell.

Temperature adaptation can also have correlated effects in viruses: Carratala *et al.* (2020) show that with adaptation to higher temperatures, viruses also evolved to handle stress induced by free chlorine, making it difficult to eliminate disease-causing viruses in wastewater-treatment plants, for example. With the use of heat shocks, Domingo-Calap *et al.* (2010) demonstrated that populations of viruses which adapted to higher temperatures also showed higher mutational robustness in the presence of mutation inducing chemicals like nitrous acid.

Finally, Knies *et al.* (2009) and Knies *et al.* (2006) addressed the phenomena of "Hotter is better" and "Hotter is wider" by the use of both experimentally and naturally evolved high temperature populations and successfully validated these phenomena in viruses. All of these studies highlight that also viruses can adapt to changing temperatures readily.

Adaptation to fluctuating temperatures

In our analysis, we have only considered evolutionary responses to constant selection temperatures, but experiments with fluctuating temperature regimes have been performed earlier-on. For example, Bennett *et al.* (1992) have used *Escherichia coli* in an experiment including intergenerational fluctuations between high and low temperatures and showed that the bacteria evolved reduced variability for fitness when assayed across a range of temperatures after selection compared to the thermal specialists evolved at specific constant temperatures. In a further experiment, Lenski & Bennett (1993) showed that even though *E. coli* was selected at fluctuating temperatures, lines adapted asymmetrically more to high than to low temperatures.

In contrast, populations of the ciliate *Paramecium caudatum* facing random daily fluctuations between high and low temperatures exhibited the evolution of a superior generalist which performed better or at least as well as the high and low temperature specialist populations (Duncan *et al.*, 2011). Similar results have been reported by Ketola *et al.* (2013) for the bacterium *Serratia marcescens*. *S. marcescens* temperature generalists also exhibited exaptation to novel environments and stresses at the cost of characteristics like invasiveness and virulence. An increasing amplitude of fluctuation in temperatures can also lead to the evolution of increased temperature optima and maximal growth rates (Bonnefond *et al.*,

2017).

However, using the dung fly *Sepsis punctum*, Berger *et al.* (2014) failed to evolve a superior generalist even though they included an intra- and intergenerational temperature fluctuation selection treatment. These authors also did not find any increase in the breadth of the TPC even though these populations showed an overall reduction in maximum fitness compared to the constant temperature selection lines. The results of the intragenerational fluctuation treatment supported the "Hotter is better" hypothesis. In addition, evolution of compensatory mechanisms like heat shock proteins and their expression levels may mask effects of fluctuating temperatures: Ketola *et al.* (2004) showed in the ciliate *Tetrahymena thermophila* that the expression of heat shock protein was highest in rapidly fluctuating environments.

The large variation between the responses to fluctuating temperature selection observed across systems may be due to an erroneous measurement of fitness: Generally, fitness of such populations is assayed at a constant temperatures, however, Ketola & Saarinen (2015) argue that here fitness should be assayed in a fluctuating environmental. Accordingly, Saarinen *et al.* (2018) showed for nine bacterial species that were selected in fluctuating temperatures, that they achieved higher yields when assayed in a fluctuating temperature assay compared to constant conditions.

Thermal adaptation and biotic interactions

In nature, adaptation to temperature will most likely be taking place in the presence of biotic interactions. Focusing in intra-specific competition, Van Doorslaer *et al.* (2009) exposed *Daphnia magna* populations to varying culling regimes, that is, different levels of intraspecific competition, while applying a thermal selection treatment simultaneously. Populations issued from a harsher culling regime had an overall higher performance at both the low and high assay temperatures when selected at high temperature, compared to populations which experienced milder culling regimes.

Similarly, the presence of a predator can also drastically affect the outcome of thermal selection (Tseng & O'Connor, 2015; Tseng *et al.*, 2019). Using *Daphnia pulex*, Tseng & O'Connor (2015) reported that selection at high temperatures only led to increased population growth rates in the presence of a predator. The presence of a predator additionally led to increased TPC width. Effects on thermal plasticity could also be mediated by bottom-up effects linked to the thermal evolution background of resources (Tseng *et al.*, 2019).

Biotic interactions may also lead to events of exaptation where adaptation to high temperatures beyond the existing thermal niche can take place without even actively selecting for that particular high temperature. Zhou *et al.* (2019) report that when the yeast *Lachancea thermotolerans* was co-cultured with bacteria, an increase in thermotolerance was observed. Similarly, Alto & Turner (2009) showed that vesicular stomatitis virus adaptation to different hosts exhibited different TPCs: Viruses which were host

generalists had a narrower TPC than viruses which were host specialists. The authors attribute this difference to the loss of thermal stability of viral genes and pleiotropic effects between viral genes for thermal adaptation, when adapting to a variety of hosts. In contrast, coevolution between a host and a bacteriophage reduced thermal adaptation in the phage (Zhang & Buckling, 2011).

In summary, biotic interactions affect the evolutionary trajectories of thermal adaptation. Be it intraspecific competition, antagonistic biotic interactions like predation or antagonistic coevolution, they change the impact of temperature stress on the temperature selected organism, either acceleration and delaying adaptation.

Conclusions

In conclusion, our results clearly show that thermal performance curves (TPCs), across the tree of life, have the potential to evolve in response to temperature selection and not only thermal limits (Logan & Cox, 2020). Our analyses indicate that thermal adaptation leads to overall niche shifts and that adaptation to higher temperature trades off with fitness at lower temperature. Clearly, these results apply strictly speaking to laboratory systems and, in nature, biotic interactions and fluctuating temperatures may modulate the picture (Buckley & Kingsolver, 2021; Kellermann & van Heerwaarden, 2019).

We found only one paper which contained a temperature selection experiment with plants which aligns well with the conclusion of Lancaster & Humphreys (2020) that knowledge about TPCs in plants remains very limited. This raises the question whether the general patterns of temperature adaptation discussed above hold in vascular plants other than algae and unicellular photosynthesizing organisms that are represented here. Along similar lines, experiments on larger organisms and ecologically impactful taxa such as marine plankton (Collins *et al.*, 2020) remain a minority which critically reduces our ability to infer responses to global warming (see also Sinclair *et al.*, 2016). While our work shows that the existing observed responses to thermal selection are encouraging, it is also clear that a larger taxonomic diversity needs to be included in temperature selection experiments in the future.

Author contributions

E.A.F. and S.P.M. conceived the study. S.P.M. gathered the data. G.Z. performed the statistical analyses. S.P.M. and E.A.F. wrote the manuscript and all authors commented on the draft.

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Code and Data availability

Data and R-code for the meta-analysis are available from XXX.

References

Alto, B. & Turner, P. 2009. Consequences of host adaptation for performance of vesicular stomatitis virus in novel thermal environments. *Evol. Ecol.* **24**: 299–315.

Angilletta, M., Huey, R. & Frazier, M. 2010. Thermodynamic Effects on Organismal Performance: Is Hotter Better? *Physiol. Biochem. Zool.* **83**: 197–206.

Arribas, M., Kubota, K., Cabanillas, L. & Lazaro, E. 2014. Adaptation to Fluctuating Temperatures in an RNA Virus Is Driven by the Most Stringent Selective Pressure. *PLoS One* **9**: e100940.

Banta, J., Ehrenreich, I., Gerard, S., Chou, L., Wilczek, A., Schmitt, J., Kover, P. & Purugganan, M. 2012. Climate envelope modelling reveals intraspecific relationships among flowering phenology, niche breadth and potential range size in *Arabidopsis thaliana*. *Ecol. Lett.* **15**: 769–77.

Bennett, A., Lenski, R. & Mittler, J. 1992. Evolutionary adaptation to temperature. I. Fitness responses of *Escherichia coli* to changes in its thermal environment. *Evolution* **46**: 16–30.

Berger, D., Walters, R.J. & Blanckenhorn, W.U. 2014. Experimental evolution for generalists and specialists reveals multivariate genetic constraints on thermal reaction norms. *J. Evol. Biol.* **27**: 1975–1989.

Betancourt, A. 2009. Genomewide Patterns of Substitution in Adaptively Evolving Populations of the RNA Bacteriophage MS2. *Genetics* **181**: 1535–1544.

Bonnefond, H., Grimaud, G., Rumin, J., Bougaran, G., Talec, A., Gachelin, M., Boutoute, M., Pruvost, E., Bernard, O. & Sciandra, A. 2017. Continuous selection pressure to improve temperature acclimation of *Tisochrysis lutea*. *PLoS One* **12**: e0183547.

Brown, I.M., Wharton, D.A. & Millar, R.B. 2004a. The influence of temperature on the life history of the Antarctic nematode *Panagrolaimus davidi*. *Nematology* **6**: 883–890.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. 2004b. Toward a metabolic theory of ecology. *Ecology* **85**: 1771–1789.

Buckley, L.B. & Kingsolver, J.G. 2021. Evolution of thermal sensitivity in changing and variable climates. *Annu. Rev. Ecol. Evol. Syst.* **52**: 563–586.

Carratala, A., Bachmann, V., Julian, T. & Kohn, T. 2020. Adaptation of Human Enterovirus to Warm Environments Leads to Resistance against Chlorine Disinfection. *Environ. Sci. Technol.* **54**: 11292–11300.

Chase, J.M. & Leibold, M.A. 2003. *Ecological Niches: Linking Classical and Contemporary Approaches.* University of Chicago Press.

Chevin, L.M. 2011. On measuring selection in experimental evolution. *Biol. Lett.* **7**: 210–213.

Chevin, L.M., Collins, S. & Lefèvre, F. 2013. Phenotypic plasticity and evolutionary demographic responses to climate change: taking theory out to the field. *Funct. Ecol.* **27**: 967–979.

Cohen, J.M., Sauer, E.L., Santiago, O., Spencer, S. & Rohr, J.R. 2020. Divergent impacts of warming weather on wildlife disease risk across climates. *Science* **370**: eabb1702.

Collins, S., Boyd, P.W. & Doblin, M.A. 2020. Evolution, microbes, and changing ocean conditions. *Annu. Rev. Mar. Sci.* **12**: 181–208.

Corbin, C., Heyworth, E.R., Ferrari, J. & Hurst, G.D.D. 2017. Heritable symbionts in a world of varying temperature. *Heredity* **118**: 10–20.

Cotto, O., Sandell, L., Chevin, L.M. & Ronce, O. 2019. Maladaptive shifts in life history in a changing environment. *Am. Nat.* **194**: 558–573.

Couper, L.I., Farner, J.E., Caldwell, J.M., Childs, M.L., Harris, M.J., Kirk, D.G., Nova, N., Shocket, M., Skinner, E.B., Uricchio, L.H., Exposito-Alonso, M. & Mordecai, E.A. 2021. How will mosquitoes adapt to climate warming? *eLife* **10**: e69630.

DeLong, J.P., Gibert, J.P., Luhring, T.M., Bachman, G., Reed, B., Neyer, A. & Montooth, K.L. 2017. The combined effects of reactant kinetics and enzyme stability explain the temperature dependence of metabolic rates. *Ecol. Evol.* **7**: 3940–3950.

Diamond, S.E., Chick, L., Perez, A., Strickler, S.A. & Martin, R.A. 2017. Rapid evolution of ant thermal tolerance across an urban-rural temperature cline. *Biol. J. Linnean Soc.* **121**: 248–257.

Domingo-Calap, P., Pereira-Gomez, M. & Sanjuan, R. 2010. Selection for thermostability can lead to the emergence of mutational robustness in an RNA virus. *J. Evol. Biol.* **23**: 2453–2460.

Drevon, D., Fursa, S.R. & Malcolm, A.L. 2017. Intercoder Reliability and Validity of WebPlotDigitizer in Extracting Graphed Data. *Behav. Modif.* **41**: 323–339.

Duncan, A.B., Fellous, S. & Kaltz, O. 2011. Temporal variation in temperature determines disease spread and maintenance in paramecium microcosm populations. *Proc. R. Soc. B-Biol. Sci.* **278**: 3412–3420, URL `http://dx.doi.org/10.1098/rspb.2011.0287`.

Duputié, A., Rutschmann, A., Ronce, O. & Chuine, I. 2015. Phenological plasticity will not help all species adapt to climate change. *Glob. Change Biol.* **21**: 3062–3073.

Eyring, H. 1935. The Activated Complex in Chemical Reactions. *J. Chem. Phys.* **3**: 107–115.

Franks, S.J., Weber, J.J. & Aitken, S.N. 2014. Evolutionary and plastic responses to climate change in terrestrial plant populations. *Evol. Appl.* **7**: 123–139.

Gillooly, J.F., Brown, J.H., West, G.B., Savage, V.M. & Charnov, E.L. 2001. Effects of size and temperature on metabolic rate. *Science* **293**: 2248–2251.

Gillooly, J.F., Charnov, E.L., West, G.B., Savage, V.M. & Brown, J.H. 2002. Effects of size and temperature ondevelopmental time. *Nature* **417**: 70–73.

Gvoždík, L. 2018. Just what is the thermal niche? *Oikos* **127**: 1701–1710.

Hao, Y.Q., Brockhurst, M.A., Petchey, O.L. & Zhang, Q.G. 2015. Evolutionary rescue can be impeded by temporary environmental amelioration. *Ecol. Lett.* **18**: 892–898.

Hector, T.E., Sgrò, C.M. & Hall, M.D. 2021. Thermal limits in the face of infectious disease: How important are pathogens? *Glob. Change Biol.* **27**: 4469–4480.

Hillaert, J., Boeye, J., Stoks, R. & Bonte, D. 2015. The evolution of thermal performance can constrain dispersal during range shifting. *J. Biol. Dyn.* **9**: 317–335.

Huey, R. & Kingsolver, J. 1993. Evolution of Resistance to High-Temperature in Ectotherms. *Am. Nat.* **142**: S21–S46.

Kellermann, V. & van Heerwaarden, B. 2019. Terrestrial insects and climate change: adaptiveresponses in key traits. *Physiol. Entomol.* **44**: 99–115.

Ketola, T., Laakso, J., Kaitala, V. & Airaksinen, S. 2004. Evolution of Hsp90 expression in *Tetrahymena thermophila* (Protozoa, Ciliata) populations exposed to thermally variable environments. *Evolution* **58**: 741–748.

Ketola, T., Mikonranta, L., Zhang, J., Saarinen, K., Örmälä, A.M., Friman, V.P., Mappes, J. & Laakso, J. 2013. Fluctuating Temperature Leads to Evolution of Thermal Generalism and Preadaptation to Novel Environments. *Evolution* **67**: 2936–2944.

Ketola, T. & Saarinen, K. 2015. Experimental evolution in fluctuating environments: tolerance measurements at constant temperatures incorrectly predict the ability to tolerate fluctuating temperatures. *J. Evol. Biol.* **28**: 800–806.

Knies, J., Kingsolver, J. & Burch, C. 2009. Hotter Is Better and Broader: Thermal Sensitivity of Fitness in a Population of Bacteriophages. *Am. Nat.* **173**: 419–430.

Knies, J.L., Izem, R., Supler, K.L., Kingsolver, J.G. & Burch, C.L. 2006. The Genetic Basis of Thermal Reaction Norm Evolution in Lab and Natural Phage Populations. *PLoS Biol.* **4**: e201.

Kokko, H. 2021. The stagnation paradox: the ever-improving but (more or less) stationary population fitness. *Proc. R. Soc. B-Biol. Sci.* **288**: 20212145.

Lancaster, L.T. & Humphreys, A.M. 2020. Global variation in the thermal tolerances of plants. *Proc. Natl. Acad. Sci. U. S. A.* **117**: 13580–13587.

Lenski, R. & Bennett, A. 1993. Evolutionary response of *Escherichia coli* to thermal stress. *Am. Nat.* **142**: S47–S64.

Logan, M.L. & Cox, C.L. 2020. Genetic constraints, transcriptome plasticity, and the evolutionary response to climate change. *Front. Genet.* **11**.

Martin, T. & Huey, R. 2008. Why "Suboptimal" Is Optimal: Jensen's Inequality and Ectotherm Thermal Preferences. *Am. Nat.* **171**: E102–E118.

Masson-Delmotte, V., Zhai, P., Pirani, A., Connors, S.L., Péan, C., Berger, S., Caud, N., Chen, Y., Goldfarb, L., Gomis, M.I., Huang, M., Leitzell, K., Lonnoy, E., Matthews, J.B.R., Maycock, T.K.,

Waterfield, T., Yelekçi, O., Yu, R. & Zhou, B. (eds) 2021. *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change.* Cambridge University Press.

McElreath, R. 2020. *Statistical Rethinking.* Chapman & Hall.

O'Dea, R.E., Lagisz, M., Jennions, M.D., Koricheva, J., Noble, D.W., Parker, T.H., Gurevitch, J., Page, M.J., Stewart, G. & Nakagawa, D.M.S. 2021. Preferred reporting items for systematic reviews and meta-analyses in ecology andevolutionary biology: a PRISMA extension. *Biol. Rev.* **96**: 1695–1722.

Parmesan, C. 2006. Ecological and Evolutionary Responses to Recent Climate Change. *Annu. Rev. Ecol. Evol. Syst.* **37**: 637–669.

Pearman, P.B., Guisan, A., Broennimann, O. & Randin, C.F. 2008. Niche dynamics in space and time. *Trends Ecol. Evol.* **23**: 149–158.

Poon, A. & Chao, L. 2004. Drift increases the advantage of sex in RNA bacteriophage Phi 6. *Genetics* **166**: 19–24.

Ratkowsky, D.A., Olley, J. & Ross, T. 2005. Unifying temperature effects on the growth rate of bacteria and the stability of globular proteins. *J. Theor. Biol.* **233**: 351–362.

Rohatgi, A. 2020. Webplotdigitizer: Version 4.2. URL `https://automeris.io/WebPlotDigitizer`.

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C. & Pounds, J.A. 2003. Fingerprints of global warming on wild animals and plants. *Nature* **421**: 57–60.

Ryu, W.S. 2017. Virus Life Cycle. *Molecular Virology of Human Pathogenic Viruses* pp. 31–45.

Saarinen, K., Laakso, J., Lindstrom, L. & Ketola, T. 2018. Adaptation to fluctuations in temperature by nine species of bacteria. *Ecol. Evol.* **8**: 2901–2910.

Savolainen, O., Bokma, F., García-Gil, R., Komulainen, P. & Repo, T. 2004. Genetic variation in cessation of growth and frost hardiness and consequences for adaptation of *Pinus sylvestris* to climatic changes. *For. Ecol. Manage.* **197**: 79–89.

Schoolfield, R.M., Sharpe, P.J.H. & Magnuson, C.E. 1981. Non-linear regression of biological temperature-dependent rate models based on absolute reaction-rate theory. *J. Theor. Biol.* **88**: 719–731.

Sexton, J.P., Montiel, J., Shay, J.E., Stephens, M.R. & Slatyer, R.A. 2017. Evolution of ecological niche breadth. *Annu. Rev. Ecol. Evol. Syst.* **48**: 183–206.

Sinclair, B.J., Marshall, K.E., Sewell, M.A., Levesque, D.L., Willett, C.S., Slotsbo, S., Dong, Y., Harley, C.D.G., Marshall, D.J., Helmuth, B.S. & Huey, R.B. 2016. Can we predict ectotherm responses to climate change usingthermal performance curves and body temperatures? *Ecol. Lett.* **19**: 1372–1385.

Sinervo, B., Méndez-de-la Cruz, F., Miles, D.B., Heulin, B., Bastiaans, E., Cruz, M.V.S., Lara-Resendiz, R., Martínez-Méndez, N., Calderón-Espinosa, M.L., Meza-Lázaro, R.N., Gadsden, H., Avila, L.J., Morando, M., Riva, I.J.D.l., Sepulveda, P.V., Rocha, C.F.D., Ibargüengoytía, N., Puntriano, C.A., Massot, M., Lepetz, V., Oksanen, T.A., Chapple, D.G., Bauer, A.M., Branch, W.R., Clobert, J. & Sites, J.W. 2010. Erosion of Lizard Diversity by Climate Change and Altered Thermal Niches. *Science* **328**: 894–899.

Thompson, P.L. & Fronhofer, E.A. 2019. The conflict between adaptation and dispersal for maintaining biodiversity in changing environments. *Proc. Natl. Acad. Sci. U. S. A.* **116**: 21061–21067.

Tseng, M., Bernhardt, J.R. & Chila, A.E. 2019. Species interactions mediate thermal evolution. *Evol. Appl.* **12**: 1463–1474.

Tseng, M. & O'Connor, M.I. 2015. Predators modify the evolutionary response of prey to temperature change. *Biol. Lett.* **11**: 20150798.

Urban, M.C., Bocedi, G., Hendry, A.P., Mihoub, J.B., Peer, G., Singer, A., Bridle, J.R., Crozier, L.G., Meester, L.D., Godsoe, W., Gonzalez, A., Hellmann, J.J., Holt, R.D., Huth, A., Johst, K., Krug, C.B., Leadley, P.W., Palmer, S.C.F., Pantel, J.H., Schmitz, A., Zollner, P.A. & Travis, J.M.J. 2016. Improving the forecast for biodiversity under climate change. *Science* **353**: aad8466–1 – aad8466–9.

Uszko, W., Diehl, S., Englund, G. & Amarasekare, P. 2017. Effects of warming on predator-prey interactions — a resource-based approach and a theoretical synthesis. *Ecol. Lett.* **20**: 513–523.

Van Doorslaer, W., Stoks, R., Duvivier, C., Bednarska, A. & De Meester, L. 2009. Population dynamics determine genetic adaptation to temperature in *Daphnia*. *Evolution* **63**: 1867–1878.

Wadgymar, S.M., Daws, S.C. & Anderson, J.T. 2017. Integrating viability and fecundity selection to illuminate the adaptive nature of genetic clines. *Evol. Lett.* **1**: 26–39.

Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.M., Hoegh-Guldberg, O. & Bairlein, F. 2002. Ecological responses to recent climate change. *Nature* **416**: 389–395.

Zhang, Q.G. & Buckling, A. 2011. Antagonistic coevolution limits population persistence of a virus in a thermally deteriorating environment. *Ecol. Lett.* **14**: 282–288.

Zhou, N., Ishchuk, O.P., Knecht, W., Compagno, C. & Piskur, J. 2019. Improvement of thermotolerance in *Lachancea thermotolerans* using a bacterial selection pressure. *J. Ind. Microbiol. Biotechnol.* **46**: 133–145.