

Variation in the rate of phenotypic plasticity among ectotherms

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Abstract

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Variation in the rate of phenotypic plasticity among ectotherms

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Abstract

An individual's fitness cost associated with environmental change depends on the rate of adaptive phenotypic plasticity, and yet our understanding of plasticity rates in an ecological and evolutionary context remains limited. We provide the first quantitative synthesis of existing plasticity rate data, focusing on acclimation of temperature tolerance in ectothermic animals, where we demonstrate applicability of a recently proposed analytical approach. The analyses reveal considerable variation in plasticity rates of this trait among species, with half-times (how long it takes for the initial deviation from the acclimated phenotype to be reduced by 50% when individuals are shifted to a new environment) ranging from 3.7 to 770.2 h. Furthermore, rates differ among higher taxa, being higher for amphibians and reptiles than for crustaceans and fishes, and with insects being intermediate. We argue that a more comprehensive understanding of phenotypic plasticity will be attained through increased focus on the rate parameter.

Introduction

Phenotypic plasticity, or the expression of different phenotypes across environments by a single genotype, is an important process by which organisms can minimize environmental impacts on fitness (Gabriel, 2005; Gabriel, Luttbegg, Sih, & Tollrian, 2005; Padilla & Adolph, 1996; Siljestam & Östman, 2017). Such plasticity can be described by two parameters. First, the capacity for plasticity determines the amount by which the phenotype can change following a shift in the environment. This parameter can be measured as the change in the slope of the relationship between trait value and environment as plasticity proceeds, from acute exposure until the full plastic response has been achieved (see Einum et al. 2019 for arguments why it is this change in the slope, and not slope *per se*, that describes plasticity). Whereas the capacity for plasticity has received considerable theoretical and empirical interest from ecologists and evolutionary biologists, empirical support for certain predictions regarding the evolution of this plasticity parameter remain equivocal. For example, it has been proposed that organisms inhabiting more variable environments should evolve greater plasticity capacities. However, this is rarely supported by empirical data (Gunderson & Stillman, 2015; Kelly, Sanford, & Grosberg, 2012; MacLean et al., 2019; Pereira, Sasaki, & Burton, 2017; Phillips et al., 2016; Sgro et al., 2010; van Heerwaarden, Kellermann, & Sgrò, 2016; van Heerwaarden, Lee, Overgaard, & Sgrò, 2014). Recently, Burton et al. (2022) suggested that this discrepancy gives reason for pause, and that greater considerations of the second parameter, the rate of plasticity, which addresses the timescale over which plastic phenotypic change occurs, might aid in bringing this field of research forward.

If the plasticity of a trait is an adaptive response, the fitness cost that an organism incurs following a change in its environment should be minimized once the phenotype becomes fully adjusted to the new environment. Hence, the rate at which the phenotype approaches this state should determine how long the individual expresses a sub-optimal phenotype, and in part, determine the magnitude of the fitness cost associated with that change in the environment. Given that organisms are unlikely to be able to predict changes in all of the relevant environmental variables they are exposed to, it seems plausible that individuals may actually spend a considerable proportion of their time having a phenotype that is not fully adjusted to their current environment. This mismatch between environment and phenotype, and associated cumulative fitness costs, will be exacerbated if plastic responses are slow relative to the timescale of environmental change. Furthermore, as pointed out by Burton et al. (2022), the rate of plasticity might even influence how the capacity for plasticity evolves, because the evolution of capacity depends on the predictability of the environment. Organisms that can rapidly implement their phenotypic response to a new environment can postpone the onset of this process closer to the time of selection in that environment than organisms that do so at a slower rate. In a temporally autocorrelated environment this would in effect make faster responding organism to more accurately 'predict' the future selective environment at the moment when they have to start adjust their phenotype. Thus, a faster rate of plasticity might effectively increase predictability in the environment, which in turn should favour the evolution of greater phenotypic plasticity capacity (Lande 2014).

Presently, a basic synthesis of plasticity rate data among taxa is lacking, and consideration of how rates of plasticity might be expected to evolve in response to environmental change is absent from current theoretical

models (Lande 2014, Siljestam & Östman 2017). This knowledge gap is mirrored by, and perhaps stems from, a lack of empirical interest in studying the evolution of rates of plasticity. Although a substantial number of empirical studies document how phenotypes change over time when introduced into new environments, these studies remain largely descriptive, fail to address evolutionary hypotheses, and very rarely (four out of 166 studies surveyed by Burton et al. 2022) attempt to provide any formal statistical quantification of the time course of plasticity. Thus, advancing our understanding of the evolution of phenotypic plasticity might arguably benefit from a shift in focus from capacities to rates of plasticity. To stimulate such a shift, we provide the first comparative analysis of published data describing rates of plasticity. In doing so, we follow recent suggestions (Burton et al. 2022) regarding the estimation of plasticity rates in a (i) standardized way, which is (ii) consistent with theory and (iii) directly comparable across taxa and traits.

We draw upon published data from studies of acclimation to temperature among ectotherms. Temperature is an environmental variable that affects all organisms, varies substantially in space and time, and which has particularly pervasive effects on biochemical, physiological and ecological processes in this group of animals (Daufresne et al. 2009). We focus our synthesis on traits describing temperature tolerance. We first determine the shape of how temperature tolerance changes over time (exponential vs. linear decay) in response to a shift in ambient temperature, as this is the first step required when calculating the rate of plasticity. After calculating rates of plasticity for each published dataset, we then investigate relationships between rates of plasticity and taxonomic class, body size, and acclimation temperature. By providing clear evidence that rates of plasticity have diverged among ectotherm classes we show that the rate of plasticity can, and does, evolve, and that increased empirical and theoretical focus on the rate parameter is likely to provide a way forward in understanding evolution of phenotypic plasticity.

Methods

Collection of data

We identified published studies documenting the rate of change in whole-body measurements of thermal tolerance in response to manipulation of ambient temperature. Specifically, we sought to identify papers where the study organisms, having been acclimated to an initial temperature for a given period of time, were transferred to a ‘new’ temperature, after which thermal tolerance was measured on subsamples of these individuals at different points in time. Our search criteria included studies that addressed tolerance of both high and low temperatures and performed measurements of critical temperatures (i.e. CT_{max}, CT_{min}), time to death or immobility, or mortality rate at a stressful temperature. An additional criterion was that measurements of thermal tolerance were made at a minimum of three time points. Using these criteria, relevant papers were identified using the following procedure. First, we included eight papers identified by Burton et al. (2022) that were based on a search in Web of Science (see Burton et al. for procedure). Second, we conducted two searches on Google Scholar during January 2022. In the first search, we used the terms “temperature” and “rate of acclimation”. The 739 hits were sorted based on relevance, and the first 200 abstracts were scanned for inclusion, resulting in a total of 55 papers (none of these appeared among the last 30 scanned abstracts). In the second search, we used the terms “temperature”, “acclimation”, “time course” and “critical”. This resulted in 30200 hits, which also were sorted based on relevance, and where the first 200 abstracts were scanned for inclusion. For this second search, 7 additional papers were identified (the majority of relevant hits had been identified in the initial search). Finally, the reference lists of papers identified above were scanned for reference to additional papers not located in any of the previous searches, resulting in a further 18 papers. Thus, a total of 88 papers were identified during this procedure. For each paper, we determined whether it presented the required data in an accessible form. Fifty-nine of the papers identified above were found to contain suitable data. Many of these contained data from several experiments (different species and/or different acclimation temperatures), and data from a total of 308 acclimation experiments from a total of 114 species were extracted from these papers. For most of the papers, data were presented in figure format only, usually as the mean tolerance of groups of individuals that had experienced the ‘new’ temperature for differing lengths of time prior to being measured for the chosen tolerance trait. We digitized such data using the WebPlotDigitizer (<https://apps.automeris.io/wpd/>). In addition to thermal

tolerance data we extracted information for the following variables: taxonomic class, species name, mean body mass of individuals used in the experiment, and acclimation temperature. For experiments where body mass information was absent we used the following procedure to obtain such data. First, we searched for information on minimum and maximum adult body size (length or mass) for the species in question. If only data on body length were available, we searched for allometries between length and mass for that species, or for species within the same genus, and used these to convert body lengths to mass. We then calculated the mean of the minimum and maximum body mass values. If no data on minimum or maximum size was found, we searched for studies that presented body sizes of adult individuals during field surveys and used the mean of these. Combining body size estimates from each of these sources yielded measurements for 290 of the 308 experiments described above, representing a total of 107 species from the following classes of ectotherms; amphibians, reptiles, insects, osteichthyes and malacostraca. For simplicity the latter two will be referred to as fishes and crustaceans, respectively.

Calculating rates of plasticity

Rates of plasticity were calculated according to the approach outlined by Burton et al. (2022). Thus, for each observation of temperature tolerance at times t we first calculated the proportion of the full plastic response that remained to be achieved, D_t , as $(z_t - z_{[q]}) / (z_0 - z_{[q]})$, where z_0 is the first measurement of the phenotype (typically measured prior to the onset of acclimation), z_t is the phenotype after acclimating for a time period t , and $z_{[q]}$ is the fully adjusted phenotype. In theory, $z_{[q]}$ is the final measurement of thermal tolerance. However, given measurement noise this may not be the case. Thus, we defined $z_{[q]}$ as the maximum (for acclimation to higher temperature) or minimum (for acclimation to lower temperature) value for a given measurement of tolerance observed. For each experiment, we considered two potential responses in plasticity of thermal tolerance. First, D_t may have a value of 1 at $t = 0$ (first measurement) and decline linearly with time with a rate λ_A given by $\lambda_A = (1 - D_t) / t$ until it reaches 0, after which it will be constant. Alternatively, D_t may have a value of 1 at $t = 0$ and decline as an exponential decay function towards 0 with rate λ_E , such that $D_t = e^{-\lambda_E t}$. Thus, for each experiment, we fitted these two types of models to the observed data. For the linear decline we fitted a piecewise regression with an intercept of 1 (at $t = 0$), which estimates the breakpoint b (i.e. the time at which D_t reaches 0), from which the rate λ_A can be calculated as $1/b$. Thus, both models estimate a single parameter, and their relative fits for a given experiment can be compared directly using their residual standard errors. Models were fitted using the function `nls_multstart` from the `nls_multstart` package (Padfield and Matheson 2020).

For most studies, z_0 was measured in individuals prior to transfer to the new temperature. It was often less clear whether experimenters had been able to measure a ‘true’ value of $z_{[q]}$, i.e. thermal tolerance after full acclimation to the new temperature had been obtained. This is a key point when measuring rates of plasticity because estimates of λ_E will be biased if full acclimation to the new environment has not been achieved (Fig. S1). However, an advantage of the exponential decay function is that achievement of full acclimation can be assessed by calculating the slope of the estimated function (i.e. $-\lambda_E e^{\lambda_E t}$) at the final acclimation time point t_n (this slope has an asymptotic value of 0). Thus, this value was included as a covariate in our analysis (see below) to control for any bias introduced by variation in maximum acclimation time among studies.

Statistical analyses

All statistical analyses were conducted in R v.4.1.2 (R Core Team, 2021). Comparisons of exponential and linear decay models showed that the former was superior to the latter in most cases (see Results). Thus, the following statistical analyses use λ_E as the dependent variable.

Inspection of the distribution of standard errors (SE) for estimates of λ_E were used to exclude experiments that had poor model fit for the exponential decline models (Fig. S2). This was based on judgement, trading-off maintaining sample size while avoiding inclusion of potentially biased estimates. Using a threshold SE value of 0.01 enabled us to retain 78% of the experiments ($n = 240$ out of 307). The statistical analyses described below use estimates obtained below this threshold. Increasing the threshold SE value to 0.02 increased inclusion rate to 88% ($n = 271$) without resulting in qualitative changes in the results (Table S1).

The bias in estimated λ_E for experiments with $SE > 0.02$ and within the range 0.01-0.02 can be observed by comparing λ_E in experiments within different SE bins (Fig. S3).

Variation in λ_E among taxonomic classes of ectothermic animals was analysed using linear mixed-effect models, fitted using the function *lme* in the package *nlme* (Pinheiro et al., 2022). The full model contained the fixed effects of class, body mass, acclimation temperature, and slope of the estimated exponential decay function at t_n , whereas species was included as a random effect.

The full model was compared to simplified ones based on AICc values using the function *dredge* from the package *MuMIn* (Barton 2020). For all analyses inspection of residual plots suggested that assumptions of their normality and homogeneity were satisfied.

Results

A total of 290 experiments could be fitted with both piecewise regression and exponential decay models (Fig. S4). The remaining 18 could not be fitted with piecewise regression, which most frequently occurred because the minimum value of D (i.e. complete acclimation) was reached at the second observation, in which case multiple breakpoints can yield an identical fit. Of these 290 experiments, comparisons of residual standard errors from models showed that the data in 62% ($n=180$) of them were best explained by exponential decay models. Furthermore, superior fit by piecewise regressions ($N = 110$ experiments) was observed primarily in experiments where thermal tolerance was measured at relatively few time points following exposure of the study organisms to the new temperature (Fig. S5). Thus, for more comprehensive experiments (i.e. greater number of measurement points in time), the shape of the plasticity rate response is better described by an exponential decay function. Thus, in all further analyses we use the estimates of λ_E (Table S2).

For the data included in the statistical analyses presented here, species-specific mean estimated λ_E was 0.0342 h^{-1} . The variation in estimated mean λ_E across species was considerable, with $SD = 0.0305$ (i.e. $CV = 89\%$). Species-specific mean λ_E ranged from 0.0009 to 0.1892 h^{-1} . Variation in λ_E was best explained by a model that included taxonomic class, acclimation temperature, and the slope of the estimated exponential decay function at t_n , while evidence for an effect of body mass was weak (Table 1). Model coefficients of the best ranked model show that plasticity rates were highest among amphibians and reptiles, lowest among fishes and crustaceans, and intermediate in insects (Table 2). This pattern was also evident when examining distributions of λ_E among these classes without correcting for the covariates fitted in the best ranked model (Fig. 1). We also observed that plasticity rates increased with acclimation temperature (Table 1, 2, Fig. 2). Finally, plasticity rates were observed to be higher when the slope of the estimated exponential decay function at t_n was shallower (Table 1). In other words, experiments where complete acclimation was more likely to have been obtained were associated with higher estimated plasticity rates. This pattern was mainly driven by the amphibian data, which had a large number of experiments with relatively steep slopes at t_n (Fig. S6). This is in the opposite direction to what might be predicted if a relationship between this slope and estimated acclimation rate is a statistical artefact (Fig. S1). Rather, the causality of this relationship is likely in the opposite direction, i.e. experiments that had a low acclimation rate were stopped *before* complete acclimation to the new temperature had occurred. Nevertheless, to evaluate if this anomaly could have influenced our results, we repeated the model comparison summarized in Table 2 but including only experiments where the slope of the estimated exponential decay function at t_n was larger than -0.002 and -0.001, respectively. For both cases, results remained qualitatively identical and showed only minor quantitative changes (Table S3 - S6).

Discussion

Here, we provide the first synthesis of plasticity rates (λ) across taxa and apply a novel method to obtain standardized and thus comparable measures of this plasticity parameter. For our focal trait, acclimation of temperature tolerance to temperature change, the shape of the plasticity responses were well described by an exponential decay function (i.e. with the rate λ_E). In other words, the absolute rate of change in temperature tolerance when an individual is shifted to a new temperature is proportional to the deviance from the phenotype when completely acclimated to that temperature. We thus validate an assumption

that has previously been made in theory describing the evolution of phenotypic plasticity (Lande 2014). In contrast, superior fit by piecewise linear regression was primarily observed in experiments with poor temporal resolution, thus demonstrating the importance of measuring phenotypes at multiple time points in the new environment to determine the optimal model to use when estimating the shape of the plasticity response.

Variation in estimated λ_E among species was considerable. To put these numbers into perspective they can be translated into half-times, or how long it takes for the initial deviation from the fully acclimated phenotype to be reduced by 50% after being shifted to a new environment, which is given as $\ln(2)/\lambda_E$. The mean observed λ_E of 0.0342 h^{-1} corresponds to a half-time of 20.3 h, whereas the minimum and maximum species-specific λ_E , estimated to 0.0009 and 0.1892 h^{-1} , correspond to half-times of 770.2 and 3.7 h, respectively (only including data used in the analyses, i.e. with $\text{SE}\lambda_E < 0.01$). Using model estimates (Table 2), half-times at 20°C when the final slope of the decay function is zero is 10.7, 15.8, 30.1, 43.3 and 40.8 h for amphibians, reptiles, insects, crustaceans and fishes, respectively. Thus, our analyses demonstrate considerable systematic variation in rates of phenotypic plasticity among these taxa. This begs the question of why such variation has evolved. One might speculate that due to the higher heat capacity of water compared to air, fishes (all species) and crustaceans (5 out of 7 species in our data) which inhabit aquatic environments experience higher temperature stability than taxa inhabiting terrestrial environments. Furthermore, aquatic habitats are often thermally stratified (lentic habitats such as lakes and oceans) or provide cold-water plumes (rivers), which allows for behavioural thermoregulation under periods of stressful temperatures (Kurylyk et al. 2015, Freitas et al. 2016, Harrison et al. 2016). This may reduce the strength of selection on rapid plasticity compared to in the terrestrial environment occupied by reptiles and insects (all species in our data). Although the amphibians also inhabit aquatic environments (particularly during juvenile life stages), their utilization of thermal refugia in deep or fast flowing water is likely limited. Unfortunately, habitat use is confounded with phylogeny in this data set, preventing direct analysis of the effect of habitat on rate of plasticity in thermal tolerance. Thus, although we do demonstrate evolutionary divergence in plasticity rates among these taxa, it remains an open question as to whether this pattern results from evolutionary adaptation to environmental conditions. However, this question could be addressed in future work that targets populations or species that experience known and contrasting patterns of environmental variability.

We observed a positive relationship between acclimation temperature and rate of plasticity in temperature tolerance. This pattern may be explained by the general relationship that exists between developmental rate and body temperature in ectotherms, which is driven by the positive effect of temperature on biochemical reactions and metabolic rate (Brown et al. 2004). It may also explain the observation that within a species, acclimation to high temperature is achieved faster than acclimation to low temperature (Burton et al. 2020). A relationship between metabolic rate and the rate of plasticity was previously hypothesized and addressed by Rohr et al. (2018), but in a less direct manner. Specifically, Rohr et al. (2018) argued that the effect of metabolic rate on rates of thermal plasticity in ectotherms should be evident as a negative relationship between body size and plasticity rate, because smaller organisms tend to have a higher mass-specific metabolic rate than larger ones. They did not however, calculate rates of plasticity from experiments that were explicitly designed to do so. Rather, they used data from experiments that measure the phenotype at only two time points (z_0 and $z_{[t]}$ in our terminology), and from this inferred how the bias in acclimation capacity caused by insufficient acclimation time was influenced by body size. Based on their results it was concluded that rates of plasticity appeared to be higher for smaller organisms. Using a more direct approach we failed to find support for a general relationship between body size and rate of thermal plasticity. Yet, our observation that the rate of plasticity in temperature tolerance is positively related to acclimation temperature suggests a role for metabolic rate in causing some of the variation in plasticity rate across experiments.

Given the general patterns in rate of plasticity observed here, further efforts in studying this plasticity parameter may be fruitful and provide a better foundation for understanding how plasticity evolves in response to environmental variation. From an empirical perspective, including a temporal-dimension in experiments that study plasticity may be included without large costs. In this respect, we make two recommendations. First, a proper choice of model (linear vs. exponential decay) for estimating lambda requires multiple measurements of the phenotype as it responds to the new environment. Our analyses indicate that five or more

measurements may be required to adequately establish the shape of the plasticity response (Fig. S5). Superficially, this requirement might appear to substantially increase the workload of such studies in comparison to studies that only estimate the capacity for plastic phenotypic change in a trait. However, once the model that best describes the shape of the plastic response to the new environment is established, a single measurement z_t after time t (which must be prior to achievement of full acclimation) in addition to those typically measured (z_0 in non-acclimated individuals and $z_{[?]}$ after the full acclimation response has been obtained) is sufficient to accurately estimate D_t , which in turn can be used to calculate the rate of plasticity ($\lambda_E = \ln(D_t)/t$ for exponential decay or $\lambda_A = (1-D_t)/t$ for linear decay). Thus, the workload in such experiments can be greatly reduced by performing a pilot experiment with sufficient temporal resolution (in terms of measurement time points) that provides a precise description of the shape of plasticity response to the new environment before performing more replicates at a lower temporal resolution to obtain the desired estimates of λ . It should be noted that λ_E and λ_A are not directly comparable, because the initial approach towards the fully adjusted phenotype is more rapid under exponential decay. Thus, the relative support for these two types of plasticity responses should be reported. As a second recommendation, experimenters should strive to ensure that complete acclimation to the new environment is achieved prior to measuring $z_{[?]}$. Our analyses show that failing to do so can, and does, lead to bias in estimation of λ_E (Fig. S1, S6). Ideally this is achieved by rearing individuals in all the alternative environments for the whole duration of the experiment (i.e. both prior to and after some of the individuals are transferred into new environments). As pointed out by Burton et al. (2022), this has rarely been done in studies of rates of plasticity. Rather, the majority of studies first acclimate the animals to a single initial environment before shifting them to a new environment and then performing repeated measures of phenotype in this new environment for what typically appears to be a pre-determined (and potentially insufficient) duration.

Natural next steps in research on evolution of plasticity would be to test for links between environmental variation and the evolution of rates of plasticity, and to provide theoretical models that address the co-evolution of plasticity rates and capacity (see Introduction). Although this is beyond the scope of the current paper, our work provides both methodology and novel insights that should stimulate future work along these lines. We also re-emphasize a point made previously (Burton et al. 2022) - that selection on the rate of plasticity might be stronger than selection on the capacity for plasticity. Evolutionary theory posits a central role for phenotypic plasticity in mitigating the fitness impact of environmental variation, but that possessing the potential for such a response is associated with a fitness cost in stable environments (Lande 2009). Fitness costs of plasticity can be categorized into costs of maintenance and costs of production. Costs of maintenance represent the investment of resources into maintaining the machinery required for detecting and responding to a change in the environment and will be paid at a constant rate independent of environmental conditions (Auld et al. 2010). In contrast, production costs are only paid when the plastic response is triggered and are compensated by the fitness benefits associated with changing the phenotype. If one assumes that the capacity for plasticity can be increased by operating the 'machinery' required to change a trait for a longer duration, this will increase production costs but not maintenance costs. Populations living in less variable environments may therefore pay a small price for maintaining their capacity for plasticity (as shown by Van Buskirk & Steiner 2009), and adaptation of this parameter of plasticity to levels of environmental fluctuations may therefore be relatively modest in magnitude. In contrast, increasing the rate of change in the same trait would require increasing the size or output of that 'machinery', with corresponding increases in maintenance costs. Populations living in less variable environments should therefore experience strong selection against maintaining rapid plasticity due to higher maintenance costs, and adaptive evolution across populations may then be expected to be more pronounced for the rate of plasticity. This line of reasoning is also consistent with theoretical results showing that maintenance costs shape the evolution of plasticity to a greater extent than production costs (Sultan & Spencer 2002). Given these considerations, and the results presented in the current study, it seems prudent to address the hypothesis that adaptation to environmental variation may be more pronounced in terms of rates of plasticity rather than capacity of plasticity. By providing clear evidence that rates of plasticity have diverged among ectotherm classes we show that it is a trait that evolves, and that increased empirical and theoretical focus on the rate parameter is likely to provide a way forward for a more comprehensive understanding of phenotypic plasticity.

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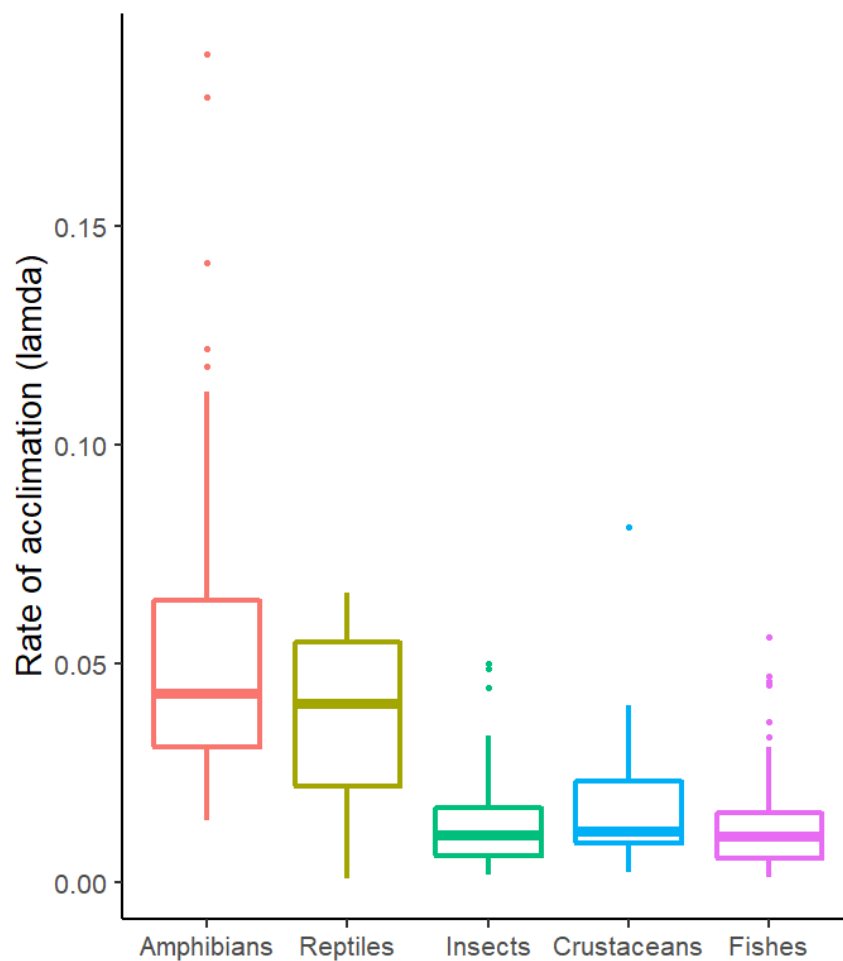


Fig. 1. Observed rates of plasticity (λ_E) in temperature tolerance for different classes of ectotherms animals. Estimates obtained from a linear mixed effect model that controls for the random effect of species as well as acclimation temperature and the slope of the estimated exponential decay function at the final measurement are given in Table 2.

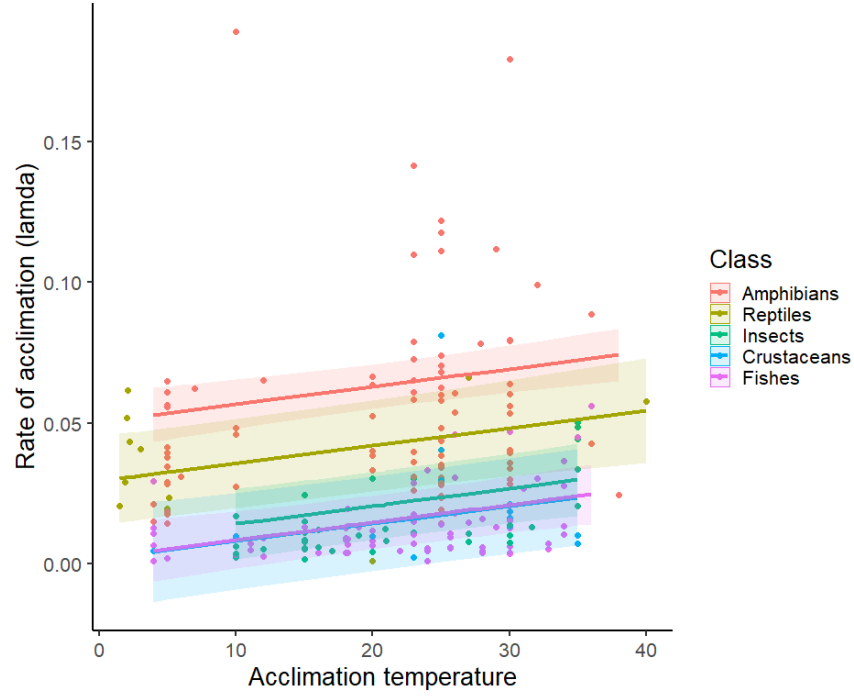


Fig. 2. Observed rates of plasticity (λ_E) in temperature tolerance as a function of acclimation temperature for different classes of ectothermic animals. Regression lines with a common slope are based on the best fitting model (Table 2), and are given for the median slope of the estimated exponential decay function at the final acclimation time point, together with 95% CI.

Table 1. 1 AICc comparisons of the three top candidate models explaining variation in rates of plasticity (λ_E) in temperature tolerance among different classes of ectothermic animals. 'Slope' is the slope of the estimated exponential decay function at the final measurement. Species identity is included as random intercepts in all models.

	K	AIC _C	Δ AIC _C	w_i
Acclimation temperature + Taxonomic class + Slope	9	-1031.8	0.00	0.73
Acclimation temperature + Taxonomic class + Slope + Body mass	10	-1029.8	2.00	0.27
Class + Slope	8	-1019.1	12.70	0.00

Table 2. Summary of the best fitting linear mixed-effect model (Table 1, re-fitted using REML) describing variation in rates of plasticity (λ_E) in thermal tolerance among different classes of ectothermic animals.

	Estimate	SE
Fixed effects		
Amphibians	0.053	0.005
Reptiles	0.032	0.008
Insects	0.011	0.007
Fishes	0.005	0.006
Crustaceans	0.004	0.009
Acclimation temperature	0.0006	0.0002

	Estimate	SE
Slope at end	7.51	1.38
Random effects (SD)		
Species	0.017	