Reduced plasticity and opportunity for selection in terrestrial ectotherm populations under climate change

Daniel W.A. Noble, Fonti Kar, Frank Seebacher, Alex Bush, & Shinichi Nakagawa

#### Affliations:

Division of Ecology and Evolution, Research School of Biology, The Australian National University, Canberra, ACT 2600, Australia
  
 Ecology and Evolution Research Centre, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW, Australia
  
 SOLES, University of Sydney, Sydney, NSW, Australia
  
 Department of Biology, Lancaster University, Liverpool, UK

## **Abstract**

## **Introduction**

Climate change is expected to result in warmer and more variable thermal environments for many organisms globally (Easterling *et al.* 2000; Ummenhofer & Meehl 2017; Suarez-Gutierrez *et al.* 2023). Greater thermal variability in the past is expected to have resulted in strong selection pressures leading to genetic adaptation and/or the evolution of adaptive phenotypic plasticity – both of which are considered important for population resilience to contemporary human-induced climate change (Chevin *et al.* 2010; Merila & Hendry 2014; Chevin & Lande 2015; Seebacher *et al.* 2015; Nunney 2016; Chevin & Hoffmann 2017). The extent to which adaptive plasticity and genetic adaptation will allow organisms to adapt to new environmental conditions is not yet clearly established (Chevin & Hoffmann 2017). Without such responses, high rates of extinction are predicted if organisms cannot track suitable habitats (Cahill *et al.* 2012; Nunney 2016). Phenotypic plasticity is expected to be the ‘first line of defence’ against changing climates by buying time for genetic adaptation to take place (i.e., the ‘plasticty first hypothesis’ - West-Eberhard 2003; see also Lande 2009). Phenotypic plasticity is predicted to evolve when environmental variability is high but predictable and the costs of plasticity is low (Dewitt *et al.* 1998; Reed *et al.* 2010; Nunney 2016; Chevin & Hoffmann 2017; Scheiner *et al.* 2020). Despite this theoretical expectation, empirical support is scant (but see Leung *et al.* 2020), likely because many organisms can behaviorally adjust micro-habitat selection to offset thermal stress, the costs of plasticity are high (Dewitt *et al.* 1998; Chevin & Lande 2015), and/or the prediction is likely only supported for specific plastic responses (i.e., active and developmental plasticity) or life-history stages.

Reversible forms of phenotypic plasticty, such as acclimitisation and behavioural plasticity, are expected to provide greater potential to buffer populations from climate impacts as responses can be fine-tuned to environments (assuming the costs of plasticty are low – Dewitt *et al.* 1998; Scheiner *et al.* 2020). Such responses are driven by changes in underlying physiology that can respond rapidly to the environment. However, studies have primarily been focused on mean physiological responses, paying little attention to changes in physiological variability (Seebacher *et al.* 2015; Havird *et al.* 2020). For example, most work has focused on the degree to which mean thermal tolerances or acclimation abilities in a population are likely to shift in response to thermal environments (Gunderson & Stillman 2015; Seebacher *et al.* 2015; Havird *et al.* 2020; Pottier *et al.* 2022), neglecting how intrapopulation variability might also be impacted. Understanding how variability in physiological rates – traits thought to be closely closely linked to fitness – are affected by climate change has important implications for understanding a populations capacity for physiological trait evolution because lack of physiological variation is expected to play a role in limiting responses to selection (i.e., the ‘opportunity for selection on a trait’) (Pelletier & Coulson 2012). Higher physiological variability may also imply greater niche breadth and inform on the extent to which populations are able to buffer against environmental change (Schindler *et al.* 2010; for example, through ‘portfolio effects’ see Bolnick *et al.* 2011; Slatyer *et al.* 2013; Zheng *et al.* 2023). Decreases in phenotypic variance may also suggest strong stabilising selection or constraints on performance, depending on the trait (Dewitt *et al.* 1998; Scheiner *et al.* 2020). Such changes in physiological trait variation may also have important ecological consequences by promotong population productivity and stability (Kooijman *et al.* 1989; Agashe 2009), species coexistence and ecosystem processes (Imura *et al.* 2003; Bolnick *et al.* 2011). The implications of changes in variance could therefore have wide-reaching consequences for understanding the capacity for populations to persist in and adapt to novel environments (Scheiner *et al.* 2020).

Periods of past climatic change have had disproportionate impacts on some ecosystems over others leading to debates over which ecosystems will be most vulnerable to contemporary climate change. Studies have highlighted species occupying terrestrial ecosystems as being particularly vulnerable given their weak acclimation abilities and greater probability of experiencing thermal extremes that overwhelm physiological homeostasis (Gunderson & Stillman 2015; Seebacher *et al.* 2015; Pinsky *et al.* 2019). Despite marine and freshwater ecosystems appearing to have greater physiological acclimation capacity (e.g., see Seebacher *et al.* 2015), it is unclear if the magnitude of physiological adjustment is sufficient. Low oxygen availability has been suggested as a major factor influencing the vulnerability of aquatic ecosystems whereas remaining close to thermal limits and greater water loss is expected to be a stronger constraint on physiological processes in terrestrial ectotherms (Verberk *et al.* 2016). Given that terrestrial ectotherms are expected to be closer to their thermal limits increases in temperature may have a stronger impact on variation in physiological rates within populations compared to aqautic ectotherms. Reduced variability may result from variances being eroded by strong selection, an inability to adjust physiological rates, or a combination of both.

Here, we use new effect sizes and meta-analysis to re-evaluate the degree to which aquatic and terrestrial ectotherms are capable of physiological plasticity. We then expand these effect sizes to allow for comparisons of variance in physiological rates to ask the following questions: 1) How much is variance in physiological rates expected to change, if at all, as temperatures rise? 2) Are temperture effects on plastic adjustments in physiolgical rates larger than changes in variance across aquatic and terrestrial ectotherms? 3) Are changes in plasticity or variance in physiological rates impacted by a population’s past climate history? and 4) How are means and variances in physiological rates expected to change under climate change?

## **Materials and Methods**

### *Literature collection*

We compiled literature on ectothermic animals that measured physiological rates (e.g., metabolic rate) at two or more temperatures after having been acclimated (or acclimatized) at these temperatures. We used data from a previous meta-analysis (Seebacher *et al.* 2015) and updated Seebacher *et al.* (2015)’s data by extracting data from suitable studies from our own searches that followed the same search protocol. More specifically, we performed a literature search on the 28th of June 2017 using the Web of Science database. We limited our search to articles or proceedings papers published in English from 2013 to 2017 (the date after Seebacher *et al.* 2015 searches were conducted) using the following topic search string: *“(acclimat* AND (therm\* OR temp*) NOT (plant* OR tree\* OR forest\* OR fung\* OR mammal\* OR marsup\* OR bird\* OR human OR exercis\* OR train\* OR hypoxi*))“*. We further limited to the following research areas: Anatomy Morphology; Biodiversity Conservation; Biology; Ecology; Endocrinology Metabolism; Entomology; Evolutionary Biology; Marine Freshwater Biology; Physiology; Respiratory System, Reproductive Biology, Zoology.

Our search resulted in 1,321 papers for screening in Rayyan (Ouzzani *et al.* 2016). We also cross-checked papers we found in our searches with a recent paper by Havird *et al.* (2020), which also updates Seebacher *et al.* (2015)’s dataset. We included any papers that were missed between our searches and those of Havird *et al.* (2020) from the dates 2013-2017. Havird *et al.* (2020) added 7 new studies between 2013-2017 (mainly because they were focused on metabolic rates), and our searches differed from theirs by only a single paper (i.e., Bulgarella *et al.* 2015). Given the physiological traits we included were broader, we had a substantial increase in additional papers that we added to Seebacher *et al.* (2015)’s dataset. More specifically, in addition to the 191 papers we included from the Seebacher *et al.* (2015) dataset, we extracted data from an extra 65 papers (with a total of 238 effects) that were published between 2013 - 2017 (a 34.03% increase in the number of published articles). Note that Seebacher *et al.* (2015) included a total of 205 publications, however, not all these contained the necessary statistics we needed to derive effect sizes and associated sampling variances (see below). While we may have missed papers, our goal was to obtain a large representative (and unbiased) sample of acclimation research rather than a comprehensive dataset. As such, our database represents the most up-to-date dataset used by Seebacher *et al.* (2015) to answer questions on acclimation across ectotherms.

We split the screening of titles and abstracts for the 1,321 papers found in our search among all authors evenly. To ensure consistency among authors in title and abstracts that should be included, prior to screening all authors went through a randomly selected set of papers together - agreeing on those that were relevant and those that were not based on our inclusion criteria (see below). Where any authors were uncertain about whether to include a paper in the sub-sample they screened, we conservatively included the paper for full text screening and discussed uncertain papers among authors to come to a decision on whether to include the paper. After title and abstract screening, we were left with a total of 149 papers for full text screening. Papers were included only if they: 1) measured a physiological rate acutely at two temperatures on a sample of animals chronically exposed to the same two temperatures for at least 1 week; and 2) where physiological rates measured were burst and sustained locomotion, metabolic rates (standard, resting, routine and maximal), heart rates, and/or enzyme activities.

### *Data Compilation*

We extracted means, standard deviations, and sample sizes for physiological rates at the two test temperatures. If there were more than two test temperatures, we choose only the test temperatures that fell within the most likely natural range of temperatures experienced by the species in question. We extracted these data from text, tables or figures of a given paper. Data were extracted from figures using the R package *metaDigitise* (Pick *et al.* 2019). We also recorded the phylum, class, order, genus and species under study and the latitude and longitude of the population that was being studied. For studies that did not provide latitude and longitude for the population, we searched for similar studies by the lab group to identify where the population was likely to have been sourced or derived from when needed. If the population was derived from the wild, we recorded the nearest latitude and longitude of the population to the field collection site. If the animals had been sourced from a commercial supplier, we took the latitude and longitude of the supplier that the paper identified the animals to have originated from. When it was not possible to find latitude and longitude using these methods, we looked up the distribution of the species in question and took the latitude and longitude of the centroid of the species’ distributional range.

### *Based Effect Sizes and Sampling Variances for Means and Variances*

Following Noble *et al.* (2022) we calculated a series of temperature corrected effect sizes that compared mean physiological rates () as well as the variability in physiological rates ( and ). These effect sizes are similar to the traditional temperature coefficient (), but with formal analytical approximations for their sampling variances. Sampling variances for effect sizes allowed us to make use of traditional meta-analytic modelling approaches.

#### *Comparing changes in mean physiological rates*

To compare mean physiological rates, we calculated the log response ratio, (Noble *et al.* 2022) as follows:

Where, and are mean physiological rates and and are the temperatures that these rates are measured. Log transformation of this ratio makes the effect size normally distributed. [Equation 1](#eq-lnq10) is essentially a temperature corrected equivalent to the log response ratio (lnRR) (Hedges *et al.* 1999; Lajeunesse 2011) when the numerator and denominator are measured at different temperatures. This allows one to compare the mean of two temperature treatments directly regardless of the temperatures that these groups have been measured. The sampling variance for [Equation 1](#eq-lnq10) can be computed as follows (as described in Noble *et al.* (2022)):

Here, and are the standard deviations and and are the sample sizes in group 1 and 2, respectively.

#### *Comparing variance in physiological rates*

Nakagawa *et al.* (2015) recently proposed analogous effect size estimates to *lnRR* that allow for comparisons of changes in variance between two groups, the log variance ratio (*lnVR*) and the log coefficient of variation (*lnCVR*). *lnVR* and *lnCVR* are ratios that describe the relative difference in trait variability between two groups. We refer readers to Nakagawa *et al.* (2015) for the equations describing *lnVR* and *lnCVR*, but these can easily be extended to their analogues (and associated sampling variance) as follows:

[Equation 3](#eq-lnq10VR) and [Equation 4](#eq-slnq10VR) describe the change in physiological rate variance ([Equation 3](#eq-lnq10VR)) across a 10°C temperature change along with its sampling variance ([Equation 4](#eq-slnq10VR)). While this is a useful metric, as discussed by Nakagawa *et al.* (2015) there is often a strong mean-variance relationship that needs to be accounted for in analysing changes in variance. As such, we calculated the coefficient of variation, which standardizes changes in variance for changes in means as follows:

where is the coefficient of variation defined as .

#### *Calculating acute and acclimation , and estimates*

Using the mean, standard deviation, and sample size for all acute and acclimation treatments of studies in our databases we derived acute and acclimation , and estimates. For all effect sizes the higher acute or acclimation temperature was in the numerator and the lower of the two temperatures in the denominator. As such, positive effect sizes suggest that the mean or variance is larger at the higher of the two temperatures, standardized to 10°C.

### *Moderator Variables*

We recorded or derived a series of moderator variables from each study that are expected to have an impact on our effect size estimates. These included the duration of acclimation in days and acclimation type (“acclimation” or “acclimatization”) given that acclimation responses are expected to depend on how long chronic temperature exposure occurs (longer exposure = better acclimation response) (Seebacher *et al.* 2015). We also recorded if the sample of animals were derived from captive or wild stocks, the life-history stage of the animals used (“adult” or “juvenile”) and the habitat type (“freshwater”, “marine” or “terrestrial”) given that Seebacher *et al.* (2015) show that these factors can impact estimates. Physiological rate measures varied widely across the studies but could generally be grouped into discrete trait categories (Seebacher *et al.* 2015). As such, using the detailed information on the trait type, and its associated units from a given study, we categorized each effect size into one of 12 trait categories. These categories included measures of whole organism performance measures including cardiac (i.e., ‘cardiac’) and muscle (‘muscle’) function, sprint speed (‘sprint’) and endurance (‘endurance’) and metabolic rates (i.e., maximal and resting metabolic rate; max MR’, ‘rest MR’, respectively). Studies also quantified various enzymatic reaction rates, including enzymes involved in general metabolic responses (categorized as ‘metabolic enzyme’), various parts of the electron transport chain, including ATPase activity (‘ATPase’), mitochondrial leak (‘mito\_leak’) and oxidation (‘mito\_oxidation’) as well as antioxidant enzymes (‘antiox’). All other traits not falling within these categories were placed into ‘other’.

### *Climate Data*

To understand how climate has impacted species’ physiological acclimation abilities we used the coordinates reported by each study to extract temperature data from terrestrial and aquatic environments. It was unclear whether climate at the locations of captive reared organisms would be representative of a population’s climate history - particularly for species reared under captive condition for many generations. Given that we were interested in understanding climate driven effects on acclimation capacity we only used studies on wild populations for climate analyses.

Monthly average temperature data were extracted from the ERA5 climate model, available from the Copernicus climate data store (Hersbach *et al.* 2020). For each population and species in the dataset we extracted a 30-year period (1950-2022) of either surface air temperature at 2 meters (0.01 resolution) for both terrestrial and freshwater taxa, or sea surface temperature for the marine taxa (at 0.25 resolution) using the *ncdf4* R package (vers. 1.22, Pierce 2021). We chose a 2-meter resolution because we believed that it more likely to reflects the micro-thermal environment experienced by terrestrial and freshwater ectotherms at those locations. For terrestrial species we also collected soil temperature as for many species this maybe more representative of microhabitat choice compared to air temperature. We fit models using both air and soil temperature and found that the results were qualitatively similar. As such, we only present results for air temperature (See Supplementary Materials).

Using the thermal time-series data for each location we summarised various metrics of thermal variability across months and years as well as estimates of thermal predictability (i.e., autocorrelation). To estimate thermal variability, we calculated the coefficient of variation (, where SD = standard deviation in temperature and M = the mean temperature for each year). To estimate thermal predictability, we calculated the auto-regressive time lag across the entire dataset. Theoretical and empirical studies of plasticity evolution have emphasised the importance of both climate variability and predictability in plasticity evolution.

We also extracted climate projections into the future to understand the effects of climate warming will have on opportunity for selection. We used the CanESM2 climate model (2005-2100) under a high emissions scenerio (RCP8.5).

### *Meta-Analysis*

We analysed our data using multilevel meta-analytic (MLMA) and meta-regression (MLMR) models in R (vers. 4.3.1) using *brms* (vers. 2.20.4 Bürkner 2017, 2018; “Stan development team. RStan” 2021) and *metafor* (vers. 4.4.0 Viechtbauer 2010). We fit both Bayesian and frequentist approaches to ensure that our results were consistent, and to create orchard plots more easily (vers. 2.0, Nakagawa *et al.* 2021a). In addition, Bayesian methods better protect against type I errors in the presence of complex sources of non-independence (Nakagawa *et al.* 2021b; Song *et al.* 2021). For our Bayesian models, we ran 4 MCMC chains, each with a warm-up of 1000 followed by 4000 sampling iterations keeping every 5 iterations for a total of 3200 samples from the posterior distribution. We used flat Gaussian priors for ‘fixed’ effects (i.e., ) and a student t-distribution for ‘random’ effects (i.e., ). We checked that all MCMC chains were mixing and had converged (i.e., ). We compared any competing models using Akaike’s Information Criteria (AIC) (if frequentist) or Wantabe Information Criteria (WIC) (if Bayesian). We deemed models with the lowest IC value to be best supported if there was a between the competing models of 2 or more. If two models were within 2 units we went with the most parsimonious model.

#### *Multi-level Meta-analysis (MLMA) Models*

We first fit multi-level meta-analysis (MLMA) models (i.e., intercept only models) for both and , that included study, species, and phylogeny as random effects to account for non-independence. We also included trait as a random effect to account for trait variation within the data. Our MLMA models allowed us to partition the variation in and among these key sources while accounting for total sampling variance in each. This allowed us to calculate total heterogeneity [i.e., ; *sensu* Nakagawa & Santos (2012); Noble *et al.* (2022)] along with various metrics describing the proportion of variance explained by each random effect level (Nakagawa & Santos 2012). We also present 95% prediction intervals which describe the expected distribution of effects from future studies (Nakagawa *et al.* 2021a; Noble *et al.* 2022).

A phylogeny was derived using the Open Tree of Life (OTL) with the *rotl* package in R (vers. 3.1.0, Michonneau *et al.* 2016), and plotted using *ggtree* (vers. 3.9.0, Yu *et al.* 2017). We resolved all polytomies in the tree. Any missing taxa were replaced with closely related species and branch lengths were computed using Grafen’s method (using power = 0.7, Grafen 1989). We used the R packages *ape* (vers. 5.7.1, Paradis & Schliep 2019) and *phytools* (vers. 1.9.16, Revell 2012) to prune the tree for individual analyses and calculate phylogenetic covariance (or correlation) matrices used in meta-analytic models.

#### *Multi-level Meta-regression (MLMR) Models*

After quantifying levels of heterogeneity, we fit a series of multi-level meta-regression (MLMR) models to test our key questions. In all models, we included the same random effects as we used in our MLMA models. Acclimation time varied from 4 to 408 days (mean (SD) = 37.98 45.19 days), and terrestrial ectotherms were acclimated for a much shorter duration (mean (SD) = 23.53 15.56, n = 125) than both freshwater (mean (SD) = 36.81 28.71, n = 430) and marine species (mean (SD) = 46.18 67.21, n = 313). Rates of acclimation have been shown to be faster for many terrestrial groups compared to aquatic organisms [e.g., amphibians and reptiles have faster rates of acclimation than fishes; See Einum & Burton (2023)], which would make it more likely that terrestrial ectotherms would show lower post acclimation . To control for these possible differences, acclimation time was mean-centered (mean = 0) and included in all our models. As such, all estimates can be interpreted as values for an average level of acclimation time (i.e., 37.98 days).

We first tested the degree to which acute and acclimation and effects varied by habitat type (i.e., terrestrial, freshwater, and marine ecosystems). Models included an interaction between effect type (i.e., acute or acclimation) and habitat. Reduced mean relative to indicates that acclimation to thermal environments results in partial compensation of physiological rates (i.e., phenotypic plasticity), whereas no differences between and suggests organisms are not capable of physiological plasticity (Havird *et al.* 2020). In contrast, a difference in relative to would imply that changes in between individual variation in physiological rates across 10C differ depending on whether acute or acclimation responses are measured. If the interaction between effect type and habitat was not supported, then we fit a model that only contained additive effects of effect type and habitat. Following on from these models, we subset each habitat type and explored how mean changed across traits. Within each habitat (marine, freshwater, and terrestrial) we fit a series of models that included an interaction between effect type (acute / acclimation) and trait category (as defined above). Variance in effects within trait categories appeared to vary depending on the trait type in question. Comparison of a model with and without heteroscedastic residual variance favored a model with heteroscedastic residual variance across trait categories (; marine = 58, freshwater = 120, and terrestrial = 12). To ensure models converged we limited to trait categories for each habitat with six or more effect sizes.

Second, we tested whether different life-stages are more or less likely to acclimate by fitting a model for each habitat type and including an interaction between life-stage (‘adult’ or ‘juvenile’) and effect type. We predicted that acclimation responses would be more likely early in development compared to later in development, but that this should depend on the habitat type given the different constraints faced by different early life stages across major habitat types.

#### *Modelling how climate change will impact on opportunity for selection*

To understand the consequences of human-induced climate change on the potential to impact the opportunity for selection on physiogical traits we fit a model that included an interaction between acclimation type, habitat type, latitude and longitude. We assumed that any change in across latitude and longitude could vary by habitat type (i.e., an interaction between habitat). We used non-linear tensors for latitude and longitude as any response could be complicated by local factors (e.g., altitude). Our model included random effects of species, trait, phylogeny and study. We predicted the expected change in for each wild population in our dataset at the specific populations latitude and longitude. To do this, we first converted the predicted to a 1C change as opoosed to 10C as follows:

[Equation 7](#eq-lCVRpred) turned the expected change across 10C to 1C. We then multiplied this predicted change by the change in air and sea surface temperatures at the locations of each population (and species) that is expected under high emissions scenerios in 2080.

### *Publication Bias*

We explored the possibility for publication bias graphically, using funnel plots, and more formally by including in our meta-regression models sampling variance (or sampling standard error) (Nakagawa *et al.* 2022). Funnel plot asymmetry may suggest a form of publication bias called the ‘file-drawer’ effect whereby low-powered studies are less likely to be published. To test whether sampling variance covaried with effect size we included it in a multi-level meta-regression model that acounted for all the random effects (study, species, trait) and fixed effects (acclimation time, type of effect, habitat, trait category and the interaction between habitat type and trait category).

## **Results**

The final dataset included a total of 91 freshwater (fishes = 48, Molluscs = 4, Amphibians = 19, Reptiles = 8, Arthropods = 10, and a single Crustacean and Nematode species), 90 marine (fishes = 47, Annelids = 2, Molluscs = 21, Echinoderms = 7, Reptiles = 1, Arthropods = 10, and a single Crustacean and Cnidarian species), and 45 terrestrial species (Annelids = 1, Molluscs = 5, Arthropods = 14, Reptiles = 12 and Amphibians = 12 along with a single Tardigrade species) ([Figure 1](#fig-1) A). We had more data on acute thermal responses (n = 1115) compared to thermal responses after an acclimation period (n = 798) because both acclimation temperatures had separate acute responses ([Figure 1](#fig-1)). While the two acute effect sizes did differ significantly from each other, on average (Acute responses were higher for animals acclimated to high temperatures – = 0.07, 95% CI: 0.04 to 0.1, = < 0.0001), they were in the same direction and only differed by ~10%. As such, we averaged the two acute effect sizes in subsequent analyses.

Most of the effect size estimates came from measurements of metabolic rates (both resting and maximal – = 190, = 3069, considering acute and acclimation effects together), metabolic enzymes ( = 61, = 2394) and whole-organism performance traits (i.e., measures of speed and endurance – = 73, = 963).

### *Terrestrial and aquatic ectotherms differ in their capacity to acclimate but acclimation does not depend on life-history stage*

Overall, and differed by only 7.88% across all habitats (95%CI: 4.77 to 11.2%). Ectotherms in marine and freshwater environments showed partial compensation of physiological rates ([Figure 1](#fig-1)B) amounting to reduced of 10.05% (95% CI: 6.1 to 13.92) in freshwater and 9.16% (95% CI: 2.74 to 15.52) in marine environments. In contrast, terrestrial ectotherms showed no acclimation (possibly even inverse acclimation) – showing a 4.42% increase in (95% CI: 0.22 to 11.12, [Figure 1](#fig-1)B). Considering acute responses of animals acclimated to high temperatures are generally slightly elevated compared to cold acclimated animals (~7%; = 0.07, 95% CI: 0.04 to 0.1, p < 0.0001), acclimatization is not likely going to provide adaptive benefits under climate change.

Nonetheless, effect heterogeneity was high (only 2.85% of the variance was the resulting of sampling varianbility, 95% CI: 2.38 to 3.32%), with most variance being explained by the specific study and type of trait (Study: 29.41% , 95% CI: 20.78 to 38.49%; Trait Type: 29.35% , 95% CI: 19.97 to 39.53%). Evolutionary relationships among taxa and species ecology explained little variation in acute and acclimation repsonses (Species: 2.39% , 95% CI: 0.01 to 8.1%; Phylogeny: 2.89% , 95% CI: 0 to 12.94%).

Different trait categories showed different accclimation responses across habitat types, however, they mirrored patterns seen overall ([Figure 2](#fig-2)). Acclimation capacity also did not vary by life-stage given that there were no differences between and between adult and juveniles ([Figure 3](#fig-3)) (Adult-Juvenile (Acute): 0, 95% CI: -0.21 to 0.2, = 0.96; Adult-Juvenile (Acclimation): 0.05, 95% CI: -0.16 to 0.38, = 0.83).

|  |
| --- |
| Figure 1- Taxonomic distribution of acute and acclimation estimates across major habitats. **A)** Phylogenetic distribution of taxa contained within the data. The total number of acute and acclimation type Q10 effect sizes are highlighted as well as whether the taxa is marine, freshwater or terrestrial. Silouettes are representative taxa of major clades within the tree. **B)** Acute and Acclimation across marine, freshwater, and terrestrial environments. **C)** across traits for marine, freshwater and terrestrial systems. Note there were no differences between acute and acclimation types. k = total number of effect size estimates while the numbers in brackets indicate the number of species. |

|  |
| --- |
| Figure 2- Acute and Acclimation lnRR q10 across traits for A) marine, B) freshwater and C) terrestrial systems |

|  |
| --- |
| Figure 3- Predicted mean acclimation and acute “” for adult and juevenile life-history stages for A) Marine, B) Freshwater and C) Terrestrial ectotherms. |

### *The opportunity for selection is reduced in terrestrial ectotherms*

The opportunity for selection, as captured by , showed a decrease across all habitat types but was especially pronouced in terrestrial and marine ectotherms. Overall, there was a 27.87% (95% CI: 10.77 to 40.91, = 0.01) reduction in variation in physiological rates for terrestrial ectotherms and a 14.94% (95% CI: 1.87 to 29.97, = 0.07) reduction in variation for marine ectotherms when temperatures increase by 10C. In contrast, freshwater ectotherms exhibited a much smaller reduction in physiological rate variance at high temperatures (8.62%, 95% CI: 0.41 to 21.78, = 0.33).

The total proportion of heterogeneity in was lower compared to ( = 23.96, 95% CI: 20.36 to 27.27), with most variation being driven by between study and trait differences (See supplemental [Figure 10](#fig-s3)). Each life-history stage exhibited the same pattern of variance change in each of the habitats ([Figure 4](#fig-cvrlh)). While traits did differ in whether they exhibited a reduction in variation in physiological rates at high temperatures reduced variance was prominant for resting metabolic rates and sprint speed ([Figure 5](#fig-cvrtrait)).

|  |
| --- |
| Figure 4- Predicted mean for adult and juevenile life-history stages for A) Marine, B) Freshwater and C) Terrestrial ectotherms. |

|  |
| --- |
| Figure 5- Acute and Acclimation across traits for A) marine, B) freshwater and C) terrestrial systems |

### *Past climate does not influence acclimation capacity or expected change in variance*

Thermal variability (i.e., ) and predictability a population experienced in its past did not explain acclimation capacity or changes in opportunity for selection (i.e., the change in physiological variability) among terrestrial, marine or freshwater populations ([Figure 6](#fig-4); [Figure 7](#fig-5)).

|  |
| --- |
| Figure 6- Bubble plot environment for wild populations by habitat. |

|  |
| --- |
| Figure 7- Bubble plot environment for wild populations by habitat. |

### Global change in opportunity for selection

Acute and acclimation responses for wild ectotherms were much less common than studies done on captive populations ( = 134, from 188 populations). Globally, there was a clear bias towards spiecies in the Northern Hemiphere ([Figure 8](#fig-fig6) A-C). Projected changes in the opportunity for selection were highly variable across the globe, with some regions showing a decrease in the opportunity for selection, while others showing an increase ([Figure 8](#fig-fig6) D). Out of the 188 populations variance was predicted to decrease in 96.28% of the locations.

Predictions of current global changes in the opportunity for selection were generally conservative with our model explaining ~ 50% of the variation in the observed data ( = 0.48, 95% CI: 0.31 to 0.6). Across habitat types climate change is predicted to result in a only a 0.43% change in variance for freshwater systems (95% CI: -7.08 to 5.8%, = 0.87), whereas we expect a 2.87% reduction in variance for marine systems (95% CI: -6.38 to 1.23%, = 0.37) and a 12.98% reduction in variance for terrestrial systems (95% CI: -20.43 to -6.7%, = < 0.0001) under a RCP8.5 climate scenerio.

|  |
| --- |
| Figure 8- Model predictions for the expected change in acclimation across the globe for terrestrial, marine and freshwater ecthotherms. Predictions consider the uncertainty in random effects (i.e., species, phylogeny, study). |

## **Discussion**

Understanding acclimation capacity and how variation in physiological rates change across populations and species is important for predicting the impacts ecological and evolutionary consequences of climate change (Chevin *et al.* 2010; Bolnick *et al.* 2011; Chevin & Hoffmann 2017). Here we show that the opportunity for selection is expected to decrease for ectotherms, but particularly so for terrestrial ectotherms (~28%). Decreases in variance in physiological rates is larger than the expected benefits from acclimation in marine and terrestrial ectotherms (marine: 9% acclimation vs. 15% reduction in variance; terrestrial: no acclimation vs 28% reduction in variance). Such effects are expected to result in a decrease in the variability in physiologcial rates for marine and terrestrial ectotherms between ~4-13% under future climate change projections.

### **Acclimation capacity and opportunity for selection is limited in response to climate change**

One explanation for why terrestrial ectotherms show minimal acclimation capacity may be related to the fact that terrestrial ectotherms, were, on average acclimated for significantly less time than ectotherms from aquatic habitats. However, rates of acclimation have been shown to be faster for many terrestrial groups compared to aquatic organisms [e.g., amphibians and reptiles have higher rates of acclimation than fishes; See Einum & Burton (2023)]. Faster rates of acclimation would therefore result in the opposite patterns to those we observed – in other words, terrestrial species would be more likely to exhibit lower compared to when controlling for acclimation time. assuming a fraction of this variation is heritable and/or it weakens selection

### **No signature of past climate on capacity for acclimation or opportunity for selection**

Theoretical models predict that plasticity should evolve in populatons experiencing greater environmental variability (spatial or temporal), particularly if oscillations are predictable over time making cues more reliable (Lande 2009; Chevin *et al.* 2010; Murren *et al.* 2015; Hendry 2016; Nunney 2016; Chevin & Hoffmann 2017). Higher spatial heterogenetiy in terrestrial ectotherms suggests that plasticity should be more likely evolve, however, we did not find evidence to this effect; possibly because of the lower predictability of thermal environments over time making cues unreliable (Hendry 2016). Empirical evidence properly testing these predictions, however, is scant. Leung *et al.* (2020) recently showed that greater plasticty in morphological traits did evolve in experimental algae populations, however, work in seed beetles. Our results suggest that such theoretical explanations may not be general but rather specific to the population, context and trait in question; a point emphaised by others.

### ***Ecological consequences of reduced variation in physiological Rates***

Variance in physiological rates decreases substantially at high temperatures with effects being especially pronouced in terrestrial ecosystems and for key traits such as metabolism and performance. Changes in variability in physiological rates, particularly energy demand, could have important consequences on the flow of energy within and between populations, communities and ecosystems that can have important consequences for population dynamics (Hendry 2016). For examaple, Kooijman *et al.* (1989) integrated individual variation in dynamic energy budget (DEB) models developed for *Daphnia magna*. They showed that greater between-individual variation in DEB parameters led to less extreme population occilations compared to scenerios with no variation (Kooijman *et al.* 1989). To date, integrating realistic changes in physiological rate variation across indiviudals into mechanistic physiological models appears to be rare.

The ecological consequences of changes in physiological rate variance across aquatic and terrestrial ecosystems remains unclear. The dearth of empirical data demonstrating changes in variance paired with a lack of theoretical models - buckley 2014, - Lawton 1991, - Nisbet especailly see Kooijman *et al.* (1989) given that they “introduce some small spread” and it results in oscillatinos dapeming..

### **Acute and acclimation responses of wild ectotherms are lower in warmer environments**

### **The opportunity for selection is expected to decrease for wild ectotherms under climate change**

### **Limitations and future directions**

## References

Agashe, D. (2009). The stabilizing effect of intraspecific genetic variation on population dynamics in novel and ancestral habitats. *The American Naturalist*, 174, 255–267.

Bolnick, D.I., Amarasekare, P., Araújo, M.S., M. Levine, R.B. andJonathan, Novak, M., Rudolf, V.H.W., *et al.* (2011). Why intraspecific trait variation matters in community ecology. *Trends in Ecology and Evolution*, 26, 183–192.

Bulgarella, M., Trewick, S.A., Godfrey, A.J.R., Sinclair, B.J. & Morgan-Richards, M. (2015). Elevational variation in adult body size and growth rate but not in metabolic rate in the tree weta hemideina crassidens. *J. Insect Physiol.*, 75, 30–38.

Bürkner, P.-C. (2017). Brms: An R package for bayesian multilevel models using stan. *J. Stat. Softw.*, 80, 1–28., doi:10.18637/jss.v080.i01.

Bürkner, P.-C. (2018). Advanced bayesian multilevel modeling with the R package brms. *R J.*, 10, 395–411.

Cahill, A.E., Aiello-Lammens, M.E., Fisher-Reid, M.C., Hua, X., Karanewsky, C.J., Ryu, H.Y., *et al.* (2012). How does climate change cause extinction? *Proceedings of the Royal Society B: Biological Sciences*, 280, 20121890.

Chevin, L.-M. & Hoffmann, A.A. (2017). Evolution of phenotypic plasticity in extreme environments. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, 372, 20160138, https://doi.org/10.1098/rstb.2016.0138.

Chevin, L.-M., Lande, R. & Mace, G.M. (2010). Adaptation, plasticity, and extinction in a changing environment: Towards a predictive theory. *PLoS Biology*, 8, e1000357, https://doi.org/10.1371/journal.pbio.1000357.

Chevin, L.M. & Lande, R. (2015). Evolution of environmental cues for phenotypic plasticity. *Evolution*, 69, 2767–2775, https:// doi.org/10.1111/evo.12755.

Dewitt, T.J., Sih, A. & Wilson, D.S. (1998). Costs and limits of phenotypic plasticity. *Trends in Ecology and Evolution*, 13, 77–81.

Easterling, D.R., Meehl, G.A., Parmesan, C., Changnon, S.A., Karl, T.R. & Mearns, L.O. (2000). Climate extremes: Observations, modelling and impacts. *Science*, 289, 2068–2074.

Einum, S. & Burton, T. (2023). Divergence in rates of phenotypic plasticty among ectotherms. *Ecol. Lett.*, 26, 147–156.

Grafen, A. (1989). The phylogenetic regression. *Philos. Trans. R. Soc. Lond. B Biol. Sci.*, 326, 119–157.

Gunderson, A.R. & Stillman, J.H. (2015). Plasticity in thermal tolerance has limited potential to buffer ectotherms from global warming. *Proceedings of the Royal Society B: Biological Sciences*, 282, 20150401.

Havird, J.C., Neuwald, J.L., Shah, A.A., Mauro, A., Marshall, C.A. & Ghalambor, C.K. (2020). Distinguishing between active plasticity due to thermal acclimation and passive plasticity due to Q10 effects: Why methodology matters. *Funct. Ecol.*, 0, 1–14.

Hedges, L.V., Gurevitch, J. & Curtis, P.S. (1999). The meta-analysis of response ratios in experimental ecology. *Ecology*, 80, 1150–1156.

Hendry, A.P. (2016). Key questions on the role of phenotypic plasticity in eco-evolutionary dynamics. *Journal of Heredity*, 107, 25–41.

Hersbach, H., Bell, B., Berrisford, P., Hirahara, S., Horányi, A., Muñoz-Sabater, J., *et al.* (2020). The ERA5 global reanalysis. *Quart. J. Roy. Meteor. Soc.*, 146, 1999–2049.

Imura, D., Toquenaga, Y. & Fujii, K. (2003). Genetic variation can promote system persistence in an experimental host-parasitoid system. *Population Ecology*, 45, 205–212.

Kooijman, S., Van der Hoeven, N. & Van der Werf, D. (1989). Population consequences of a physiological model for individuals. *Functional Ecology*, 325–336.

Lajeunesse, M.J. (2011). On the meta-analysis of response ratios for studies with correlated and multi-group designs. *Ecology*, 92, 2049–2055.

Lande, R. (2009). Adaptation to an extraordinary environment by evolution of phenotypic plasticity and genetic assimilation. *Journal of Evolutionary Biology*, 22, 1435–1446.

Leung, C., Rescan, M., Grulois, D. & Chevin, L. (2020). 2020. *Ecology Letters*, 23, 1664–1672.

Merila, J. & Hendry, A.P. (2014). Climate change, adaptation, and phenotypic plasticity: The problem and the evidence. *Evolutionary Applications*, 7, 1–14., doi:10. 1111/eva.12137.

Michonneau, F., Brown, J.W. & Winter, D.J. (2016). Rotl: An R package to interact with the open tree of life data. *Methods Ecol. Evol.*, 7, 1476-1481. doi:10.1111/2041-210X.12593.

Murren, C., Auld, J., Callahan, H., Ghalambor, C., Handelsman, C., Heskel, M., *et al.* (2015). Constraints on the evolution of phenotypic plasticity: Limits and costs of phenotype and plasticity. *Heredity*, 115, 293–301.

Nakagawa, S., Lagisz, M., Jennions, M.D., Koricheva, J., Daniel W. A. Noble, T.H.P., Sánchez-Tójar, A., *et al.* (2022). Methods for testing publication bias in ecological and evolutionary meta-analyses. *Methods in Ecology and Evolution*, 13, 4–21.

Nakagawa, S., Lagisz, M., O’Dea, R.E., Rutkowska, J., Yang, Y., Noble, D.W.A., *et al.* (2021a). The orchard plot: Cultivating forest plots for use in ecology, evolution and beyond. *Research Synthesis Methods*, 12, 4–12.

Nakagawa, S., Poulin, R., Mengersen, K., Reinhold, K., Engqvist, L., Lagisz, M., *et al.* (2015). Meta-analysis of variation: Ecological and evolutionary applications and beyond. *Methods Ecol. Evol.*, 6, 143–152.

Nakagawa, S. & Santos, E.S.A. (2012). Methodological issues and advances in biological meta-analysis. *Evol. Ecol.*, 26, 1253–1274.

Nakagawa, S., Senior, A.M., Viechtbauer, W. & Noble, D.W.A. (2021b). An assessment of statistical methods for non-independent data in ecological meta-analyses: comment. *Ecology*, in press., https://doi.org/10.1002/ecy.3490.

Noble, D.W.A., Pottier, P., Lagisz, M., Burke, S., Drobniak, S.M., O’Dea, R.E., *et al.* (2022). Meta-analytic approaches and effect sizes to account for “nuisance heterogeneity” in comparative physiology. *J. Exp. Biol.*, 225, jeb243225.

Nunney, L. (2016). Adapting to a changing environment: Modeling the interaction of directional selection and plasticity. *Journal of Heredity*, 107, 15–24.

Ouzzani, M., Hammady, H., Fedorowicz, Z. & Elmagarmid, A. (2016). Rayyan—a web and mobile app for systematic reviews. *Syst. Rev.*, 5, 210–220.

Paradis, E. & Schliep, K. (2019). Ape 5.0: An environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, 35, 526–528.

Pelletier, F. & Coulson, T. (2012). A new metric to calculate the opportunity for selection on quantitative characters. *Evolutionary Ecology Research*, 14, 729–742.

Pick, J.L., Nakagawa, S. & Noble, D.W.A. (2019). Reproducible, flexible and high throughput data extraction from primary literature: The metaDigitise R package. *Methods Ecol. Evol.*, 10, 426–431.

Pierce, D. (2021). ncdf4: Interface to unidata netCDF (version 4 or earlier) format data files.

Pinsky, M.L., Eikeset, A.M., McCauley, D.J., Payne, J.L. & Sunday, J.M. (2019). Greater vulnerability to warming of marine versus terrestrial ectotherms. *Nature*, 569, 108–111.

Pottier, P., Burke, S., Zhang, R.Y., Noble, D.W., Schwanz, L.E., Drobniak, S.M., *et al.* (2022). Developmental plasticity in thermal tolerance: Ontogenetic variation, persistence, and future directions. *Ecology Letters*, 25, 2245–2268.

Reed, T.E., Waples, R.S., Schindler, D.E., Hard, J.J. & Kinnison, M.T. (2010). Phenotypic plasticity and population viability: The importance of environmental predictability. *Proceedings of the Royal Society B: Biological Sciences*, 277, 3391–3400.

Revell, L.J. (2012). Phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, 3, 217–223.

Scheiner, S.M., Barfield, M. & Holt, R.D. (2020). The genetics of phenotypic plasticity. XVII. Response to climate change. *Evolutionary Applications*, 13, 388–399.

Schindler, D.E., Hilborn, R., Chasco, B., Boatright, C.P., Quinn, T.P., Rogers, L.A., *et al.* (2010). Population diversity and the portfolio effect in an exploited species. *Nature*, 465, 609–613.

Seebacher, F., White, C.R. & Franklin, C.E. (2015). Physiological plasticity increases resilience of ectothermic animals to climate change. *Nat. Clim. Chang.*, 5, 61.

Slatyer, R.A., Hirst, M. & Sexton, J.P. (2013). Niche breadth predicts geographical range size: A general ecological pattern. *Ecology Letters*, 16, 1104–1114.

Song, C., Peacor, S.D., Osenberg, C.W. & Bence, J.R. (2021). An assessment of statistical methods for nonindependent data in ecological meta-analyses. *Ecology*, e03184.

Stan development team. RStan: The R interface to stan. (2021). *R package version 2. 21. 3. https://mc-stan. org/.*

Suarez-Gutierrez, L., Müller, W.A. & Marotzke, J. (2023). Extreme heat and drought typical of an end-of-century climate could occur over europe soon and repeatedly. *Communications Earth & Environment*, 4, 415, https://doi.org/10.1038/s43247-023-01075-y.

Ummenhofer, C.C. & Meehl, G.A. (2017). Extreme weather and climate events with ecological relevance: A review. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, 372, 20160135, http://doi.org/10.1098/rstb.2016.0135.

Verberk, W.C.E.P., Bartolini, F., Marshall, D.J., Pörtner, H.-O., Terblanche, J.S., White, C.R., *et al.* (2016). Can respiratory physiology predict thermal niches? *Annals of the New York Academy of Sciences*, 1365, 73–88.

Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor package. *J. Stat. Softw.*, 36, 1–48. URL: https://www.jstatsoft.org/v36/i03/.

West-Eberhard, M.J. (2003). *Developmental plasticity and evolution.* Oxford University Press, New York.

Yu, G., Smith, D., Zhu, H., Guan, Y. & Lam, T.T.-Y. (2017). Ggtree: An R package for visualization and annotation of phylogenetic trees with their covariates and other associated data. *Methods Ecol. Evol.*, 8, 28–36, doi:10.1111/2041–210X.12628.

Zheng, S., Hu, J., Ma, Z., Lindenmayer, D. & Liu, J. (2023). Increases in intraspecific body size variation are common among north american mammals and birds between 1880 and 2020. *Nature Ecology and Evolution*, 7, 347–354, https://doi.org/10.1038/s41559-022-01967-w.

## Supplemental Results and Figures

#### Comparing raw variance changes using

Analysis of suggested that variance increases with higher temperatures across all habitat types, with terrestrial ectotherms having the smallest increase in variance ([Figure 9](#fig-s1)). **?@tbl-s1**

|  |
| --- |
| Figure 9- lnVR |

| **Parameter** | **Estimate** | **Est.Error** | **l-95% CI** | **u-95% CI** |
| --- | --- | --- | --- | --- |
| **Fixed Effects** | | | | |
| Intercept | 0.4932 | 0.10684 | 0.2984 | 0.7281 |
| Acclimation Time (z scaled) | -0.0001 | 0.00071 | -0.0015 | 0.0013 |
| Acclimation Effect | -0.0247 | 0.04247 | -0.1097 | 0.0593 |
| Habitat (Marine) | -0.0024 | 0.09890 | -0.1957 | 0.1968 |
| Habitat (Terrestrial) | -0.2032 | 0.10196 | -0.3956 | -0.0049 |
| Acclimation\*Marine | -0.0857 | 0.07817 | -0.2389 | 0.0700 |
| **Random Effects** |  |  |  |  |
| Study | 0.3647 | 0.03944 | 0.2910 | 0.4434 |
| Phylogeny | 0.1194 | 0.09729 | 0.0043 | 0.3630 |
| Species | 0.0821 | 0.05471 | 0.0041 | 0.2017 |
| Trait | 0.3134 | 0.04159 | 0.2386 | 0.3975 |

#### Plots of for multi-level models

|  |
| --- |
| Figure 10- estimates. A) B) and C) . |

#### Publicaton Bias Analysis

Funnel plots did not show any noticable deviation from the typical funnel shape for any of the effect size estimates ([Figure 11](#fig-s2)).

|  |
| --- |
| Figure 11- Funnel plot of precision (1/sampling standard error) against effect size for A) log response ratio (), B)log coefficient of variance ratio () and C) log variance ratio (). Both acute (‘green’) and acclimation (‘orange’) effect sizes are plotted. |