Limited plasticity but increased variance in physiological rates across ectotherm populations under climate change

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Abstract

Climate change causes warmer and more variable temperatures globally, impacting physiological rates and function in ectothermic animals. Acclimation of physiological rates can help maintain function. However, it is unresolved how variance in physiological rates changes with temperature despite its potential ecological and evolutionary importance. We tested whether thermal variation affects physiological traits in ectotherms by conducting a meta-analysis (>1900 effects from 226 species), and applying new effect sizes that quantify how trait mean and variance change as temperature increases. We show that variance in physiological rates increases at higher temperatures, but that the magnitude of change depends on habitat. Freshwater and marine ectotherms are capable of acclimation and have the greatest increase in variance. In contrast, terrestrial ectotherms lack the capacity for acclimation and have smaller increases in variance. Simulations suggest that these patterns may result from differences in among-individual variation in thermal breadth and optima of performance curves across habitats. Our results highlight the greater vulnerability of terrestrial ectotherms to climate change because limited increases in variance may provide less raw material for evolutionary adaptation. Considering both acclimation capacity and variance in physiological rates side-by-side is therefore important for understanding how climate change will impact populations.

Introduction

Climate change is expected to result in warmer and more variable thermal environments globally (Easterling *et al.* 2000; Ummenhofer & Meehl 2017; Suarez-Gutierrez *et al.* 2023). Greater thermal variability is predicted to pose strong selection pressure that leads to genetic adaptation and/or the evolution of adaptive phenotypic plasticity – both of which are considered important for population resilience to human-induced climate change (Chevin *et al.* 2010; Merila & Hendry 2014; Chevin & Lande 2015; Seebacher *et al.* 2015, 2023; Nunney 2016; Chevin & Hoffmann 2017; Cooke *et al.* 2021). Without plasticity or adaptation, high extinction rates are expected unless organisms can migrate to track suitable habitats (Cahill *et al.* 2012; Nunney 2016).

Reversible phenotypic plasticity, such as physiological acclimation, is relatively rapid and can be fine-tuned to environmental conditions making it the first 'line-of-defense' against environmental change (Dewitt *et al.* 1998; Scheiner *et al.* 2020). For example, physiological rates are known to speed up as temperature increases because of the thermodynamic effects on chemical reaction rates – so called 'acute' temperature responses (Figure 1). However, longer-lasting (days-weeks) temperature increases that move environmental conditions away from thermal optima of physiological rate functions (i.e., thermal performance curves) can be mitigated by acclimation, which adjust reaction rates (Seebacher *et al.* 2015; Havird *et al.* 2020). Physiological acclimation is driven by endocrine and epigenetic processes that change the underlying physiology to allow organisms to maintain physiological performance around a fitness optimum despite changes in the environment (Little *et al.* 2013; Taff & Vitousek 2016; Seebacher & Simmonds 2019). Acclimation therefore alters acute thermal sensitivity to offset the potentially negative effects of acute temperature changes (e.g., higher energetic demands). Acclimation, however, does not necessarily result in complete compensation in response to environmental change (*sensu* Huey *et al.* 1999). Rather, increased physiological rates are often only partially compensated (Huey *et al.* 1999; Havird *et al.* 2020).

Acclimation is expected to evolve in populations experiencing high but predictable environmental variability, and when the costs of plasticity are low (Dewitt *et al.* 1998; Reed *et al.* 2010; Nunney 2016; Chevin & Hoffmann 2017; Scheiner *et al.* 2020). Thermal variation and predictability differ across habitats (terrestrial, marine and freshwater) (Steele *et al.* 2019), and it may be expected that organisms within these habitats vary in their capacity for acclimation. Rohr *et al.* (2018) show relationships between acclimation capacity, latitude and body size suggesting climate could be an important driver of acclimation responses. In addition, species occupying terrestrial habitats exhibit weaker acclimation capacities and, therefore may be particularly vulnerable to climate change given their greater probability of experiencing thermal extremes that overwhelm physiological homeostasis (Hoffmann *et al.* 2013; Gunderson & Stillman 2015; Seebacher *et al.* 2015; Morley *et al.* 2019). In contrast, marine and freshwater organisms appear to have greater physiological acclimation capacity (e.g., Seebacher *et al.* 2015; Pottier *et al.* 2022). However, the focus of research up to now has been primarily on mean physiological responses neglecting how variability in physiological processes might also be impacted by higher temperatures.

As mean physiological rates increase with temperature it is likely that intrapopulation variability will also be impacted. Positive mean-variance relationships are common across biology suggesting that, as physiological rates increase with temperature, so too should variability [i.e., Taylor's Law; Giometto *et al.* (2015)]. Differences in the shape of thermal performance curves (thermal breadth, maximal performance and thermal optima) can reflect among-individual variability at higher temperatures, which can also differ between different levels of biological organisation, environmental conditions, and acclimation responses (Angilletta 2009; Schulte *et al.* 2011; Tattersall *et al.* 2012; Rezende & Bozinovic 2019). Presumably, increases in variation in physiological rates reflects environment-mediated changes to underlying regulatory networks, which can lead to an increased variation in phenotypic outcomes (Costanzo *et al.* 2021; Matthey-Doret *et al.* 2020). Quantifying levels of among-individual variation in thermal performance curves is important to understand their capacity to evolve, as well as the resilience of populations to environmental change (Careau *et al.* 2014).

Importantly, changes in physiological rate variability are expected to have consequences for the flow of energy within and between populations, communities, and ecosystems (Bolnick *et al.* 2011; Hendry 2016; Barneche *et al.* 2021; Sanderson *et al.* 2023; Seebacher *et al.* 2023). Generally, more variable populations are predicted to be associated with broader niches, have increased growth rates, and decreased vulnerability to environmental change, lowering extinction risk (i.e., "portfolio effects" *sensu* Schindler *et al.* 2010, and see also Bolnick *et al.* 2011; Forsman 2014; Forsman 2015; Hart *et al.* 2016; Hendry 2016; Pörtner 2021). In addition, if phenotypic and genetic variation in physiological rates are correlated and linked to fitness, reduced phenotypic variation may limit responses to selection and reduce the capacity of populations to evolve (Hoffmann & Sgrò 2011; Pelletier & Coulson 2012). Therefore, maintaining intrapopulation

variability in physiological rates in a warmer world may be important for population resilience to climate change.

Here, we use meta-analysis to establish the current state-of-knowledge of the extent to which aquatic and terrestrial ectotherms are capable of physiological plasticity. We then developed new effect sizes to quantify how variance in physiological rates changes with temperature to ask the following questions regarding acclimation-induced changes in trait means and variances: 1) Does variance in physiological rates change as temperatures rise? 2) Are temperature effects on means of physiological rates greater than changes in variance across aquatic and terrestrial ectotherms? 3) How do changes in trait mean and variance relate to different life-stages, traits, and habitats? 4) Are changes in mean and variance of physiological rates impacted by past climate history? 5) How are 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. We extracted data from an extra 65 papers (with a total of 238 effects; a 34.03% increase in the number of published articles). For full details on the search protocol, see the *Supplementary Materials*, where we also provide a PRISMA flow diagram of our extraction process (Figure S1).

Data Compilation

We extracted means, standard deviations, and sample sizes for physiological rates measured at the two test temperatures that coincided with acclimation temperatures (Figure 1A). If there were more than two temperatures, we chose only the temperatures that fell within the most likely natural range of temperatures experienced by the species in question (Figure 1). 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, and the latitude and longitude from where the experimental animals were sourced. For studies that did not provide latitude and longitude for the population, we searched for similar studies by the same lab group to identify where the population was likely to have been sourced. If the experimental animals were derived from the wild, we recorded the nearest latitude and longitude of the field collection site. If the animals were sourced from a commercial supplier, we took the latitude and longitude of the supplier. 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.

Q_{10} 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 ($lnRR_{Q_{10}}$) as well as the variability in physiological rates ($lnVR_{Q_{10}}$ and $lnCVR_{Q_{10}}$) (Figure 1). These effect sizes are similar to the traditional temperature coefficient (Q_{10}), but with formal analytical approximations of their sampling variances. Sampling variances for effect sizes allowed us to make use of traditional meta-analytic modelling approaches.

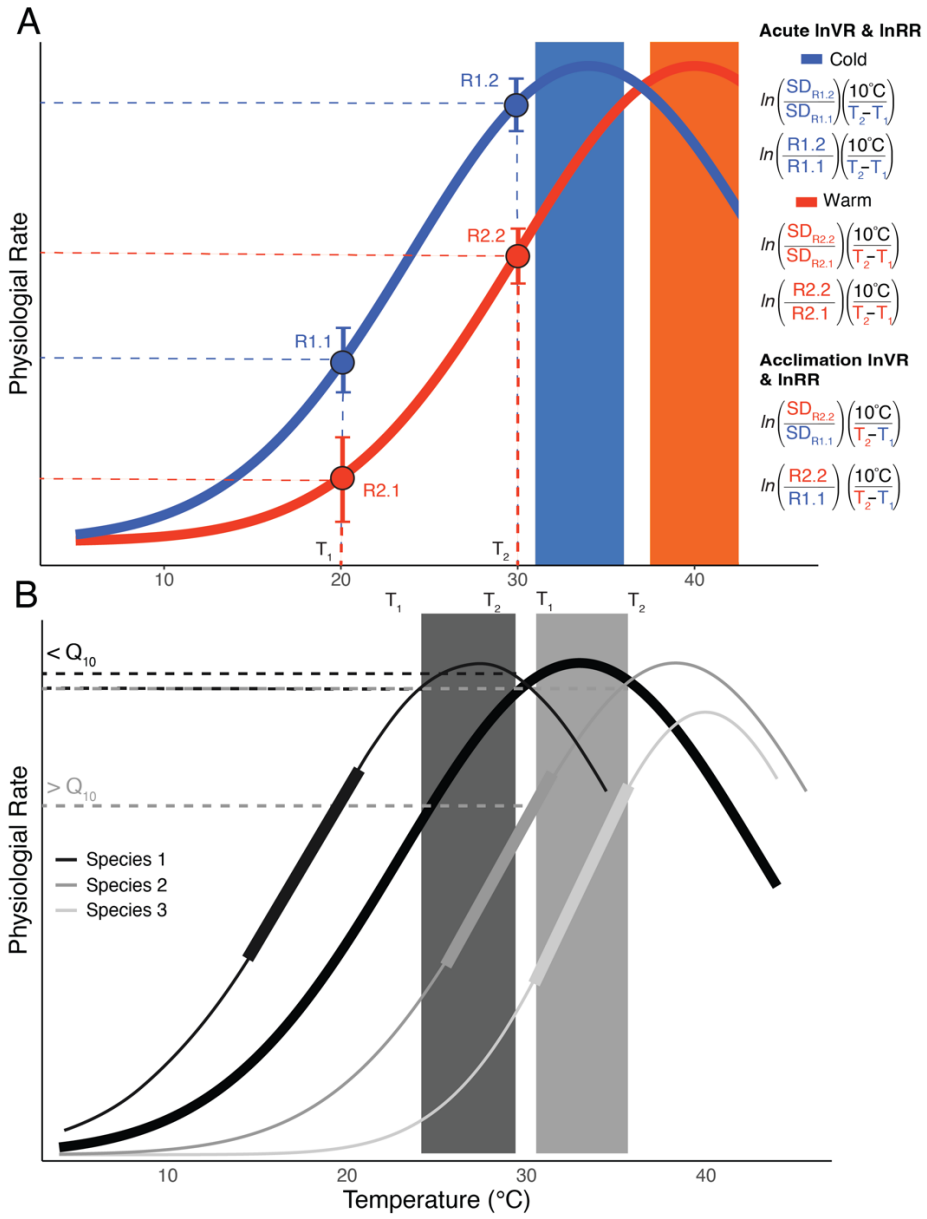

Figure 1- Calculations of acute and acclimation $lnVR_{Q_{10}}$ and $lnRR_{Q_{10}}$. (A) Two idealised thermal performance curves for animals held at 'cold' ('blue') temperatures and warm ('red') temperatures. Shaded blue and red areas are the thermal optima of the performance curves. Physiological rates are measured for a sample of ectotherms at two different temperatures along the thermal performance curves (T_1 = 20°C and T_2 = 30°C) for both curves. At each temperature a mean physiological rate (R) (points) and its standard deviation (SD) (error bars above and below mean) are estimated. R1.1 and R1.2 are the rates and associated SD (subscripted) for the cold acclimated animals at temperature 1 and 2, respectively. R2.1 and R2.2 are the rates and associated SD (subscripted) for the warm acclimated animals at temperature 1 and 2, respectively. An example of how acute and acclimation $lnVR_{Q_{10}}$ and $lnRR_{Q_{10}}$ are calculated from the treatments within the study is provided on the right-hand side of the figure with reference to each of the four possible groups. Two acute effect sizes can be calculated, one for the cold acclimated animals and one for the warm acclimated animals. (B) Species are expected, *a priori*, to vary in their thermal performance curves (thin lines) around an average (thick black line). We restricted our data to areas of each species' performance curve that fell within the natural thermal range of the species (thick lines on each species-level curve). However, given it was not possible to measure the full performance curve for each species some test temperatures within studies may have converged on or moved past the thermal optima. In such

cases, we expected our Q_{10} effect sizes to be smaller as indicated by comparing the black dashed lines to grey dashed lines.

Comparing changes in mean physiological rates

To compare mean physiological rates, we calculated the log Q_{10} response ratio, $lnRR_{Q_{10}}$ (Noble *et al.* 2022) as follows:

$$lnRR_{Q_{10}} = ln\left(\frac{R_2}{R_1}\right)\left(\frac{10^{\circ}C}{T_2 - T_1}\right) \qquad (1)$$

Where, R_1 and R_2 are mean physiological rates at temperatures T_1 and T_2, respectively. Log transformation of this ratio makes the effect size normally distributed. Equation 1 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 comparisons of the means from two temperature treatments directly regardless of the absolute measurement temperatures. The sampling variance for Equation 1 can be computed as follows (as described in Noble *et al.* 2022):

$$s_{lnRR_{Q_{10}}} = \left(\frac{SD_2^2}{R_2^2 N_2} + \frac{SD_1^2}{R_1^2 N_1}\right)\left(\frac{10^{\circ}C}{T_2 - T_1}\right)^2 \qquad (2)$$

Here, SD_1^2 and SD_2^2 are the standard deviations, and N_1 and N_2 are the sample sizes of the groups measured at T_1 and T_2, respectively (Figure 1A).

Comparing variance in physiological rates

Nakagawa *et al.* (2015) 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 Q_{10} analogues (and associated sampling variance) as follows:

$$lnVR_{Q_{10}} = ln\left(\frac{SD_2}{SD_1}\right)\left(\frac{10^{\circ}C}{T_2 - T_1}\right) \qquad (3)$$

$$s_{lnVR_{Q_{10}}} = \left(\frac{1}{2(N_2 - 1)} + \frac{1}{2(N_1 - 1)}\right)\left(\frac{10^{\circ}C}{T_2 - T_1}\right)^2 \qquad (4)$$

where parameters are defined above. Equation 3 and Equation 4 describe the change in physiological rate variance (Equation 3) normalised to a 10°C temperature change along with its sampling variance (Equation 4). As discussed by Nakagawa *et al.* (2015) there is often a strong mean-variance relationship. As such, the coefficient of variation is often used because it permits standardisation of changes in variance as mean trait values change:

$$lnCVR_{Q_{10}} = ln\left(\frac{\mathrm{CV}_2}{\mathrm{CV}_1}\right)\left(\frac{10^{\circ}C}{T_2 - T_1}\right) \qquad (5)$$

$$s_{lnCVR_{Q_{10}}} = \left[\frac{(\mathrm{SD}_1)^2}{N_1(R_1)^2} + \frac{(\mathrm{SD}_2)^2}{N_2(R_2)^2} + \frac{1}{2(N_1 - 1)} + \frac{1}{2(N_2 - 1)}\right]\left(\frac{10^{\circ}C}{T_2 - T_1}\right)^2 \qquad (6)$$

where CV is the coefficient of variation defined as SD/R. We refer to $lnCVR_{Q_{10}}$ as relative variance because variance changes are relative to the mean. While we analyse $lnCVR_{Q_{10}}$ it does make the assumption that SD

is directly proportional to the mean, and given that we are analysing the mean alongside the variance we present results on $lnCVR_{Q_{10}}$ in the supplement.

Calculating acute and acclimation $\boldsymbol{lnRR_{Q_{10}}}$, $\boldsymbol{lnVR_{Q_{10}}}$ and $\boldsymbol{lnCVR_{Q_{10}}}$ estimates

R_1, R_2, SD_1^2 and SD_2^2 can all be taken from samples of organisms measured acutely at two temperatures or after having been acclimated these same temperatures (Figure 1A). For studies that measure acute and acclimated responses we used the mean, standard deviation, and sample size to derive both acute and acclimation $lnRR_{Q_{10}}$, $lnVR_{Q_{10}}$ and $lnCVR_{Q_{10}}$ estimates. For studies that only measured R_1, R_2, SD_1^2 and SD_2^2 acutely we could only calculate acute versions of these effect size estimates. For all effect sizes the higher temperature was in the numerator and the lower of the two temperatures in the denominator. As such, positive effect sizes indicate that the mean (i.e., $lnRR_{Q_{10}}$), variance ($lnVR_{Q_{10}}$) or relative variance (i.e., $lnCVR_{Q_{10}}$) is larger at the higher of the two temperatures (numerator) when standardized to 10°C. Importantly, our effect sizes, as with Q_{10} more generally, all assume that the effect of temperature on physiological rates (or changes in variance) is log-linear (see Figure 1B & *Supplementary Materials* for further discussion). We test and control for any violations of these assumptions in our analysis (see below).

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. This included the duration of acclimation in days given that acclimation responses may depend on how long chronic temperature exposure occurs. 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 Q_{10} estimates. Physiological rate measures varied widely across the studies but could generally be grouped into two broad categories that included whole-organism measures, which all integrate a diversity of physiological and biochemical processes, and biochemical processes (e.g., enzyme reaction rates, proton leak) (Seebacher *et al.* 2015; Rezende & Bozinovic 2019). We explore differences across more detailed trait categories in *Supplemental Materials*, but note sample sizes are limited for many traits. Traits that could not be categorised into these two we classified as 'Other'.

Meta-Analysis

We analysed our data using multilevel meta-analytic (MLMA) and meta-regression (MLMR) models in R (vers. 4.2.1) using *brms* (vers. 2.19.0 Bürkner 2017, 2018; "Stan development team. RStan" 2021) and *metafor* (vers. 4.6.0 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, 2023). In addition, Bayesian methods better protect against type I errors in the presence of complex sources of non-independence (Noble *et al.* 2017; Nakagawa *et al.* 2021b; Song *et al.* 2021). In all cases, frequentist and Bayesian models resulted in the same conclusions. 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 minimum of 3200 samples from the posterior distribution. We used flat Gaussian priors for 'fixed' effects (i.e.,$N(0,10)$) and a student t-distribution for 'random' effects (i.e., $student_t(3,0,10)$). We checked that all MCMC chains were mixing and had converged (i.e., $R_{hat} = 1$).

Multi-level Meta-analysis (MLMA) Models

We first fit multi-level meta-analysis (MLMA) models (i.e., intercept-only models) for both $lnRR_{Q_{10}}$ and $lnVR_{Q_{10}}$, that included study, species, trait type, and phylogeny as random effects to account for non-independence and identify sources of variability. We refer to this model structure as "Model 1" in the results. Our MLMA models allowed us to partition the variation in $lnRR_{Q_{10}}$ and $lnVR_{Q_{10}}$ among these key sources

while accounting for total sampling variance in each. This allowed us to calculate the proportion of total heterogeneity [i.e., I^2_{total}; *sensu* Nakagawa & Santos (2012); Noble *et al.* (2022)] along with various I^2 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 for 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. 3.0.14) (Michonneau *et al.* 2016), and plotted using *ggtree* (vers. 3.6.2) (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). Models fit using correlation matrices computed with different power (p) parameters (from 0.5 – 1.0) had nearly identical AIC_c. As such, we used an intermediate value of p = 0.7. We used the R packages *ape* (vers. 5.7.1) (Paradis & Schliep 2019) and *phytools* (vers. 1.5.1) (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 $\pm$ SD = 37.98 $\pm$ 45.19 days), and terrestrial ectotherms were acclimated for a much shorter duration (mean $\pm$ SD = 23.53 $\pm$ 15.56 days, n = 125) than freshwater (mean $\pm$ SD = 36.81 $\pm$ 28.71 days, n = 430) and marine species (mean $\pm$ SD = 46.18 $\pm$ 67.21 days, n = 313). To control for these differences, acclimation time was mean-centered (mean = 0) and included in all our models, although it was not a strong predictor of effect size variation in any of our models (*Supplementary Materials*, Figure S3).

In addition to the acclimation period, all our models corrected for possible violations of the log-linearity assumption associated with effect size calculations (Figure 1; and see *Supplementary Materials* Figure S2). We predicted that, if $lnRR_{Q_{10}}$ and $lnVR_{Q_{10}}$ were not strictly log-linear there would be a decrease in average effect size for studies applying higher temperature treatments, because these temperatures are expected to either converge on or cross the thermal optima of the performance curve causing reaction rates to decelerate or decrease beyond T_{op} (Michaletz & Garen 2024). The benefit of this approach is that we could still use Q_{10} as an effect size while statistically correcting for the potential non-linearity that would be expected in the data at high treatment temperatures. Given that our data included a wide range of species and habitats, we also included a random slope of maximum temperature that varied across species because we expected that species would vary in their thermal performance curves, which would be reflected in experimental treatments. We mean-centered the maximum temperature and included it in our models.

With acclimation time and maximum temperature as moderators in all our models we proceeded to build separate models that tested our core questions. All estimates from our models are therefore conditioned on an average acclimation time (i.e., 37.98 days) and an average maximum temperature (i.e., 23°C) across the dataset.

We first tested the extent to which acute and acclimation $lnRR_{Q_{10}}$ and $lnVR_{Q_{10}}$ effect sizes varied between habitat types (i.e., terrestrial, freshwater, and marine). Models included an interaction between effect type (i.e., acute or acclimation) and habitat (referred to as "Model 2"). Reduced mean $lnRR_{Q_{10_{acclimation}}}$ relative to $lnRR_{Q_{10_{acute}}}$ indicates that acclimation to thermal environments results in (partial) compensation of physiological rates (i.e., phenotypic plasticity), whereas no differences between $lnRR_{Q_{10_{acute}}}$ and $lnRR_{Q_{10_{acclimation}}}$ indicates that organisms did not acclimate (Seebacher *et al.* 2015; Havird *et al.* 2020). In

contrast, a difference in $lnVR_{Q_{10}{}_{acclimation}}$ relative to $lnVR_{Q_{10}{}_{acute}}$ would show that changes in between-individual variation differ between acute responses and acclimation responses.

Second, we tested whether acute and acclimation $lnRR_{Q_{10}}$ and $lnVR_{Q_{10}}$ differed between whole-organism versus biochemical traits across habitats by fitting an model with an interaction between type, habitat and trait category (referred to as "Model 3"). We expected that whole-organism traits would be more likely to maintain variation in physiological function and be less likely to acclimate because whole-organism function relies on a greater number of biochemical reactions each with different thermal sensitivities (Fields 2001; Angilletta 2009).

Third, we tested whether different life-stages were 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 (referred to as "Model 4"). We predicted that acclimation responses would be more likely early in development compared to later in development as this pattern has been shown in previous studies (e.g., Moghadam *et al.* 2019), but that this should depend on the habitat type given the different constraints faced by different early life stages across major habitat types.

Finally, we tested whether the change in $lnRR_{Q_{10}{}_{acclimation}}$ and $lnVR_{Q_{10}}$ were predicted by climate variability (CV) (details on climate data can be found in the *Supplementary Materials*). We only used $lnRR_{Q_{10}{}_{acclimation}}$ $lnVR_{Q_{10}{}_{acclimation}}$ for these models because our predictions were specifically focused on acclimation responses; though there were no differences between $lnVR_{Q_{10}{}_{acclimation}}$ and $lnVR_{Q_{10}{}_{acute}}$. We fit models that included an interaction between habitat type and thermal coefficient of variability (CV) as moderators (referred to as "Model 5"). We also explored whether environmental predictability explained capacity for acclimation; we estimated predictability as the correlation of temperatures across months at a given location. However, such analyses are challenging to interpret because the temporal scale that is biologically relevant to different organisms will be different making the choice of lag to estimate the correlation difficult to apply across taxa. As such, we report a simple analysis in the *Supplementary Materials* but note that it does not differ from our CV analysis.

Modelling how climate change can impact relative variance in physiological rates

To explore the potential consequences of the impacts that human-induced climate change may have on variance in physiological rates we fit a model that included an interaction between acclimation type, habitat type, latitude and longitude (referred to as "Model 6"). We assumed that any change in $lnVR_{Q_{10}}$ 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 $lnVR_{Q_{10}}$ for each wild population in our dataset at its specific populations latitude and longitude. We first converted the predicted $lnVR_{Q_{10}}$ to a 1°C change as opposed to 10°C:

$$lnVR_{Q_1} = \frac{lnVR_{Q_{10}}}{10} \qquad (7)$$

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 scenarios in 2080.

Publication Bias

We explored the possibility for publication bias graphically using funnel plots, and more formally by including the square root of the inverse effective sample size ($\sqrt{1/ne}$) in our meta-regression models (Nakagawa *et al.* 2022). Funnel plot asymmetry indicates a form of publication bias called the 'file-drawer'

effect whereby low-powered studies are less likely to be published. However, graphical approaches do not account for sources of non-independence and high heterogeneity which can drive apparent funnel asymmetry (Nakagawa *et al.* 2022). As such, we included $\sqrt{1/ne}$ as a moderator in a multilevel meta-regression model that accounted for all the random (i.e, study, species, trait) and fixed effects (acclimation time, type of effect, habitat, trait category and the interaction between habitat type and trait category). There was no evidence for publication bias, and results are presented in the *Supplementary Materials* (see Figure S14).

Identifying patterns of among-individual variance in performance curves contributing to variance increases

We conducted a simple simulation as a sensitivity analysis to better understand the characteristics of performance curves that could lead to our observed changes in variance across temperatures and habitats. The simulation varied among-individual variation in performance curves to identify the parameters that could produce the results we observed. To simulate performance curves, we used an asymmetrical Gaussian function (Angilletta 2009):

$$P_T = 2\epsilon^{-\frac{(T-\delta)^2}{2\sigma^2}}\Phi\left(\alpha\frac{T-\delta}{\sigma}\right) \qquad (8)$$

where T is temperature, δ is the optimal temperature (the temperature where performance is maximized), σ the performance breadth, and α the skewness of the curve (see Figure S15 in *Supplementary Materials* for example curves). We simulated n = 1000 individual performance curves by varying the amount of between individual variance on each of the key parameters (δ, σ) in all possible combinations from 0.01 to 2. We also varied α, but this did not impact our conclusions and so we kept among-individual variation fixed for each simulation (at 0.01). From the population of performance curves, we took the standard deviation at two temperatures (18 and 28°C) to calculate $lnVR_{Q_{10}}$ and identify potential parameter spaces that could produce observed patterns in our empirical data.

Results

Data Summary

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 2). We had more data on acute thermal responses (n = 1115) compared to acclimation responses (n = 798) because acute responses were reported for each of the two acclimation temperatures (Figure 2). The two acute $lnRR_{Q_{10}}$ effect sizes (Figure 1A) differed significantly from each other (β = 0.07, 95% CI: 0.03 to 0.1, p_{MCMC} = < 0.0001) with animals acclimated to high temperatures having slightly higher average $lnRR_{Q_{10}}$ (μ = 0.62, 95% CI: 95% CI: 0.51 to 0.72, p_{MCMC} = < 0.0001, Q_{10} = 1.85) compared to animals at lower temperatures (μ = 0.55, 95% CI: 95% CI: 0.44 to 0.66, p_{MCMC} = < 0.0001, Q_{10} = 1.73) (Figure S4). However, on average they were in the same direction and only differed by ~10%. Hence, we averaged the two acute $lnRR_{Q_{10}}$ effect sizes in subsequent analyses.

Most of the effect size estimates came from measurements of metabolic rates (both resting and maximal – $N_{species}$ = 190, $N_{effects}$ = 1023), metabolic enzyme rates ($N_{species}$ = 61, $N_{effects}$ = 798) and whole-organism performance traits (i.e., measures of locomotor speed and endurance – $N_{species}$ = 73, $N_{effects}$ = 321).

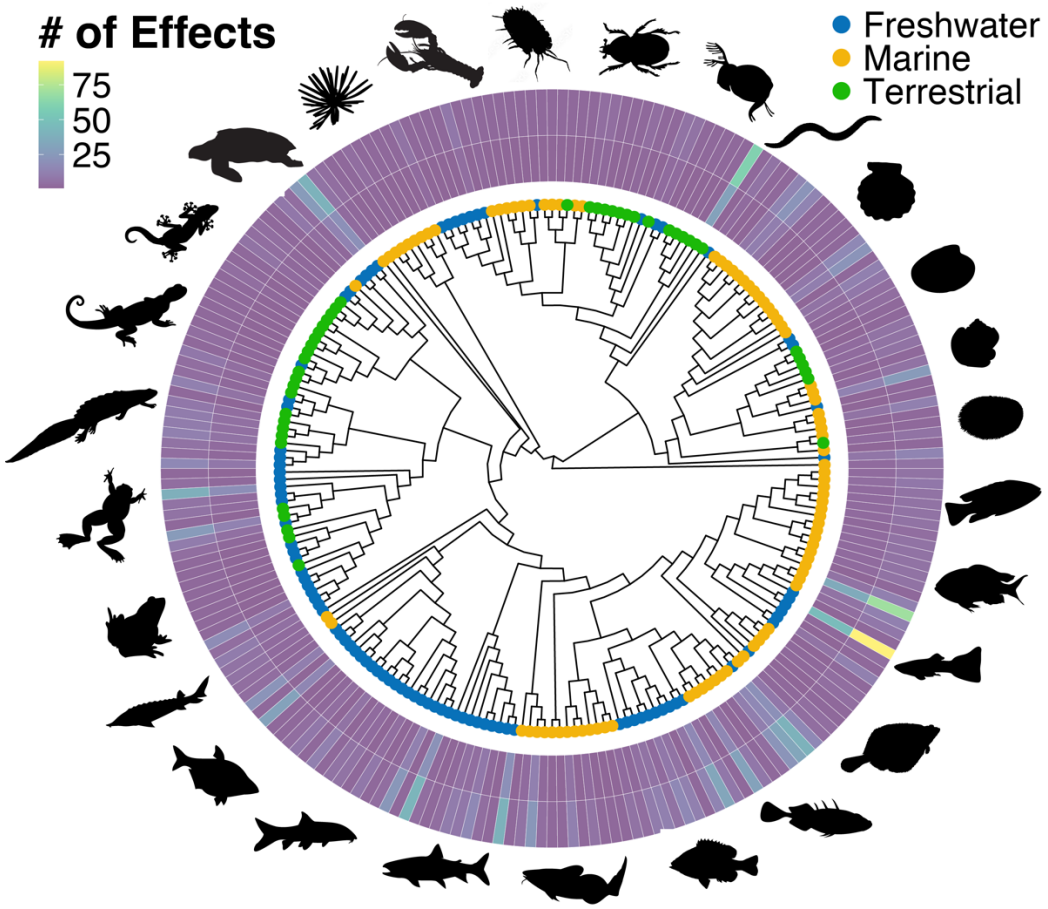

Figure 2- Phylogenetic distribution of acute and acclimation $lnRR_{Q_{10}}$ and $lnVR_{Q_{10}}$ estimates across major habitats. The total number of acute and acclimation $lnRR_{Q_{10}}$ and $lnVR_{Q_{10}}$ effect sizes are indicated by the coloured bars, and the colouring at the tips of the phylogeny indicates marine, freshwater, and terrestrial habitats. Silhouettes are only representative taxa of major clades within the tree.

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

Results from "Model 1" (see "Meta-Analysis" above) show that effect heterogeneity was high (only 2.85% of the variance was the result of sampling variability, 95% CI: 2.38 to 3.32%), and most variance was 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 (i.e., species random effect) explained little variation in acute and acclimation responses (Species: 2.39%, 95% CI: 0.01 to 8.1%; Phylogeny: 2.89% , 95% CI: 0 to 12.94%). These patterns were similar for $lnVR_{Q_{10}}$ (see *Supplementary Materials*, Figure S12).

Physiological rates increased more in terrestrial ectotherms (μ = 0.62, 95% CI: 0.49 to 0.75) compared to marine (μ = 0.52, 95% CI: 0.41 to 0.64) and freshwater ectotherms (μ = 0.56, 95% CI: 0.46 to 0.67), but did not differ significantly betweem aquatic and terrestrial habiatats (Terrestrial - Marine: β = 0.1, 95% CI: -0.03 to 0.23, p_{MCMC} = 0.14; Terrestrial - Freshwater: β = 0.06, 95% CI: -0.04 to 0.17, p_{MCMC} = 0.24) ("Model 2"). However, capacity for acclimation depended on the habitat. Ectotherms in marine and freshwater environments showed partial compensation of physiological rates (Figure 3A) amounting to reduced $lnRR_{Q_{10_{acclimation}}}$ of 17.11% (95% CI: -24.2 to -10.61) in freshwater and 16.05% (95% CI: -26.92 to -4.67)

in marine environments. In contrast, terrestrial ectotherms showed no acclimation with a 6.52% increase in $lnRR_{Q_{10}{}_{acclimation}}$ (95% CI: -5.94 to 20.47, Figure 3A).

Across habitats, the extent to which whole-organism versus biochemical traits acclimated varied ("Model 3"; Figure 4A-C). Biochemical traits acclimated to a greater extent compared to whole-organism traits in marine habitats (Figure 4B), whereas both whole-organism and biochemical traits acclimated similarly in freshwater ectotherms (Figure 4C). Neither trait category acclimated in terrestrial ectotherms (Figure 4A).

Acclimation capacity did not vary consistently by life-history stage with no differences in $lnRR_{Q_{10}{}_{acclimation}}$ and $lnRR_{Q_{10}{}_{acute}}$ between adult and juveniles, except for marine habitats where adults acclimated to a greater extent ("Model 4"; Figure 5A-C). Averaging over acute and acclimation effects there were also no differences between adults and juveniles within habitats (Adult-Juvenile: Terrestrial: -0.07, 95% CI: -0.39 to 0.22, p_{MCMC} = 0.67; Marine: 0, 95% CI: -0.21 to 0.22, p_{MCMC} = 0.98; Freshwater: 0, 95% CI: -0.12 to 0.11, p_{MCMC} = 0.94).

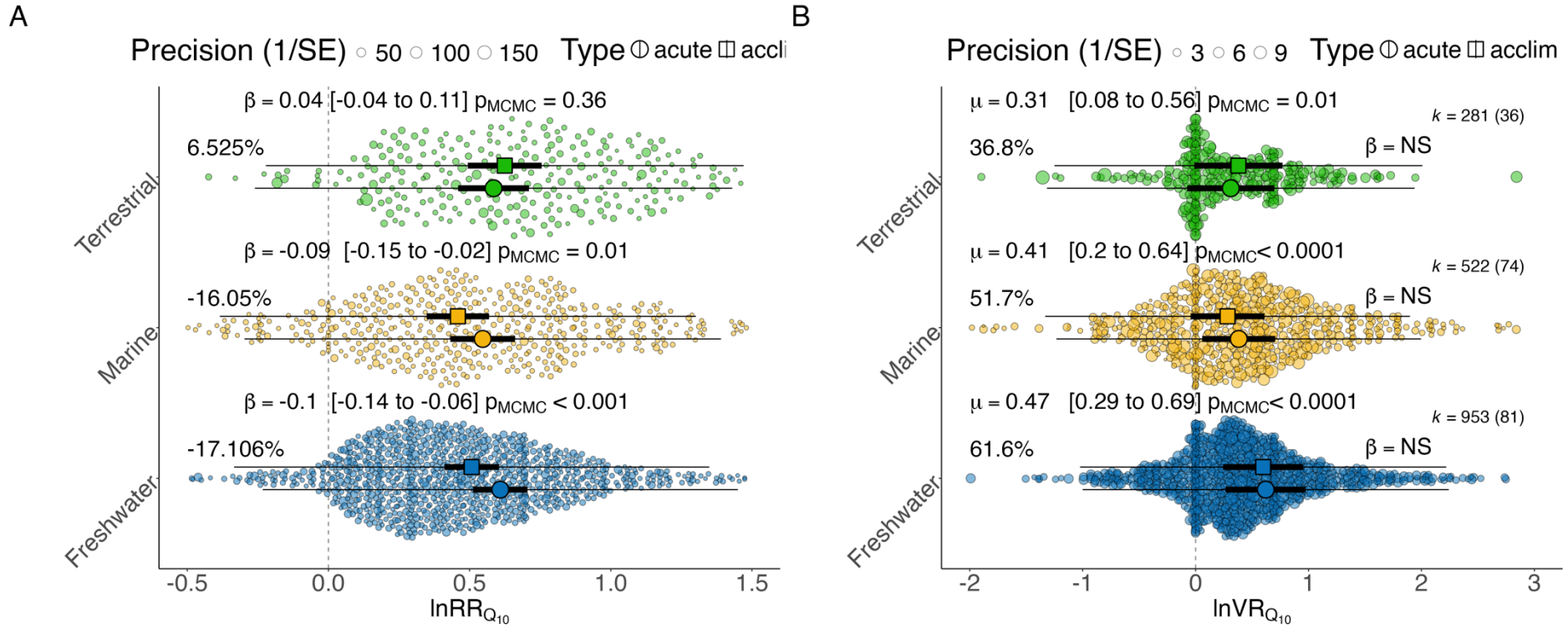

Figure 3- Meta-analysis results for different habitats. In both panels, thick bars are 95% confidence intervals (CI) and thin bars 95% prediction intervals (PI). β values are the contrasts between acute and acclimation means within each habitat. μ values are the overall meta-analytic means averaged across acute and acclimation types within each habitat type. In both cases, their 95% CI's are indicated within square brackets. p_{MCMC} values are the posterior probability of the contrast or overall meta-analytic mean being different from zero. (A) Mean acute and acclimation $lnRR_{Q_{10}}$ across ectotherms in marine, freshwater, and terrestrial habitats. Overall mean physiological rates (μ) across the habitats are provided in the results for simplicity and only contrasts between acute and acclimation $lnRR_{Q_{10}}$ are shown (B) Mean acute and acclimation $lnVR_{Q_{10}}$ across ectotherms in marine, freshwater and terrestrial habitats. For both plots, k = total number of effect size estimates while the numbers in brackets indicate the number of species. Sample sizes are the same for panel A and B. For ease of visualisation, all the raw data plotted for both acute and acclimation type effect sizes are presented as circles.

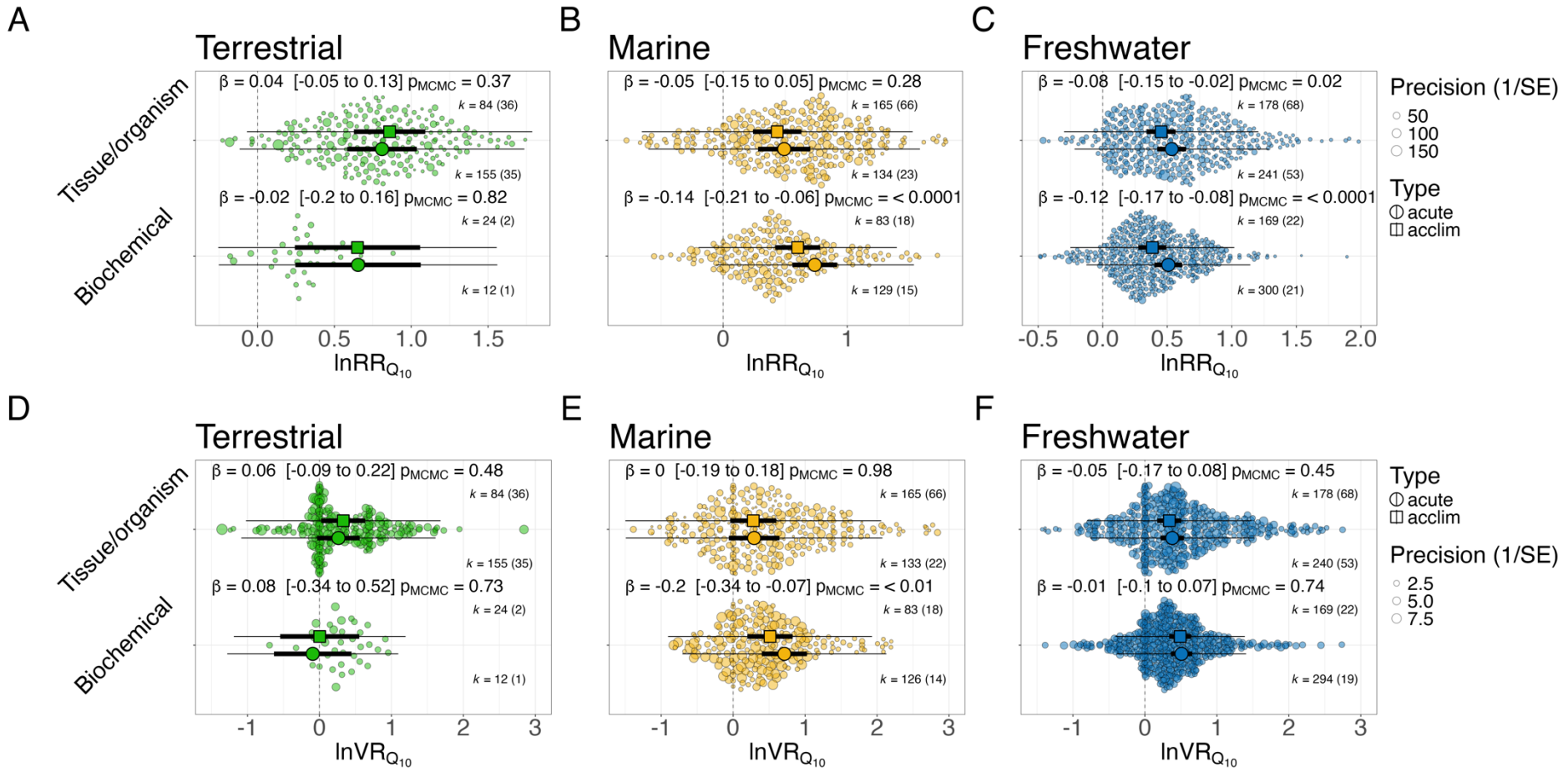

Figure 4- Meta-analysis results for organismal and biochemical trait categories. Estimated mean acclimation and acute $lnRR_{Q_{10}}$ (A-C) and $lnVR_{Q_{10}}$ (D-F) effect sizes for tissue/whole-orgamism traits and biochemical traits across terrestrial (A & D), marine (B & E) and freshwater (C & F) ectotherms. Across all plots, thick bars indicate 95% confidence intervals and thin bars indicate 95% prediction intervals. k = total number of effect size estimates while the numbers in brackets indicate the number of species. For ease of visualisation, raw data for both trait categories are presented but points are not distinguished by different symbols.

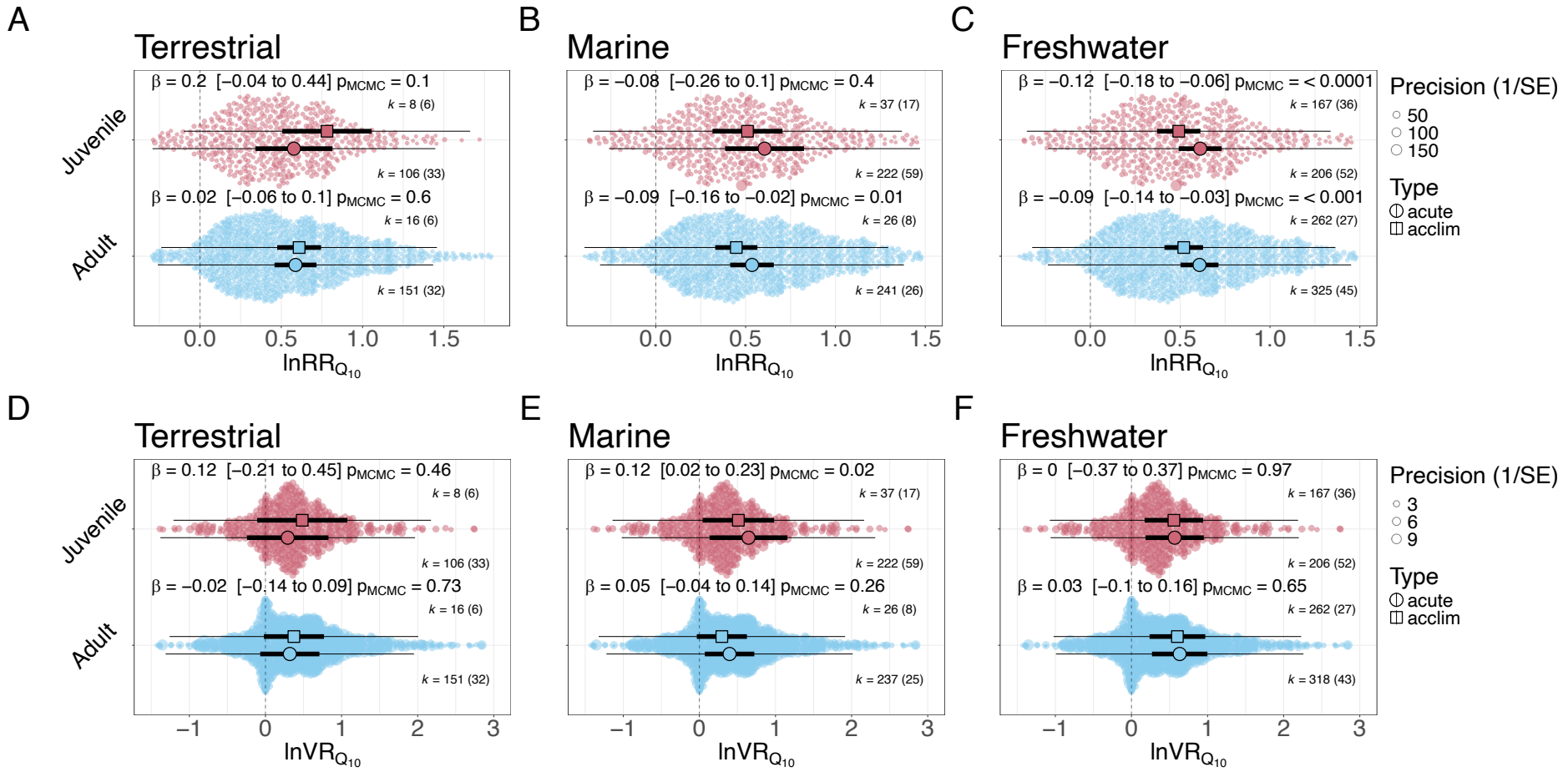

Figure 5- Meta-analysis results for different life stages. Estimated mean acclimation and acute $lnRR_{Q_{10}}$ (A-C) and $lnVR_{Q_{10}}$ (D-F) for adult (a) and juvenile (j) life-history stages for terrestrial (A & D), marine (B & E) and freshwater (C & F) ectotherms. Across all plots, thick bars indicate 95% confidence intervals and thin bars indicate 95% prediction intervals. k = total number of effect size estimates while the numbers in brackets indicate the number of species. For ease of visualisation, raw data for both adult and juvenile life-history stages are presented but points are not distinguished by different symbols. β values are the contrasts between acute and acclimation means within each life stage. p_{MCMC} values are the posterior probability of the contrast being different from zero.

Variation in physiological rates increases but to a greater extent in aquatic compared terrestrial ectotherms

Variance in physiological rates ($lnVR_{Q_{10}}$) showed an increase with increasing temperature across all habitat types (Figure 3B). Overall, there was a 36.76% (95% CI: 8.43 to 74.52, p_{MCMC} = 0.01) increase in physiological rate variance for terrestrial ectotherms, a 51.67% (95% CI:21.95 to 89.49, p_{MCMC} = < 0.01) increase in variation for marine ectotherms and a 61.59% (95% CI: 33.8 to 99.58, p_{MCMC} = < 0.0001) increase in variance for freshwater ectotherms across 10°C (Figure 3; results from "Model 2"). Analysis of $lnCVR_{Q_{10}}$, which accounts for changes in mean physiological rates, also showed that the relative variance for terrestrial ectotherms decreased compared to marine and freshwater ectotherms, suggesting that increases in variance are less than expected for ectotherms occupying terrestrial habitats (See *Supplementary Materials,* Figure S6).

Physiological rate variance increased significantly more in freshwater compared to terrestrial ectotherms for acute responses (β = 0.2, 95% CI: 0 to 0.4, p_{MCMC} = 0.05), but not for acclimation responses because increases in rates were dampened by acclimation resulting in smaller increases in variance (β = 0.12, 95% CI: -0.1 to 0.34, p_{MCMC} = 0.3). While marine ectotherms had larger increases in variance compared to terrestrial ectotherms these were not significant (Acute: β = 0.18, 95% CI: -0.07 to 0.43, p_{MCMC} = 0.15; Acclimation: β = 0.01, 95% CI: -0.25 to 0.26, p_{MCMC} = 0.9)(Figure 3B). Marine and freshwater habitats did not differ in the extent of variance increases at higher temperatures (Acute: β = 0.03, 95% CI: -0.18 to 0.23, p_{MCMC} = 0.79; Acclimation: β = 0.1, 95% CI: -0.09 to 0.3, p_{MCMC} = 0.3). There were no differences between $lnVR_{Q_{10}{acute}}$ and $lnVR_{Q_{10}{acclimation}}$ within any habitat (Figure 3B). Differences in variance between habitats were driven by different scaling relationships between mean and variance with slopes varying across habitat types (see *Supplementary Materials* scaling analyses, Table S1 & Figure S5).

$lnVR_{Q_{10}}$ values from our simulations matched our empirical results in particular areas of parameter space (Figure 6). For a given among-individual variance in thermal breadth, terrestrial ectotherms are predicted to have lower among-individual variance in thermal optima compared to marine and freshwater ectotherms (Figure 6). In contrast, terrestrial ectotherms are expected to have higher levels of among-individual variance in thermal breadth when controlling for among-individual variance in thermal optima (Figure 6).

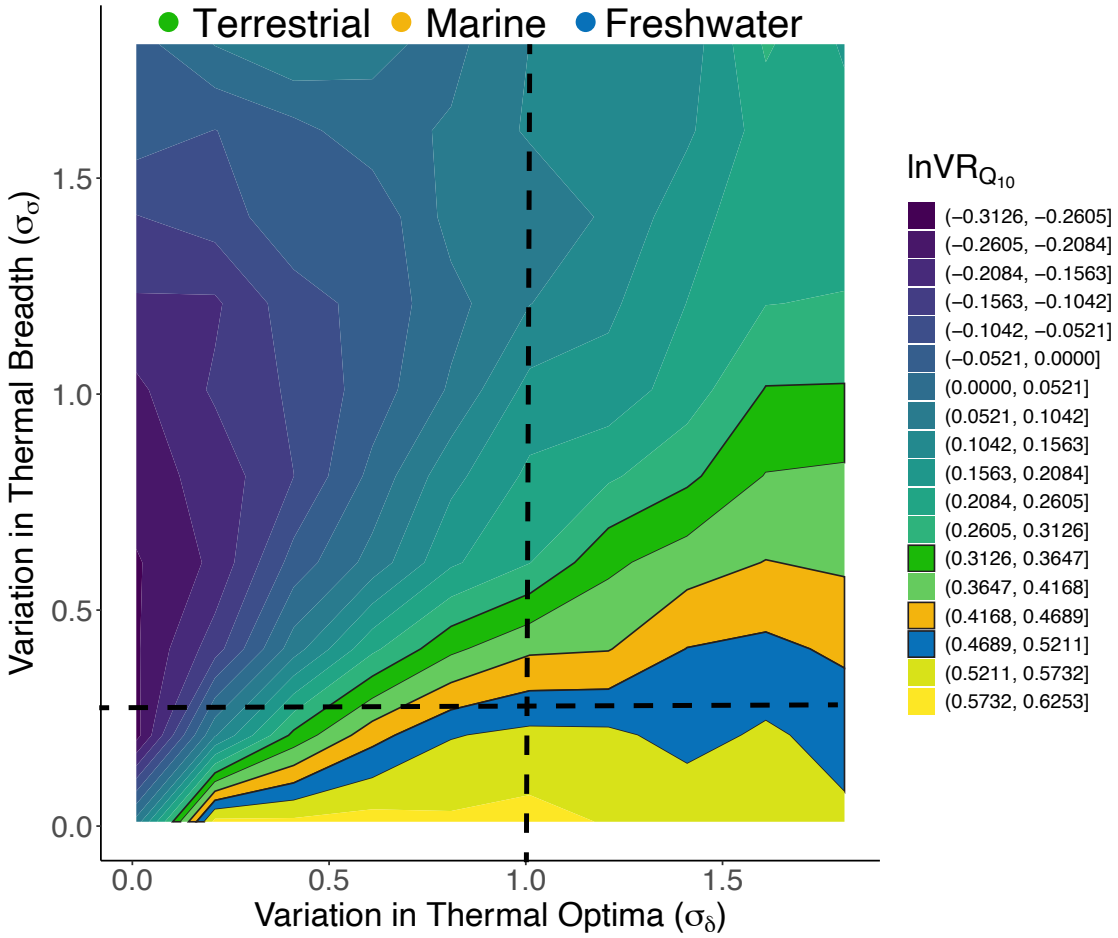

Figure 6- Results from sensitivity analysis. Expected $lnVR_{Q_{10}}$ from simulated performance curves when varying among-individual variance in thermal breadth (σ_δ = {0.01, 2}) and thermal optima (σ_σ = {0.01, 2}) while fixing the rate variance constant (σ_α = 0.01). In all simulations, population parameters were δ = 35, σ = 9, α = -15, and n = 1000 individuals were simulated for each combination of σ_δ and σ_σ. The parameter space that matches the observed mean $lnVR_{Q_{10}}$ for terrestrial (green), marine (orange) and freshwater (blue) ectotherms is highlighted. Dashed lines indicate the relative differences between the three habitat types when holding one variance parameter constant.

Across habitats biochemical processes tended to result in greater increases in variance at higher temperatures, but this was only significant for marine ectotherms (biochemical/whole-organism contrasts: Marine: β = 0.36, 95% CI: 0.02 to 0.71, p_{MCMC} = 0.04; Freshwater: β = 0.11, 95% CI: -0.11 to 0.33, p_{MCMC} = 0.32; Terrestrial: β = 0.19, 95% CI: -0.34 to 0.72, p_{MCMC} = 0.48) (Figure 4D-F; "Model 3"). Variance increases for biochemical traits was reduced during acclimation in marine ectotherms (Figure 4E).

Each life-history stage exhibited the same pattern of variance change in each of the habitats (Adult-Juvenile contrasts: Marine: β = 0.15, 95% CI: -0.19 to 0.53, p_{MCMC} = 0.41; Freshwater: β = 0.02, 95% CI: -0.16 to 0.2, p_{MCMC} = 0.8; Terrestrial: β = 0.02, 95% CI: -0.36 to 0.4, p_{MCMC} = 0.92), with no differences between acute and acclimation effect types ("Model 4"; Figure 5).

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

Thermal variability (i.e., CV) experienced by a population in the past did not explain acclimation capacity (Figure 7A–C) or changes in physiological rate variance (Figure 7D–F) among terrestrial, marine or freshwater populations ("Model 5").

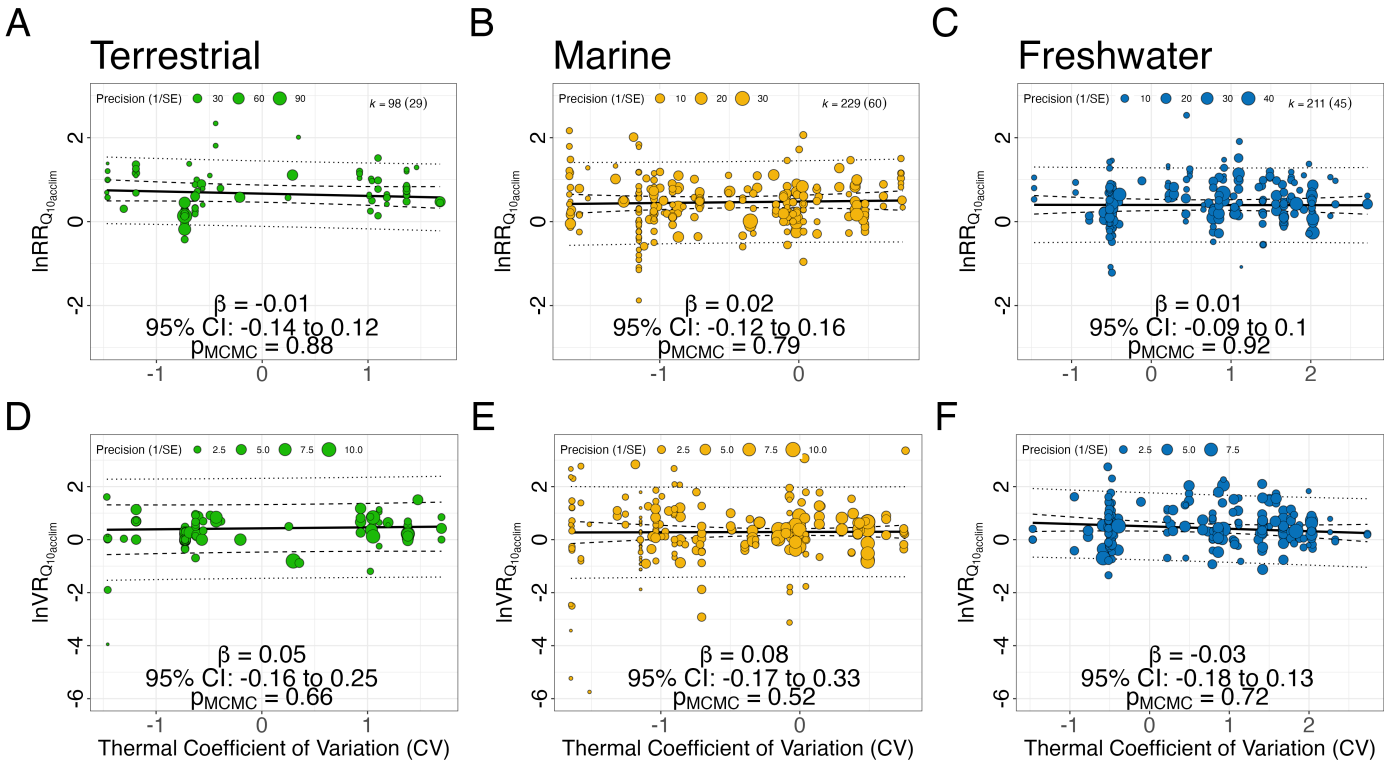

Figure 7- Past climate variability did not predict acclimation responses. Predicted mean acclimation (thick black line) $lnRR_{Q_{10}{}_{acclim}}$ (A-C) and $lnVR_{Q_{10}{}_{acclim}}$ (E-G) as a function of the Thermal Coefficient of Variation (CV) for wild populations across marine, freshwater and terrestrial habitats. Dashed lines indicate 95% confidence intervals and dotted lines indicate 95% prediction intervals. Model slope (β) along with the 95% CI and p_{MCMC} values for the slopes are shown for each habitat.

Changes in physiological rate variance under climate change

Measurements of acute and acclimation responses from wild ectotherms were much less common than from captive populations ($N_{species}$ = 134, from 188 wild populations). Globally, there was a clear bias towards species in the Northern Hemisphere (Figure 8A-C). Projected changes in physiological rate variance were highly variable across the globe, however, variance was predicted to increase at all locations.

Using the ERA5 climate model, predictions of current global changes in physiological rate variance were generally conservative with our model explained ~ 43% of the variation in the observed data (R^2 = 0.43, 95% CI: 0.33 to 0.51). Climate change is predicted to result, on average, in a 28.67% increase in variance for freshwater systems (95% CI: 15.43 to 47.16%, p_{MCMC} = < 0.0001), a 15.63% increase in marine systems (95% CI: 0.59 to 30.41%, p_{MCMC} = < 0.0001), and a 13.03% increase in terrestrial systems (95% CI: 7.13 to 19.4%, p_{MCMC} = < 0.0001) under a RCP8.5 climate scenario (Figure 8D). All results are taken from "Model 6".

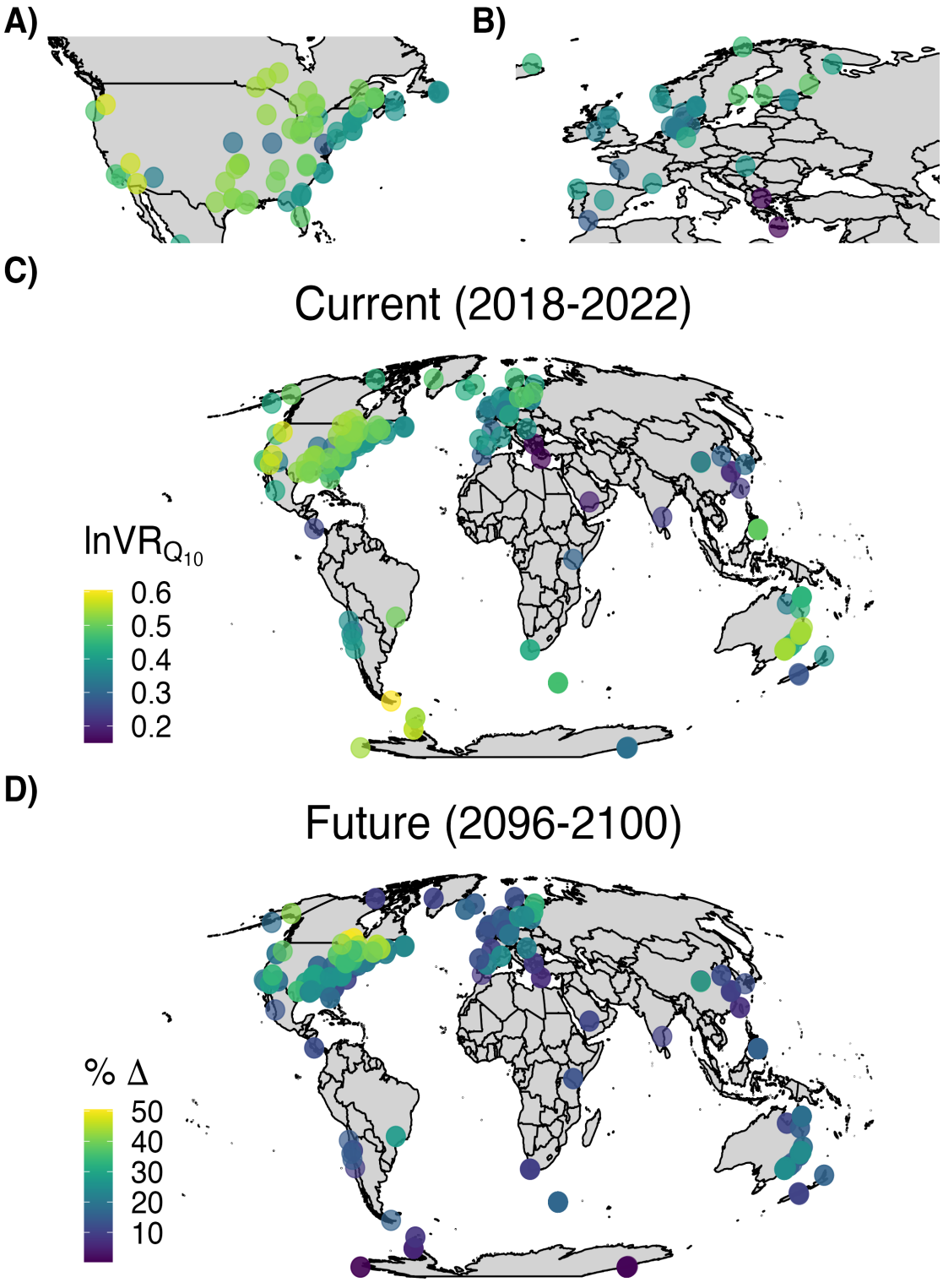

Figure 8- Potential effects of climate change on trait variance. Model predictions for the expected change in $lnVR_{Q_{10}}$ across the globe for terrestrial, marine and freshwater ectotherms. Predicted change in physiological rate variance for each population based on current temperatures (average from 2018-2022; A-C) as well as the expected change from current temperatures based on future temperature predictions (average from 2096-2100, D). Future climate predictions are the increase in variance expected under a RCP8.5 climate scenario relative to current climate conditions (% change).

Discussion

Understanding acclimation capacity and how variation in physiological rates change across populations and species is important for predicting the ecological and evolutionary consequences of climate change (Chevin *et al.* 2010; Bolnick *et al.* 2011; Bush *et al.* 2016; Chevin & Hoffmann 2017; Sanderson *et al.* 2023; Seebacher *et al.* 2023; Urban *et al.* 2023). Here we show that both acclimation responses ($lnRR_{Q_{10}}$) and increases in physiological rate variance ($lnVR_{Q_{10}}$) of ectotherms varied across habitats. Our results uncover an hitherto unrecognised dynamic where the benefits of partial acclimation are paralleled by increases in trait variance that depend on habitat in ways that may have impacts on how ectotherm populations will be able to adapt to increased temperatures.

Acclimation capacities vary among habitats but are often still limited

We show that the capacity for acclimation of physiological rates differs across habitats. Our findings confirm previous results that quantify the different capacity of terrestrial, marine and freshwater ectotherms to acclimate (Gunderson & Stillman 2015; Seebacher *et al.* 2015; Morley *et al.* 2019). Our analysis confirms findings by Seebacher *et al.* (2015), Gunderson & Stillman (2015) and Morley *et al.* (2019) that all show a general inability of terrestrial ectotherms to physiologically acclimate. These consistent results are interesting given the different physiological traits measured in these meta-analyses (i.e., thermal limits versus physiological rates).

The change in acclimation Q_{10} we found in our expanded dataset was similar to Seebacher *et al.* (2015) for freshwater organisms (~17%), but higher in marine ectotherms (decrease of 16% versus ~10% in Seebacher *et al.* 2015), and opposite in terrestrial ectotherms (increase of ~6% compared to an ~8% decrease in Seebacher *et al.* 2015). The difference observed in terrestrial ectotherms between studies may be due to additional data from terrestrial species added in our analysis, and to the use of newly derived Q_{10} effect sizes that allowed us to control for sampling variance. Greater capacity for acclimation in aquatic organisms may be the result of fewer opportunities for behavioural thermoregulation in aquatic environments making physiological remodeling important for maintaining homeostasis (Gunderson & Stillman 2015; Morley *et al.* 2019). Importantly, even though marine and freshwater ectotherms were capable of partial acclimation, on average, the effect size was small (amounting to Q_{10} dropping from ~1.8 to 1.6), suggesting that acclimation provides limited scope for aquatic ectotherms to adjust their physiology to higher temperatures.

Biochemical traits (e.g., enzyme activities) were more likely to acclimate compared to whole-organism traits as predicted, but only for marine ectotherms, presumably because of the less complicated physiological networks that underlie specific biochemical processes (Schulte *et al.* 2011). However, whole-organism and biochemical traits acclimated to the same extent in freshwater ectotherms. Differences between marine and freshwater ectotherms do not appear to be related to the types of traits measured across the habitats but rather that the traits responded differently. However, it is important to note that whole-organism traits in marine ectotherms did respond in the same direction and of a similar magnitude to freshwater ectotherms, so it is possible the difference in marine habitats is simply a sampling artefact.

Increased variability in physiological rates across habitats: adaptive potential of physiological processes in the face of climate change?

Contrary to acclimation capacity variance in physiological rates increased across habitats with effect sizes being 3-5 times larger than those observed for acclimation of mean trait values. Mechanistically, it is unclear what exactly is contributing to the increased variation in physiological rates at higher temperatures, but it is likely the result of increased among-individual variability in how biochemical, cellular and physiological processes function at higher temperatures to maintain homeostasis (Somero 1995; Fields 2001; Angilletta 2009; Schulte *et al.* 2011; Tattersall *et al.* 2012). Higher temperatures increase membrane fluidity affecting

electrochemical gradients and impacting protein structure and function (Somero 1995; Fields 2001; Tattersall *et al.* 2012). Such challenges (among others) may expose among-individual variation within a population. Indeed, there is considerable variation in acclimation capacity among individuals which would increase variance in thermal performance curves within populations (Schulte *et al.* 2011; Loughland & Seebacher 2020).

Importantly, increased variance in physiological rates was not equal among terrestrial, marine and freshwater ectotherms, with increases in variance being higher in freshwater ectotherms (~60% increase / 10°C) compared to terrestrial ectotherms (~36% increase / 10°C). One possible hypothesis for the differences in variability we observed across habitats could be that among-individual variation in key parameters affecting the shape of thermal performance curves differ between habitats (Huey & Kingsolver 1989; Angilletta 2009; Tattersall *et al.* 2012; Rezende & Bozinovic 2019). Our simulations suggest that theoretical and observed $lnVR_{Q_{10}}$ match when thermal performance curves have different among-individual variance in thermal optima and breadth across habitats making this hypothesis plausible. Such patterns across habitats are expected given that terrestrial ectotherms should be adapted to more extreme and variable thermal environments. Theoretical models also suggest that populations with greater temporal environmental variability exhibit greater thermal breadth (Lynch & Gabriel 1987). However, we did not find support that thermal variation co-varied with $lnVR_{Q_{10}}$ (see below), as would be expected. The relevance of analyses of thermal variability will depend on temporal variation in temperature that is biologically relevant – a challenging feat across diverse taxa, but worthy of future investigation.

Our results further highlight the potential vulnerability of terrestrial ectotherms to climate change. Assuming that changes in variation in physiological rates are underpinned by genetic variation, and that there is a genetic correlation with fitness, smaller increases in physiological variance could limit adaptation in terrestrial habitats more than aquatic habitats in the future (Hoffmann & Sgrò 2011; Urban *et al.* 2023). For example, under climate change we expect an increase in variance in physiological rates of only ~13% in terrestrial habitats whereas for freshwater habitats we expect variation in physiological rates to increase by ~30%. Importantly, responses to selection will also depend on the magnitude and direction of genetic covariances with other traits, which need consideration. There will obviously be limits to variance increases, and we predict that organisms closer to their upper thermal limits (CT_{max}) will have lower $lnVR_{Q_{10}}$ values compared to those farther away from CT_{max}. Some evidence points to possible differences across habitats in upper thermal limits already (Gunderson & Stillman 2015; Pinsky *et al.* 2019), making this a fruitful future question to explore.

Plasticity and variance in physiological rates do not differ between life stages

Acclimation capacities are expected to differ between life-stages because of distinct patterns of dispersal, habitat use and behaviour that force earlier life stages to cope with more variable environmental conditions which can also lead to developmental constraints on how physiological systems respond later in life (Stearns 1976; Angilletta 2009; Martin 2015; Sinclair *et al.* 2016; Noble *et al.* 2018; O'Dea *et al.* 2019; Pottier *et al.* 2022). In addition, plastic responses are also expected to be costly (Dewitt *et al.* 1998; Angilletta 2009), such costs can be magnified in later life reducing the capacity for plasticity (e.g., Rossi *et al.* 2019). These processes can also result in changes to intrapopulation variation in physiological rates at higher temperatures but the direction of change between early and adult life stages is likely to depend on the costs of adjusting physiological processes, energy reserves at different life stages, and the extent to which early life experiences constrain plasticity.

Despite these expectations, our analysis does not show any significant differences between early and late life acclimation capacities and little change in the variance in physiological rates across habitats. This may not be too surprising given that such responses are likely context or trait-dependent (Moghadam *et al.* 2019; Carter & Sheldon 2020). The lack of differences we observed may be because both juvenile and adult animals

occupy similar thermal niches, disperse to a similar extent and exhibit comparable thermoregulatory behaviors making physiological responses to temperature similar. A focus on collecting more detailed information on behaviour, dispersal and thermal environments experienced by different life stages is likely to provide a more complete picture on when plasticity differs. We would also encourage more empirical focus on this question and its potential ecological and evolutionary implications.

Past climate does not influence capacity for physiological acclimation or changes in variance

Theoretical models predict that plasticity should evolve in populations experiencing greater environmental variability (spatial or temporal), particularly when fluctuations are predictable over time to make environmental cues reliable (Lande 2009; Chevin *et al.* 2010; Reed *et al.* 2010; Murren *et al.* 2015; Hendry 2016; Nunney 2016; Chevin & Hoffmann 2017). Higher spatial and temporal heterogeneity in terrestrial habitats (Steele *et al.* 2019) therefore suggest that plasticity is more likely to evolve in terrestrial environments. However, if thermal variability is too high and unpredictable, the rates of acclimation decrease and there are increased costs associated with re-modelling physiological processes (Angilletta 2009) it would instead be expected that phenotypes are canalised during development (Angilletta 2009; Seebacher *et al.* 2015; Leung *et al.* 2020, 2023; Loughland & Seebacher 2020; Rescan *et al.* 2022). The lack of acclimation in terrestrial ectotherms we observed is consistent with the latter hypothesis, and is supported by other meta-analyses of heat tolerance (Gunderson & Stillman 2015; Barley *et al.* 2021) suggesting that there are costs to being plastic or that the environmental signals are insufficient to trigger endocrine and epigenetic mechanisms that lead to plasticity when environments are not predictable (Hendry 2016; Leung *et al.* 2020).

Whether population capacity for acclimation is related to the thermal variability (or predictability) it experiences is equivocal. We show no relationship between acclimation capacity and thermal variability in marine, freshwater and terrestrial habitats. Our results are consistent with Gunderson & Stillman (2015) who show no relationship between plasticity in heat tolerance and latitude or thermal seasonality. However, other analyses on heat tolerance limits have found relationships between latitude (a proxy for seasonality) (Morley *et al.* 2019) or even direct measures of thermal variability (Verberk *et al.* 2024). Seebacher *et al.* (2015) also found that acclimation capacity was related to a populations thermal variability, however, relationships depended on the habitat and traits in question, and tropical animals showed greater acclimation capacity. Discrepancies across studies could be related to the taxa included in analyses (e.g., Morley *et al.* 2019), different traits or possibly the fact that different climate projections/models are being used to quantify thermal variability. Latitude covaries with a diversity of different ecological attributes aside from temperature (Louthan *et al.* 2021), which means it may be capturing other aspects of the environment that affect acclimation capacity. In addition, modelling realistic microenvironments across such diverse taxa is also challenging because it is unclear what the most appropriate spatial and temporal scale might be that is of evolutionary relevance. Historical temperature time series' may not be representative of the selective environment a population has experienced making relationships between capacity for acclimation and temperature variability (or predictability) difficult to pin down.

Conclusions and future directions

Enhanced knowledge of how variation in physiological rates vary across populations and species, and the degree to which they can be adjusted in response to the environment leads to more informed predictions about the ecological and evolutionary dynamics of natural populations (Forsman 2015; Cooke *et al.* 2021; Sanderson *et al.* 2023; Seebacher *et al.* 2023). We show general patterns across taxa and habitats that provide a foundation to understand the relationship between plasticity and trait variance, as well as particular trade-offs that could impact the benefits (or lack thereof) of acclimation. It is important to recognise, however, that these patterns do not necessarily apply to all populations. Substantial variation in acclimation responses and changes in variance exist among populations and traits, as evidenced by wide prediction intervals and

substantial study- and trait-level variance estimates, which is consistent with our understanding of factors influencing variation in performance curves across taxa (Tattersall *et al.* 2012; Rezende & Bozinovic 2019). Conservation efforts are often targeted at particular populations or species, and taxonomic differences are important in this context. Regardless, quantitative measures of the changes in variance in physiological rates could be better incorporated into physiological and ecological models to provide more nuanced, and possibly more realistic, predictions about the impacts of climate change on natural populations. While we do not yet understand the relative contribution of environmental and genetic factors to variance changes, models could better decouple how different levels of heritability and total variance impact evolutionary and ecological predictions. Our meta-analysis now provides the opportunity to parameterise such models, and ensure they are better aligned with empirical findings.

Many fascinating questions remain unanswered that will require greater focus on the consequences of changes in variance (rather than just the mean). Particularly interesting questions include: How do differences in physiological rate variance change energy flow across trophic levels within communities? What are the biochemical, cellular, and physiological mechanisms that underlie differences in physiological rate variance across habitats? Are changes in variance in one trait associated with changes in other traits, or do some traits increase while others decrease? Are changes in physiological rate variance correlated with changes in genetic variation? Answers to these questions will require integrative approaches that combine empirical and theoretical work across multiple levels of biological organisation but will likely provide useful advances in understanding the full consequences that climate change will have on ectotherms across major ecosystems globally.

Acknowledgements

We would like to thank Malgorzata Lagisz for helping sort out the phylogeny used in our analysis and Enrico Rezende for discussions around alternative implementations of thermal performance curves. We are also grateful to three anonymous reviewers who all provided extremely constructive feedback that greatly improved the manuscript.

Funding

DWAN is supported by an Australian Research Council (ARC) Future Fellowship (FT220100276) and ARC Discovery Project DP210101152. SN is supported by ARC Discovery Project Grants DP210100812 and DP230101248. FS is supported by ARC Discovery Project Grant DP220101342.

Data and code availability

All data and code used to reproduce analyses can be found on GitHub at: https://github.com/daniel1noble/Q10_meta_analysis and is deposited in Zenodo (https://doi.org/10.5281/zenodo.11123600).

Author contributions

Conceptualization: DWAN, FK, FS, SN; Methodology: DWAN, AB, FK, FS, SN; Investigation: DWAN, FK, FS, SN; Visualization: DWAN; Supervision: DWAN, SN, FS; Writing—original draft: DWAN; Writing—review & editing: DWAN, AB, FK, FS, SN.

Conflict of interest

Authors declare that they have no competing interests.

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Supplemental Materials

Literature Search Protocol and PRISMA flow diagram

We performed a literature search using the Web of Science database for 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 the dataset of Seebacher *et al.* (2015)'s. We included any papers that were missed between our searches and those of Havird *et al.* (2020). Havird *et al.* (2020) added 7 new studies (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 than Havird *et al.* (2020), 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; 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 since Seebacher *et al.* (2015) to answer questions on physiological rates across ectotherms.

We split the screening of titles and abstracts for the 1,321 papers found in our search among DWAN, FK, FS, and SN evenly. To ensure consistency among authors in title and abstract inclusion, relevant authors went through a randomly selected set of papers together before the formal screening to calibrate selection of papers based on our inclusion criteria (see below). In cases of disagreement regarding inclusion, we conservatively included the paper for full text screening and discussed uncertain papers among authors to come to a decision. After title and abstract screening, there was 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. Importantly, as in Seebacher *et al.* (2015), we only included studies that manipulated temperatures within normal thermal ranges for the species.

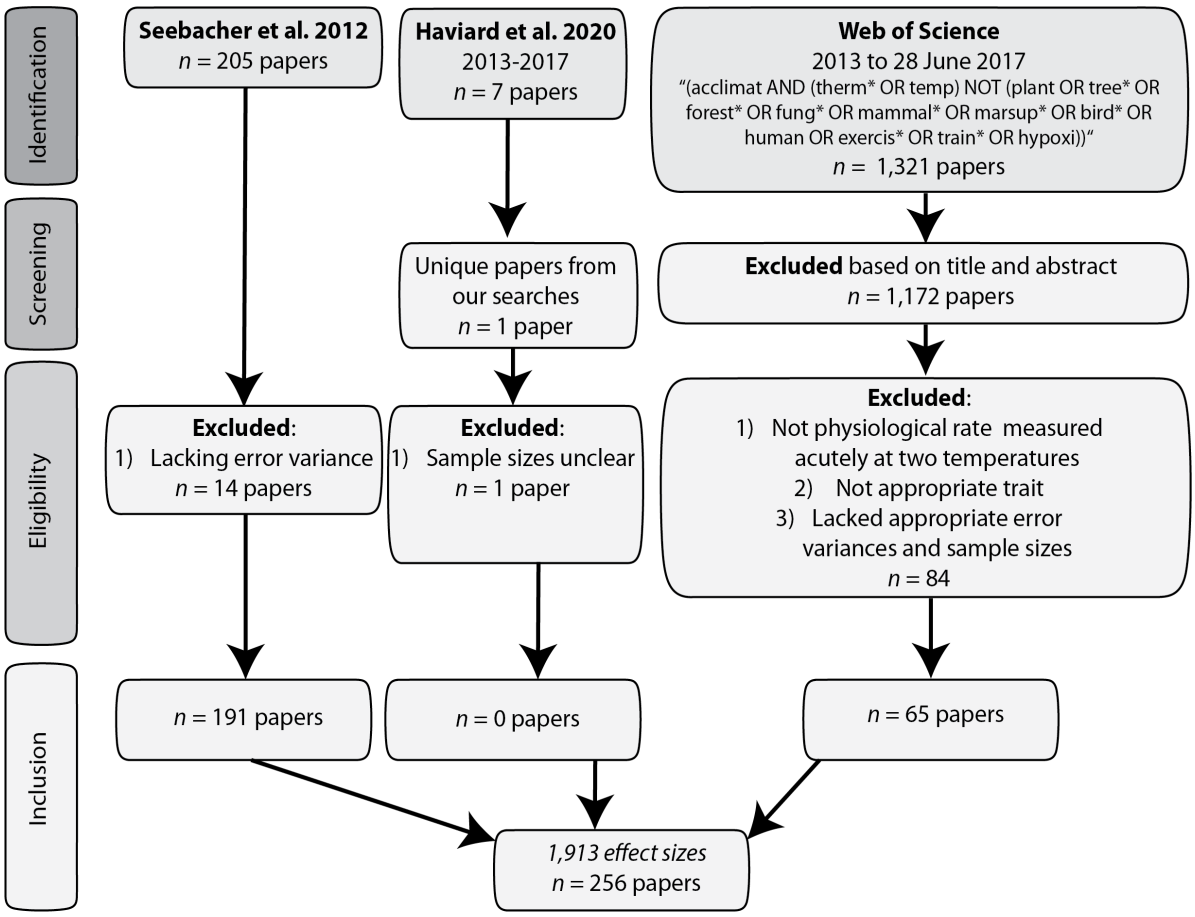

Figure S1- PRISMA flow diagram of the literature search and screening process.

Further discussions on the assumptions of $lnRR_{Q_{10}}$, $lnVR_{Q_{10}}$ and $lnCVR_{Q_{10}}$ estimates

$lnRR_{Q_{10}}$, $lnCVR_{Q_{10}}$ and $lnVR_{Q_{10}}$, as with Q_{10} more generally, all assume that the effect of temperature on physiological rates (or changes in relative variance) is log-linear. While this is likely in our data given that we restricted our analysis of Q_{10} to standard operating temperatures for a given species, it may not always be satisfied given the diversity of species in our dataset. Q_{10} (Hoff 1884) has been used extensively in the physiological literature to successfully address a multitude of questions (Seebacher *et al.* 2015; e.g., Havird *et al.* 2020). However, there is a preference for using a Boltzmann – Arrhenius (BA) relationship (or its extension, the Sharpe-Schoolfield model (Molnár *et al.* 2017; Michaletz & Garen 2024)) to model thermal effects on physiological rates (Gillooly *et al.* 2001; Michaletz & Garen 2024). While debate still exists over the utility of Q_{10} when modelling temperature-dependence it is important to recognise that both BA and Q_{10} can exhibit curvilinearity as temperatures increase (as discussed in (Michaletz & Garen 2024)). White *et al.* (2012) also showed that the BA model may not always perform better. For example, in eukaryotes, modelling thermal dependence using Q_{10} provided a 5.8-fold better fit to metabolic rate data than the BA relationship (White *et al.* 2012). Given that studies included in our analysis never measured full performance curves at acute and acclimation temperatures it was not possible for us to compare different models of thermal dependence. Nonetheless, Q_{10}-based effect sizes remain the most practical effect-size for comparing thermal dependence when using existing empircial data, with the benefit that these effects having convenient properties that make them suitable for meta-analysis. Nonetheless, we control for possible violations of the log-linearity assumption in our analyses.

Exploring the impact of maximum treatment temperature on $lnRR_{Q_{10}}$

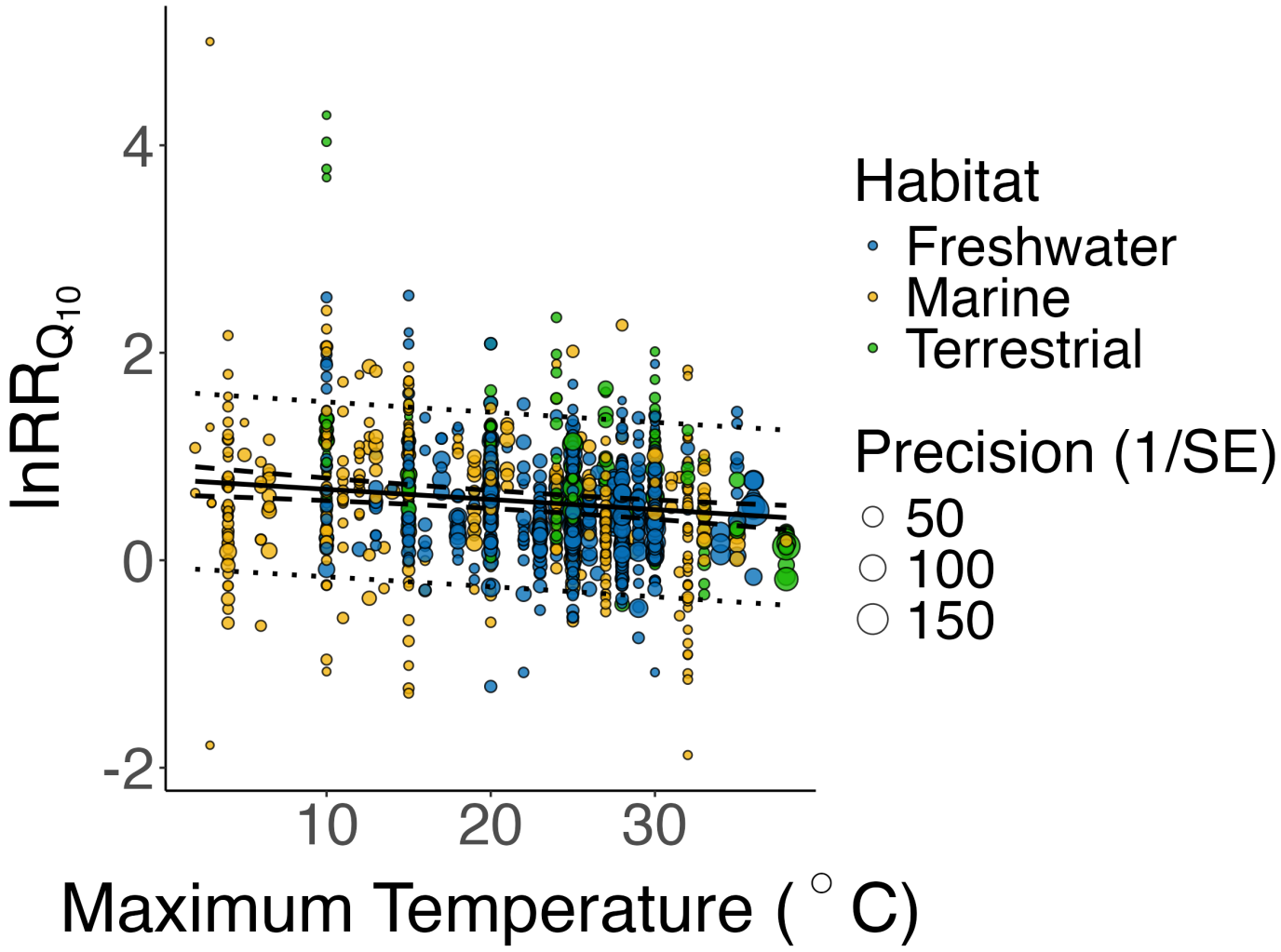

Figure S2- Bubble plot of the relationship between $lnRR_{Q_{10}}$ and maximum temperature used in treatments within a study.

How acclimation time is related to $lnRR_{Q_{10}}$

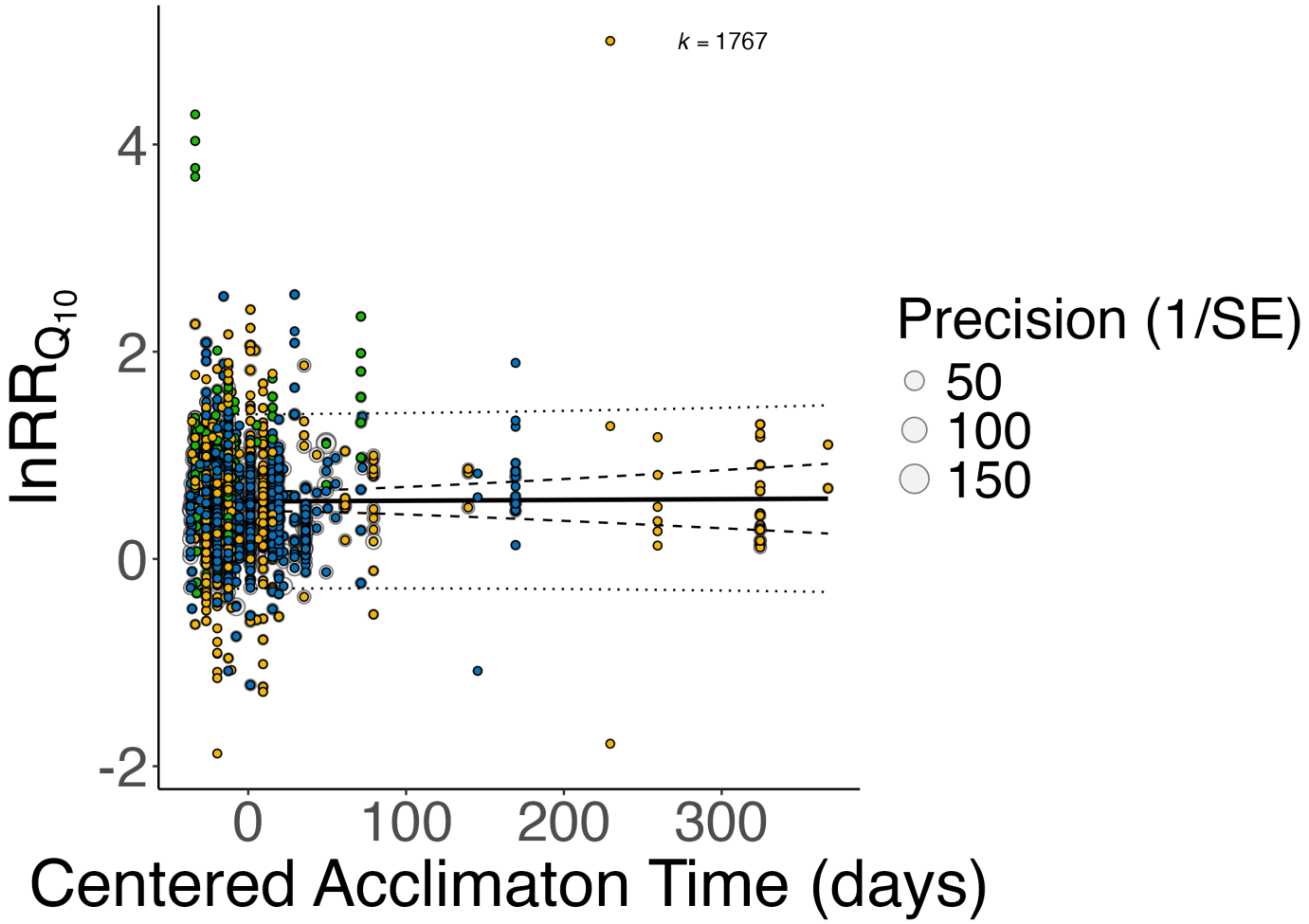

Figure S3- Bubble plot of the relationship between $lnRR_{Q_{10}}$ and acclimation time for terrestrial (green), marine (orange) and freshwater (blue) habitats. Acclimation time is centered around the mean acclimation time (37.5 days) in the data. Not all studies reported acclimation time hence the total number of effects, *k*, was 1767.

Comparing cool and warm acclimated acute responses

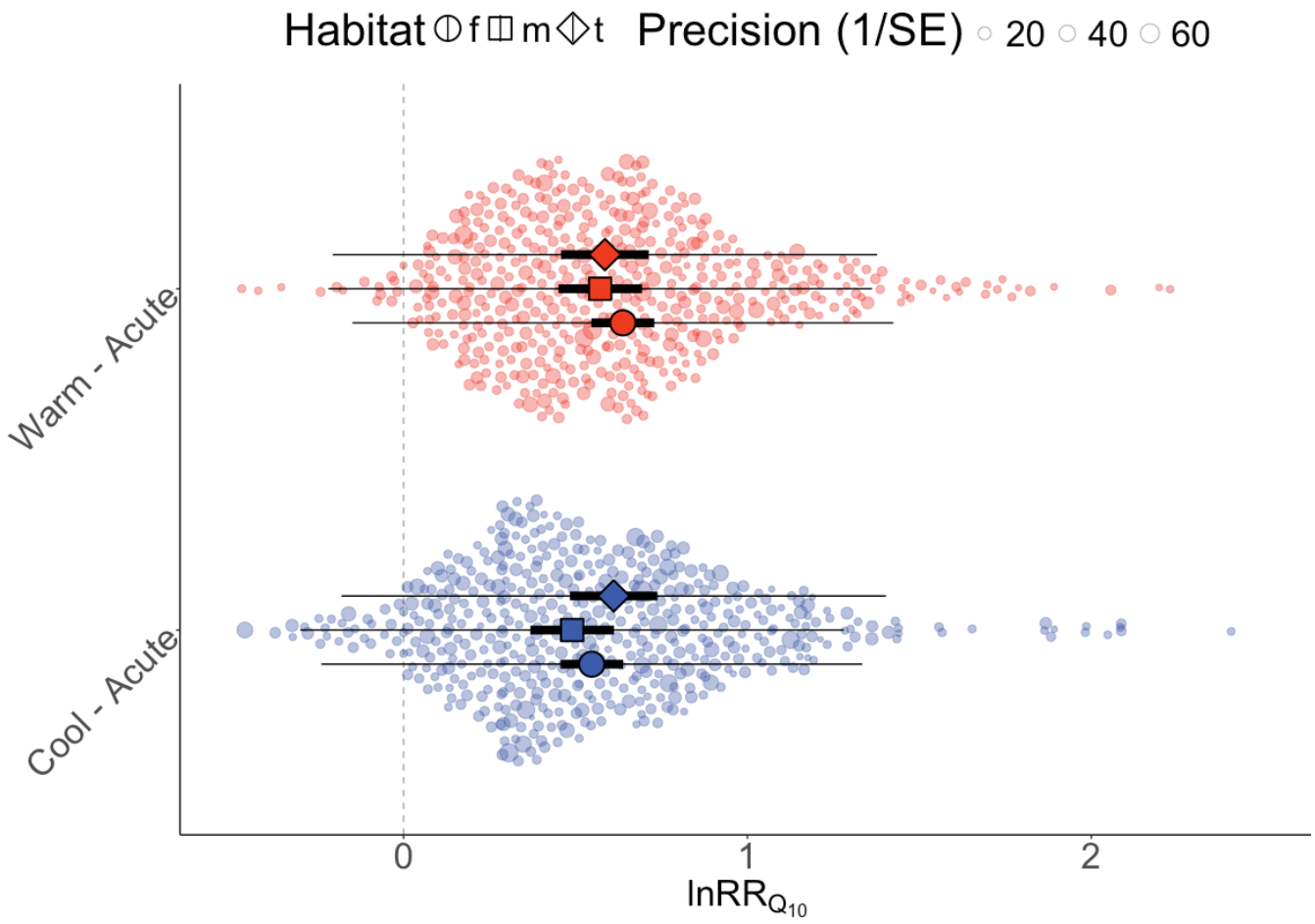

Figure S4- Mean acute $lnRR_{Q_{10}}$ for cool (blue) and warm (red) acclimated populations for terrestrial (diamonds), marine (square) and freshwater (circle) habitats. Note that points in each category show the full distribution of data irrespective of habitat for simplicity. *k* = total number of effect size estimates while the numbers in brackets indicate the number of species. Thick bars indicate 95% confidence intervals and thin bars indicate 95% prediction intervals. Note that means for all three habitats are displayed but there is weak evidence that the means differ between habitats given models with and without an interaction with habitat are equally supported. Note that x-axis is truncated for ease of visualisation. Sample sizes for each habitat for acute warm and cold are: marine [warm = (131, 38, 29), cold = (136, 41, 32)], freshwater [warm = (294, 76, 61), cold = (293, 77, 63)], terrestrial [warm = (83, 31, 35), cold = (84, 31, 35)]. Numbers within brackets are number of effects, number of studies and number of species.

Climate data

To understand how climate is related to a species' physiological acclimation abilities and changes in variance 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 72-year period (1950-2022) of either surface air temperature (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. 1.21, Pierce 2021). We chose surface temperature because we believed that it was more likely to reflect the micro-thermal environment experienced by terrestrial and freshwater ectotherms at those locations.

Using the thermal time-series data for each location we calculated 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 ($\frac{SD}{M}$, where SD = standard deviation in temperature and M = the mean temperature for each year). We also estimated thermal predictability, by calculating the auto-regressive time lag across months (i.e., a measure of how correlated temperatures were between months), however, identifying biologically relevant lags for such diverse taxa is challenging. As such, we present a coarse analysis using this metric of thermal predictability in the *Supplemental Materials* below.

Lastly, to illustrate the effects that climate warming could have on physiological rate variance we also extracted climate projections into the future. We used the CanESM2 climate model (2005-2100) [vers. 1.2.0; Hufkens *et al.* (2019)] under a high emissions scenario (RCP8.5).

Mean-variance relationships to understand patterns in $lnCVR_{Q_{10}}$

We explored mean-variance relationships for the acute and acclimation responses across all traits and habitats. We estimated the scaling relationship between log standard deviation in physiological rates [log(SD)] and log mean physiological rates [log(mean)], accounting for non-independence resulting from effects coming from the same species, study and traits (i.e., random effects of species, study and trait) as done in our main analyses. We also included an interaction between log(mean) and habitat type to better understand how the scaling relationship between log(SD) and log(mean) varies across habitats.

Overall, we found that the relationship between log(mean) and log(SD) of the acute and acclimation responses was generally linear (Figure S5). Overall, the scaling relationship between log(SD) and log(mean) was sub-linear across all habitats (Table S1), however, ectotherms from terrestrial habitats had much shallower slopes than marine and freshwater ectotherms, particularly at higher treatment temperatures, indicating increased mean physiological rates generally do not result in higher between individual variance in physiological rates (Table S1). Interestingly, in marine ectotherms the slope was highest at cooler temperatures, whereas the slope was suppressed when acclimated and/or measured at higher temperatures (i.e., r.1. compared to r1.2, r2.1, r2.2) (Table S1). In freshwater ectotherms, there we some differences in scaling relationships but they were all fairly comparable no matter what acclimation and test temperature (Table S1).

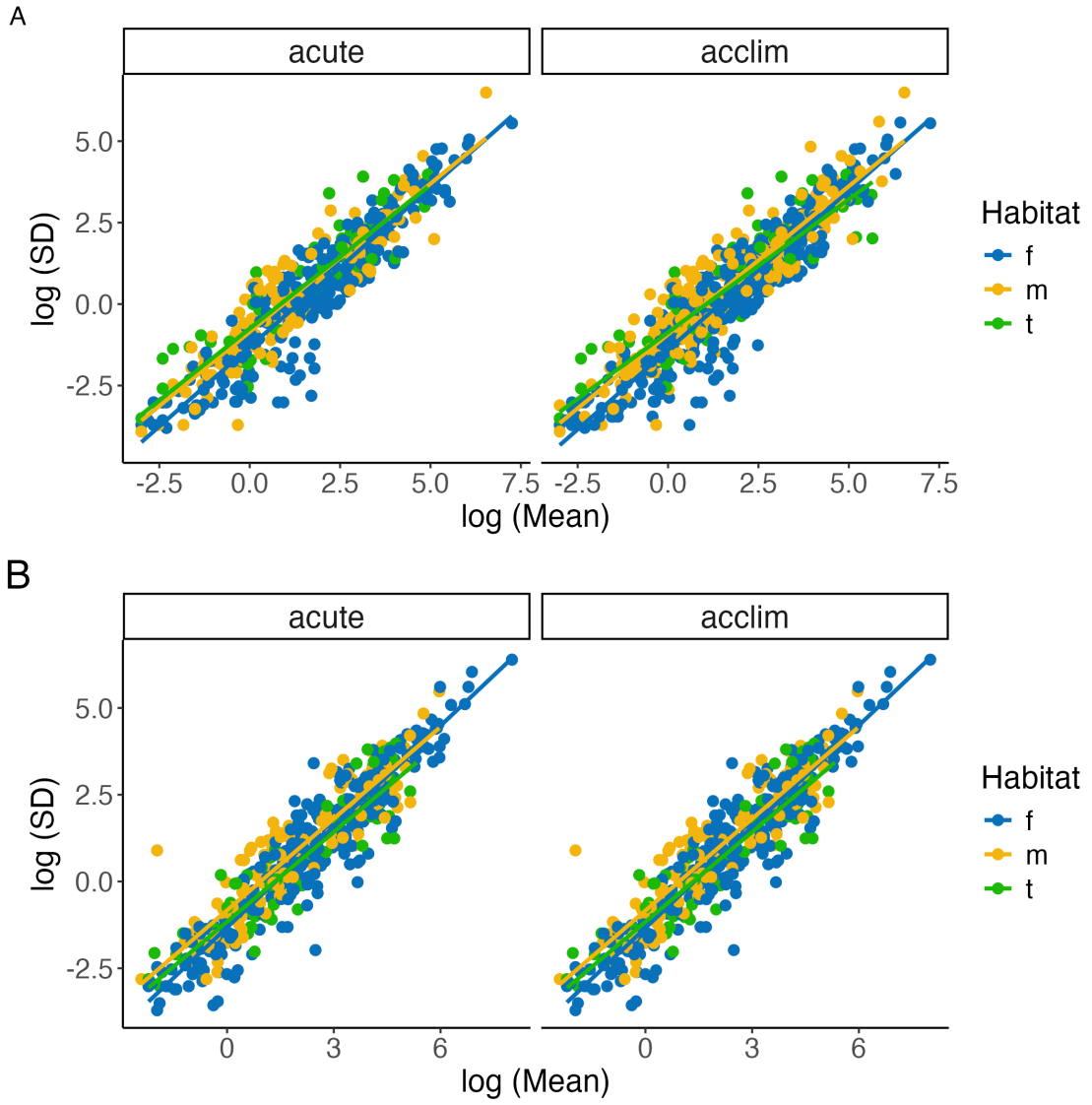

Figure S5- Mean-standard deviation relationships for the acute and acclimation responses across all habitats. Relationships are depicted for the low temperature treatment of the study (A) and high temperature treatment (B).

Table S1: Slopes and 95% credible intervals (lower = 2.5% and upper = 97.5%) of log transformed standard deviation (log(SD)) and log transformed mean (log(mean)) for each of the four treatment types (r1.1, r1.2, r2.1, r2.2). Note that r1.1 and r2.2 represent measurements of physiological rates of acclimated animals and measured at their respective acclimation temperature. In contrast, r1.2 and r2.1 are acute measurements. See Figure 1 in main manuscript for full details on treatments.

Type	Treatment	Habitat	Slope	2.5%	97.5%
Acclimation	r1.1	Freshwater	0.92	0.89	0.96
Acute	r1.2	Freshwater	0.95	0.91	0.98
Acute	r2.1	Freshwater	0.94	0.91	0.97
Acclimation	r2.2	Freshwater	0.98	0.94	1.01
Acclimation	r1.1	Marine	0.99	0.93	1.03
Acute	r1.2	Marine	0.90	0.84	0.95
Acute	r2.1	Marine	0.91	0.86	0.96
Acclimation	r2.2	Marine	0.90	0.85	0.95
Acclimation	r1.1	Terrestrial	0.83	0.75	0.90
Acute	r1.2	Terrestrial	0.82	0.75	0.90
Acute	r2.1	Terrestrial	0.75	0.67	0.82
Acclimation	r2.2	Terrestrial	0.73	0.66	0.81

Comparing relative variance changes using $lnCVR_{Q_{10}}$

Overall, analyses with $lnCVR_{Q_{10}}$ showed similar patterns to those with $lnVR_{Q_{10}}$, except that, because of rates being taken into consideration and there being strong mean-variance relationships, the patterns were generally opposite in direction. Either way, the relative differences are quite similar. Overall, analysis of $lnCVR_{Q_{10}}$ suggested that relative variance decreased with higher temperatures across all habitat types, with terrestrial ectotherms having the largest decrease in relative variance (Figure S6). There were also no major differences in the relative differences among broad trait categories (Figure S7) or life-history stages (Figure S8).

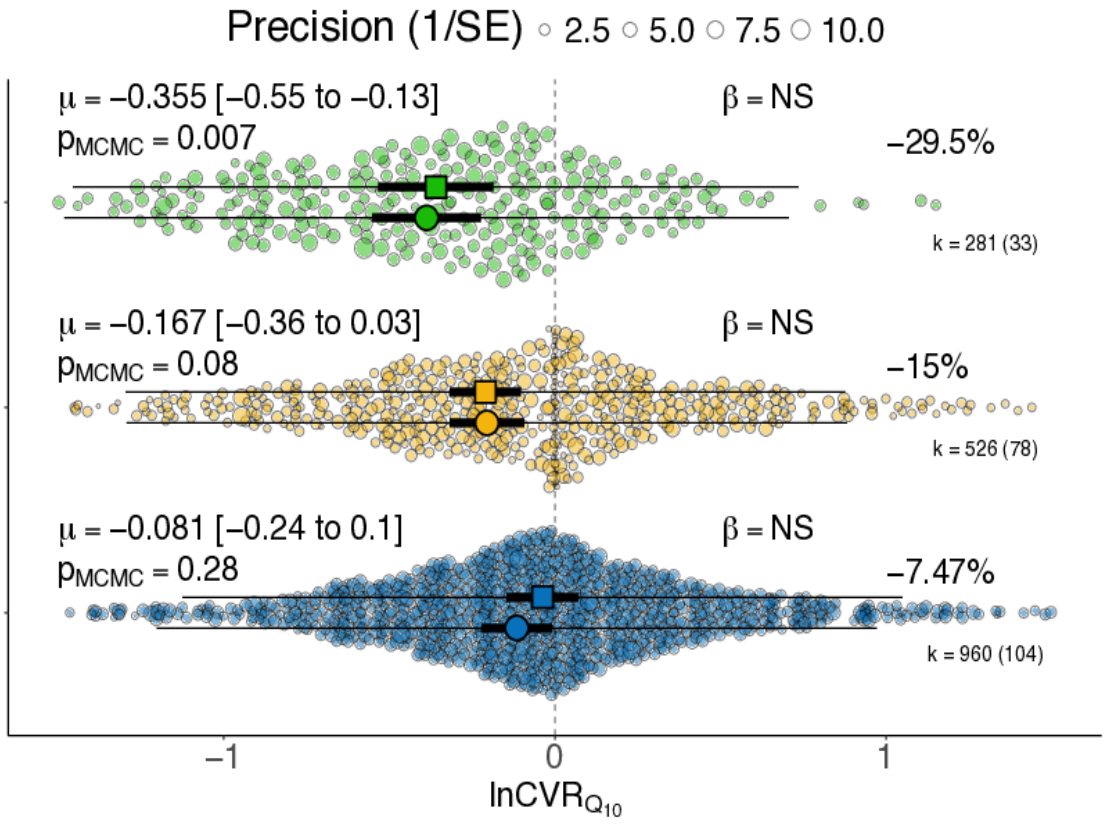

Figure S6- Estimated mean acute and acclimation $lnCVR_{Q_{10}}$ for marine, freshwater and terrestrial habitats. The percentage change in variance is also back calculated. Note that these are raw variances and do not account for changes in mean physiological rates. k = total number of effect size estimates while the numbers in brackets indicate the number of species. Thick bars are 95% confidence intervals (CI) and thin bars 95% prediction intervals (PI). β values are the contrasts between acute and acclimation means within each habitat with 'NS' signifiying no significant differences. μ values are the overall meta-analytic means averaged across acute and acclimation types within each habitat type. In both cases, their 95% CI's are indicated within square brackets. p_{MCMC} values are the posterior probability of the contrast or overall meta-analytic mean being different from zero. For ease of visualisation, all the raw data plotted for both acute and acclimation type effect sizes are presented as circles.

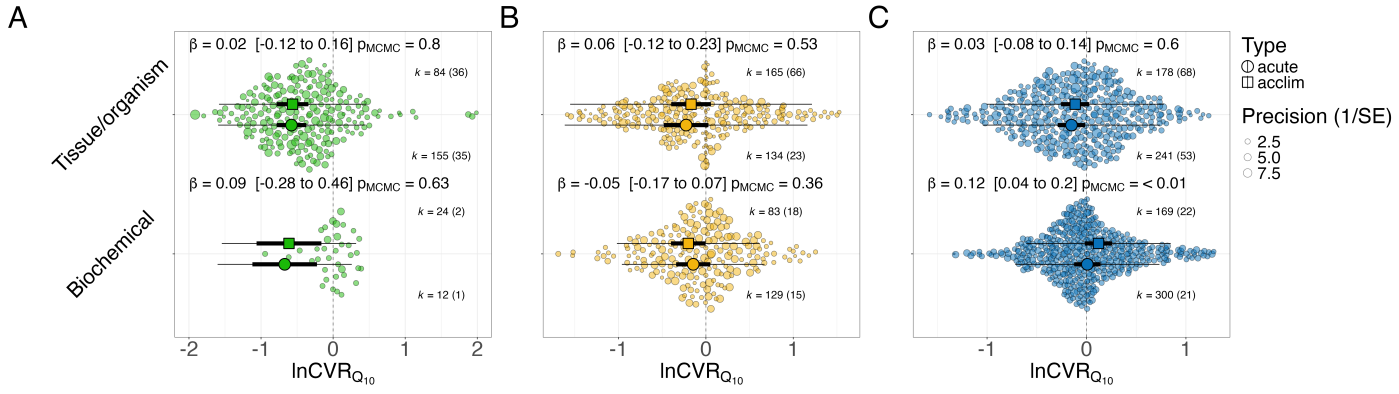

Figure S7- Estimated mean acclimation and acute $lnCVR_{Q_{10}}$ for tissue/whole-orgamism traits and biochemical traits across terrestrial (A), marine (B) and freshwater (C) habitats. Across all plots, thick bars indicate 95% confidence intervals and thin bars indicate 95% prediction intervals. k = total number of effect size estimates while the numbers in brackets indicate the number of species. For ease of

visualisation, raw data for both trait categories are presented but points are not distinguished by different symbols. β values are the contrasts between acute and acclimation means within each life stage. p_{MCMC} values are the posterior probability of the contrast being different from zero.

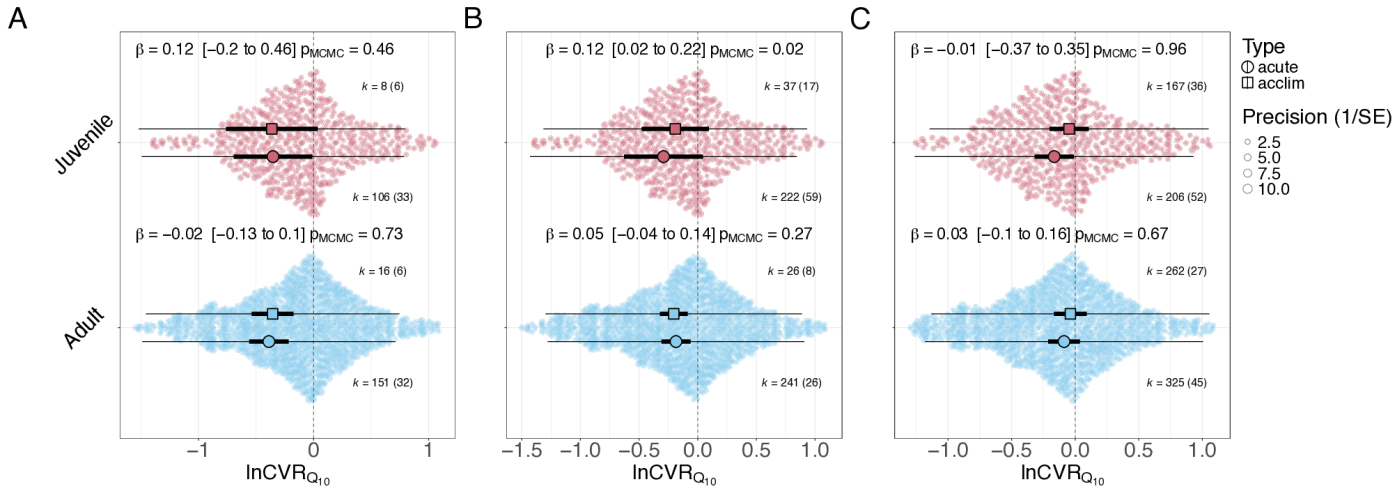

Figure S8- Estimated mean acclimation and acute $lnCVR_{Q_{10}}$ for adult (a) and juvenile (j) life-history stages for terrestrial (A), marine (B) and freshwater (C) ectotherms. Across all plots, thick bars indicate 95% confidence intervals and thin bars indicate 95% prediction intervals. k = total number of effect size estimates while the numbers in brackets indicate the number of species. For ease of visualisation, raw data for both adult and juvenile life-history stages are presented but points are not distinguished by different symbols. β values are the contrasts between acute and acclimation means within each life stage. p_{MCMC} values are the posterior probability of the contrast being different from zero.

Acute and acclimation for detailed trait categories across marine, freshwater and terrestrial taxa

In addition to the broader trait categories we fit models to understand how acute and acclimation effect sizes varied across more detailed trait categories. To achieve this, 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 ('Proton Leak') and oxidation ('OXPHOS', short for Oxidative Phosphorylation), as well as antioxidant enzymes ('antiox'). All other traits not falling within these categories were placed into 'other'.

Acclimation capacity varied across trait categories and habitat with measures of resting metabolic rate, including associated biochemical reactions like oxidative phosphorylation (OXPHOS) and ATPase activity, acclimating in marine and freshwater ectotherms (Figure S9). Whether variation in physiological rates changes also depended on trait type, with freshwater ectotherms generally maintaining variance in physiological rates better than marine and freshwater ectotherms (Figure S10 & Figure S11). We note though that some traits have very small sample sizes on their own and should be interpreted with caution.

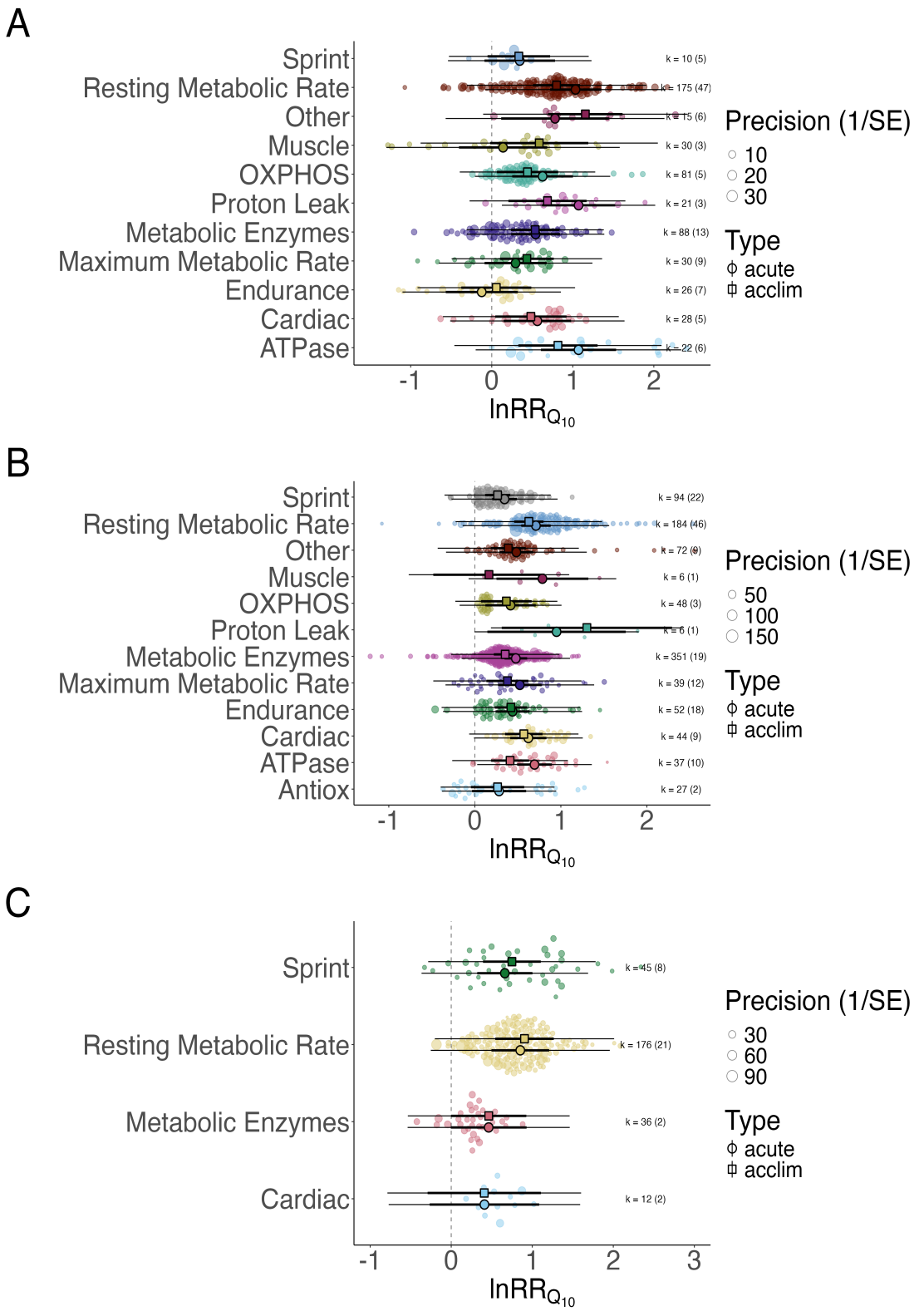

Figure S9- Acute and Acclimation $lnRR_{Q_{10}}$ across detailed trait categories for A) marine, B) freshwater and C) terrestrial systems. k = total number of effect size estimates while the numbers in brackets indicate the number of species. Thick bars indicate 95% confidence intervals and thin bars indicate 95% prediction intervals. The x-axis is truncated for ease of visualisation. See methods section "Moderator Variables" for a full description of the trait categories.

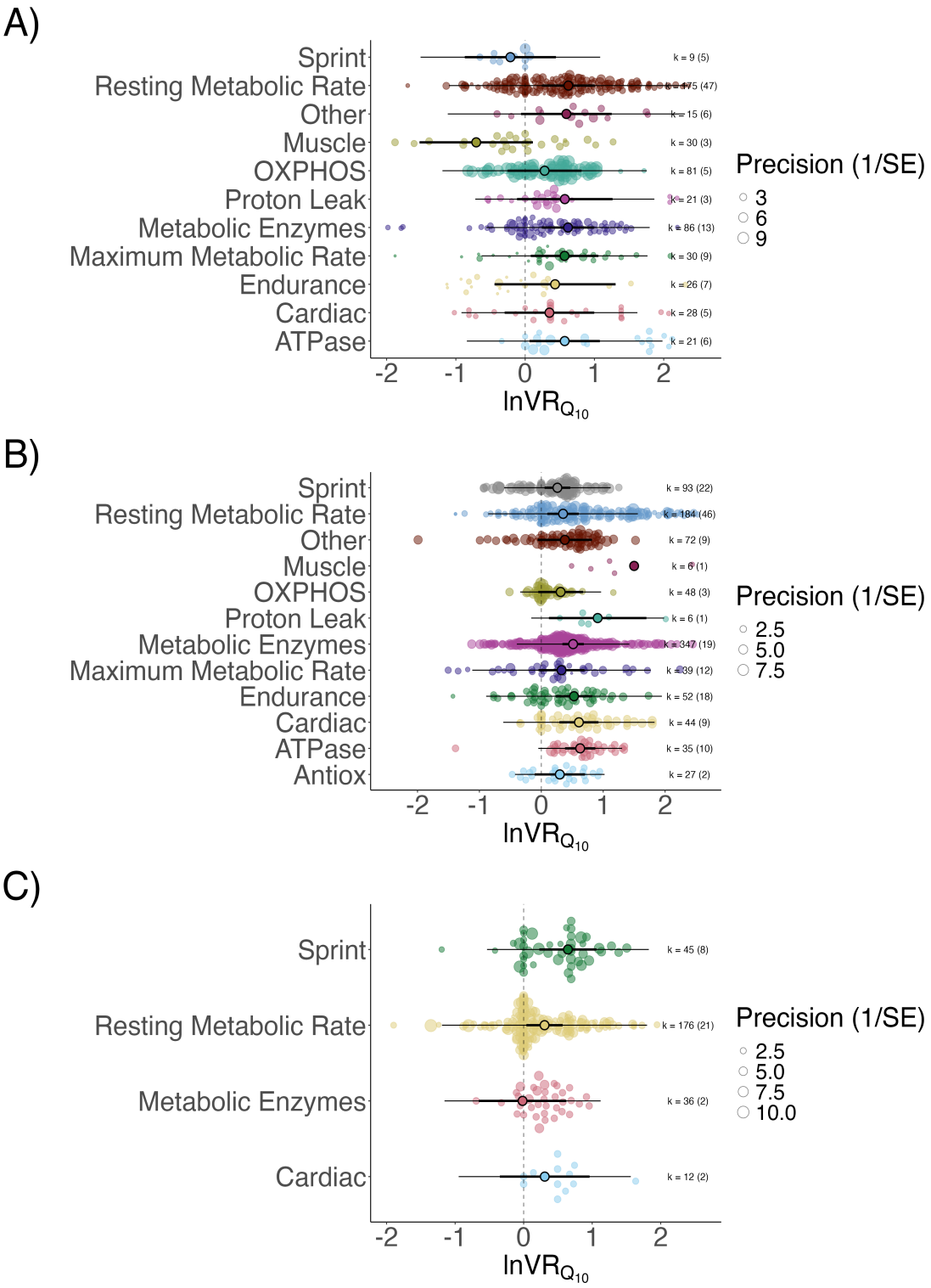

Figure S10- Acute and acclimation $lnVR_{Q_{10}}$ across traits for A) marine, B) freshwater and C) terrestrial systems. k = total number of effect size estimates while the numbers in brackets indicate the number of species. Thick bars indicate 95% confidence intervals and thin bars indicate 95% prediction intervals. The x-axis is truncated for ease of visualisation. See methods section "Moderator Variables" for a full description of the trait categories.

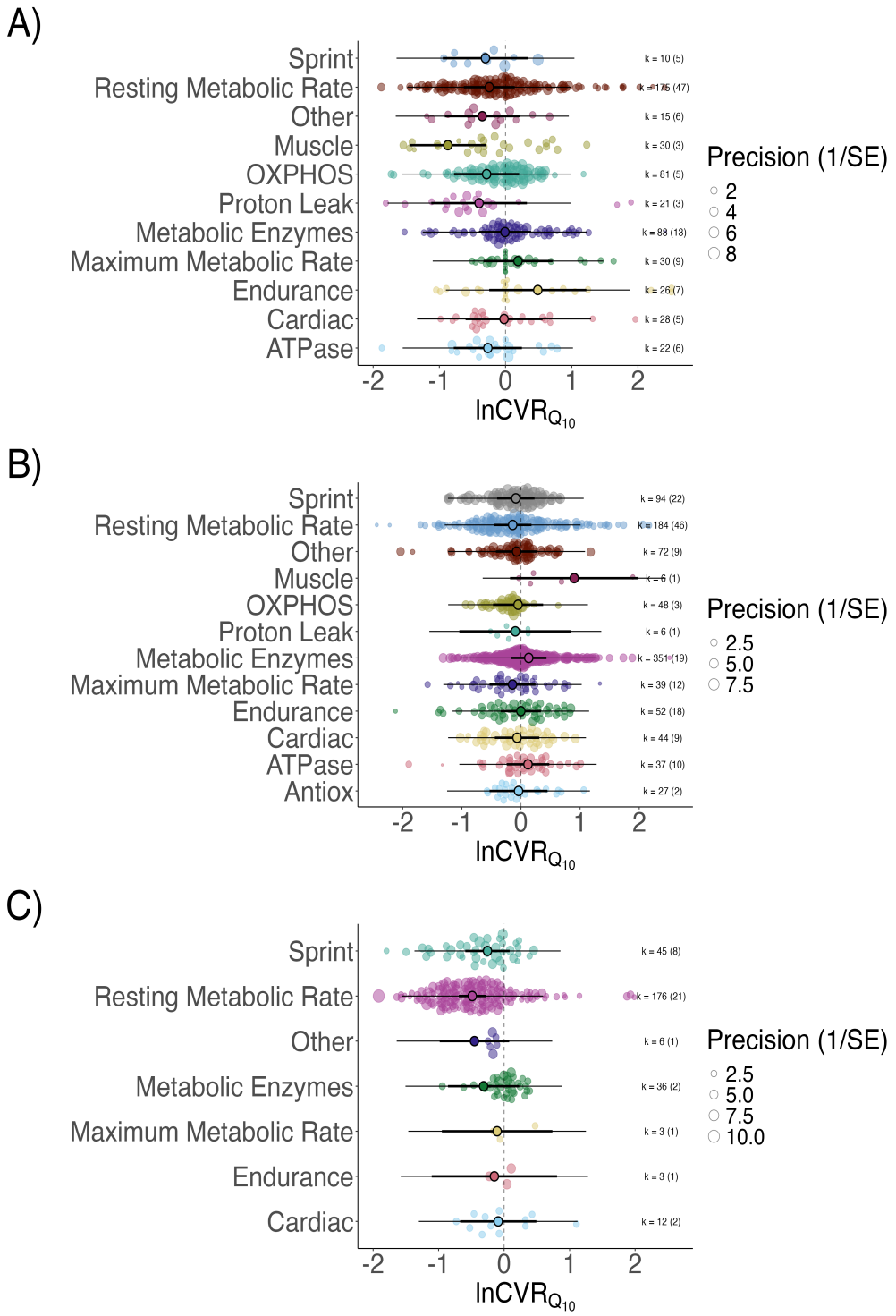

Figure S11- Acute and acclimation $lnCVR_{Q_{10}}$ across traits for A) marine, B) freshwater and C) terrestrial systems. k = total number of effect size estimates while the numbers in brackets indicate the number of species. Thick bars indicate 95% confidence intervals and thin bars indicate 95% prediction intervals. The x-axis is truncated for ease of visualisation. See methods section "Moderator Variables" for a full description of the trait categories.

Plots of I^2 for multilevel models

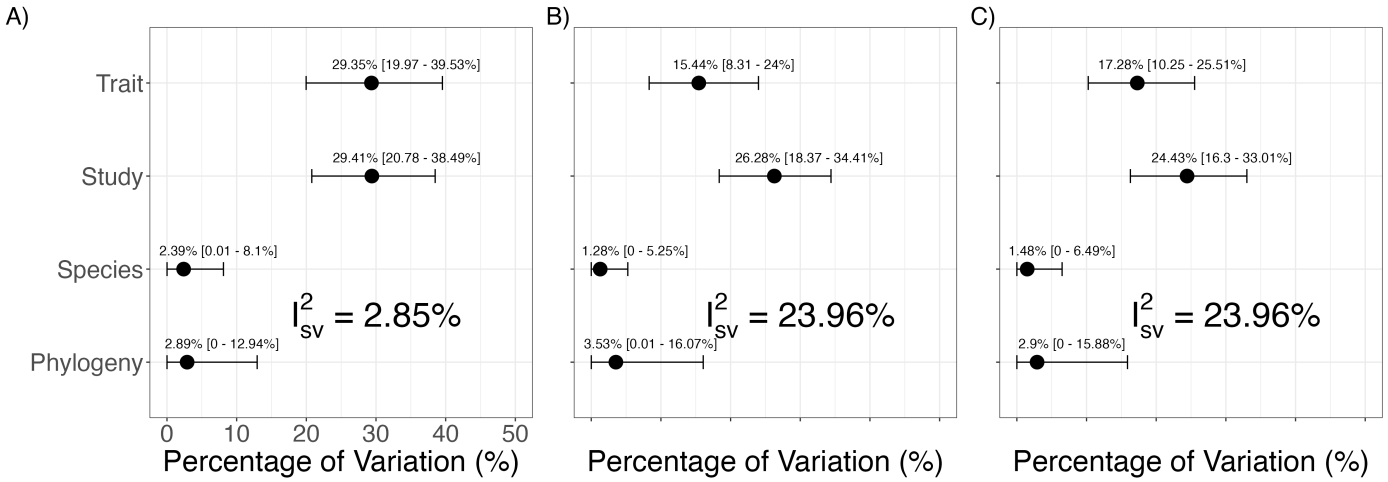

Figure S12- I^2 estimates. A) $lnRR_{Q_{10}}$ B) $lnCVR_{Q_{10}}$ and C) $lnVR_{Q_{10}}$.

Environmental predictability

Theoretical models highlight the importance of environmental predictability in selecting for plastic responses. However, capturing environmental predictability is challenging given that it is unclear which timescale one should select. For example, is it more important to look at correlation between temperatures monthly or seasonally. In addition, such temporal resolution will likely depend on the species in question given that for some species fine-grained thermal predictability maybe more important compared to others.

With these limitations in mind, we used our temperature time series to calculate auto regressive correlation in temperature across the entire time series. We then modeled how this measure of thermal predictability was related to plasticity. We found no relationship between our estimate of environmental predictability and effect sizes (Figure S13).

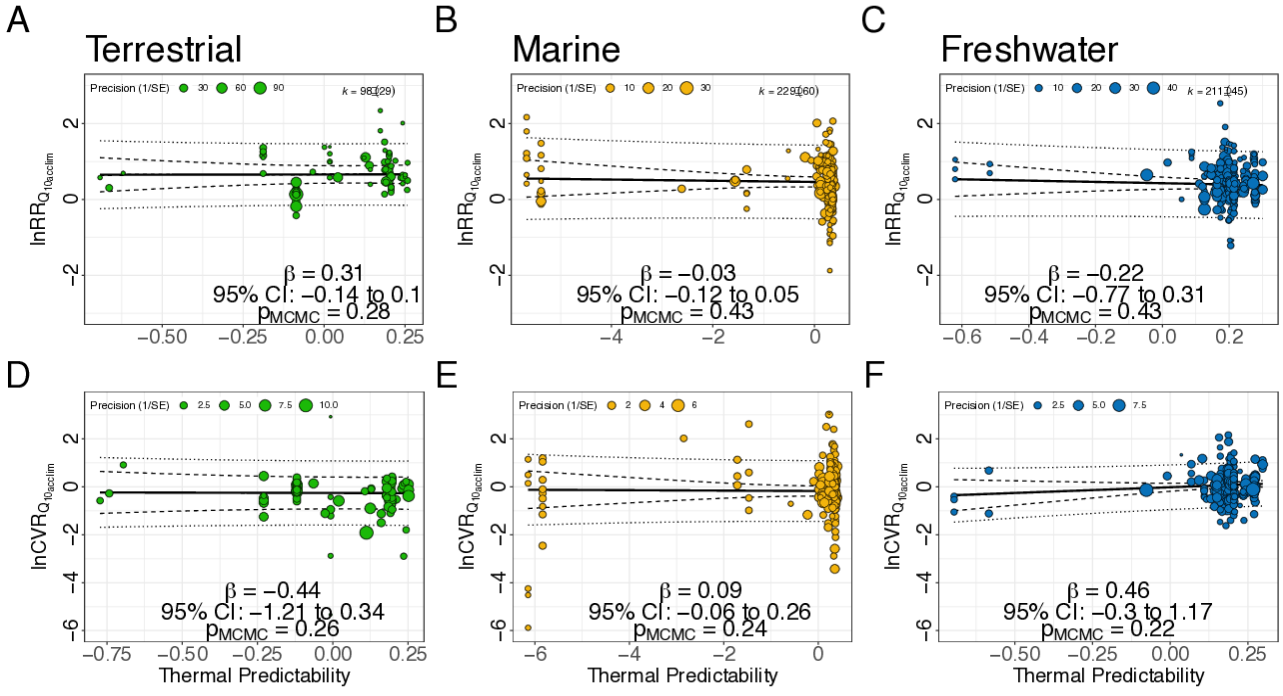

Figure S13- Predicted mean acclimation (thick black line) $lnRR_{Q_{10}{}_{acclim}}$ (A) and $lnCVR_{Q_{10}{}_{acclim}}$ (B) as a function of the thermal predictability for wild populations across marine, freshwater and terrestrial habitats. Dashed lines indicate 95% confidence intervals and dotted lines indicate 95% prediction intervals. Model slope (β) along with the 95% CI and p_{MCMC} values for the slopes are shown for each habitat.

Publication bias analysis

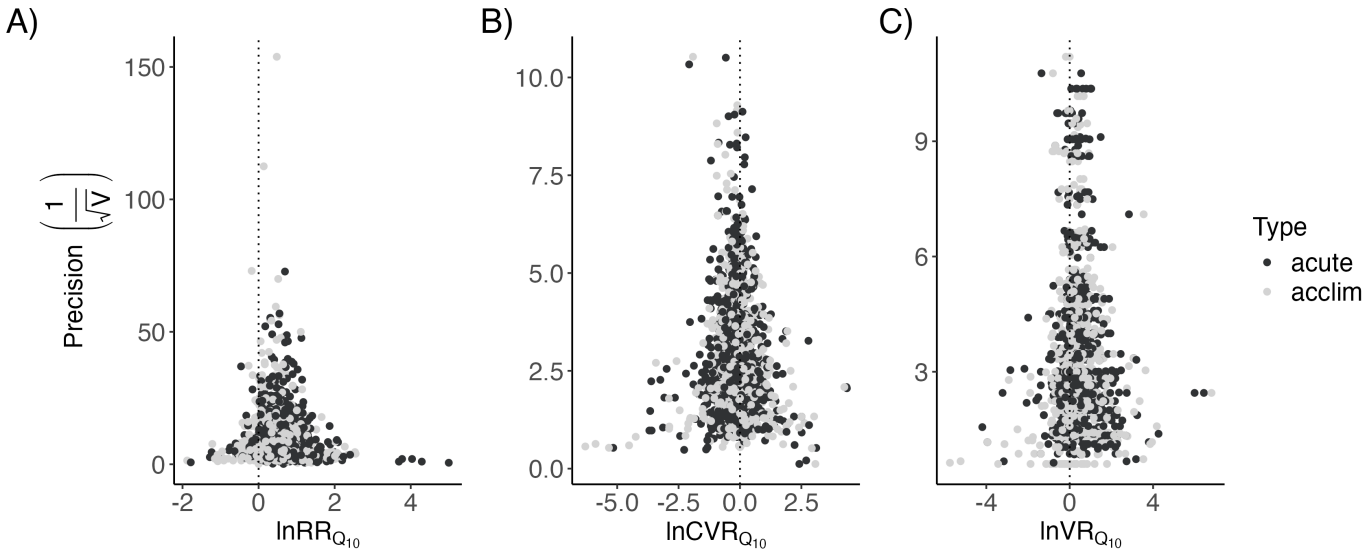

Figure S14- Funnel plot of precision (1/sampling standard error) against effect size for A) log response ratio Q_{10} ($lnRR_{Q_{10}}$), B) log coefficient of variance ratio Q_{10} ($lnCVR_{Q_{10}}$) and C) log variance ratio Q_{10} ($lnVR_{Q_{10}}$). Both acute ('black') and acclimation ('grey') effect sizes are plotted.

Funnel plots did not show any noticeable deviation from the typical funnel shape for any of the effect size estimates (Figure S14). Meta-regression models including sampling standard error as a moderator also suggested no relationship with effect size for $lnRR_{Q_{10}}$ (β = -0.09, 95% CI: -0.35 to 0.17, p_{MCMC} = 0.48), $lnCVR_{Q_{10}}$ (β = 0.04, 95% CI: -0.41 to 0.49, p_{MCMC} = 0.85) or $lnVR_{Q_{10}}$ (β = -0.07, 95% CI: -0.57 to 0.44, p_{MCMC} = 0.79) was not significant indicating little evidence for publication bias.

Performance Curve Simulations

To better understand the characteristics of the performance curves in a sample that would lead to observed changes in variance (and relative variance) across temperature we conducted a simple simulation. To simulate performance curves, we used an asymmetrical Gaussian function (Equation 9):

$$P_T = 2\epsilon^{-\frac{(T-\delta)^2}{2\sigma^2}}\Phi\left(\alpha\frac{T-\delta}{\sigma}\right) \qquad (9)$$

where T is the temperature gradient, δ is the optimal temperature (the temperature where performance is maximized), σ is the performance breadth, and α is the skewness of the performance function or rate variation. To understand how each parameter impacts the shape of performance curves, we simulated 40 individuals with varying amounts of between individual variation in performance breadth, optima and rate variation. We then calculated the relative variance in performance across the temperature gradient as the variance in performance at each temperature divided by the maximum performance at that temperature. This simple analysis identified thermal optima and breath as being the major factors likely leading to the observed patterns in $lnVR_{Q_{10}}$ we identify in our meta-analysis.

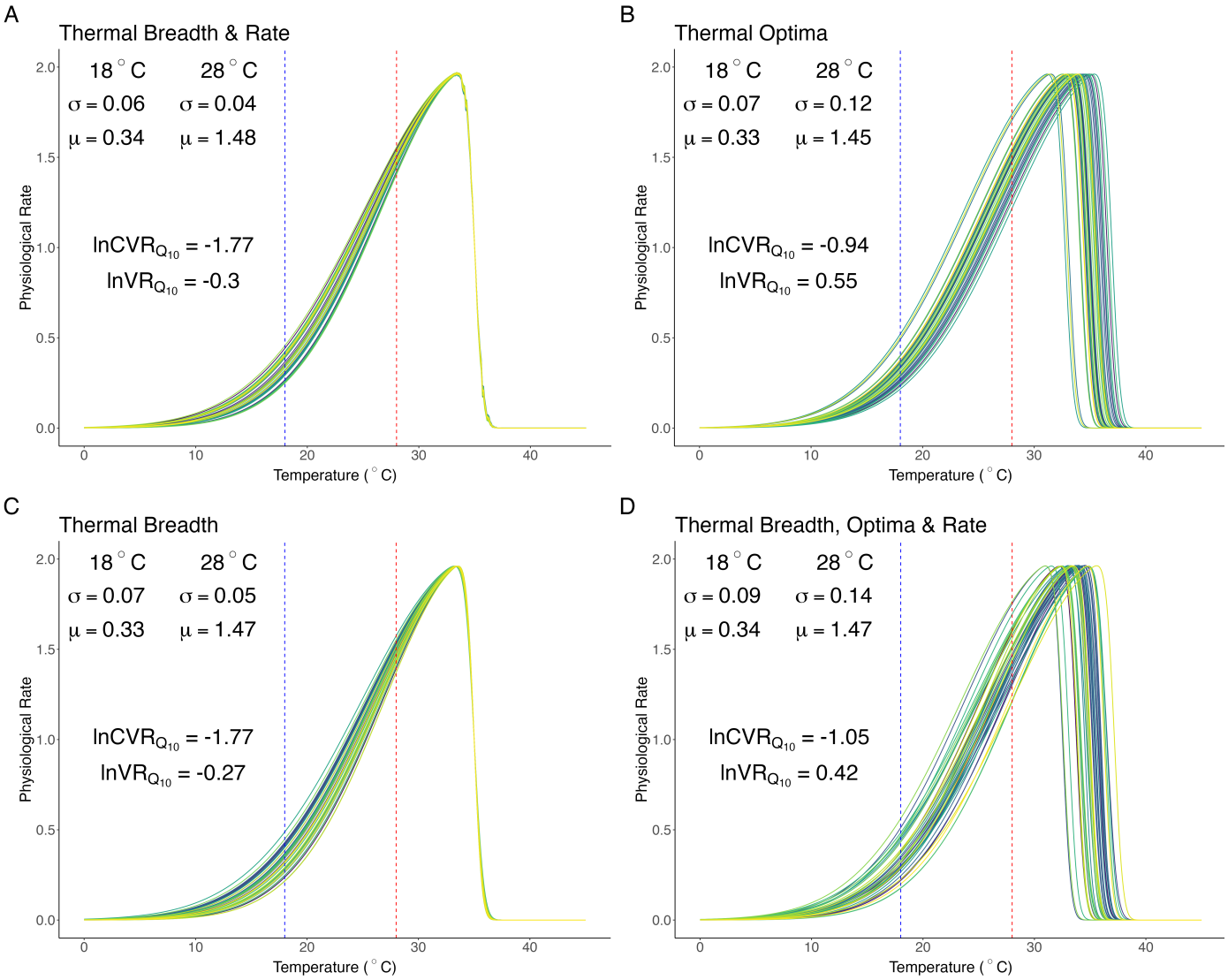

Figure S15- Simulated performance curves for n = 40 individuals in four hypothetical scenerios with varying performance breadth (σ), optima (δ) and skewness (α). Individual performance curves are different colours. $lnCVR_{Q_{10}}$ is calculated as the log transformed ratio of the coefficient of variance (CV) in performance at the higher temperature divided by the CV in performance at that temperature at each point along the curve. $lnVR_{Q_{10}}$ is calculated as the log transformed ratio of the standard deviation in performance at the higher temperature divided by the standard deviation in performance at that temperature. The dashed red line indicates the higher temperature (28°C) and the dashed blue line indicates the lower temperature (18°C). Note that the mean (μ) and standard deviation (σ) of physiological rates are shown for each temperature. In all simulations, δ = 35, σ = 9 and α = -15, while between individual variation for σ_δ = 1, σ_σ = 0.5 and σ_α = 0.5.

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