

# Reduced plasticity and variance in physiological rates of ectotherm populations under climate change

Daniel W.A. Noble<sup>1</sup> ‡, Fonti Kar<sup>2</sup>, Alex Bush<sup>4</sup>, Frank Seebacher<sup>3</sup> †, & Shinichi Nakagawa<sup>2</sup> †

## Affiliations:

<sup>1</sup> Division of Ecology and Evolution, Research School of Biology, The Australian National University, Canberra, ACT 2600, Australia

<sup>2</sup> Ecology and Evolution Research Centre, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW, Australia

<sup>3</sup> School of Life and Environmental Sciences, University of Sydney, Sydney, NSW 2006, Australia

<sup>4</sup> Department of Biology, Lancaster University, Liverpool, UK

† contributed equally

‡ corresponding author, daniel.noble@anu.edu.au

**Running title:** Reduced physiological rate variation in ectotherms

**Author Email Addresses:** Fonti Kar – f.kar@unsw.edu.au; Alex Bush, alex.bush@lancaster.ac.uk; Frank Seebacher, frank.seebacher@sydney.edu.au; Shinichi Nakagawa, s.nakagawa@unsw.edu.au.

**Statement of authorship:** 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.

**Data accessibility statement:** All data and code used to reproduce analyses can be found on GitHub at: [https://github.com/daniel1noble/Q10\\_meta\\_analysis](https://github.com/daniel1noble/Q10_meta_analysis).

**Article Type:** Synthesis

**Word Counts:** Abstract: 202; Main Text: 6752

**Number of References:** 85

**Number of Figures:** 5

**Number of Tables:** 0

**Number of Boxes:** 0

## Abstract

Climate change is expected to result in warmer and more variable thermal environments globally. Maintaining phenotypic variability in physiological rates and adjusting them in response to extreme temperatures (plasticity) is essential for allowing populations to adapt to climate change. Yet, incorporating both plasticity and changes in phenotypic variation when predicting the impacts of climate change on populations is often ignored. Using newly developed effect size estimates and meta-analysis (>1900 effects from 226 species), we show that across habitats relative variance in physiological rates decreases at higher temperatures. Freshwater ectotherms are capable of acclimating and have the smallest reductions in relative variance. Marine organisms also showed a capacity to acclimate to higher temperatures, but capacity for plasticity traded-off with a reduction in relative variance in physiological rates at higher temperatures. Relative variance reductions were particularly pronounced for terrestrial ectotherms, and this coincided with a lack of capacity for acclimation, highlighting the vulnerability of terrestrial ectotherms to climate change. Our results show that beneficial acclimation responses in some ecosystems (marine and freshwater) may trade-off with reductions in physiological rate variance that can have important evolutionary and ecological ramifications that affect our understanding of how climate change will impact populations now and in the future.

## Introduction

Climate change is expected to result in warmer but also more variable thermal environments globally (Easterling *et al.* 2000; Ummenhofer & Meehl 2017; Suarez-Gutierrez *et al.* 2023). Greater thermal variability in the past should result in strong selection pressures that lead 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, 2023; Nunney 2016; Chevin & Hoffmann 2017; Cooke *et al.* 2021). Without plasticity or adaptation, high extinction rates are predicted unless organisms can migrate to track suitable habitats (Cahill *et al.* 2012; Nunney 2016). Phenotypic plasticity is expected to be the ‘first line of defence’ against changing climates, thereby buying time for genetic adaptation to take place (i.e., the ‘plasticity first hypothesis’) (West-Eberhard 2003; Lande 2009). Phenotypic plasticity is predicted to evolve when environmental variability is high but predictable and the costs of plasticity are 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), or the prediction is only supported for specific life-history stages.

Reversible phenotypic plasticity, such as acclimation, is expected to provide greater potential to buffer populations from climate impacts as responses are relatively rapid and can therefore be fine-tuned to proximate environmental conditions (assuming the costs of plasticity are low) (Dewitt *et al.* 1998; Scheiner *et al.* 2020). Acclimation is driven by endocrine and epigenetic processes that change the underlying physiology to facilitate a rapid response to the environment (Little *et al.* 2013; Taff & Vitousek 2016; Seebacher & Simmonds 2019). However, the focus up to now has been primarily on mean physiological responses. For example, mean thermal tolerances or acclimation capacities 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). However, it is possible that intrapopulation variability might also be impacted in addition to the mean. Understanding how variability in physiological rates – traits thought to be closely linked to fitness – are affected by climate change is important because lack of physiological variation can limit responses to selection (i.e., the ‘opportunity for selection on a trait’) (Pelletier & Coulson 2012). Higher physiological variance in a population may also indicate greater niche breadth which can buffer populations against environmental change (i.e., the portfolio effect) (Schindler *et al.* 2010; Bolnick *et al.* 2011; Slatyer *et al.* 2013; Sanderson *et al.* 2023; Zheng *et al.* 2023). Decreases in phenotypic variance also suggests strong stabilising selection or reflects constraints on performance (Dewitt *et al.* 1998; Scheiner *et al.* 2020). Changes in physiological trait variation may also have important ecological consequences by promoting population productivity and stability (Kooijman *et al.* 1989; Agashe 2009), species coexistence and ecosystem processes (Imura *et al.* 2003; Bolnick *et al.* 2011; Hart *et al.* 2016; Sanderson *et al.* 2023). The implications of changes in variance could, therefore, have wide-reaching consequences for understanding the capacity of populations to persist in and adapt to novel environments but to date there are few data testing the importance of variances in this context (Scheiner *et al.* 2020).

Periods of past climatic change have had disproportionate impacts on some ecosystems over others raising the question of which ecosystems will be most vulnerable to contemporary climate change. Species occupying terrestrial ecosystems are thought to be particularly vulnerable given their weak acclimation abilities and greater probability of experiencing thermal extremes that overwhelm physiological homeostasis (Hoffmann *et al.* 2013; Gunderson & Stillman 2015; Seebacher *et al.* 2015). However, this conclusion has been questioned given that marine ectotherms have recently been shown

to be closer to their upper thermal limits compared to terrestrial species (Pinsky *et al.* 2019). Marine and freshwater ecosystems appear to have greater physiological acclimation capacity (e.g., Seebacher *et al.* 2015; Pottier *et al.* 2022). However, it is unclear if the magnitude of physiological adjustment is sufficient to compensate for potentially negative environmental effects, particularly when temperature interacts with other abiotic changes. Low oxygen availability may be 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, an increase in temperature may have a stronger impact on variation in physiological rates within populations compared to aquatic ectotherms which may have important cascading effects on energy transfer and productivity across different ecosystems (Barneche *et al.* 2021; Seebacher *et al.* 2023).

Here, we use meta-analysis to re-evaluate the degree to which aquatic and terrestrial ectotherms are capable of physiological plasticity. We then developed new effect sizes to quantify how variance in physiological rates change with temperature to ask the following questions: 1) How much is variance in physiological rates expected to change, if at all, as temperatures rise? 2) Are temperature effects on plastic adjustments in physiological rates larger than changes in variance across aquatic and terrestrial ectotherms? 3) Are changes in plasticity or variance in physiological rates impacted by past climate history? 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 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, 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 by 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. We provide a PRISMA flow diagram of our extraction process in the *Supplement* (see Figure S1).

### ***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 chose 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, 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<sub>10</sub> 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 ( $\ln RR_{Q_{10}}$ ) as well as the variability in physiological rates ( $\ln VR_{Q_{10}}$  and  $\ln CVR_{Q_{10}}$ ). 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.

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

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

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

Where,  $R_1$  and  $R_2$  are mean physiological rates and  $T_1$  and  $T_2$  are the temperatures at which these rates are measured. Log transformation of this ratio makes the effect size normally distributed. Equation 1 is essentially a temperature corrected equivalent to the log response ratio ( $\ln RR$ ) (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)):

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

Here,  $SD_1^2$  and  $SD_2^2$  are the standard deviations and  $N_1$  and  $N_2$  are the sample sizes in group 1 and 2, respectively.

### ***Comparing variance in physiological rates***

Nakagawa *et al.* (2015) proposed analogous effect size estimates to  $\ln RR$  that allow for comparisons of changes in variance between two groups, the log variance ratio ( $\ln VR$ ) and the log coefficient of variation ( $\ln CVR$ ).  $\ln VR$  and  $\ln CVR$  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  $\ln VR$  and  $\ln CVR$ , but these can easily be extended to their  $Q_{10}$  analogues (and associated sampling variance) as follows:

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

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

Equation 3 and Equation 4 describe the change in physiological rate variance (Equation 3) across a  $10^\circ C$  temperature change along with its sampling variance (Equation 4). 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:

$$\ln CVR_{Q_{10}} = \ln \left( \frac{CV_2}{CV_1} \right) \left( \frac{10^\circ C}{T_2 - T_1} \right) \quad (5)$$

$$s_{\ln CVR_{Q_{10}}} = \left[ \frac{(SD_1)^2}{N_1 (R_1)^2} + \frac{(SD_2)^2}{N_2 (R_2)^2} + \frac{1}{2(N_1 - 1)} + \frac{1}{2(N_2 - 1)} \right] \left( \frac{10^\circ C}{T_2 - T_1} \right)^2 \quad (6)$$

where  $CV$  is the coefficient of variation defined as  $SD/R$ . We refer to  $\ln CVR_{Q_{10}}$  as relative variance because variance changes are relative to the mean.

### ***Calculating acute and acclimation $\ln RR_{Q_{10}}$ , $\ln VR_{Q_{10}}$ and $\ln CVR_{Q_{10}}$ 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  $\ln RR_{Q_{10}}$ ,  $\ln VR_{Q_{10}}$  and  $\ln CVR_{Q_{10}}$  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  $10^\circ C$ .

### ***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  $Q_{10}$  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 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. 1.22, 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. For terrestrial species we estimated soil temperatures as 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. We therefore only present results for air temperature.

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). 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.

Lastly, to illustrate the effects that climate warming could have on physiological rate variance we also extracted climate projections and calculated thermal variability and predictability for the future. We used the CanESM2 climate model (2005-2100) under a high emissions scenario (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, n.d.). 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). 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.,  $N(0,10)$ ) 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.,  $R_{hat} = 1$ ). 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  $\Delta IC$  between the competing models of 2 or more. If two models were within 2  $\Delta IC$  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  $\ln RR_{Q_{10}}$  and  $\ln CVR_{Q_{10}}$ , 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  $\ln RR_{Q_{10}}$  and  $\ln CVR_{Q_{10}}$  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 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) =  $37.98 \pm 45.19$  days), and terrestrial ectotherms were acclimated for a much shorter duration (mean (SD) =  $23.53 \pm 15.56$ , n = 125) than both freshwater (mean (SD) =  $36.81 \pm 28.71$ , n = 430) and marine species (mean (SD) =  $46.18 \pm 67.21$ , 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  $\ln RR_{Q_{10}}$ . 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  $\ln RR_{Q_{10}}$  and  $\ln CVR_{Q_{10}}$  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  $\ln RR_{Q_{10}acclimation}$  relative to  $\ln RR_{Q_{10}acute}$  indicates that acclimation to thermal environments results in partial compensation of physiological rates (i.e., phenotypic plasticity), whereas no differences between  $\ln RR_{Q_{10}acute}$  and



$\ln RR_{Q_{10}^{acclimation}}$  suggests organisms are not capable of physiological plasticity (Seebacher *et al.* 2015; Havird *et al.* 2020). In contrast, a difference in  $\ln CVR_{Q_{10}^{acclimation}}$  relative to  $\ln CVR_{Q_{10}^{acute}}$  would imply that changes in between individual variation in physiological rates across 10°C 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  $\ln RR_{Q_{10}}$  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 ( $\Delta AIC_c$ ; 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 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.

### ***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 physiological traits we fit a model that included an interaction between acclimation type, habitat type, latitude and longitude. We assumed that any change in  $\ln CVR_{Q_{10}}$  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  $\ln CVR_{Q_{10}}$  for each wild population in our dataset at the specific populations latitude and longitude. To do this, we first converted the predicted  $\ln CVR_{Q_{10}}$  to a 1°C change as opposed to 10°C as follows:

$$\ln CVR_{Q_1} = \frac{\ln CVR_{Q_{10}}}{10} \quad (7)$$

Equation 7 turned the expected change across 10°C to 1°C. 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 accounted 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 A). We had more data on acute thermal responses ( $n = 1115$ ) compared to thermal responses after an acclimation period ( $n = 798$ ) because acute responses were reported for each of the two acclimation temperatures (Figure 1). The two acute  $\ln RR_{Q_{10}}$  effect sizes differed significantly from each other (acute responses were greater for animals acclimated to high temperatures –  $\beta = 0.07$ , 95% CI: 0.04 to 0.1,  $p_{MCMC} = < 0.0001$ ), but on average they were in the same direction and only differed by ~10%. As such, we averaged the two acute  $\ln RR_{Q_{10}}$  effect sizes in subsequent analyses.

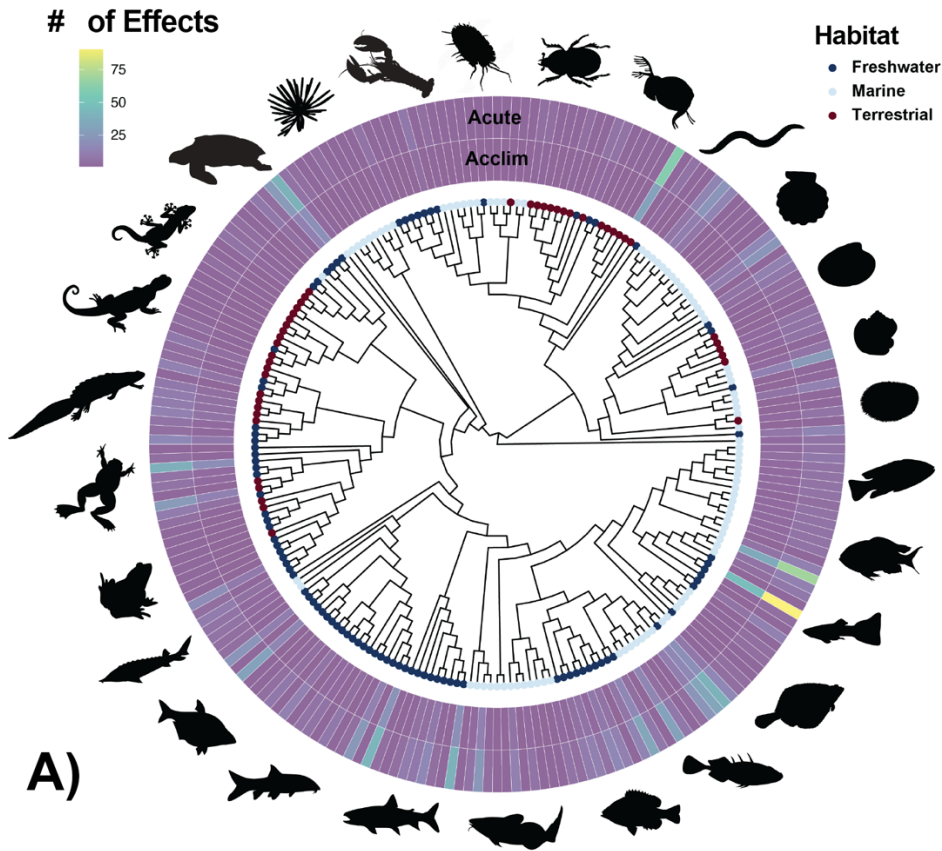
Most of the effect size estimates came from measurements of metabolic rates (both resting and maximal –  $N_{species} = 190$ ,  $N_{effects} = 1023$ , considering acute and acclimation effects together), metabolic enzyme rates ( $N_{species} = 61$ ,  $N_{effects} = 798$ ) and whole-organism performance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

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

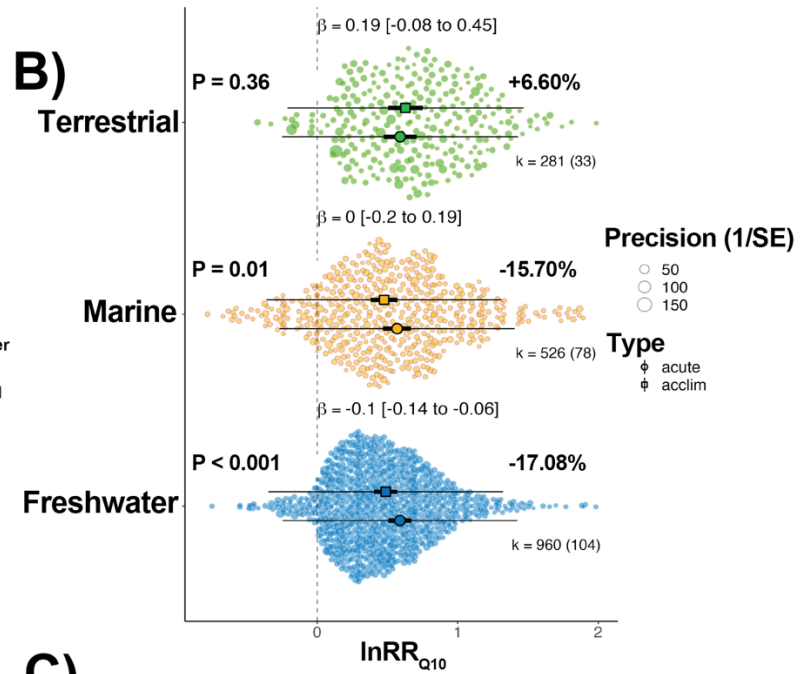
Overall,  $\ln RR_{Q_{10}acclimation}$  was 8.72% lower than  $\ln RR_{Q_{10}acute}$  across all habitats (95%CI: -15.14 to -2.45%). Ectotherms in marine and freshwater environments showed partial compensation of physiological rates (Figure 1B) amounting to reduced  $\ln RR_{Q_{10}acclimation}$  of 17.08% (95% CI: -24.32 to -10.19) in freshwater and 15.7% (95% CI: -25.96 to -4.79) in marine environments. In contrast, terrestrial ectotherms showed no acclimation (possibly even inverse acclimation) – showing a 6.6% increase in  $\ln RR_{Q_{10}acclimation}$  (95% CI: -6.56 to 21.19, Figure 1B).

Nonetheless, 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%).

Different trait categories showed different acclimation responses across habitat types, however, they mirrored overall patterns (see Supplement; Figure S2). Acclimation capacity also did not vary by life-history stage and there were no differences between  $\ln RR_{Q_{10}acclimation}$  and  $\ln RR_{Q_{10}acute}$  between adult and juveniles (Figure 2 A-C) (Adult-Juvenile (Acute): 0, 95% CI: -0.21 to 0.2,  $p_{MCMC} = 0.96$ ; Adult-Juvenile (Acclimation): 0.05, 95% CI: -0.16 to 0.38,  $p_{MCMC} = 0.83$ ).



B)



C)

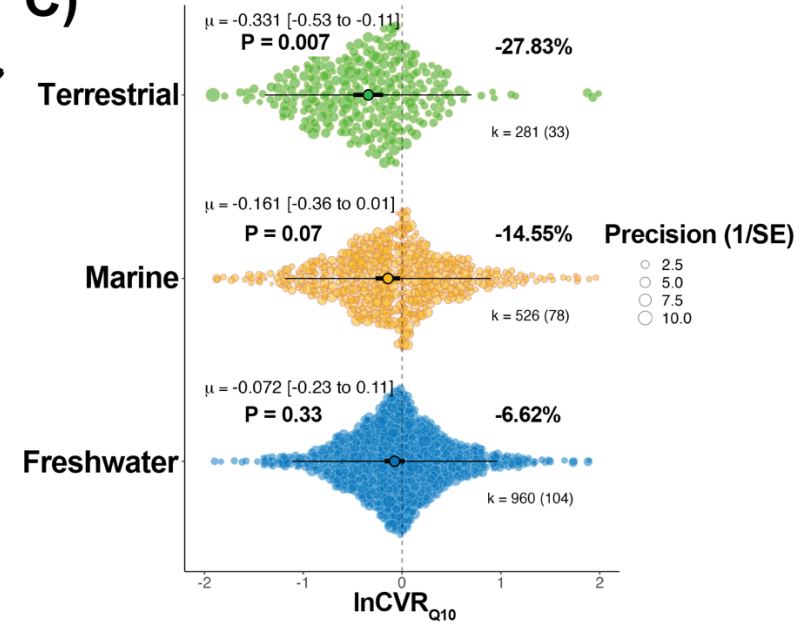


Figure 1- Taxonomic distribution of acute and acclimation  $Q_{10}$  estimates across major habitats. **A)** Phylogenetic distribution of taxa contained within the data. The total number of acute and acclimation  $Q_{10}$  effect sizes are highlighted as well as whether the taxa are marine, freshwater or terrestrial. Silhouettes are representative taxa of major clades within the tree. **B)** Mean acute and acclimation  $\ln RR_{Q_{10}}$  across marine, freshwater, and terrestrial systems. **C)** Mean  $\ln CVR_{Q_{10}}$  across traits for marine, freshwater and terrestrial systems. Note there were no differences between acute and acclimation  $Q_{10}$  types.  $k$  = 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).

#### 4 ***Reduced variation in physiological rates in terrestrial and marine ectotherms***

5 Relative variance in physiological rates ( $\ln CVR_{Q_{10}}$ ) showed a decrease with increasing temperature across all  
 6 habitat types, which was especially pronounced in terrestrial and marine ectotherms. Overall, there was a  
 7 27.87% (95% CI: 10.77 to 40.91,  $p_{MCMC} = 0.01$ ) reduction in relative physiological rate variance for  
 8 terrestrial ectotherms and a 14.94% (95% CI: 1.87 to 29.97,  $p_{MCMC} = 0.07$ ) reduction in relative variation for  
 9 marine ectotherms when temperatures increased by 10°C. In contrast, freshwater ectotherms exhibited a  
 10 smaller reduction in relative physiological rate variance at high temperatures (8.62%, 95% CI: 0.41 to 21.78,  
 11  $p_{MCMC} = 0.33$ ).

12 The total proportion of heterogeneity in  $\ln CVR_{Q_{10}}$  was lower compared to  $\ln RR_{Q_{10}}$  ( $I_{sv}^2 = 23.96$ , 95% CI:  
 13 20.36 to 27.27), with most variation being driven by between-study and trait differences (see Supplement;  
 14 Figure S5). Each life-history stage exhibited the same pattern of variance change in each of the habitats  
 15 (Figure 2). Reduced relative variance was particularly prominent for resting metabolic rates and sprint speed  
 16 although traits differed in whether they exhibited a reduction in variation in physiological rates at high  
 17 temperatures (Figure S3).

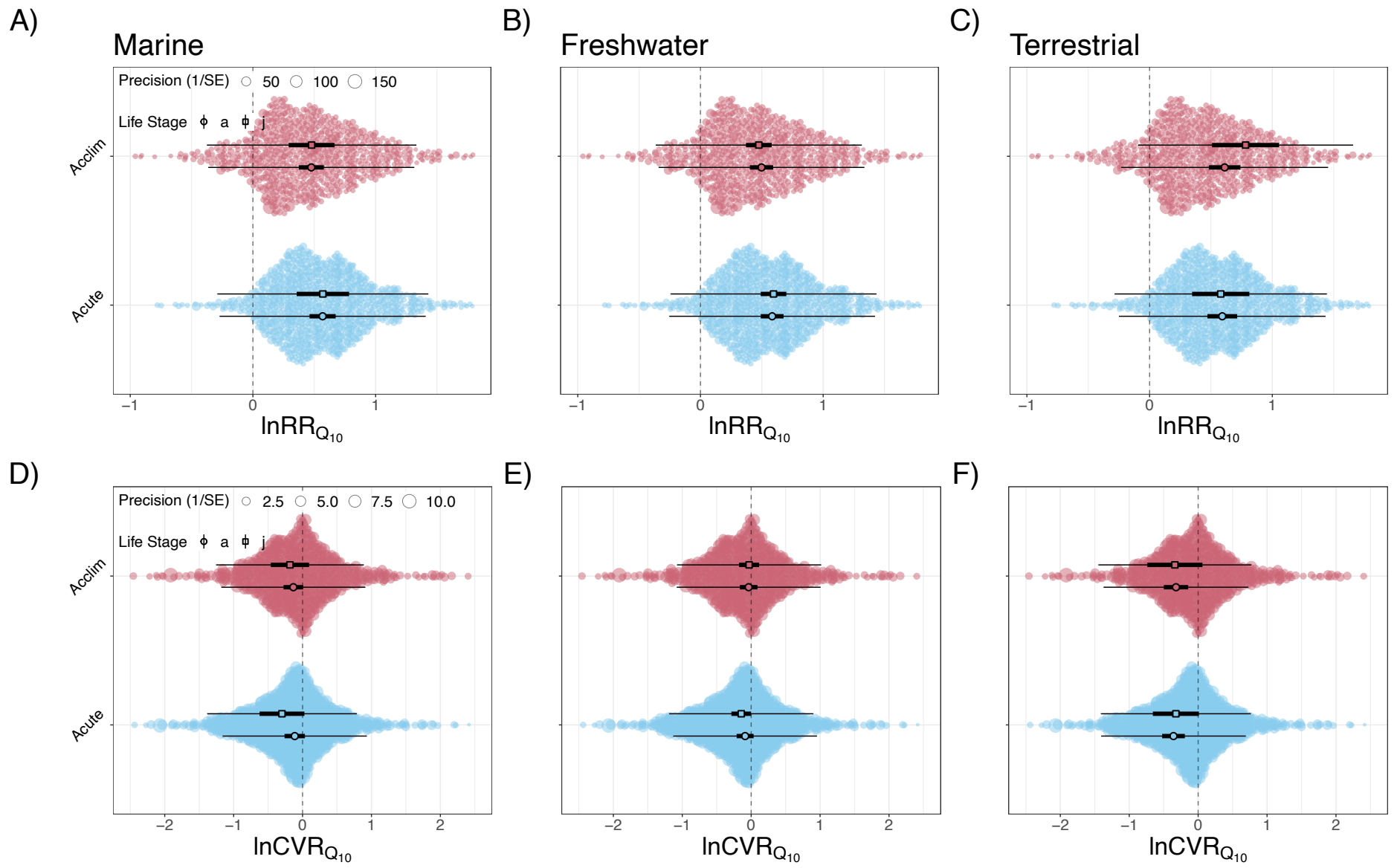


Figure 2- Estimated mean acclimation and acute  $\ln RR_{Q_{10}}$  (A-C) and  $\ln CVR_{Q_{10}}$  (D-F) for adult and juvenile life-history stages for Marine (A & D), Freshwater (B & E) and Terrestrial (C & F) ectotherms.  $k$  = total number of effect size estimates while the numbers in brackets indicate the number of species. Thick bars indicate 95% confidence intervals and thin bars indicate 95% prediction intervals. Raw data for both adult and juvenile life-history stages also presented but points are not distinguished by different symbols for ease of presentation.

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

21 Thermal variability (i.e.,  $CV$ ) and predictability experienced by a population in the past did not explain  
22 acclimation capacity or changes in physiological rate variance among terrestrial, marine or freshwater  
23 populations (Figure 3; Figure 4).

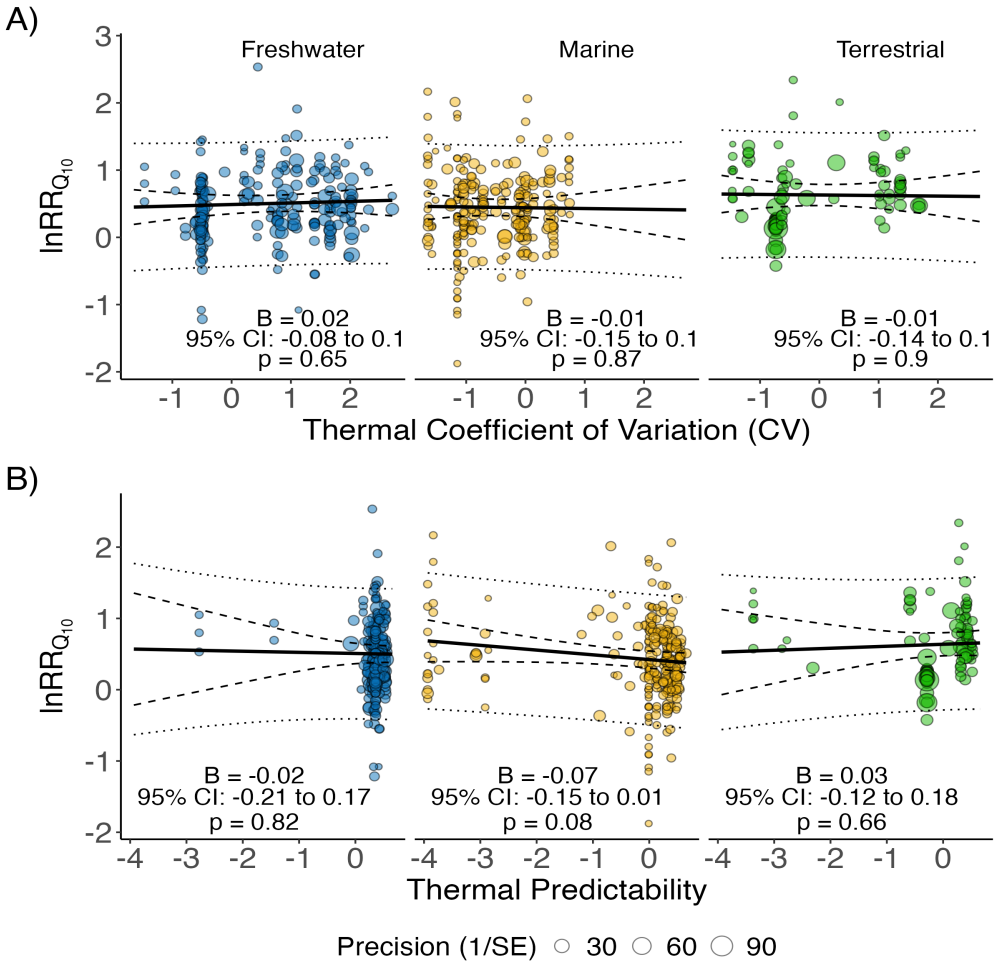


Figure 3- Predicted mean (thick black line)  $\ln RR_{Q_{10}}$  as a function of the Thermal Coefficient of Variation (CV) (A) and thermal predictability (B) for wild populations across marine, freshwater and terrestrial habitats. Dashed lines indicate 95% confidence intervals and dotted lines indicate 95% prediction intervals. Model slope ( $\beta$ ) along with the 95% CI and  $p_{MCMC}$  value is shown for each habitat.

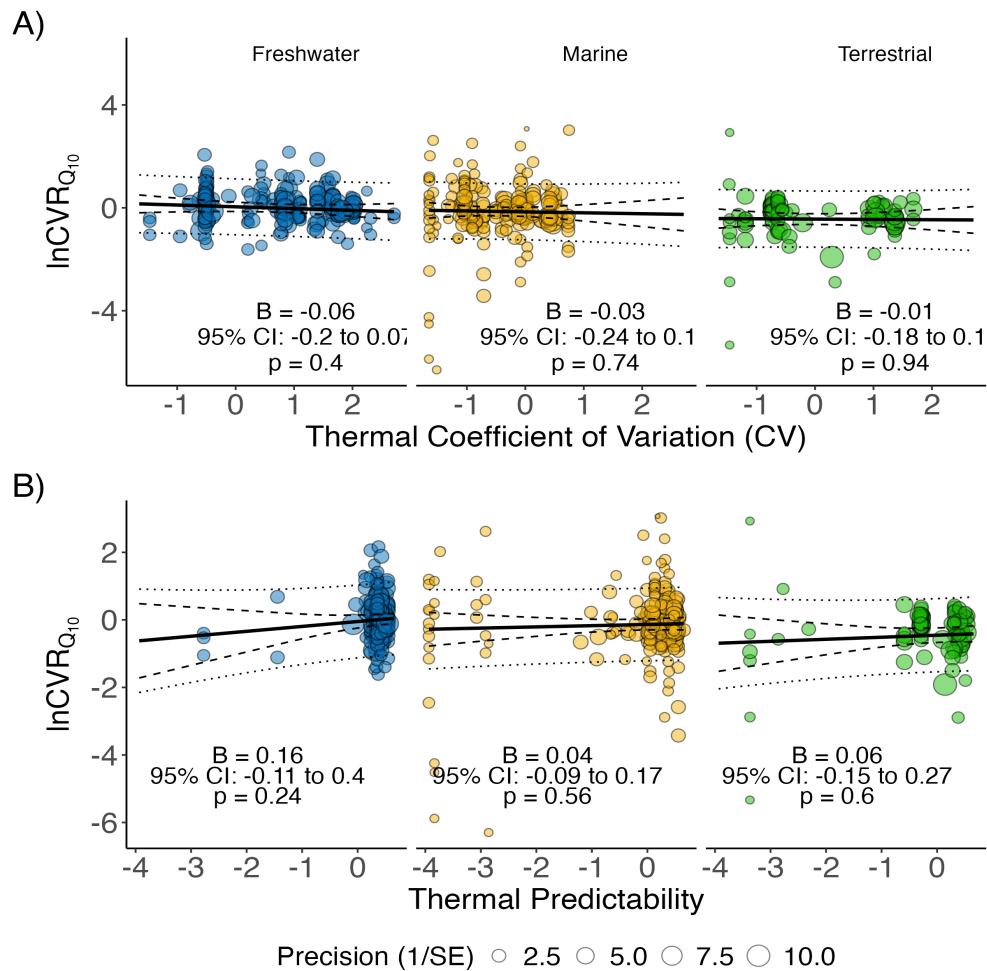


Figure 4- Predicted mean (thick black line)  $\ln CVR_{Q_{10}}$  as a function of the Thermal Coefficient of Variation (CV) (A) and thermal predictability (B) for wild populations across marine, freshwater and terrestrial habitats. Dashed lines indicate 95% confidence intervals and dotted lines indicate 95% prediction intervals. Model slope ( $\beta$ ) along with the 95% CI and  $p_{MCMC}$  value is shown for each habitat.

## 25 **Changes in physiological rate variance under climate change**

26 Measurements of acute and acclimation responses from wild ectotherms were much less common than from  
 27 captive populations ( $N_{species} = 134$ , from 188 wild populations). Globally, there was a clear bias towards  
 28 species in the Northern Hemisphere (Figure 5 A-C). Projected changes in physiological rate variance were  
 29 highly variable across the globe, with some regions showing a decrease in physiological rate variance, while  
 30 others showing an increase (Figure 5 D). However, out of the 188 populations, relative variance was  
 31 predicted to decrease in 98.94% of the locations.

32 Using the ERA5 climate model, predictions of current global changes in physiological rate variance were  
 33 generally conservative with our model explaining  $\sim 50\%$  of the variation in the observed data ( $R^2 = 0.48$ ,  
 34 95% CI: 0.31 to 0.6). Across habitat types climate change is predicted to result in a 0.33% change in relative  
 35 variance for freshwater systems (95% CI: -6.2 to 6.48%,  $p_{MCMC} = 0.89$ ), a 2.87% reduction in relative  
 36 variance for marine systems (95% CI: -6.34 to 1.23%,  $p_{MCMC} = 0.37$ ), and a 12.17% reduction in relative  
 37 variance for terrestrial systems (95% CI: -19.45 to -6.13%,  $p_{MCMC} = < 0.0001$ ) under a RCP8.5 climate  
 38 scenerio.

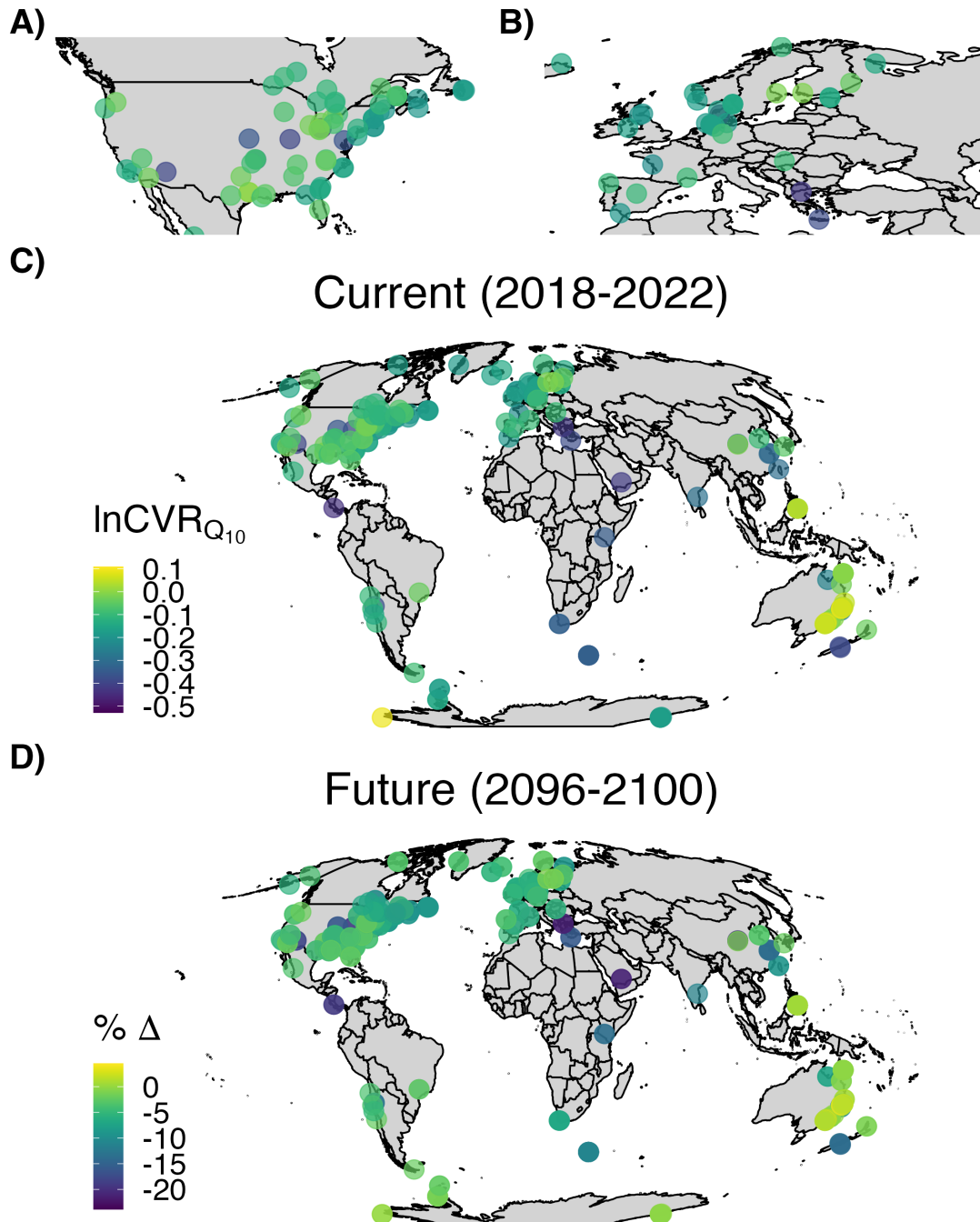


Figure 5- Model predictions for the expected change in acclimation  $\ln\text{CVR}_{Q_{10}}$  across the globe for terrestrial, marine and freshwater ectotherms. Predictions consider the uncertainty in random effects (i.e., species, phylogeny, study). Predicted change in physiological rate variance (relative 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 reduction in relative variance expected under a RCP8.5 climate scenario relative to current climate conditions (% change).

## 39 Discussion

40 Understanding acclimation capacity and how variation in physiological rates changes across populations and  
 41 species is important for predicting the ecological and evolutionary consequences of climate change (Chevin  
 42 *et al.* 2010; Bolnick *et al.* 2011; Bush *et al.* 2016; Chevin & Hoffmann 2017; Sanderson *et al.* 2023;



43 Seebacher *et al.* 2023). Here, we show that the relative variance ( $\ln\text{CVR}_{Q_{10}}$ ) in physiological rates of  
44 ectotherms decreased across terrestrial, marine and freshwater ecosystems as temperatures increase, with the  
45 decrease being particularly pronounced in terrestrial ectotherms (~28%). These effects are expected to result in  
46 a decrease in the variability in physiological rates for marine and terrestrial ectotherms between ~4-13%  
47 under future climate change projections. Our results uncover an hitherto unrecognised dynamic where the  
48 benefits of acclimation may be counteracted by a decrease in trait variance.

### 49 ***Consequences of reduced plasticity and variance in physiological rates across ectotherms***

50 Understanding the interplay between plasticity and genetic adaptation has important implications for  
51 predicting population resilience to climate change (Chevin *et al.* 2010; Hoffmann & Sgrò 2011; Merilä &  
52 Hendry 2014; Bush *et al.* 2016; Cooke *et al.* 2021; Seebacher *et al.* 2023; Urban *et al.* 2023). For example,  
53 incorporating phenotypic plasticity and adaptation into species distribution models dampens the predicted  
54 contraction of distributions in the face of climate change (e.g., Bush *et al.* 2016). In addition, it may be  
55 expected that reductions in variance impact the ‘opportunity for selection’ by reducing the strength of  
56 selection and/or the genetic variance exposed to selection, thereby reducing the capacity to evolve under  
57 climate change (Hoffmann & Sgrò 2011; Urban *et al.* 2023). Quantifying the degree of plasticity and  
58 genetic/phenotypic variation in key physiological responses is therefore recognised as being critical to  
59 informing projections for organisms threatened by climate change (Cooke *et al.* 2021).

60 We show that acclimation of physiological rates and changes relative variance differ across habitats. In  
61 freshwater habitats, acclimation responses will likely be beneficial and this coincides with relatively little  
62 reduction in the relative variance thereby maintaining the raw material for selection to operate. In contrast,  
63 acclimation responses of marine organisms are associated with a nearly equal reduction in relative variance  
64 so that the beneficial effects of acclimation trade-off against reduced potential for selection at high  
65 temperatures. In terrestrial ectotherms, relative variance reductions are particularly pronounced, and this  
66 coincides with a general inability to acclimate. Terrestrial ectotherms are therefore most vulnerable to climate  
67 because both compensations for potentially negative effect of temperature via acclimation, and adaptation to  
68 novel conditions are relatively ineffective. However, terrestrial species have greater opportunity for  
69 behavioural microhabitat selection which will decrease the impacts of climate change at least in complex,  
70 thermally heterogeneous environments (Huey *et al.* 2012).

71 Our findings highlight the potential vulnerability of terrestrial and marine ectotherms to climate change. Our  
72 meta-analytic results provide percentage changes of relative variances and acclimation responses that can be  
73 used to parameterise models (e.g., species distribution models) (Bush *et al.* 2016; DeMarche *et al.* 2019) to  
74 predict species distributions or assess population resilience in the face of climate warming. Our results also  
75 define the range of biological responses observed across diverse taxa (e.g., through prediction intervals)  
76 providing opportunities to incorporate realistic biological variation into the modelling process.

### 77 ***Plasticity and variance in physiological rates do not differ between life-stages***

78 Life-history stages often occupy different ecological niches and exhibit different physiological responses,  
79 levels of plasticity, and patterns of mortality in response to temperature. As such, it is becoming increasingly  
80 important to understand how climate change will impact different life-history stages (Petitgas *et al.* 2013;  
81 Levy *et al.* 2015). Greater plasticity in early life-stages of development is expected to be important to  
82 increase resilience to the effects of climate change because early life-stages are often particularly vulnerable  
83 periods in development (Stearns 1976; Martin 2015). We show that there were generally similar patterns  
84 between early and late life stages across a diversity of taxa, both in terms of variance changes and the  
85 capacity for plasticity. On average, our results show that early life stages are not more vulnerable to the  
86 impacts of climate change. However, our general meta-analytic findings do not imply that early life stages  
87 are not always less plastic, but that such responses are likely context or trait dependent (Moghadam *et al.*  
88 2019; Carter & Sheldon 2020). For example, Moghadam *et al.* (2019) showed that larval *Drosophila* were

89 more plastic in their heat hardening responses compared to adults. In contrast, Carter & Sheldon (2020)  
90 showed greater thermal plasticity in metabolism for adults but little in pupae of *Onthophagus taurus*. Despite  
91 variation in the literature, very few studies measure multiple life-history stages within the same population.  
92 In future research, there needs to be more studies that explicitly compare differences in plasticity among life  
93 stages across multiple traits within the same population.

#### 94 ***Ecological consequences of reduced variation in physiological rates***

95 Variance reductions in metabolism and performance (e.g., sprint speed) were most strongly impacted by  
96 increased temperature. Changes in variability of traits governing energy demand could have important  
97 consequences on the flow of energy within and between populations, communities, and ecosystems (Hendry  
98 2016; Barneche *et al.* 2021; Sanderson *et al.* 2023; Seebacher *et al.* 2023). More variable populations,  
99 genetically and/or phenotypically, are predicted to be associated with broader niches, reduced intraspecific  
100 competition, increased growth rate, decreased vulnerability to environmental change and lower extinction  
101 risk (Bolnick *et al.* 2011; Forsman 2014, 2015; Hart *et al.* 2016; Hendry 2016). Maintaining intrapopulation  
102 variability in physiological rates in a warmer world may therefore be important for population resilience to  
103 climate change. For example, Kooijman *et al.* (1989) integrated individual variation in dynamic energy  
104 budget (DEB) models developed for *Daphnia magna*. They showed that greater between-individual variation  
105 in DEB parameters led to less extreme population fluctuations compared to scenarios with no variation  
106 (Kooijman *et al.* 1989). Our results suggest that terrestrial ectotherms will likely face greater challenges to  
107 adapting to climate change (Hoffmann *et al.* 2013; Gunderson & Stillman 2015; Pottier *et al.* 2022), leading  
108 to greater rates of extinction and reduced productivity in terrestrial ecosystems. However, data testing the  
109 impacts of changes in variance on populations are limited to very few taxa. Future experimentation across a  
110 broader range of taxa should manipulate levels of variance to understand its ecological outcomes.

#### 111 ***No signature of past climate on capacity for physiological plasticity***

112 Theoretical evolutionary models predict that plasticity should evolve in populations experiencing greater  
113 environmental variability (spatial or temporal), particularly when oscillations are predictable over time to  
114 make environmental cues more reliable (Lande 2009; Chevin *et al.* 2010; Reed *et al.* 2010; Murren *et al.*  
115 2015; Hendry 2016; Nunney 2016; Chevin & Hoffmann 2017). Higher spatial and temporal heterogeneity in  
116 terrestrial ecosystems (Steele *et al.* 2019) suggests that plasticity should be more likely to evolve in terrestrial  
117 environments. However, we did not find evidence to this effect. Our finding is consistent with other meta-  
118 analyses (Gunderson & Stillman 2015; Barley *et al.* 2021) with thermal tolerance (which we did not consider  
119 here). Modelling correct microenvironments for over 200 species across such diverse habitats is challenging.  
120 The lack of a relationship between physiological plasticity and environmental variability and predictability  
121 could be due the fact that ectotherms simply seek out microhabitats that make their environment quite stable  
122 (Huey *et al.* 2012). Therefore, it is possible that more fine-scale resolution of the habitats that organisms  
123 occupy will elucidate expected patterns. Randomly fluctuating environments have been suggested to select  
124 for reduced plasticity, particularly if plastic responses are costly and this has been demonstrated by a number  
125 of empirical studies (Leung *et al.* 2020, 2023; Rescan *et al.* 2022). For example, using seed beetles  
126 (*Callosobruchus maculatus*), Hallsson & Björklund (2012) showed that experimentally evolving populations  
127 under randomly fluctuating thermal conditions did not show any increase in plasticity, but had reduced  
128 plasticity. Leung *et al.* (2020) also showed reduced plasticity in morphological traits of experimentally  
129 evolving algae populations (*Dunaliella salina*) when environments were less predictable (see also Leung *et al.*  
130 2023). While it is unclear how these findings relate directly to acclimation because they integrate multiple  
131 forms of plasticity, they do suggest that there are costs to being plastic or that the environmental signals are  
132 insufficient to trigger endocrine and epigenetic mechanisms that lead to plasticity when environments are not  
133 predictable (Hendry 2016; Leung *et al.* 2020). The fact that aquatic ectotherms did show a capacity to  
134 acclimate suggests that environmental predictability, which is expected to be higher in aquatic environments,  
135 may be more important than environmental variability in driving the evolution of plasticity.

## 136 **Conclusions and future directions**

137 Enhanced knowledge of how variation in physiological rates vary across populations and species and the  
138 degree to which they can be adjusted in response to the environment may lead to more informed predictions  
139 about the ecological and evolutionary dynamics of natural populations (Forsman 2015; Cooke *et al.* 2021;  
140 Sanderson *et al.* 2023; Seebacher *et al.* 2023). While we show general patterns across taxa and habitats it is  
141 important to recognise that this does not mean such patterns apply to all populations. Substantial variation in  
142 acclimation responses and changes in variance exist among populations as evidenced by wide prediction  
143 intervals. Nonetheless, changes in the relative variance in physiological rates could be better incorporated  
144 into physiological and ecological models to provide more nuanced and possibly more realistic predictions  
145 about the impacts of climate change on natural populations. While we do not yet understand the relative  
146 contribution of environmental and genetic factors to variances changes, models could better decouple how  
147 different levels of heritability with different total variance impact evolutionary and ecological predictions.  
148 Our meta-analysis now provides the opportunity to parameterise models and ensure they are better aligned  
149 with empirical findings. Nonetheless, many fascinating questions remain unanswered that will require greater  
150 focus on the consequences of changes in variance (rather than just the mean). Particularly interesting  
151 questions include: How does a reduction in physiological rate variance change energy flow across tropic  
152 levels within communities? What are the biochemical, cellular, and physiological mechanisms that underly  
153 reduced variance in physiological rates? Are reductions in variance in one trait associated with reductions in  
154 correlated traits, or do some traits increase while others decrease? How much of the reduction in variance is  
155 driven by lower levels of genetic variance? Answers to these questions will require integrative approaches  
156 that combine empirical and theoretical work across multiple levels of biological organisation but will likely  
157 provide useful advances in understanding the full consequences that climate change will have on ectotherms  
158 across all major ecosystems.

## 159 **Funding**

160 DWAN is supported by an Australian Research Council (ARC) Future Fellowship (FT220100276) and ARC  
161 Discovery Project (DP210101152). SN is supported by ARC Discovery Project Grants (DP210100812 and  
162 DP230101248).

## 163 **Conflict of interest**

164 Authors declare that they have no competing interests.

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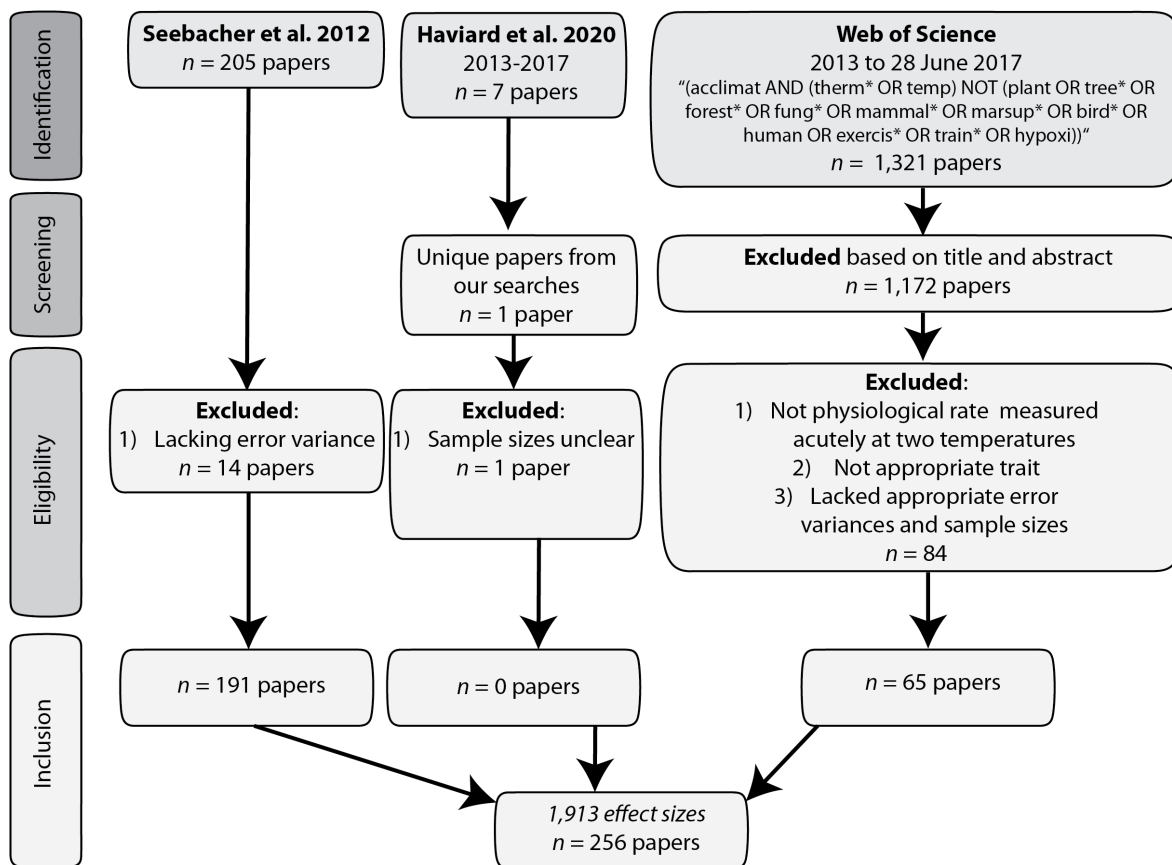


Figure S1- PRISMA flow diagram of the literature search and screening process.

Acute and acclimation  $\ln RR_{Q_{10}}$  for different trait categories across marine, freshwater and terrestrial taxa

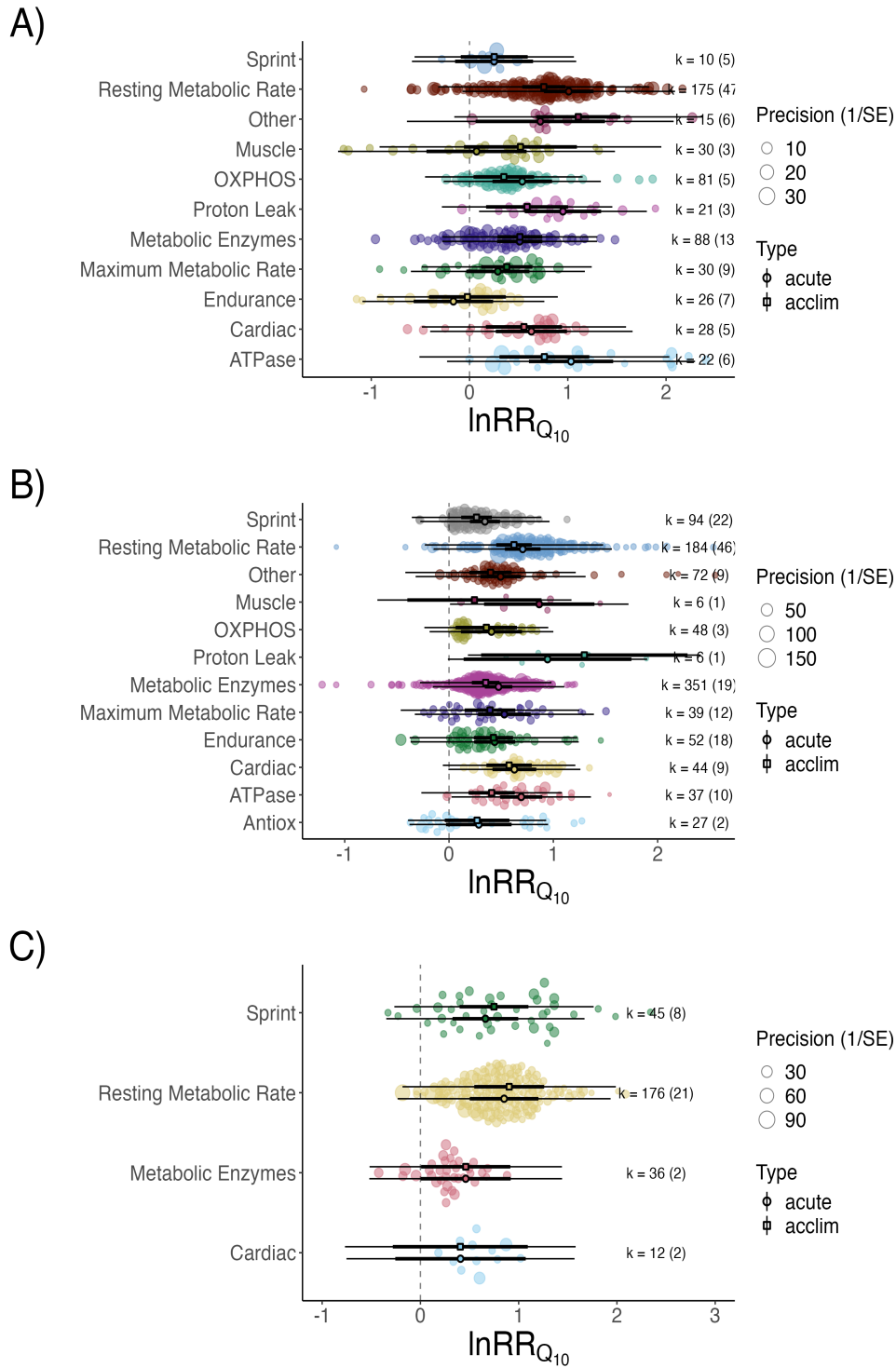


Figure S2- Acute and Acclimation  $\ln RR_{Q_{10}}$  across traits for A) marine, B) freshwater and C) terrestrial systems. k = total number of effect size estimates while the numbers in brackets indicate the number of species. Thick bars indicate 95% confidence intervals and thin bars indicate 95% prediction intervals. The x-axis is truncated for ease of visualisation.

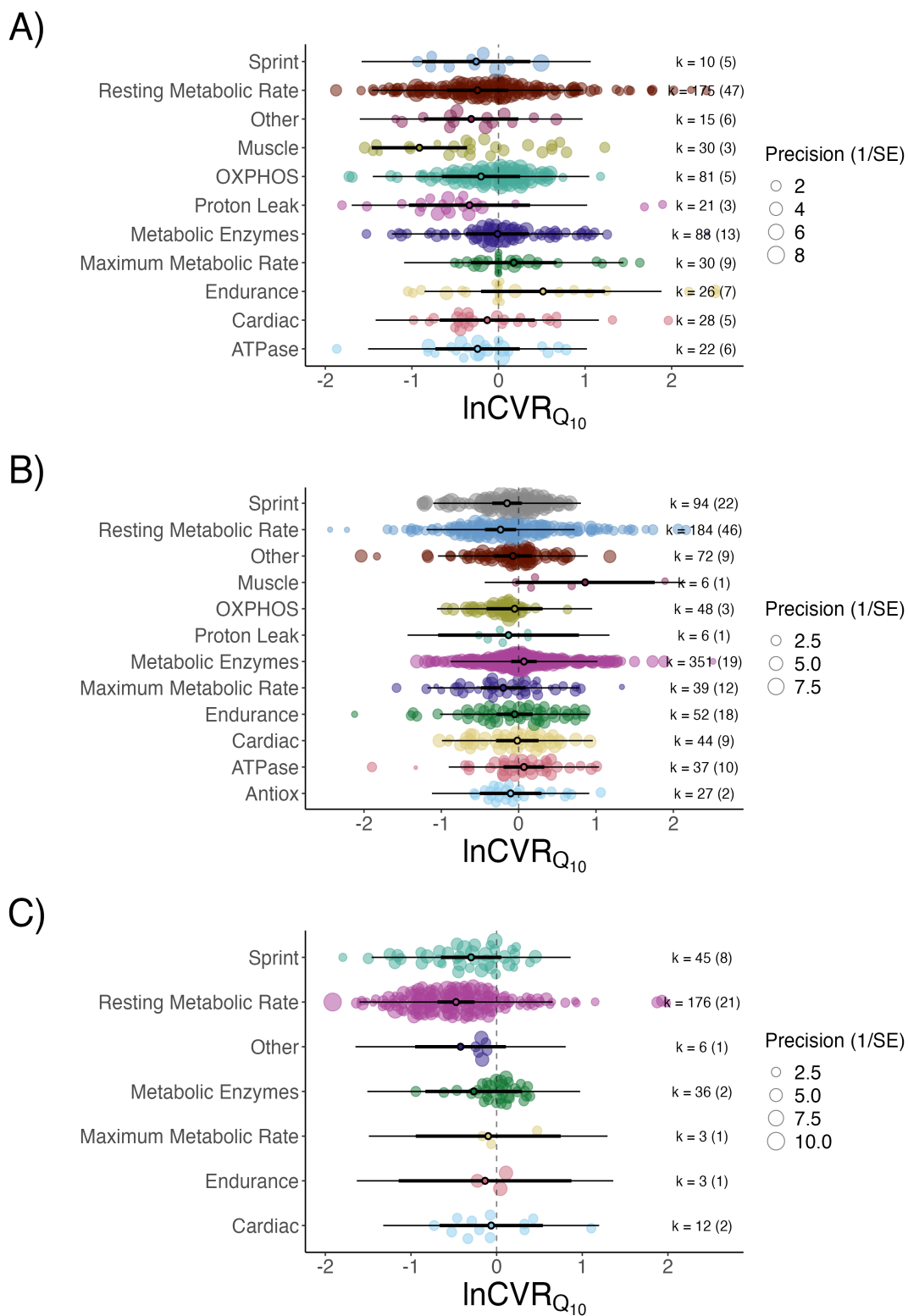


Figure S3- Acute and Acclimation  $\ln\text{CVR}_{Q_{10}}$  across traits for A) marine, B) freshwater and C) terrestrial systems.  $k$  = total number of effect size estimates while the numbers in brackets indicate the number of species. Thick bars indicate 95% confidence intervals and thin bars indicate 95% prediction intervals. The x-axis is truncated for ease of visualisation.

368 **Comparing raw variance changes using  $\ln VR_{Q_{10}}$**

369 Analysis of  $\ln VR_{Q_{10}}$  suggested that variance increases with higher temperatures across all habitat types, with  
 370 terrestrial ectotherms having the smallest increase in variance (Figure S4; Table S1).

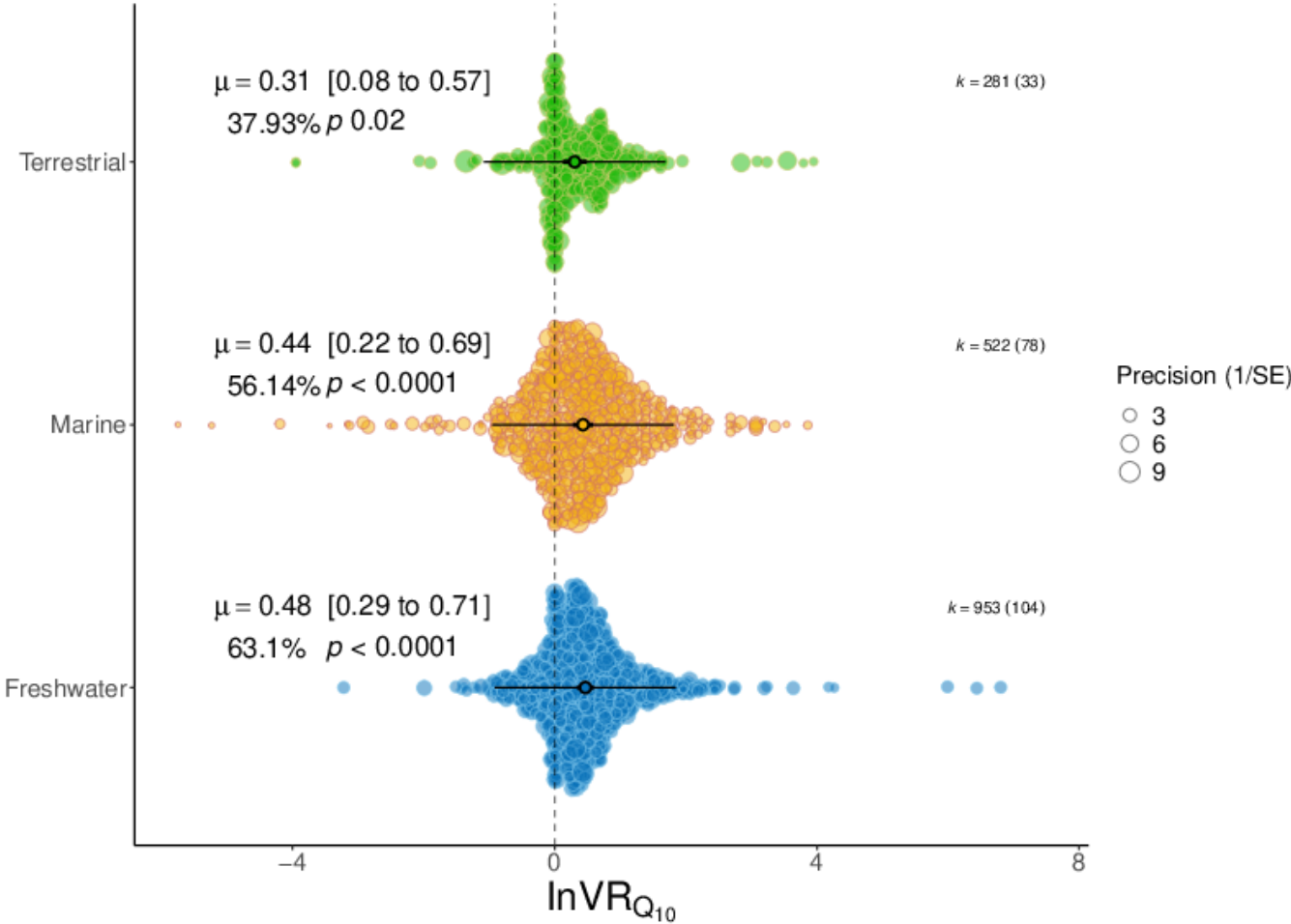


Figure S4- Estimated mean  $\ln VR_{Q_{10}}$  for marine, freshwater and terrestrial systems. Note there were no differences between acute and acclimation  $Q_{10}$  types so they were averaged. Thick black bars are 95% confidence intervals (CI's) and thin bars 95% prediction intervals (PI's). The percentage 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.

Table S1 – Model estimates, standard error, and 95% credible intervals comparing changes in acute and acclimation  $\ln VR_{Q_{10}}$  across habitat types. Model estimates are based off 1,253 effect sizes from 139 studies.

Parameter	Estimate	Est.Error	I-95% CI	u-95% CI
<b>Fixed Effects</b>				
Intercept	0.4932	0.10684	0.2984	0.7281
Acclimation Time (z scaled)	-0.0001	0.00071	-0.0015	0.0013

Parameter	Estimate	Est.Error	I-95% CI	u-95% CI
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
<b>Random Effects</b>				
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

371 **Plots of  $I^2$  for multi-level models**

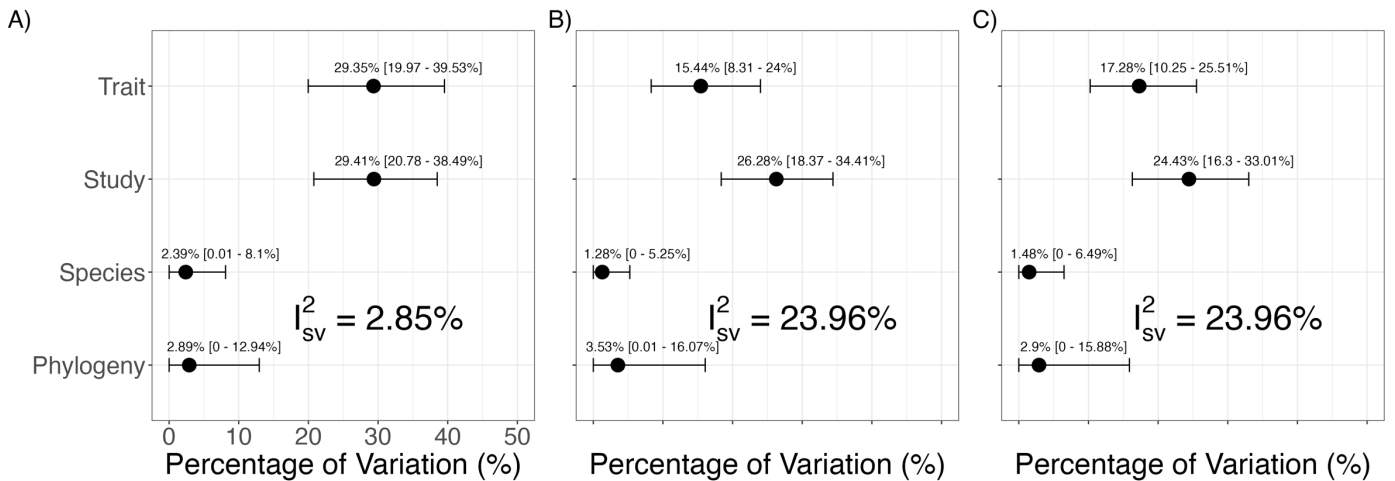


Figure S5-  $I^2$  estimates. A)  $lnRR_{Q_{10}}$  B)  $lnCVR_{Q_{10}}$  and C)  $lnVR_{Q_{10}}$ .

372 **Publication Bias Analysis**

373 Funnel plots did not show any noticeable deviation from the typical funnel shape for any of the effect size  
 374 estimates (Figure S6).

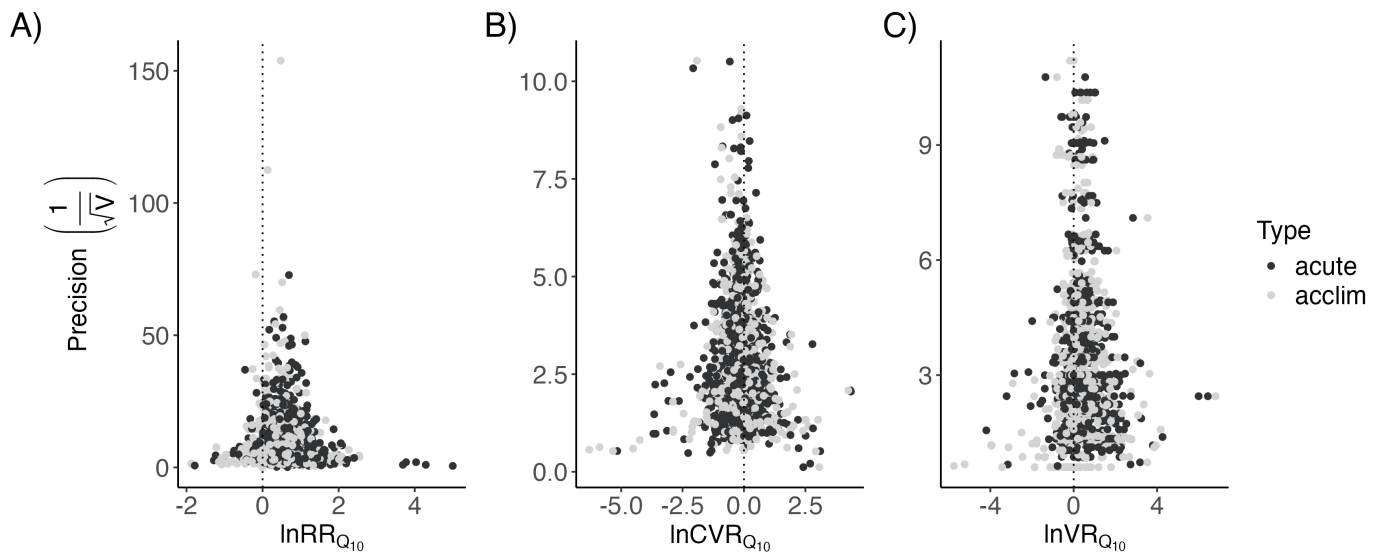


Figure S6- Funnel plot of precision (1/sampling standard error) against effect size for A) log response ratio  $Q_{10}$  ( $\ln RR_{Q_{10}}$ ), B) log coefficient of variance ratio  $Q_{10}$  ( $\ln CVR_{Q_{10}}$ ) and C) log variance ratio  $Q_{10}$  ( $\ln VR_{Q_{10}}$ ). Both acute ('green') and acclimation ('orange') effect sizes are plotted.