

# 1 **Reduced plasticity and variance in physiological rates of ectotherm** 2 **populations under climate change**

3 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> †

## 4 **Affiliations:**

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

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

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

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

11 † contributed equally

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

13 **Running head:** Reduced physiological rate variation in ectotherms

## 14 **Abstract**

15 Climate change is expected to result in warmer and more variable thermal environments globally. Greater  
16 thermal variability is expected to result in strong selection pressures leading to genetic adaptation and/or the  
17 evolution of adaptive phenotypic plasticity. Such responses depend on genetic and phenotypic variability.  
18 However, most work has focused on changes in mean phenotypic responses to climate warming ignoring  
19 how temperature may also change phenotypic variability. Phenotypic variability may be particularly  
20 important at extreme, high temperatures, which would facilitate selection of resistant individuals or promote  
21 plasticity (acclimation) and thereby increase resilience to heat waves. Using newly developed effect size  
22 estimates and meta-analysis (>1900 effects from 226 species), we show that across habitats relative variance  
23 in physiological rates decreased at higher temperatures. Freshwater ectotherms are capable of acclimating  
24 and have the smallest reductions in relative variance. Marine organisms also showed a capacity to acclimate  
25 to higher temperatures, but capacity for plasticity traded-off with a reduction in relative variance in  
26 physiological rates at higher temperatures. Relative variance reductions were particularly pronounced for  
27 terrestrial ectotherms, and this coincided with a lack of capacity for acclimation, highlighting the  
28 vulnerability of terrestrial ectotherms to climate change. Neither life-history stage nor past climate explained  
29 effect variability. Our results show that beneficial acclimation responses may trade-off with reductions in  
30 physiological rate variance. This trade-off could constrain evolutionary responses to climate change and  
31 reduce the potential benefits of portfolio effects. These findings have important evolutionary and ecological  
32 ramifications that affect our understanding of how climate change will impact populations now and in the  
33 future.

## 34 **Introduction**

35 Climate change is expected to result in warmer but also more variable thermal environments globally  
36 (Easterling *et al.* 2000; Ummenhofer & Meehl 2017; Suarez-Gutierrez *et al.* 2023). Greater thermal  
37 variability in the past should result in strong selection pressures that lead to genetic adaptation and/or the  
38 evolution of adaptive phenotypic plasticity – both of which are considered important for population resilience  
39 to contemporary human-induced climate change (Chevin *et al.* 2010; Merila & Hendry 2014; Chevin &  
40 Lande 2015; Seebacher *et al.* 2015, 2023; Nunney 2016; Chevin & Hoffmann 2017; Cooke *et al.* 2021).  
41 Without plasticity or adaptation, high extinction rates are predicted unless organisms can migrate to track

42 suitable habitats (Cahill *et al.* 2012; Nunney 2016). Phenotypic plasticity is expected to be the ‘first line of  
43 defence’ against changing climates, thereby buying time for genetic adaptation to take place (i.e., the  
44 ‘plasticity first hypothesis’)(West-Eberhard 2003; Lande 2009). Phenotypic plasticity is predicted to evolve  
45 when environmental variability is high but predictable and the costs of plasticity are low (Dewitt *et al.* 1998;  
46 Reed *et al.* 2010; Nunney 2016; Chevin & Hoffmann 2017; Scheiner *et al.* 2020). Despite this theoretical  
47 expectation, empirical support is scant (but see (Leung *et al.* 2020)), likely because many organisms can  
48 behaviorally adjust micro-habitat selection to offset thermal stress, the costs of plasticity are high (Dewitt *et*  
49 *al.* 1998; Chevin & Lande 2015), or the prediction is only supported for specific life-history stages.

50 Reversible phenotypic plasticity, such as acclimation, is expected to provide greater potential to buffer  
51 populations from climate impacts as responses are relatively rapid and can therefore be fine-tuned to  
52 proximate environmental conditions (assuming the costs of plasticity are low) (Dewitt *et al.* 1998; Scheiner  
53 *et al.* 2020). Acclimation is driven by endocrine and epigenetic processes that change the underlying  
54 physiology to facilitate a rapid response to the environment (Little *et al.* 2013; Taff & Vitousek 2016;  
55 Seebacher & Simmonds 2019). However, the focus up to now has been primarily on mean physiological  
56 responses. For example, mean thermal tolerances or acclimation capacities in a population are likely to shift  
57 in response to thermal environments (Gunderson & Stillman 2015; Seebacher *et al.* 2015; Havird *et al.* 2020;  
58 Pottier *et al.* 2022). However, it is possible that intrapopulation variability might also be impacted in addition  
59 to the mean. Understanding how variability in physiological rates – traits thought to be closely linked to  
60 fitness – are affected by climate change is important because lack of physiological variation can limit  
61 responses to selection (i.e., the ‘opportunity for selection on a trait’) (Pelletier & Coulson 2012). Higher  
62 physiological variance in a population may also indicate greater niche breadth which can buffer populations  
63 against environmental change (i.e., the portfolio effect) (Schindler *et al.* 2010; Bolnick *et al.* 2011; Slatyer *et*  
64 *al.* 2013; Sanderson *et al.* 2023; Zheng *et al.* 2023). Decreases in phenotypic variance also suggests strong  
65 stabilising selection or reflects constraints on performance (Dewitt *et al.* 1998; Scheiner *et al.* 2020).  
66 Changes in physiological trait variation may also have important ecological consequences by promoting  
67 population productivity and stability (Kooijman *et al.* 1989; Agashe 2009), species coexistence and  
68 ecosystem processes (Imura *et al.* 2003; Bolnick *et al.* 2011; Hart *et al.* 2016; Sanderson *et al.* 2023). The  
69 implications of changes in variance could, therefore, have wide-reaching consequences for understanding the  
70 capacity of populations to persist in and adapt to novel environments but to date there are few data testing the  
71 importance of variances in this context (Scheiner *et al.* 2020).

72 Periods of past climatic change have had disproportionate impacts on some ecosystems over others raising  
73 the question of which ecosystems will be most vulnerable to contemporary climate change. Species  
74 occupying terrestrial ecosystems are thought to be particularly vulnerable given their weak acclimation  
75 abilities and greater probability of experiencing thermal extremes that overwhelm physiological homeostasis  
76 (Hoffmann *et al.* 2013; Gunderson & Stillman 2015; Seebacher *et al.* 2015). However, this conclusion has  
77 been questioned given that marine ectotherms have recently been shown to be closer to their upper thermal  
78 limits compared to terrestrial species (Pinsky *et al.* 2019). Marine and freshwater ecosystems appear to have  
79 greater physiological acclimation capacity (e.g., Seebacher *et al.* 2015; Pottier *et al.* 2022). However, it is  
80 unclear if the magnitude of physiological adjustment is sufficient to compensate for potentially negative  
81 environmental effects, particularly when temperature interacts with other abiotic changes. Low oxygen  
82 availability may be a major factor influencing the vulnerability of aquatic ecosystems, whereas remaining  
83 close to thermal limits and greater water loss is expected to be a stronger constraint on physiological  
84 processes in terrestrial ectotherms (Verberk *et al.* 2016). Given that terrestrial ectotherms are expected to be  
85 closer to their thermal limits, an increase in temperature may have a stronger impact on variation in  
86 physiological rates within populations compared to aquatic ectotherms which may have important cascading  
87 effects on energy transfer and productivity across different ecosystems (Barneche *et al.* 2021; Seebacher *et*  
88 *al.* 2023).

89 Here, we use meta-analysis to re-evaluate the degree to which aquatic and terrestrial ectotherms are capable  
90 of physiological plasticity. We then developed new effect sizes effect sizes to quantify how variance in

91 physiological rates change with temperature to ask the following questions: 1) How much is variance in  
92 physiological rates expected to change, if at all, as temperatures rise? 2) Are temperature effects on plastic  
93 adjustments in physiological rates larger than changes in variance across aquatic and terrestrial ectotherms?  
94 3) Are changes in plasticity or variance in physiological rates impacted by past climate history? 4) How are  
95 means and variances in physiological rates expected to change under climate change?

## 96 **Materials and Methods**

### 97 *Literature collection*

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

109 Our search resulted in 1,321 papers for screening in Rayyan (Ouzzani *et al.* 2016). We also cross-checked  
110 papers we found in our searches with a recent paper by Havird *et al.* (2020), which also updates the dataset of  
111 Seebacher *et al.* (2015)'s. We included any papers that were missed between our searches and those of  
112 Havird *et al.* (2020). Havird *et al.* (2020) added 7 new studies (mainly because they were focused on  
113 metabolic rates), and our searches differed from theirs by only a single paper (i.e., Bulgarella *et al.* 2015).  
114 Given the physiological traits we included were broader, we had a substantial increase in additional papers  
115 that we added to Seebacher *et al.* (2015)'s dataset. More specifically, in addition to the 191 papers we  
116 included from the Seebacher *et al.* (2015) dataset, we extracted data from an extra 65 papers (with a total of  
117 238 effects; a 34.03% increase in the number of published articles). Note that Seebacher *et al.* (2015)  
118 included a total of 205 publications, however, not all these contained the necessary statistics we needed to  
119 derive effect sizes and associated sampling variances (see below). While we may have missed papers, our  
120 goal was to obtain a large representative (and unbiased) sample of acclimation research rather than a  
121 comprehensive dataset. As such, our database represents the most up-to-date dataset used by Seebacher *et al.*  
122 (2015) to answer questions on physiological rates across ectotherms.

123 We split the screening of titles and abstracts for the 1,321 papers found in our search among DWAN, FK, FS,  
124 and SN evenly. To ensure consistency among authors in title and abstract inclusion, relevant authors went  
125 through a randomly selected set of papers together before the formal screening to calibrate selection of  
126 papers based on our inclusion criteria (see below). In cases of disagreement regarding inclusion, we  
127 conservatively included the paper for full text screening and discussed uncertain papers among authors to  
128 come to a decision. After title and abstract screening, there was a total of 149 papers for full text screening.  
129 Papers were included only if they: 1) measured a physiological rate acutely at two temperatures on a sample  
130 of animals chronically exposed to the same two temperatures for at least 1 week; and 2) where physiological  
131 rates measured were burst and sustained locomotion, metabolic rates (standard, resting, routine and  
132 maximal), heart rates, and/or enzyme activities. We provide a PRISMA flow diagram of our extraction  
133 process in the *Supplement* (see Figure S1).

## 134 **Data Compilation**

135 We extracted means, standard deviations, and sample sizes for physiological rates at the two test  
136 temperatures. If there were more than two test temperatures, we chose only the test temperatures that fell  
137 within the most likely natural range of temperatures experienced by the species in question. We extracted  
138 these data from text, tables or figures of a given paper. Data were extracted from figures using the R package  
139 *metaDigitise* (Pick *et al.* 2019). We also recorded the phylum, class, order, genus and species, and the  
140 latitude and longitude from where the experimental animals were sourced. For studies that did not provide  
141 latitude and longitude for the population, we searched for similar studies by the same lab group to identify  
142 where the population was likely to have been sourced. If the experimental animals were derived from the  
143 wild, we recorded the nearest latitude and longitude of the field collection site. If the animals were sourced  
144 from a commercial supplier, we took the latitude and longitude of the supplier. When it was not possible to  
145 find latitude and longitude using these methods, we looked up the distribution of the species in question and  
146 took the latitude and longitude of the centroid of the species' distributional range.

## 147 **$Q_{10}$ Based Effect Sizes and Sampling Variances for Means and Variances**

148 Following Noble *et al.* (2022) we calculated a series of temperature-corrected effect sizes that compared  
149 mean physiological rates ( $\ln RR_{Q_{10}}$ ) as well as the variability in physiological rates ( $\ln VR_{Q_{10}}$  and  $\ln CVR_{Q_{10}}$ ).  
150 These effect sizes are similar to the traditional temperature coefficient ( $Q_{10}$ ), but with formal analytical  
151 approximations of their sampling variances. Sampling variances for effect sizes allowed us to make use of  
152 traditional meta-analytic modelling approaches.

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

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

$$156 \quad \ln RR_{Q_{10}} = \ln \left( \frac{R_2}{R_1} \right) \left( \frac{10^\circ C}{T_2 - T_1} \right) \quad (1)$$

157 Where,  $R_1$  and  $R_2$  are mean physiological rates and  $T_1$  and  $T_2$  are the temperatures at which these rates are  
158 measured. Log transformation of this ratio makes the effect size normally distributed. Equation 1 is  
159 essentially a temperature corrected equivalent to the log response ratio ( $\ln RR$ ) (Hedges *et al.* 1999;  
160 Lajeunesse 2011) when the numerator and denominator are measured at different temperatures. This allows  
161 comparisons of the means from two temperature treatments directly regardless of the absolute measurement  
162 temperatures. The sampling variance for Equation 1 can be computed as follows (as described in Noble *et al.*  
163 (2022)):

$$164 \quad s_{\ln RR_{Q_{10}}} = \left( \frac{SD_2^2}{R_2^2 N_2} + \frac{SD_1^2}{R_1^2 N_1} \right) \left( \frac{10^\circ C}{T_2 - T_1} \right)^2 \quad (2)$$

165 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,  
166 respectively.

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

168 Nakagawa *et al.* (2015) proposed analogous effect size estimates to  $\ln RR$  that allow for comparisons of  
169 changes in variance between two groups, the log variance ratio ( $\ln VR$ ) and the log coefficient of variation  
170 ( $\ln CVR$ ).  $\ln VR$  and  $\ln CVR$  are ratios that describe the relative difference in trait variability between two  
171 groups. We refer readers to Nakagawa *et al.* (2015) for the equations describing  $\ln VR$  and  $\ln CVR$ , but these  
172 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°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°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

211 whether climate at the locations of captive reared organisms would be representative of a population's  
212 climate history - particularly for species reared under captive condition for many generations. Given that we  
213 were interested in understanding climate driven effects on acclimation capacity we only used studies on wild  
214 populations for climate analyses.

215 Monthly average temperature data were extracted from the ERA5 climate model, available from the  
216 Copernicus climate data store (Hersbach *et al.* 2020). For each population and species in the dataset we  
217 extracted a 72-year period (1950-2022) of either surface air temperature (0.01° resolution) for both terrestrial  
218 and freshwater taxa, or sea surface temperature for the marine taxa (at 0.25° resolution) using the *ncdf4* R  
219 package (vers. 1.22, Pierce 2021). We chose surface temperature because we believed that it was more likely  
220 to reflect the micro-thermal environment experienced by terrestrial and freshwater ectotherms at those  
221 locations. For terrestrial species we estimated soil temperatures as this maybe more representative of  
222 microhabitat choice compared to air temperature. We fit models using both air and soil temperature and  
223 found that the results were qualitatively similar. We therefore only present results for air temperature.

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

230 Lastly, to illustrate the effects that climate warming could have on physiological rate variance we also  
231 extracted climate projections and calculated thermal variability and predictability for the future. We used the  
232 CanESM2 climate model (2005-2100) under a high emissions scenario (RCP8.5).

## 233 ***Meta-Analysis***

234 We analysed our data using multilevel meta-analytic (MLMA) and meta-regression (MLMR) models in R  
235 (vers. 4.3.1) using *brms* (vers. 2.20.4 Bürkner 2017, 2018; “Stan development team. RStan” 2021) and  
236 *metafor* (vers. 4.4.0 Viechtbauer 2010). We fit both Bayesian and frequentist approaches to ensure that our  
237 results were consistent, and to create orchard plots more easily (vers. 2.0, Nakagawa *et al.* 2021a, n.d.). In  
238 addition, Bayesian methods better protect against type I errors in the presence of complex sources of non-  
239 independence (Noble *et al.* 2017; Nakagawa *et al.* 2021b; Song *et al.* 2021). For our Bayesian models, we ran  
240 4 MCMC chains, each with a warm-up of 1000 followed by 4000 sampling iterations keeping every 5  
241 iterations for a total of 3200 samples from the posterior distribution. We used flat Gaussian priors for ‘fixed’  
242 effects (i.e.,  $N(0,10)$ ) and a student t-distribution for ‘random’ effects (i.e.,  $student_t(3,0,10)$ ). We checked  
243 that all MCMC chains were mixing and had converged (i.e.,  $R_{hat} = 1$ ). We compared any competing models  
244 using Akaike’s Information Criteria (AIC) (if frequentist) or Wantabe Information Criteria (WIC) (if  
245 Bayesian). We deemed models with the lowest IC value to be best supported if there was a  $\Delta IC$  between the  
246 competing models of 2 or more. If two models were within 2  $\Delta IC$  units we went with the most parsimonious  
247 model.

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

249 We first fit multi-level meta-analysis (MLMA) models (i.e., intercept-only models) for both  $\ln RR_{Q_{10}}$  and  
250  $\ln CVR_{Q_{10}}$ , that included study, species, and phylogeny as random effects to account for non-independence.  
251 We also included trait as a random effect to account for trait variation within the data. Our MLMA models  
252 allowed us to partition the variation in  $\ln RR_{Q_{10}}$  and  $\ln CVR_{Q_{10}}$  among these key sources while accounting for  
253 total sampling variance in each. This allowed us to calculate the proportion of total heterogeneity [i.e.,  $I^2_{total}$ ;  
254 *sensu* Nakagawa & Santos (2012); Noble *et al.* (2022)] along with various  $I^2$  metrics describing the  
255 proportion of variance explained by each random effect level (Nakagawa & Santos 2012). We also present

256 95% prediction intervals which describe the expected distribution of effects from future studies (Nakagawa *et*  
257 *al.* 2021a; Noble *et al.* 2022).

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

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

265 After quantifying levels of heterogeneity, we fit a series of multi-level meta-regression (MLMR) models to  
266 test our key questions. In all models, we included the same random effects as we used in our MLMA models.  
267 Acclimation time varied from 4 to 408 days (mean (SD) = 37.98 ± 45.19 days), and terrestrial ectotherms  
268 were acclimated for a much shorter duration (mean (SD) = 23.53 ± 15.56, n = 125) than both freshwater  
269 (mean (SD) = 36.81 ± 28.71, n = 430) and marine species (mean (SD) = 46.18 ± 67.21, n = 313). Rates of  
270 acclimation have been shown to be faster for many terrestrial groups compared to aquatic organisms [e.g.,  
271 amphibians and reptiles have faster rates of acclimation than fishes; See Einum & Burton (2023)], which  
272 would make it more likely that terrestrial ectotherms would show lower post acclimation  $\ln RR_{Q_{10}}$ . To control  
273 for these possible differences, acclimation time was mean-centered (mean = 0) and included in all our  
274 models. As such, all estimates can be interpreted as values for an average level of acclimation time (i.e.,  
275 37.98 days).

276 We first tested the degree to which acute and acclimation  $\ln RR_{Q_{10}}$  and  $\ln CVR_{Q_{10}}$  effects varied by habitat  
277 type (i.e., terrestrial, freshwater, and marine ecosystems). Models included an interaction between effect type  
278 (i.e., acute or acclimation) and habitat. Reduced mean  $\ln RR_{Q_{10}acclimation}$  relative to  $\ln RR_{Q_{10}acute}$  indicates  
279 that acclimation to thermal environments results in partial compensation of physiological rates (i.e.,  
280 phenotypic plasticity), whereas no differences between  $\ln RR_{Q_{10}acute}$  and  $\ln RR_{Q_{10}acclimation}$  suggests  
281 organisms are not capable of physiological plasticity (Seebacher *et al.* 2015; Havird *et al.* 2020). In contrast,  
282 a difference in  $\ln CVR_{Q_{10}acclimation}$  relative to  $\ln CVR_{Q_{10}acute}$  would imply that changes in between individual  
283 variation in physiological rates across 10°C differ depending on whether acute or acclimation responses are  
284 measured. If the interaction between effect type and habitat was not supported, then we fit a model that only  
285 contained additive effects of effect type and habitat. Following on from these models, we subset each habitat  
286 type and explored how mean  $\ln RR_{Q_{10}}$  changed across traits. Within each habitat (marine, freshwater, and  
287 terrestrial) we fit a series of models that included an interaction between effect type (acute / acclimation) and  
288 trait category (as defined above). Variance in effects within trait categories appeared to vary depending on  
289 the trait type in question. Comparison of a model with and without heteroscedastic residual variance favored  
290 a model with heteroscedastic residual variance across trait categories ( $\Delta AIC_c$ ; marine = 58, freshwater = 120,  
291 and terrestrial = 12). To ensure models converged we limited to trait categories for each habitat with six or  
292 more effect sizes.

293 Second, we tested whether different life-stages are more or less likely to acclimate by fitting a model for each  
294 habitat type and including an interaction between life-stage ('adult' or 'juvenile') and effect type. We  
295 predicted that acclimation responses would be more likely early in development compared to later in  
296 development as this pattern has been shown in previous studies (e.g., Moghadam *et al.* 2019), but that this  
297 should depend on the habitat type given the different constraints faced by different early life stages across  
298 major habitat types.

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

300 To understand the consequences of human-induced climate change on the potential to impact the opportunity  
301 for selection on physiological traits we fit a model that included an interaction between acclimation type,  
302 habitat type, latitude and longitude. We assumed that any change in  $\ln\text{CVR}_{Q_{10}}$  across latitude and longitude  
303 could vary by habitat type (i.e., an interaction between habitat). We used non-linear tensors for latitude and  
304 longitude as any response could be complicated by local factors (e.g., altitude). Our model included random  
305 effects of species, trait, phylogeny and study. We predicted the expected change in  $\ln\text{CVR}_{Q_{10}}$  for each wild  
306 population in our dataset at the specific populations latitude and longitude. To do this, we first converted the  
307 predicted  $\ln\text{CVR}_{Q_{10}}$  to a 1°C change as opposed to 10°C as follows:

$$308 \quad \ln\text{CVR}_{Q_1} = \frac{\ln\text{CVR}_{Q_{10}}}{10} \quad (7)$$

309 Equation 7 turned the expected change across 10°C to 1°C. We then multiplied this predicted change by the  
310 change in air and sea surface temperatures at the locations of each population (and species) that is expected  
311 under high emissions scenarios in 2080.

## 312 **Publication Bias**

313 We explored the possibility for publication bias graphically, using funnel plots, and more formally by  
314 including in our meta-regression models sampling variance (or sampling standard error) (Nakagawa *et al.*  
315 2022). Funnel plot asymmetry may suggest a form of publication bias called the ‘file-drawer’ effect whereby  
316 low-powered studies are less likely to be published. To test whether sampling variance covaried with effect  
317 size we included it in a multi-level meta-regression model that accounted for all the random effects (study,  
318 species, trait) and fixed effects (acclimation time, type of effect, habitat, trait category and the interaction  
319 between habitat type and trait category).

## 320 **Results**

321 The final dataset included a total of 91 freshwater (fishes = 48, molluscs = 4, amphibians = 19, reptiles = 8,  
322 arthropods = 10, and a single crustacean and nematode species), 90 marine (fishes = 47, annelids = 2,  
323 molluscs = 21, echinoderms = 7, reptiles = 1, arthropods = 10, and a single crustacean and cnidarian species),  
324 and 45 terrestrial species (annelids = 1, molluscs = 5, arthropods = 14, reptiles = 12 and amphibians = 12  
325 along with a single tardigrade species) (Figure 1 A). We had more data on acute thermal responses (n =  
326 1115) compared to thermal responses after an acclimation period (n = 798) because acute responses were  
327 reported for each of the two acclimation temperatures (Figure 1). The two acute  $\ln\text{RR}_{Q_{10}}$  effect sizes differed  
328 significantly from each other (acute responses were greater for animals acclimated to high temperatures –  $\beta =$   
329 0.07, 95% CI: 0.04 to 0.1,  $p_{\text{MCMC}} = < 0.0001$ ), but on average they were in the same direction and only  
330 differed by ~10%. As such, we averaged the two acute  $\ln\text{RR}_{Q_{10}}$  effect sizes in subsequent analyses.

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

## 335 **Terrestrial and aquatic ectotherms differ in their capacity to acclimate but acclimation** 336 **does not depend on life-history stage**

337 Overall,  $\ln\text{RR}_{Q_{10\text{acclimation}}}$  was 8.72% lower than  $\ln\text{RR}_{Q_{10\text{acute}}}$  across all habitats (95%CI: -15.14 to -2.45%).  
338 Ectotherms in marine and freshwater environments showed partial compensation of physiological rates



339 (Figure 1B) amounting to reduced  $\ln RR_{Q_{10}acclimation}$  of 17.08% (95% CI: -24.32 to -10.19) in freshwater and  
340 15.7% (95% CI: -25.96 to -4.79) in marine environments. In contrast, terrestrial ectotherms showed no  
341 acclimation (possibly even inverse acclimation) – showing a 6.6% increase in  $\ln RR_{Q_{10}acclimation}$  (95% CI: -  
342 6.56 to 21.19, Figure 1B).

343 Nonetheless, effect heterogeneity was high (only 2.85% of the variance was the result of sampling  
344 variability, 95% CI: 2.38 to 3.32%), and most variance was explained by the specific study and type of trait  
345 (Study: 29.41% , 95% CI: 20.78 to 38.49%; Trait Type: 29.35% , 95% CI: 19.97 to 39.53%). Evolutionary  
346 relationships among taxa and species ecology (i.e., species random effect) explained little variation in acute  
347 and acclimation responses (Species: 2.39% , 95% CI: 0.01 to 8.1%; Phylogeny: 2.89% , 95% CI: 0 to  
348 12.94%).

349 Different trait categories showed different acclimation responses across habitat types, however, they mirrored  
350 overall patterns (see Supplement; Figure S2). Acclimation capacity also did not vary by life-history stage and  
351 there were no differences between  $\ln RR_{Q_{10}acclimation}$  and  $\ln RR_{Q_{10}acute}$  between adult and juveniles (Figure 2  
352 A-C) (Adult-Juvenile (Acute): 0, 95% CI: -0.21 to 0.2,  $p_{MCMC} = 0.96$ ; Adult-Juvenile (Acclimation): 0.05,  
353 95% CI: -0.16 to 0.38,  $p_{MCMC} = 0.83$ ).

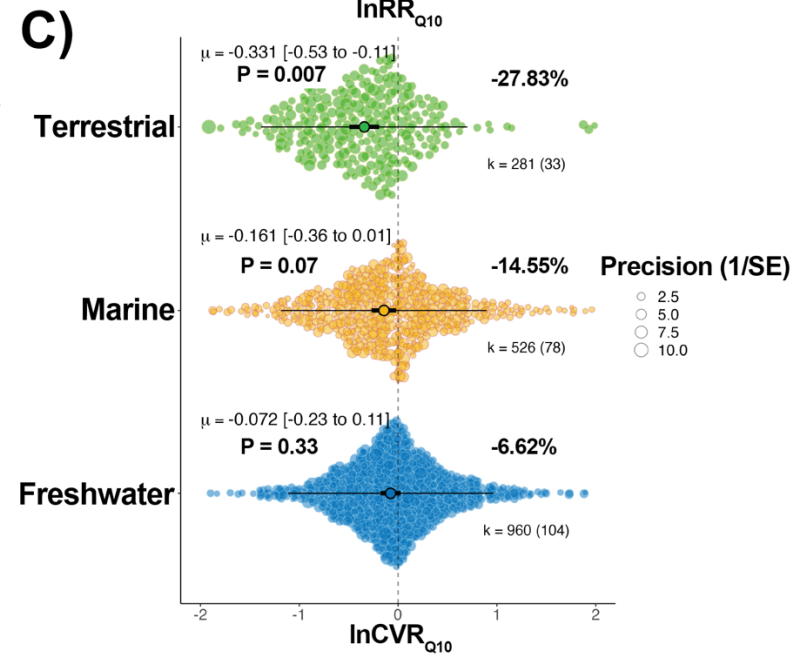
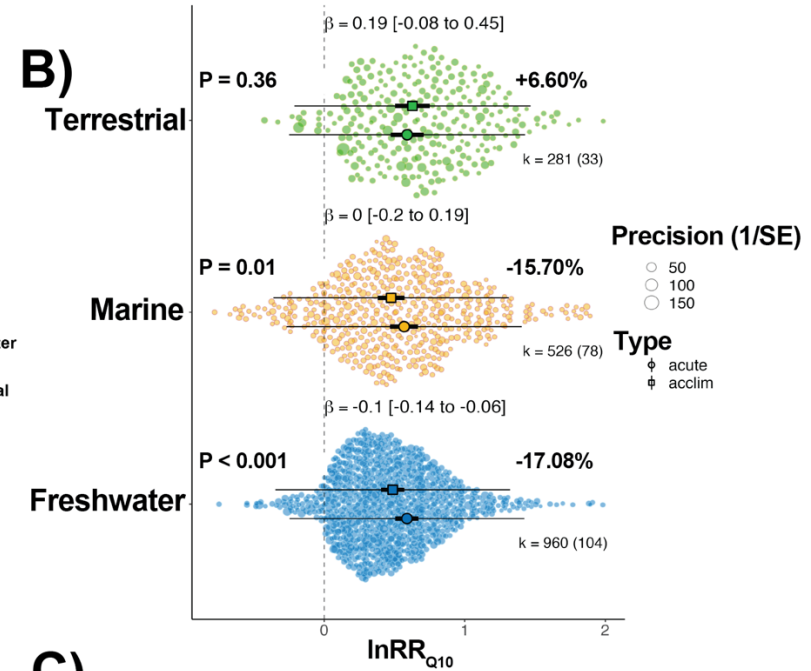
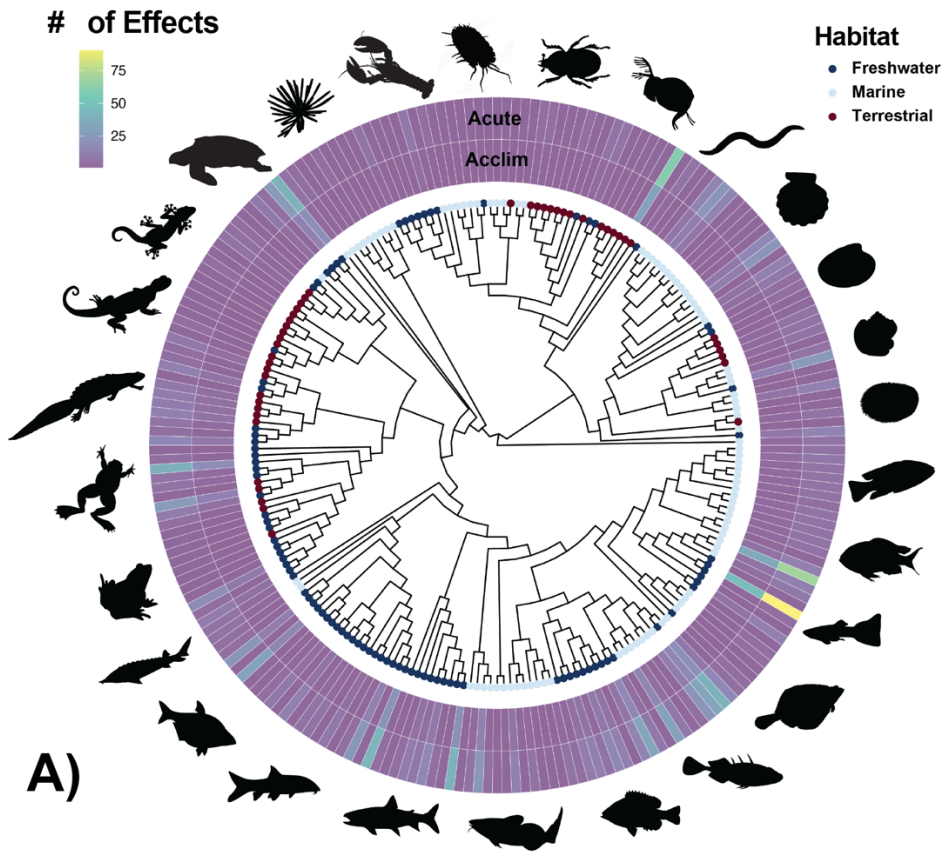


Figure 1- Taxonomic distribution of acute and acclimation  $Q_{10}$  estimates across major habitats. **A)** Phylogenetic distribution of taxa contained within the data. The total number of acute and acclimation  $Q_{10}$  effect sizes are highlighted as well as whether the taxa are marine, freshwater 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).

357 ***Reduced variation in physiological rates in terrestrial and marine ectotherms***

358 Relative variance in physiological rates ( $\ln CVR_{Q_{10}}$ ) showed a decrease with increasing temperature across all  
 359 habitat types, which was especially pronounced in terrestrial and marine ectotherms. Overall, there was a  
 360 27.87% (95% CI: 10.77 to 40.91,  $p_{MCMC} = 0.01$ ) reduction in relative physiological rate variance for  
 361 terrestrial ectotherms and a 14.94% (95% CI: 1.87 to 29.97,  $p_{MCMC} = 0.07$ ) reduction in relative variation for  
 362 marine ectotherms when temperatures increased by 10°C. In contrast, freshwater ectotherms exhibited a  
 363 smaller reduction in relative physiological rate variance at high temperatures (8.62%, 95% CI: 0.41 to 21.78,  
 364  $p_{MCMC} = 0.33$ ).

365 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:  
 366 20.36 to 27.27), with most variation being driven by between-study and trait differences (see Supplement;  
 367 Figure S5). Each life-history stage exhibited the same pattern of variance change in each of the habitats  
 368 (Figure 2). Reduced relative variance was particularly prominent for resting metabolic rates and sprint speed  
 369 although traits differed in whether they exhibited a reduction in variation in physiological rates at high  
 370 temperatures (Figure S3).

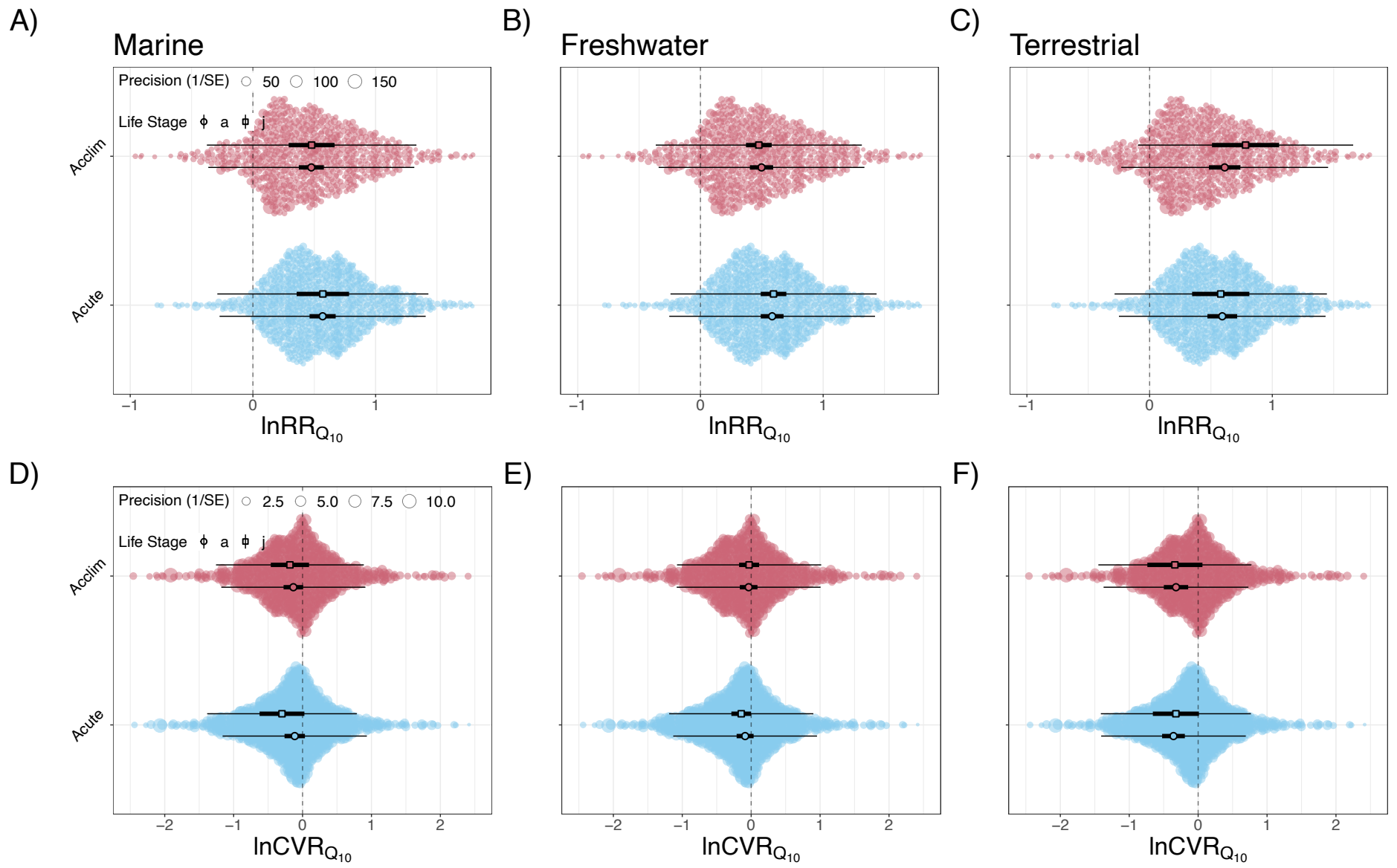


Figure 2- Estimated mean acclimation and acute  $\ln RR_{Q_{10}}$  (A-C) and  $\ln CVR_{Q_{10}}$  (D-F) for adult and juvenile life-history stages for Marine (A & D), Freshwater (B & E) and Terrestrial (C & F) ectotherms.  $k$  = total number of effect size estimates while the numbers in brackets indicate 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.

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

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

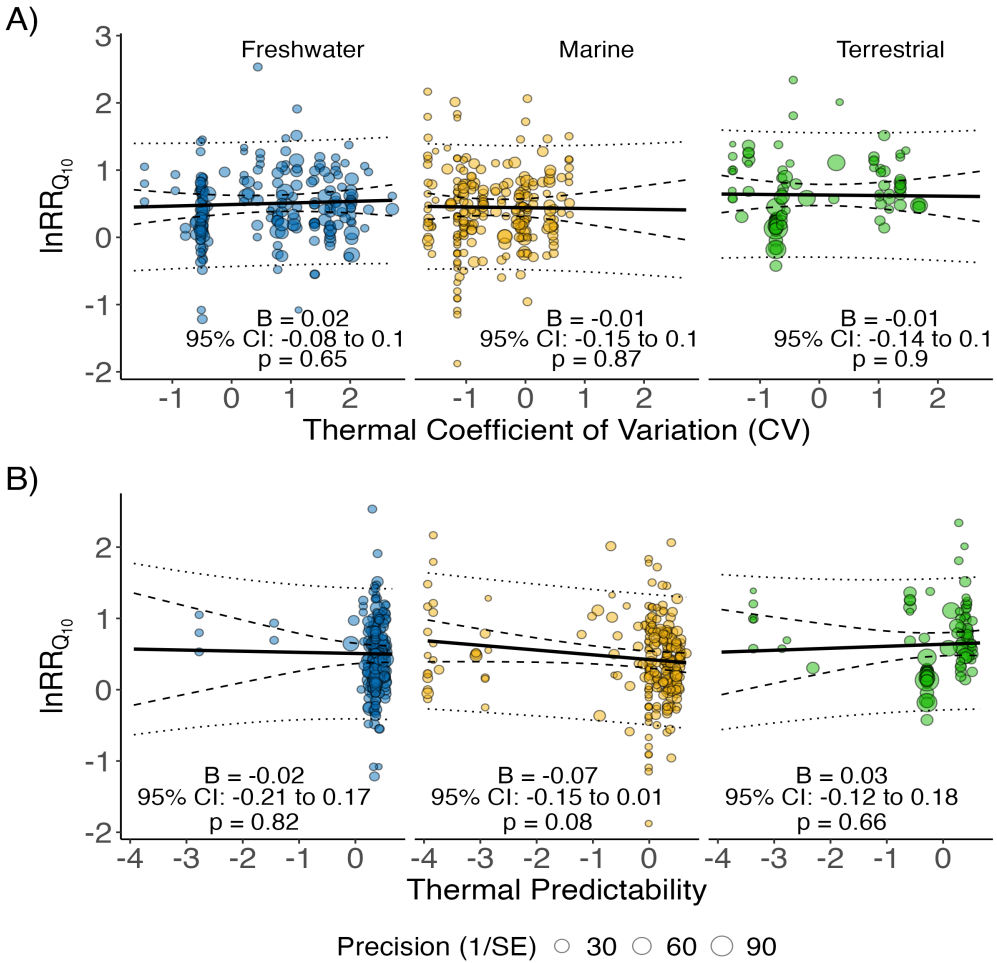


Figure 3- Predicted mean (thick black line)  $\ln RR_{Q_{10}}$  as a function of the Thermal Coefficient of Variation (CV) (A) and thermal predictability (B) for wild populations across marine, freshwater and terrestrial habitats. Dashed lines indicate 95% confidence intervals and dotted lines indicate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

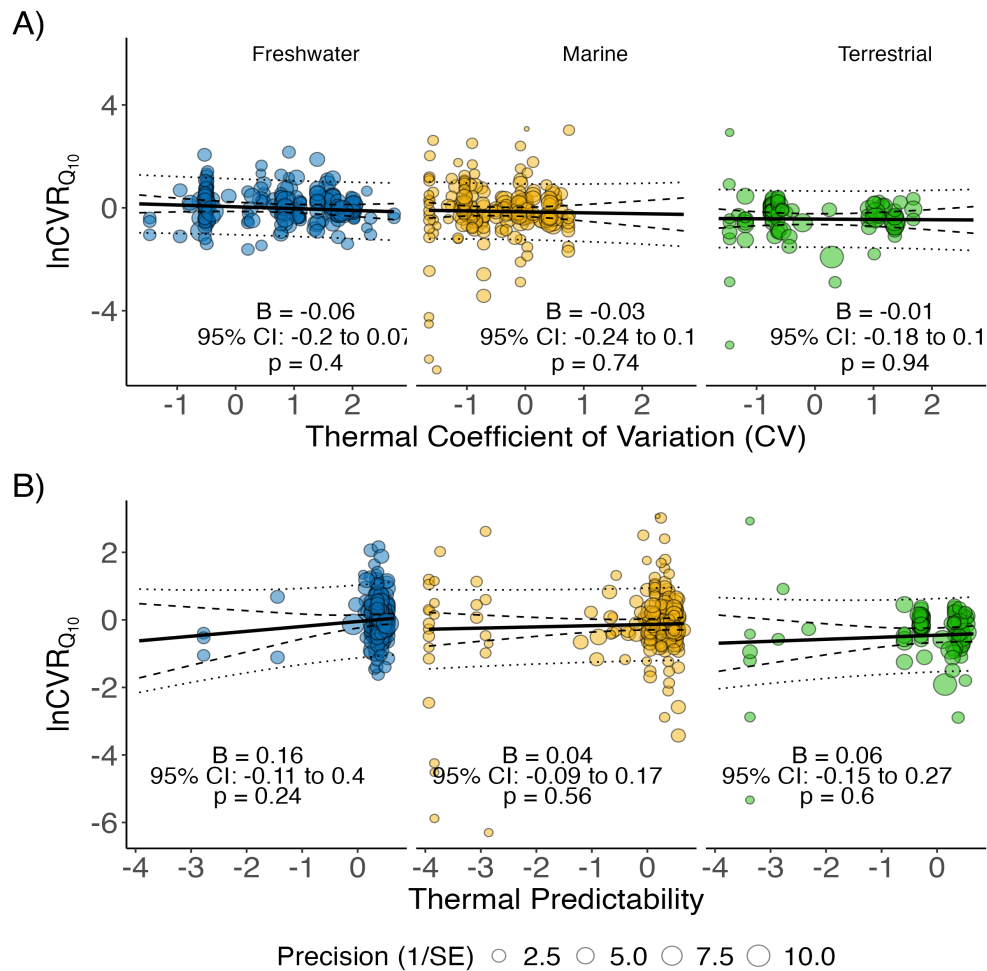


Figure 4- Predicted mean (thick black line)  $\ln CVR_{Q_{10}}$  as a function of the Thermal Coefficient of Variation (CV) (A) and thermal predictability (B) for wild populations across marine, freshwater and terrestrial habitats. Dashed lines indicate 95% confidence intervals and dotted lines indicate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

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

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

385 Using the ERA5 climate model, predictions of current global changes in physiological rate variance were  
 386 generally conservative with our model explaining  $\sim 50\%$  of the variation in the observed data ( $R^2 = 0.48$ ,  
 387 95% CI: 0.31 to 0.6). Across habitat types climate change is predicted to result in a 0.33% change in relative  
 388 variance for freshwater systems (95% CI: -6.2 to 6.48%,  $p_{MCMC} = 0.89$ ), a 2.87% reduction in relative  
 389 variance for marine systems (95% CI: -6.34 to 1.23%,  $p_{MCMC} = 0.37$ ), and a 12.17% reduction in relative  
 390 variance for terrestrial systems (95% CI: -19.45 to -6.13%,  $p_{MCMC} = < 0.0001$ ) under a RCP8.5 climate  
 391 scenario.

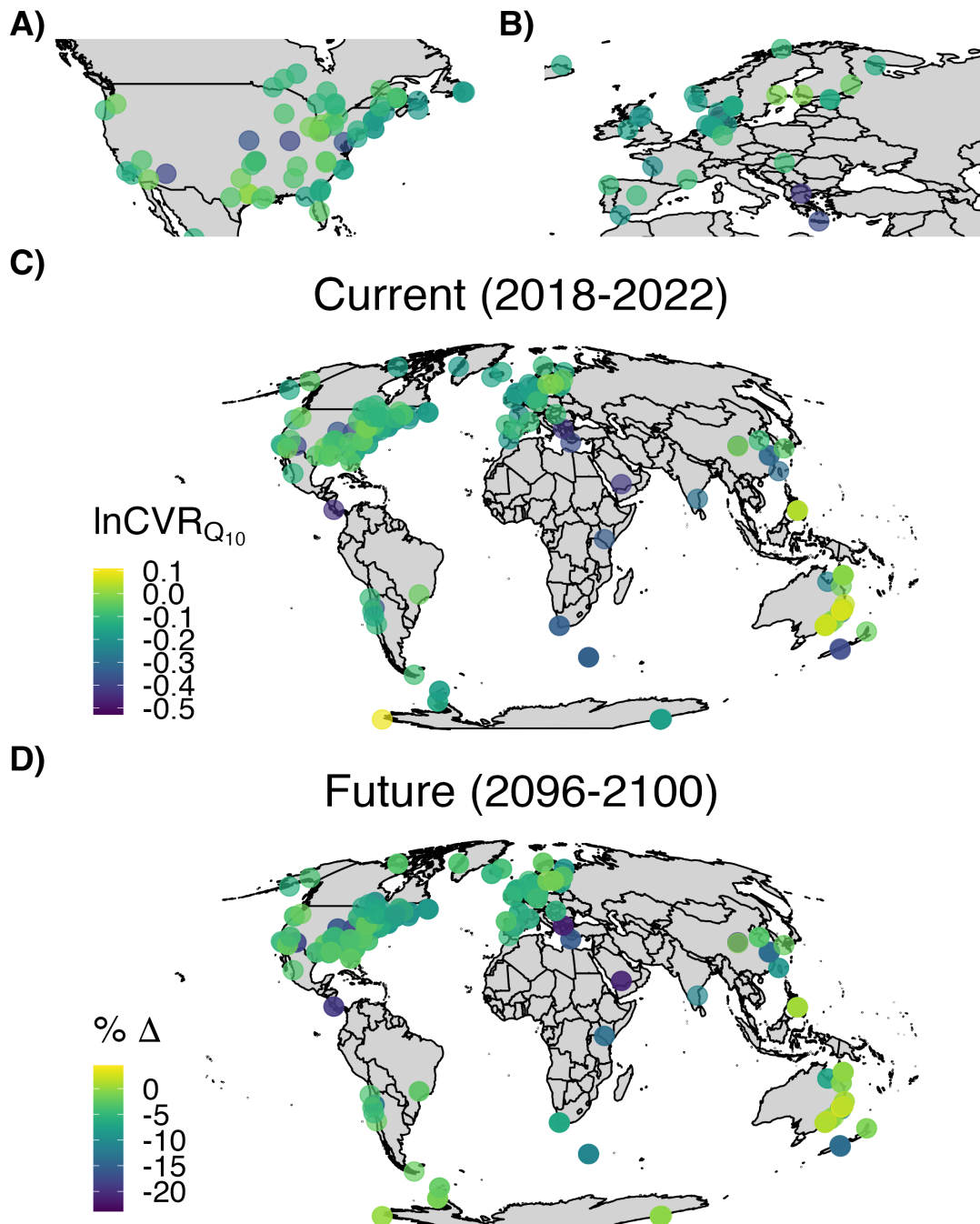


Figure 5- Model predictions for the expected change in acclimation  $\ln\text{CVR}_{Q_{10}}$  across the globe for terrestrial, marine and freshwater ectotherms. Predictions consider the uncertainty in random effects (i.e., species, phylogeny, study). Predicted change in physiological rate variance (relative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

## 392 Discussion

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

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

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

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

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

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

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

431 Life-history stages often occupy different ecological niches and exhibit different physiological responses,  
432 levels of plasticity, and patterns of mortality in response to temperature. As such, it is becoming increasingly  
433 important to understand how climate change will impact different life-history stages (Petitgas *et al.* 2013;  
434 Levy *et al.* 2015). Greater plasticity in early life-stages of development is expected to be important to  
435 increase resilience to the effects of climate change because early life-stages are often particularly vulnerable  
436 periods in development (Stearns 1976; Martin 2015). We show that there were generally similar patterns  
437 between early and late life stages across a diversity of taxa, both in terms of variance changes and the  
438 capacity for plasticity. On average, our results show that early life stages are not more vulnerable to the  
439 impacts of climate change. However, our general meta-analytic findings do not imply that early life stages  
440 are not always less plastic, but that such responses are likely context or trait dependent (Moghadam *et al.*  
441 2019; Carter & Sheldon 2020). For example, Moghadam *et al.* (2019) showed that larval *Drosophila* were



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

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

448 Variance reductions in metabolism and performance (e.g., sprint speed) were most strongly impacted by  
449 increased temperature. Changes in variability of traits governing energy demand could have important  
450 consequences on the flow of energy within and between populations, communities, and ecosystems (Hendry  
451 2016; Barneche *et al.* 2021; Sanderson *et al.* 2023; Seebacher *et al.* 2023). More variable populations,  
452 genetically and/or phenotypically, are predicted to be associated with broader niches, reduced intraspecific  
453 competition, increased growth rate, decreased vulnerability to environmental change and lower extinction  
454 risk (Bolnick *et al.* 2011; Forsman 2014, 2015; Hart *et al.* 2016; Hendry 2016). Maintaining intrapopulation  
455 variability in physiological rates in a warmer world may therefore be important for population resilience to  
456 climate change. For example, Kooijman *et al.* (1989) integrated individual variation in dynamic energy  
457 budget (DEB) models developed for *Daphnia magna*. They showed that greater between-individual variation  
458 in DEB parameters led to less extreme population fluctuations compared to scenarios with no variation  
459 (Kooijman *et al.* 1989). Our results suggest that terrestrial ectotherms will likely face greater challenges to  
460 adapting to climate change (Hoffmann *et al.* 2013; Gunderson & Stillman 2015; Pottier *et al.* 2022), leading  
461 to greater rates of extinction and reduced productivity in terrestrial ecosystems. However, data testing the  
462 impacts of changes in variance on populations are limited to very few taxa. Future experimentation across a  
463 broader range of taxa should manipulate levels of variance to understand its ecological outcomes.

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

465 Theoretical evolutionary models predict that plasticity should evolve in populations experiencing greater  
466 environmental variability (spatial or temporal), particularly when oscillations are predictable over time to  
467 make environmental cues more reliable (Lande 2009; Chevin *et al.* 2010; Reed *et al.* 2010; Murren *et al.*  
468 2015; Hendry 2016; Nunney 2016; Chevin & Hoffmann 2017). Higher spatial and temporal heterogeneity in  
469 terrestrial ecosystems (Steele *et al.* 2019) suggests that plasticity should be more likely to evolve in terrestrial  
470 environments. However, we did not find evidence to this effect. Our finding is consistent with other meta-  
471 analyses (Gunderson & Stillman 2015; Barley *et al.* 2021) with thermal tolerance (which we did not consider  
472 here). Modelling correct microenvironments for over 200 species across such diverse habitats is challenging.  
473 The lack of a relationship between physiological plasticity and environmental variability and predictability  
474 could be due the fact that ectotherms simply seek out microhabitats that make their environment quite stable  
475 (Huey *et al.* 2012). Therefore, it is possible that more fine-scale resolution of the habitats that organisms  
476 occupy will elucidate expected patterns. Randomly fluctuating environments have been suggested to select  
477 for reduced plasticity, particularly if plastic responses are costly and this has been demonstrated by a number  
478 of empirical studies (Leung *et al.* 2020, 2023; Rescan *et al.* 2022). For example, using seed beetles  
479 (*Callosobruchus maculatus*), Hallsson & Björklund (2012) showed that experimentally evolving populations  
480 under randomly fluctuating thermal conditions did not show any increase in plasticity, but had reduced  
481 plasticity. Leung *et al.* (2020) also showed reduced plasticity in morphological traits of experimentally  
482 evolving algae populations (*Dunaliella salina*) when environments were less predictable (see also Leung *et al.*  
483 2023). While it is unclear how these findings relate directly to acclimation because they integrate multiple  
484 forms of plasticity, they do suggest that there are costs to being plastic or that the environmental signals are  
485 insufficient to trigger endocrine and epigenetic mechanisms that lead to plasticity when environments are not  
486 predictable (Hendry 2016; Leung *et al.* 2020). The fact that aquatic ectotherms did show a capacity to  
487 acclimate suggests that environmental predictability, which is expected to be higher in aquatic environments,  
488 may be more important than environmental variability in driving the evolution of plasticity.

## 489 ***Conclusions and future directions***

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

## 512 **Funding**

513 DWAN is supported by an Australian Research Council (ARC) Future Fellowship (FT220100276) and ARC  
514 Discovery Project (DP210101152). SN is supported by ARC Discovery Project Grants (DP210100812 and  
515 DP230101248).

## 516 **Data and code availability**

517 All data and code used to reproduce analyses can be found on GitHub at:  
518 [https://github.com/daniellnoble/Q10\\_meta\\_analysis](https://github.com/daniellnoble/Q10_meta_analysis).

## 519 **Author contributions**

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

## 523 **Conflict of interest**

524 Authors declare that they have no competing interests.

## 525 **References**

526

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

- 529 Barley, J.M., Cheng, B.S., Sasaki, M., Gignoux-Wolfsohn, S., Hays, C.G., Putnam, A.B., *et al.* (2021).  
530 Limited plasticity in thermally tolerant ectotherm populations: Evidence for a trade-off. *Proceedings of the*  
531 *Royal Society B*, 288, 20210765.
- 532 Barneche, D.R., Hulatt, C.J., Dossena, M., Padfield, D., Woodward, G., Trimmer, M., *et al.* (2021). Warming  
533 impairs trophic transfer efficiency in a long-term field experiment. *Nature*, 592, 76–79.
- 534 Bolnick, D.I., Amarasekare, P., Araújo, M.S., M. Levine, R.B. and Jonathan, Novak, M., Rudolf, V.H.W., *et*  
535 *al.* (2011). Why intraspecific trait variation matters in community ecology. *Trends in Ecology and*  
536 *Evolution*, 26, 183–192.
- 537 Bulgarella, M., Trewick, S.A., Godfrey, A.J.R., Sinclair, B.J. & Morgan-Richards, M. (2015). Elevational  
538 variation in adult body size and growth rate but not in metabolic rate in the tree weta *hemideina crassidens*.  
539 *J. Insect Physiol.*, 75, 30–38.
- 540 Bürkner, P.-C. (2017). Brms: An R package for bayesian multilevel models using stan. *J. Stat. Softw.*, 80, 1–  
541 28., doi:10.18637/jss.v080.i01.
- 542 Bürkner, P.-C. (2018). Advanced bayesian multilevel modeling with the R package brms. *R J.*, 10, 395–411.
- 543 Bush, A., Mokany, K., Catullo, R., Hoffmann, A., Kellermann, V., Sgrò, C., *et al.* (2016). Incorporating  
544 evolutionary adaptation in species distribution modelling reduces projected vulnerability to climate  
545 change. *Ecology letters*, 19, 1468–1478.
- 546 Cahill, A.E., Aiello-Lammens, M.E., Fisher-Reid, M.C., Hua, X., Karanewsky, C.J., Ryu, H.Y., *et al.* (2012).  
547 How does climate change cause extinction? *Proceedings of the Royal Society B: Biological Sciences*, 280,  
548 20121890.
- 549 Carter, A.W. & Sheldon, K.S. (2020). Life stages differ in plasticity to temperature fluctuations and uniquely  
550 contribute to adult phenotype in onthophagus taurus dung beetles. *Journal of Experimental Biology*, 223,  
551 jeb227884.
- 552 Chevin, L.-M. & Hoffmann, A.A. (2017). Evolution of phenotypic plasticity in extreme environments.  
553 *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, 372, 20160138,  
554 <https://doi.org/10.1098/rstb.2016.0138>.
- 555 Chevin, L.-M., Lande, R. & Mace, G.M. (2010). Adaptation, plasticity, and extinction in a changing  
556 environment: Towards a predictive theory. *PLoS Biology*, 8, e1000357,  
557 <https://doi.org/10.1371/journal.pbio.1000357>.
- 558 Chevin, L.M. & Lande, R. (2015). Evolution of environmental cues for phenotypic plasticity. *Evolution*, 69,  
559 2767–2775, <https://doi.org/10.1111/evo.12755>.
- 560 Cooke, S.J., Bergman, J.N., Madliger, C.L., Cramp, R.L., Beardall, J., Burness, G., *et al.* (2021). One  
561 hundred research questions in conservation physiology for generating actionable evidence to inform  
562 conservation policy and practice. *Conservation Physiology*, 9, coab009.
- 563 DeMarche, M.L., Doak, D.F. & Morris, W.F. (2019). Incorporating local adaptation into forecasts of species'  
564 distribution and abundance under climate change. *Global Change Biology*, 25, 775–793.
- 565 Dewitt, T.J., Sih, A. & Wilson, D.S. (1998). Costs and limits of phenotypic plasticity. *Trends in Ecology and*  
566 *Evolution*, 13, 77–81.
- 567 Easterling, D.R., Meehl, G.A., Parmesan, C., Changnon, S.A., Karl, T.R. & Mearns, L.O. (2000). Climate  
568 extremes: Observations, modelling and impacts. *Science*, 289, 2068–2074.

- 569 Einum, S. & Burton, T. (2023). Divergence in rates of phenotypic plasticity among ectotherms. *Ecol. Lett.*,  
570 26, 147–156.
- 571 Forsman, A. (2014). Effects of genotypic and phenotypic variation on establishment are important for  
572 conservation, invasion, and infection biology. *Proceedings of the National Academy of Sciences*, 111, 302–  
573 307.
- 574 Forsman, A. (2015). Rethinking phenotypic plasticity and its consequences for individuals, populations and  
575 species. *Heredity*, 115, 276–284.
- 576 Grafen, A. (1989). The phylogenetic regression. *Philos. Trans. R. Soc. Lond. B Biol. Sci.*, 326, 119–157.
- 577 Gunderson, A.R. & Stillman, J.H. (2015). Plasticity in thermal tolerance has limited potential to buffer  
578 ectotherms from global warming. *Proceedings of the Royal Society B: Biological Sciences*, 282, 20150401.
- 579 Hallsson, L.R. & Björklund, M. (2012). Selection in a fluctuating environment leads to decreased genetic  
580 variation and facilitates the evolution of phenotypic plasticity. *Journal of evolutionary biology*, 25, 1275–  
581 1290.
- 582 Hart, S.P., Schreiber, S.J. & Levine, J.M. (2016). How variation between individuals affects species  
583 coexistence. *Ecology letters*, 19, 825–838.
- 584 Havird, J.C., Neuwald, J.L., Shah, A.A., Mauro, A., Marshall, C.A. & Ghalambor, C.K. (2020).  
585 Distinguishing between active plasticity due to thermal acclimation and passive plasticity due to Q10  
586 effects: Why methodology matters. *Funct. Ecol.*, 0, 1–14.
- 587 Hedges, L.V., Gurevitch, J. & Curtis, P.S. (1999). The meta-analysis of response ratios in experimental  
588 ecology. *Ecology*, 80, 1150–1156.
- 589 Hendry, A.P. (2016). Key questions on the role of phenotypic plasticity in eco-evolutionary dynamics.  
590 *Journal of Heredity*, 107, 25–41.
- 591 Hersbach, H., Bell, B., Berrisford, P., Hirahara, S., Horányi, A., Muñoz-Sabater, J., *et al.* (2020). The ERA5  
592 global reanalysis. *Quart. J. Roy. Meteor. Soc.*, 146, 1999–2049.
- 593 Hoffmann, A.A., Chown, S.L. & Clusella-Trullas, S. (2013). Upper thermal limits in terrestrial ectotherms:  
594 How constrained are they? *Functional Ecology*, 27, 934–949.
- 595 Hoffmann, A.A. & Sgrò, C.M. (2011). Climate change and evolutionary adaptation. *Nature*, 470, 479–485.
- 596 Huey, R.B., Kearney, M.R., Krockenberger, A., Holtum, J.A., Jess, M. & Williams, S.E. (2012). Predicting  
597 organismal vulnerability to climate warming: Roles of behaviour, physiology and adaptation.  
598 *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367, 1665–1679.
- 599 Imura, D., Toquenaga, Y. & Fujii, K. (2003). Genetic variation can promote system persistence in an  
600 experimental host-parasitoid system. *Population Ecology*, 45, 205–212.
- 601 Kooijman, S., Van der Hoeven, N. & Van der Werf, D. (1989). Population consequences of a physiological  
602 model for individuals. *Functional Ecology*, 325–336.
- 603 Lajeunesse, M.J. (2011). On the meta-analysis of response ratios for studies with correlated and multi-group  
604 designs. *Ecology*, 92, 2049–2055.
- 605 Lande, R. (2009). Adaptation to an extraordinary environment by evolution of phenotypic plasticity and  
606 genetic assimilation. *Journal of Evolutionary Biology*, 22, 1435–1446.

- 607 Leung, C., Grulois, D., Quadrana, L. & Chevin, L.-M. (2023). Phenotypic plasticity evolves at multiple  
608 biological levels in response to environmental predictability in a long-term experiment with a halotolerant  
609 microalga. *Plos Biology*, 21, e3001895.
- 610 Leung, C., Rescan, M., Grulois, D. & Chevin, L. (2020). 2020. *Ecology Letters*, 23, 1664–1672.
- 611 Levy, O., Buckley, L.B., Keitt, T.H., Smith, C.D., Boateng, K.O., Kumar, D.S., *et al.* (2015). Resolving the  
612 life cycle alters expected impacts of climate change. *Proceedings of the Royal Society B: Biological*  
613 *Sciences*, 282, 20150837.
- 614 Little, A.G., Kunisue, T., Kannan, K. & Seebacher, F. (2013). Thyroid hormone actions are temperature-  
615 specific and regulate thermal acclimation in zebrafish (*danio rerio*). *Bmc Biology*, 11, 1–15.
- 616 Martin, T.E. (2015). Age-related mortality explains life history strategies of tropical and temperate songbirds.  
617 *Science*, 349, 966–970.
- 618 Merila, J. & Hendry, A.P. (2014). Climate change, adaptation, and phenotypic plasticity: The problem and  
619 the evidence. *Evolutionary Applications*, 7, 1–14., doi:10. 1111/eva.12137.
- 620 Merilä, J. & Hendry, A.P. (2014). Climate change, adaptation, and phenotypic plasticity: The problem and  
621 the evidence. *Evolutionary applications*, 7, 1–14.
- 622 Michonneau, F., Brown, J.W. & Winter, D.J. (2016). Rotl: An R package to interact with the open tree of life  
623 data. *Methods Ecol. Evol.*, 7, 1476-1481. doi:10.1111/2041-210X.12593.
- 624 Moghadam, N.N., Ketola, T., Pertoldi, C., Bahrndorff, S. & Kristensen, T.N. (2019). Heat hardening capacity  
625 in *drosophila melanogaster* is life stage-specific and juveniles show the highest plasticity. *Biology letters*,  
626 15, 20180628.
- 627 Murren, C., Auld, J., Callahan, H., Ghalambor, C., Handelsman, C., Heskell, M., *et al.* (2015). Constraints on  
628 the evolution of phenotypic plasticity: Limits and costs of phenotype and plasticity. *Heredity*, 115, 293–  
629 301.
- 630 Nakagawa, S., Lagisz, M., Jennions, M.D., Koricheva, J., Daniel W. A. Noble, T.H.P., Sánchez-Tójar, A., *et*  
631 *al.* (2022). Methods for testing publication bias in ecological and evolutionary meta-analyses. *Methods in*  
632 *Ecology and Evolution*, 13, 4–21.
- 633 Nakagawa, S., Lagisz, M., O’Dea, R.E., Pottier, P., Rutkowska, J., Senior, A.M., *et al.* (n.d.). orchaRd 2.0:  
634 An r package for visualising meta-analyses with orchard plots. *Methods in Ecology and Evolution*, 14,  
635 2003–2010.
- 636 Nakagawa, S., Lagisz, M., O’Dea, R.E., Rutkowska, J., Yang, Y., Noble, D.W.A., *et al.* (2021a). The orchard  
637 plot: Cultivating forest plots for use in ecology, evolution and beyond. *Research Synthesis Methods*, 12, 4–  
638 12.
- 639 Nakagawa, S., Poulin, R., Mengersen, K., Reinhold, K., Engqvist, L., Lagisz, M., *et al.* (2015). Meta-analysis  
640 of variation: Ecological and evolutionary applications and beyond. *Methods Ecol. Evol.*, 6, 143–152.
- 641 Nakagawa, S. & Santos, E.S.A. (2012). Methodological issues and advances in biological meta-analysis.  
642 *Evol. Ecol.*, 26, 1253–1274.
- 643 Nakagawa, S., Senior, A.M., Viechtbauer, W. & Noble, D.W.A. (2021b). An assessment of statistical  
644 methods for non-independent data in ecological meta-analyses: comment. *Ecology*, in press.,  
645 <https://doi.org/10.1002/ecy.3490>.

- 646 Noble, D.W.A., Lagisz, M., O’Dea, R.E. & Nakagawa, S. (2017). Non-independence and sensitivity analyses  
647 in ecological and evolutionary meta-analyses. *Molecular Ecology*, 26, 2410–2425.
- 648 Noble, D.W.A., Pottier, P., Lagisz, M., Burke, S., Drobniak, S.M., O’Dea, R.E., *et al.* (2022). Meta-analytic  
649 approaches and effect sizes to account for “nuisance heterogeneity” in comparative physiology. *J. Exp.*  
650 *Biol.*, 225, jeb243225.
- 651 Nunney, L. (2016). Adapting to a changing environment: Modeling the interaction of directional selection  
652 and plasticity. *Journal of Heredity*, 107, 15–24.
- 653 Ouzzani, M., Hammady, H., Fedorowicz, Z. & Elmagarmid, A. (2016). Rayyan—a web and mobile app for  
654 systematic reviews. *Syst. Rev.*, 5, 210–220.
- 655 Paradis, E. & Schliep, K. (2019). Ape 5.0: An environment for modern phylogenetics and evolutionary  
656 analyses in R. *Bioinformatics*, 35, 526–528.
- 657 Pelletier, F. & Coulson, T. (2012). A new metric to calculate the opportunity for selection on quantitative  
658 characters. *Evolutionary Ecology Research*, 14, 729–742.
- 659 Petitgas, P., Rijnsdorp, A.D., Dickey-Collas, M., Engelhard, G.H., Peck, M.A., Pinnegar, J.K., *et al.* (2013).  
660 Impacts of climate change on the complex life cycles of fish. *Fisheries Oceanography*, 22, 121–139.
- 661 Pick, J.L., Nakagawa, S. & Noble, D.W.A. (2019). Reproducible, flexible and high throughput data  
662 extraction from primary literature: The metaDigitise R package. *Methods Ecol. Evol.*, 10, 426–431.
- 663 Pierce, D. (2021). ncd4: Interface to unidata netCDF (version 4 or earlier) format data files.
- 664 Pinsky, M.L., Eikeset, A.M., McCauley, D.J., Payne, J.L. & Sunday, J.M. (2019). Greater vulnerability to  
665 warming of marine versus terrestrial ectotherms. *Nature*, 569, 108–111.
- 666 Pottier, P., Burke, S., Zhang, R.Y., Noble, D.W., Schwanz, L.E., Drobniak, S.M., *et al.* (2022).  
667 Developmental plasticity in thermal tolerance: Ontogenetic variation, persistence, and future directions.  
668 *Ecology Letters*, 25, 2245–2268.
- 669 Reed, T.E., Waples, R.S., Schindler, D.E., Hard, J.J. & Kinnison, M.T. (2010). Phenotypic plasticity and  
670 population viability: The importance of environmental predictability. *Proceedings of the Royal Society B:*  
671 *Biological Sciences*, 277, 3391–3400.
- 672 Rescan, M., Leurs, N., Grulois, D. & Chevin, L.-M. (2022). Experimental evolution of environmental  
673 tolerance, acclimation, and physiological plasticity in a randomly fluctuating environment. *Evolution*  
674 *Letters*, 6, 522–536.
- 675 Revell, L.J. (2012). Phytools: An R package for phylogenetic comparative biology (and other things).  
676 *Methods Ecol. Evol.*, 3, 217–223.
- 677 Sanderson, S., Bolnick, D.I., Kinnison, M.T., O’Dea, R.E., Gorné, L.D. & Hendry, A.P. (2023).  
678 Contemporary changes in phenotypic variation, and the potential consequences for eco-evolutionary  
679 dynamics. *Ecology Letters*, 26, S127–S139.
- 680 Scheiner, S.M., Barfield, M. & Holt, R.D. (2020). The genetics of phenotypic plasticity. XVII. Response to  
681 climate change. *Evolutionary Applications*, 13, 388–399.
- 682 Schindler, D.E., Hilborn, R., Chasco, B., Boatright, C.P., Quinn, T.P., Rogers, L.A., *et al.* (2010). Population  
683 diversity and the portfolio effect in an exploited species. *Nature*, 465, 609–613.

- 684 Seebacher, F., Narayan, E., Rummer, J.L., Tomlinson, S. & Cooke, S.J. (2023). How can physiology best  
685 contribute to wildlife conservation in a warming world? *Conservation Physiology*, 11, coad038.
- 686 Seebacher, F. & Simmonds, A.I. (2019). Histone deacetylase activity mediates thermal plasticity in zebrafish  
687 (*danio rerio*). *Scientific Reports*, 9, 8216.
- 688 Seebacher, F., White, C.R. & Franklin, C.E. (2015). Physiological plasticity increases resilience of  
689 ectothermic animals to climate change. *Nat. Clim. Chang.*, 5, 61.
- 690 Slatyer, R.A., Hirst, M. & Sexton, J.P. (2013). Niche breadth predicts geographical range size: A general  
691 ecological pattern. *Ecology Letters*, 16, 1104–1114.
- 692 Song, C., Peacor, S.D., Osenberg, C.W. & Bence, J.R. (2021). An assessment of statistical methods for  
693 nonindependent data in ecological meta-analyses. *Ecology*, e03184.
- 694 Stan development team. RStan: The R interface to stan. (2021). *R package version 2. 21. 3*. <https://mc-stan.org/>.
- 695
- 696 Stearns, S.C. (1976). Life-history tactics: A review of the ideas. *The Quarterly review of biology*, 51, 3–47.
- 697 Steele, J.H., Brink, K.H. & Scott, B.E. (2019). Comparison of marine and terrestrial ecosystems: Suggestions  
698 of an evolutionary perspective influenced by environmental variation. *ICES Journal of Marine Science*, 76,  
699 50–59.
- 700 Suarez-Gutierrez, L., Müller, W.A. & Marotzke, J. (2023). Extreme heat and drought typical of an end-of-  
701 century climate could occur over Europe soon and repeatedly. *Communications Earth & Environment*, 4,  
702 415, <https://doi.org/10.1038/s43247-023-01075-y>.
- 703 Taff, C.C. & Vitousek, M.N. (2016). Endocrine flexibility: Optimizing phenotypes in a dynamic world?  
704 *Trends in ecology & evolution*, 31, 476–488.
- 705 Ummenhofer, C.C. & Meehl, G.A. (2017). Extreme weather and climate events with ecological relevance: A  
706 review. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, 372,  
707 20160135, <http://doi.org/10.1098/rstb.2016.0135>.
- 708 Urban, M.C., Swaegers, J., Stoks, R., Snook, R.R., Otto, S.P., Noble, D.W., *et al.* (2023). When and how can  
709 we predict adaptive responses to climate change? *Evolution Letters*.
- 710 Verberk, W.C.E.P., Bartolini, F., Marshall, D.J., Pörtner, H.-O., Terblanche, J.S., White, C.R., *et al.* (2016).  
711 Can respiratory physiology predict thermal niches? *Annals of the New York Academy of Sciences*, 1365,  
712 73–88.
- 713 Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor package. *J. Stat. Softw.*, 36, 1–48.  
714 URL: <https://www.jstatsoft.org/v36/i03/>.
- 715 West-Eberhard, M.J. (2003). *Developmental plasticity and evolution*. Oxford University Press, New York.
- 716 Yu, G., Smith, D., Zhu, H., Guan, Y. & Lam, T.T.-Y. (2017). Ggtree: An R package for visualization and  
717 annotation of phylogenetic trees with their covariates and other associated data. *Methods Ecol. Evol.*, 8,  
718 28–36, doi:10.1111/2041-210X.12628.
- 719 Zheng, S., Hu, J., Ma, Z., Lindenmayer, D. & Liu, J. (2023). Increases in intraspecific body size variation are  
720 common among north American mammals and birds between 1880 and 2020. *Nature Ecology and*  
721 *Evolution*, 7, 347–354, <https://doi.org/10.1038/s41559-022-01967-w>.

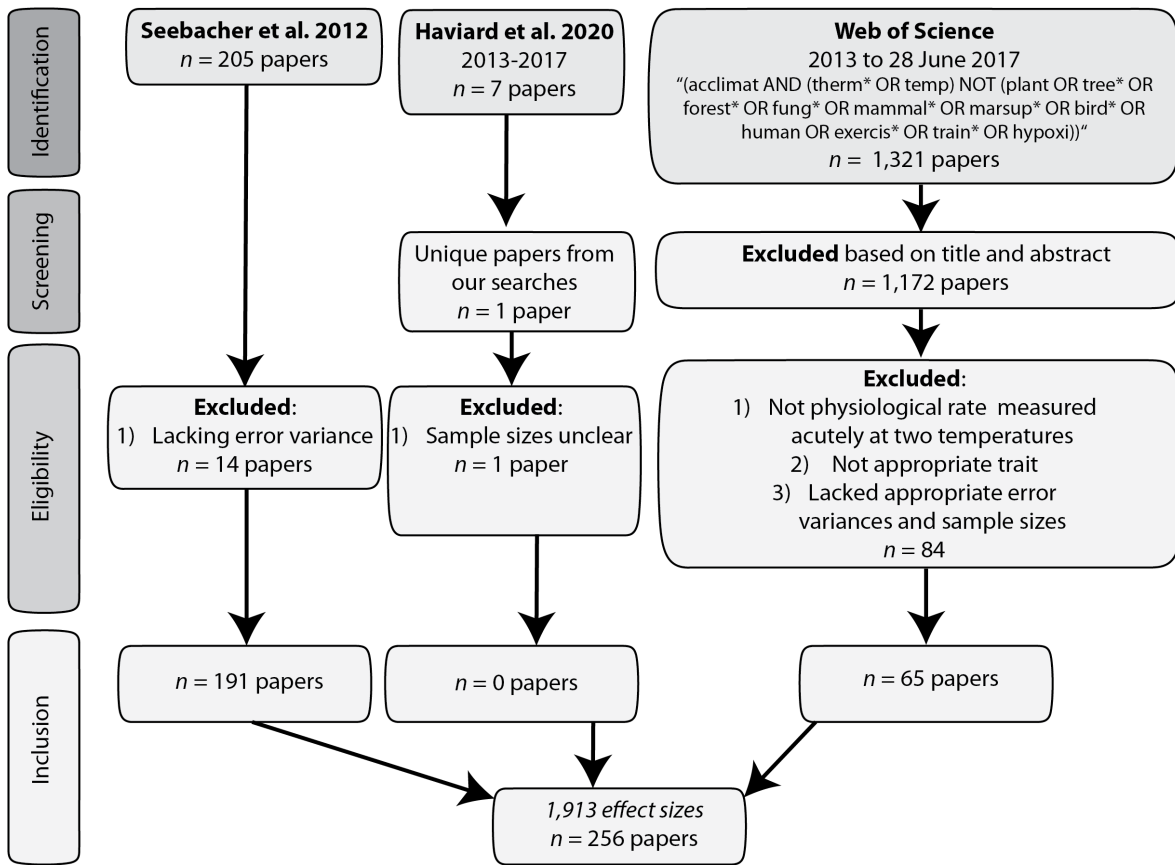


Figure S1- PRISMA flow diagram of the literature search and screening process.



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

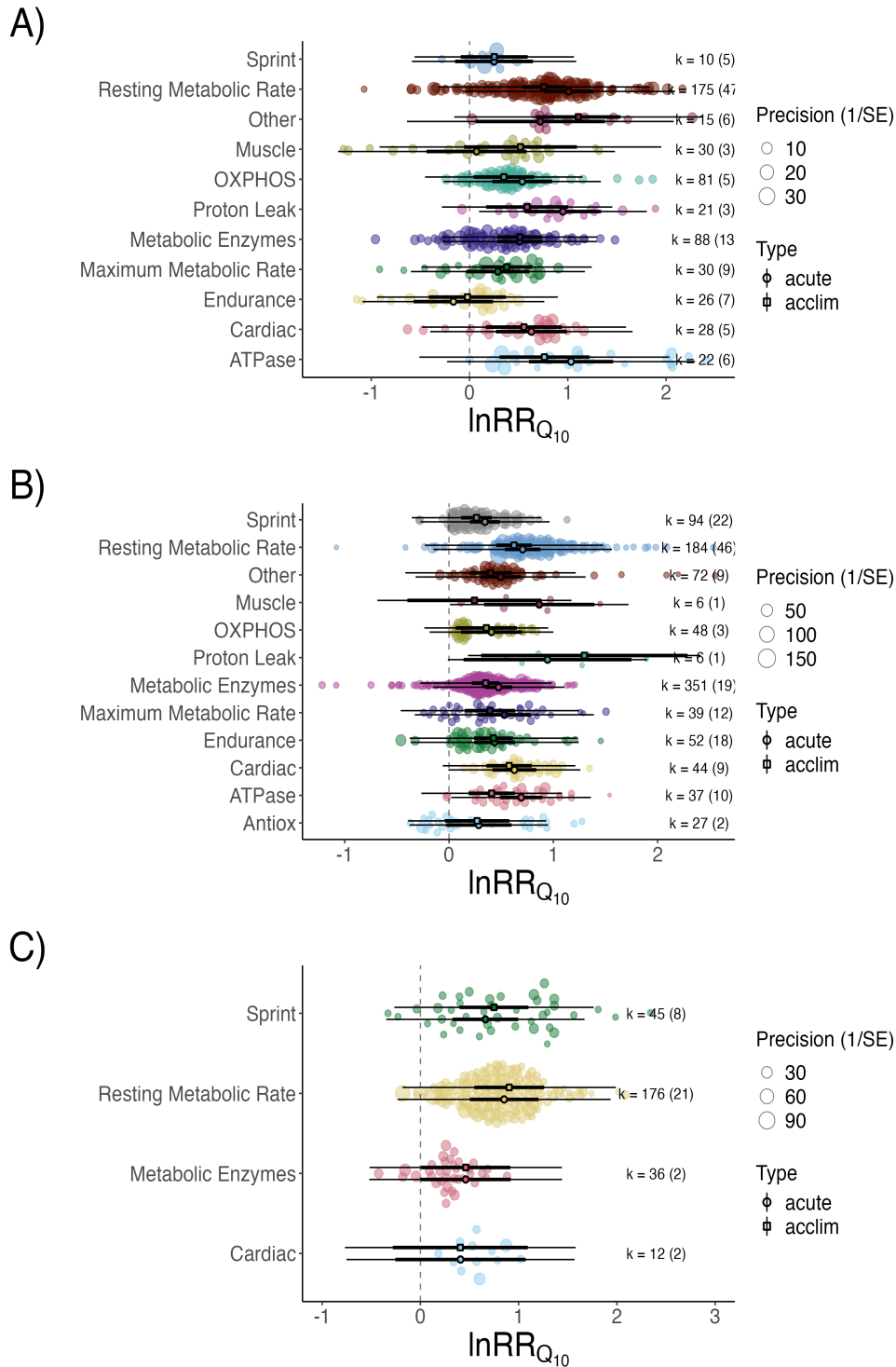


Figure S2- Acute and Acclimation  $\ln RR_{Q_{10}}$  across traits for A) marine, B) freshwater and C) terrestrial systems.  $k$  = total number of effect size estimates while the numbers in brackets indicate the number of species. Thick bars indicate 95% confidence intervals and thin bars indicate 95%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

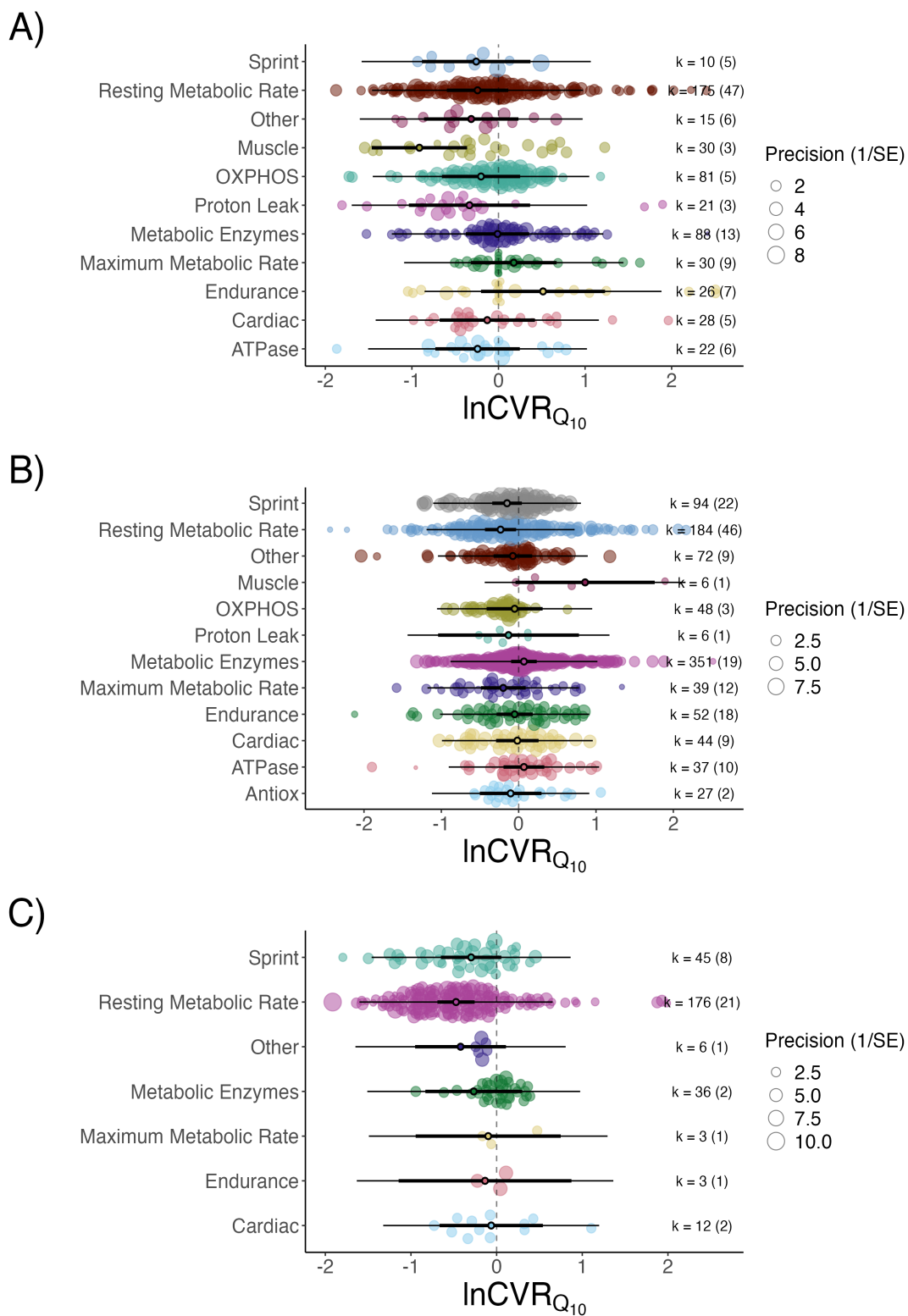


Figure S3- Acute and Acclimation  $\ln\text{CVR}_{Q_{10}}$  across traits for A) marine, B) freshwater and C) terrestrial systems.  $k$  = total number of effect size estimates while the numbers in brackets indicate the number of species. Thick bars indicate 95% confidence intervals and thin bars indicate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

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

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

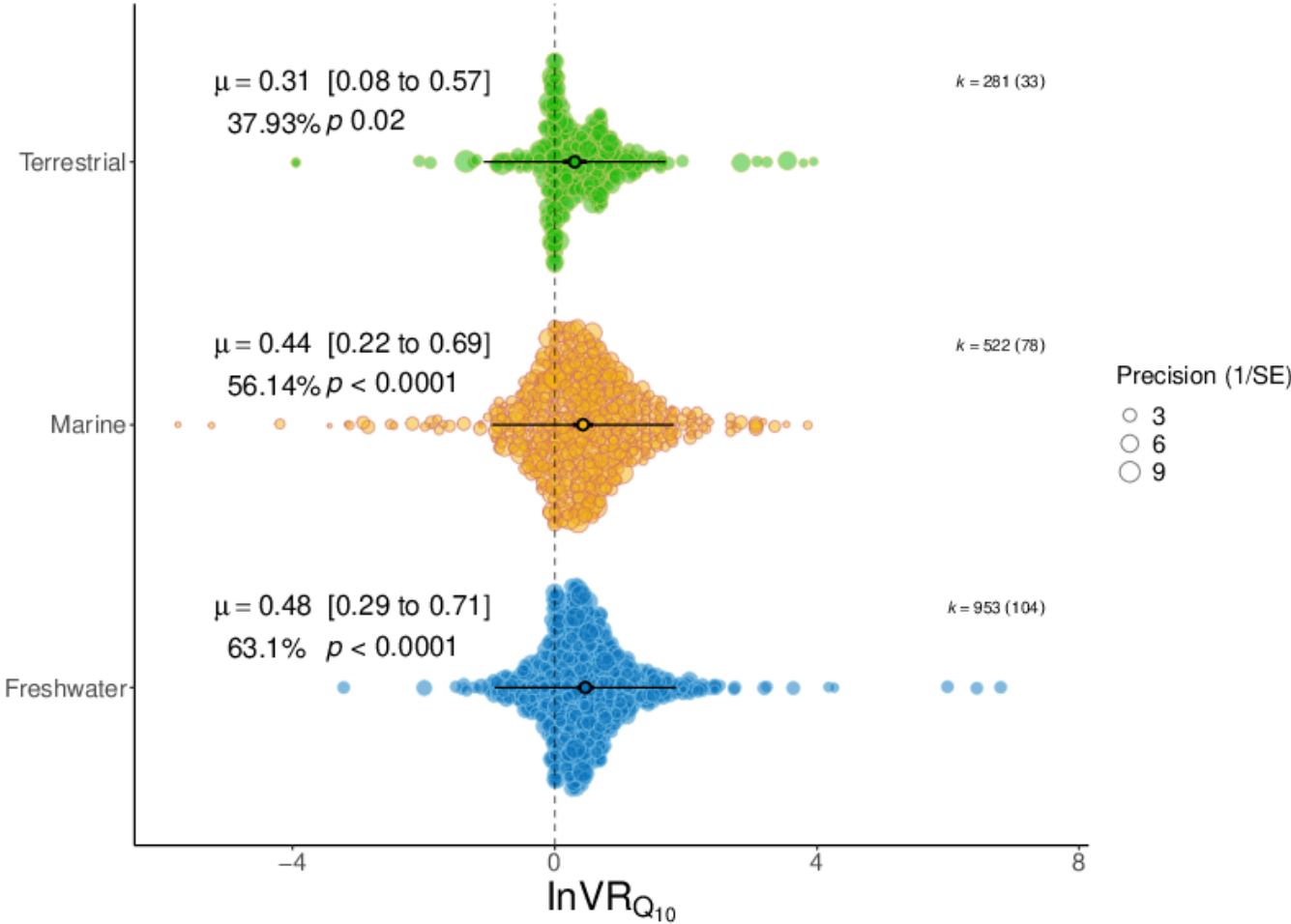


Figure S4- Estimated mean  $\ln VR_{Q_{10}}$  for marine, freshwater and terrestrial systems. Note there were no differences between acute and acclimation  $Q_{10}$  types so they were averaged. Thick black bars are 95% confidence intervals (CI's) and thin bars 95% prediction intervals (PI's). The percentage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

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

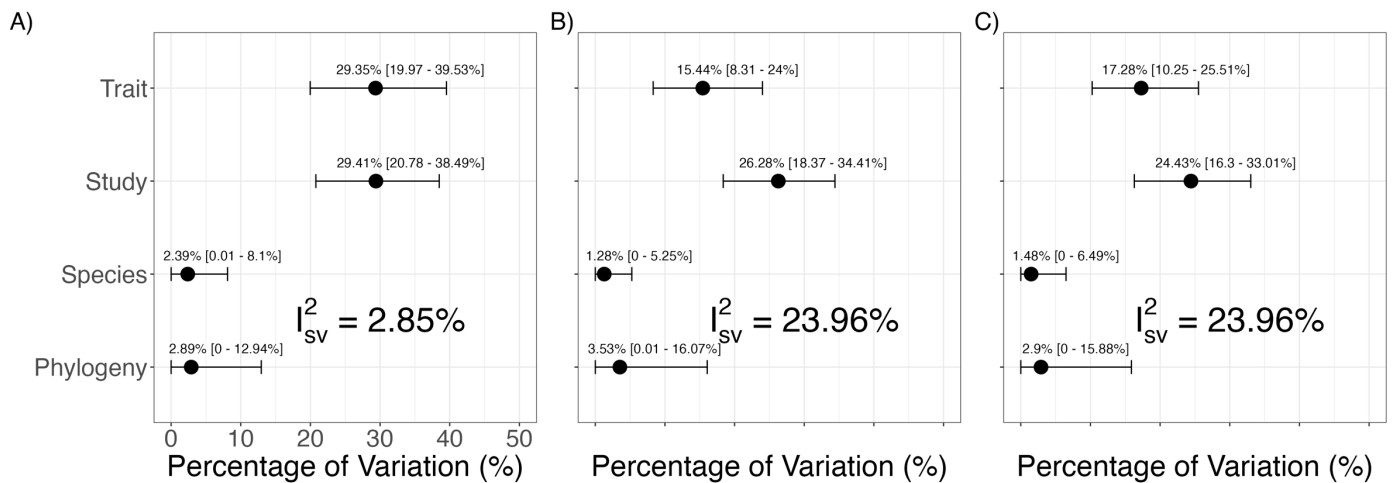


Figure S5-  $I^2$  estimates. A)  $lnRR_{Q_{10}}$  B)  $lnCVR_{Q_{10}}$  and C)  $lnVR_{Q_{10}}$ .

732 **Publication Bias Analysis**

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

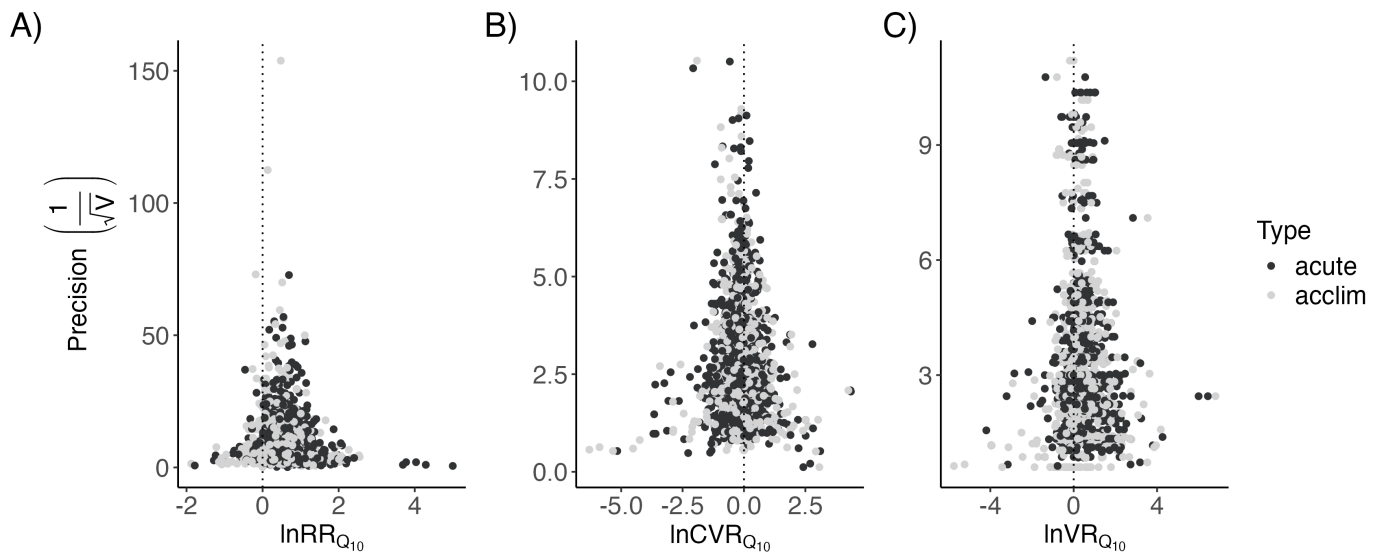


Figure S6- Funnel plot of precision (1/sampling standard error) against effect size for A) log response ratio  $Q_{10}$  ( $\ln RR_{Q_{10}}$ ), B) log coefficient of variance ratio  $Q_{10}$  ( $\ln CVR_{Q_{10}}$ ) and C) log variance ratio  $Q_{10}$  ( $\ln VR_{Q_{10}}$ ). Both acute ('green') and acclimation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