

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

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13 **Abstract**

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

33 **Main**

34 Climate change is expected to result in warmer but also more variable thermal environments globally¹⁻³.
35 Greater thermal variability in the past should result in strong selection pressures that lead to genetic
36 adaptation and/or the evolution of adaptive phenotypic plasticity – both of which are considered important
37 for population resilience to contemporary human-induced climate change⁴⁻¹¹. Without plasticity or
38 adaptation, high extinction rates are predicted unless organisms can migrate to track suitable habitats^{9,12}.
39 Phenotypic plasticity is expected to be the ‘first line of defence’ against changing climates, thereby buying
40 time for genetic adaptation to take place (i.e., the ‘plasticity first hypothesis’)^{13,14}. Phenotypic plasticity is
41 predicted to evolve when environmental variability is high but predictable and the costs of plasticity are
42 low^{7,9,15-17}. Despite this theoretical expectation, empirical support is scant (but see¹⁸), likely because many

43 organisms can behaviorally adjust micro-habitat selection to offset thermal stress, the costs of plasticity are
44 high^{6,16}, or the prediction is only supported for specific life-history stages.

45 Reversible phenotypic plasticity, such as acclimation, is expected to provide greater potential to buffer
46 populations from climate impacts as responses are relatively rapid and can therefore be fine-tuned to
47 proximate environmental conditions (assuming the costs of plasticity are low)^{15,16}. Acclimation is driven by
48 endocrine and epigenetic processes that change the underlying physiology to facilitate a rapid response to the
49 environment^{19–21}. However, the focus up to now has been primarily on mean physiological responses. For
50 example, mean thermal tolerances or acclimation capacities in a population are likely to shift in response to
51 thermal environments^{4,22–24}. However, it is possible that intrapopulation variability might also be impacted in
52 addition to the mean. Understanding how variability in physiological rates – traits thought to be closely
53 linked to fitness – are affected by climate change is important because lack of physiological variation can
54 limit responses to selection (i.e., the ‘opportunity for selection on a trait’)²⁵. Higher physiological variance in
55 a population may also indicate greater niche breadth which can buffer populations against environmental
56 change (i.e., the portfolio effect)^{26–29}. Decreases in phenotypic variance also suggests strong stabilising
57 selection or reflects constraints on performance^{15,16}. Changes in physiological trait variation may also have
58 important ecological consequences by promoting population productivity and stability^{30,31}, species
59 coexistence and ecosystem processes^{26,32,33}. The implications of changes in variance could, therefore, have
60 wide-reaching consequences for understanding the capacity of populations to persist in and adapt to novel
61 environments but to date there are few data testing the importance of variances in this context¹⁵.

62 Periods of past climatic change have had disproportionate impacts on some ecosystems over others raising
63 the question of which ecosystems will be most vulnerable to contemporary climate change. Species
64 occupying terrestrial ecosystems are thought to be particularly vulnerable given their weak acclimation
65 abilities and greater probability of experiencing thermal extremes that overwhelm physiological
66 homeostasis^{4,22,34}. However, this conclusion has been questioned given that marine ectotherms have recently
67 been shown to be closer to their upper thermal limits compared to terrestrial species³⁵. Marine and freshwater
68 ecosystems appear to have greater physiological acclimation capacity^{e.g., 4,24}. However, it is unclear if the
69 magnitude of physiological adjustment is sufficient to compensate for potentially negative environmental
70 effects, particularly when temperature interacts with other abiotic changes. Low oxygen availability may be a
71 major factor influencing the vulnerability of aquatic ecosystems, whereas remaining close to thermal limits
72 and greater water loss is expected to be a stronger constraint on physiological processes in terrestrial
73 ectotherms³⁶. Given that terrestrial ectotherms are expected to be closer to their thermal limits, an increase in
74 temperature may have a stronger impact on variation in physiological rates within populations compared to
75 aquatic ectotherms which may have important cascading effects on energy transfer and productivity across
76 different ecosystems^{10,37}.

77 Here, we use meta-analysis to re-evaluate the degree to which aquatic and terrestrial ectotherms are capable
78 of physiological plasticity. We then developed new effect sizes effect sizes to quantify how variance in
79 physiological rates change with temperature to ask the following questions: 1) How much is variance in
80 physiological rates expected to change, if at all, as temperatures rise? 2) Are temperature effects on plastic
81 adjustments in physiological rates larger than changes in variance across aquatic and terrestrial ectotherms?
82 3) Are changes in plasticity or variance in physiological rates impacted by past climate history? 4) How are
83 means and variances in physiological rates expected to change under climate change?

84 Results

85 Using a large database on physiological rates⁴ for marine, freshwater and terrestrial ectotherms we apply new
86 effect size estimates³⁸ that capture changes in mean physiological rates ($\ln RR_{Q_{10}}$), and changes in their
87 relative variance ($\ln CVR_{Q_{10}}$), standardised to a 10°C temperature difference. These standardised effects sizes
88 can be converted to percentage differences to permit comparisons between the relative magnitudes of rate
89 changes resulting from acclimation and relative variance changes at high temperatures. Acclimation

90 responses can be determined by comparing acclimation $\ln RR_{Q_{10}}$ ($\ln RR_{Q_{10}acclimation}$) to acute $\ln RR_{Q_{10}}$
91 ($\ln RR_{Q_{10}acute}$) from ectotherms acclimated to different temperatures. The difference in $\ln RR_{Q_{10}acclimation}$
92 compared to $\ln RR_{Q_{10}acute}$ measures the extent of acclimation (i.e., plasticity).

93 The final dataset included a total of 91 freshwater (fishes = 48, molluscs = 4, amphibians = 19, reptiles = 8,
94 arthropods = 10, and a single crustacean and nematode species), 90 marine (fishes = 47, annelids = 2,
95 molluscs = 21, echinoderms = 7, reptiles = 1, arthropods = 10, and a single crustacean and cnidarian species),
96 and 45 terrestrial species (annelids = 1, molluscs = 5, arthropods = 14, reptiles = 12 and amphibians = 12
97 along with a single tardigrade species) (Figure 1 A). We had more data on acute thermal responses (n =
98 1115) compared to thermal responses after an acclimation period (n = 798) because acute responses were
99 reported for each of the two acclimation temperatures (Figure 1). The two acute $\ln RR_{Q_{10}}$ effect sizes differed
100 significantly from each other (acute responses were greater for animals acclimated to high temperatures – $\beta =$
101 0.07, 95% CI: 0.04 to 0.1, $p_{MCMC} = < 0.0001$), but on average they were in the same direction and only
102 differed by ~10%. As such, we averaged the two acute $\ln RR_{Q_{10}}$ effect sizes in subsequent analyses.

103 Most of the effect size estimates came from measurements of metabolic rates (both resting and maximal –
104 $N_{species} = 190$, $N_{effects} = 1023$, considering acute and acclimation effects together), metabolic enzyme rates
105 ($N_{species} = 61$, $N_{effects} = 798$) and whole-organism performance traits (i.e., measures of speed and
106 endurance – $N_{species} = 73$, $N_{effects} = 32$).

107 ***Terrestrial and aquatic ectotherms differ in their capacity to acclimate but acclimation*** 108 ***does not depend on life-history stage***

109 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%).
110 Ectotherms in marine and freshwater environments showed partial compensation of physiological rates
111 (Figure 1B) amounting to reduced $\ln RR_{Q_{10}acclimation}$ of 17.08% (95% CI: -24.32 to -10.19) in freshwater and
112 15.7% (95% CI: -25.96 to -4.79) in marine environments. In contrast, terrestrial ectotherms showed no
113 acclimation (possibly even inverse acclimation) – showing a 6.6% increase in $\ln RR_{Q_{10}acclimation}$ (95% CI: -
114 6.56 to 21.19, Figure 1B).

115 Nonetheless, effect heterogeneity was high (only 2.85% of the variance was the result of sampling
116 variability, 95% CI: 2.38 to 3.32%), and most variance was explained by the specific study and type of trait
117 (Study: 29.41% , 95% CI: 20.78 to 38.49%; Trait Type: 29.35% , 95% CI: 19.97 to 39.53%). Evolutionary
118 relationships among taxa and species ecology (i.e., species random effect) explained little variation in acute
119 and acclimation responses (Species: 2.39% , 95% CI: 0.01 to 8.1%; Phylogeny: 2.89% , 95% CI: 0 to
120 12.94%).

121 Different trait categories showed different acclimation responses across habitat types, however, they mirrored
122 overall patterns (see Supplement; Figure S2). Acclimation capacity also did not vary by life-history stage and
123 there were no differences between $\ln RR_{Q_{10}acclimation}$ and $\ln RR_{Q_{10}acute}$ between adult and juveniles (Figure 2
124 A-C) (Adult-Juvenile (Acute): 0, 95% CI: -0.21 to 0.2, $p_{MCMC} = 0.96$; Adult-Juvenile (Acclimation): 0.05,
125 95% CI: -0.16 to 0.38, $p_{MCMC} = 0.83$).

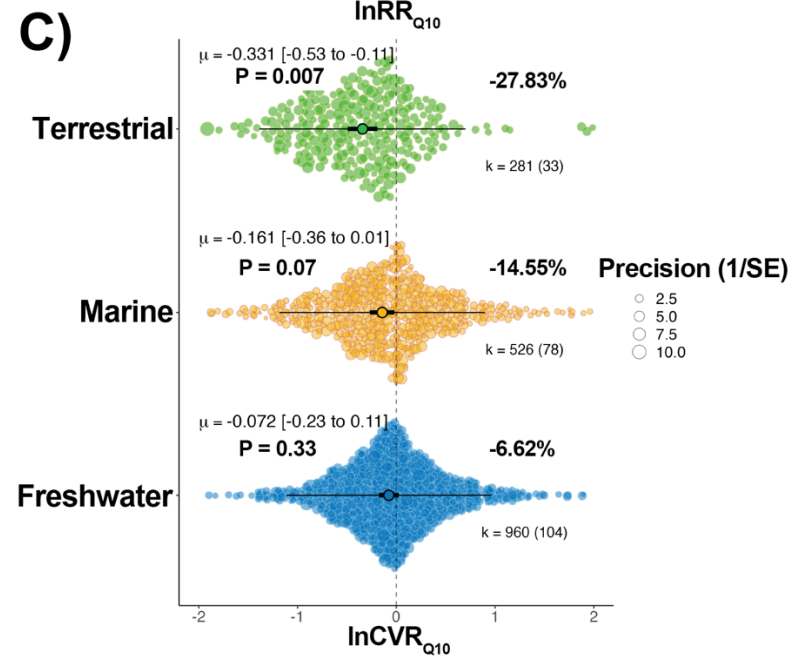
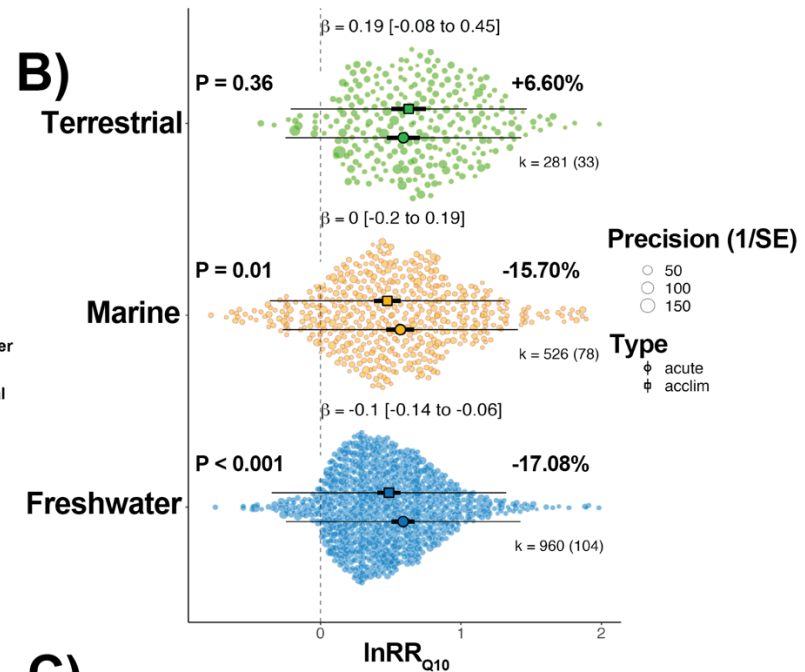
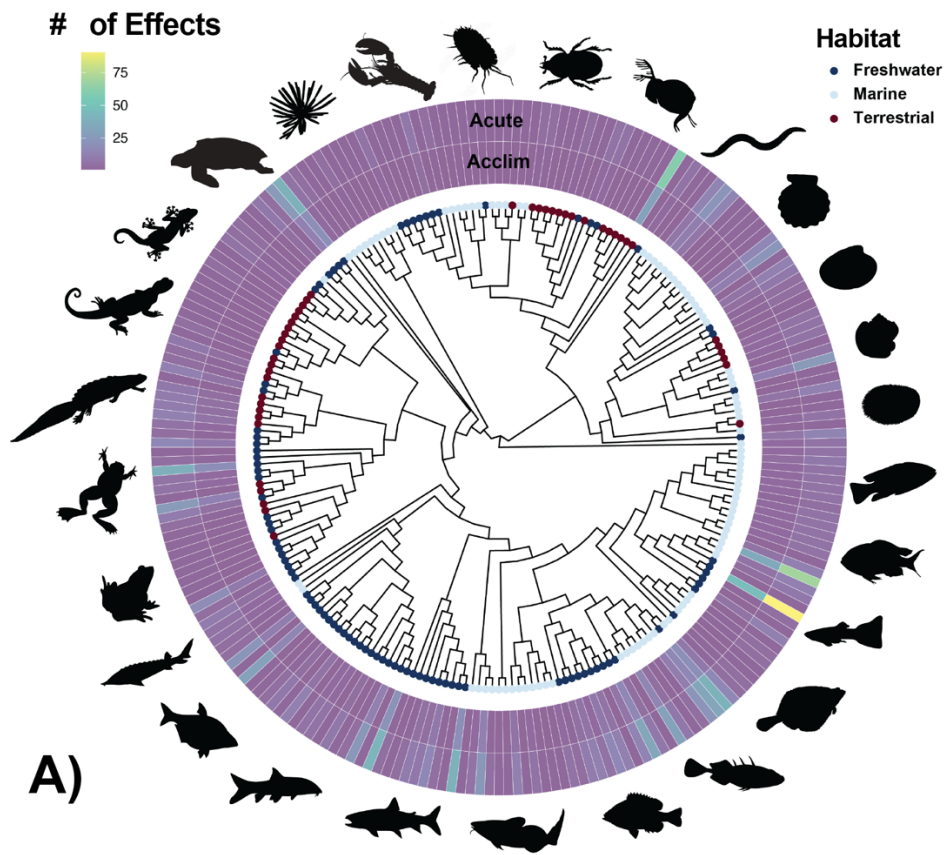


Figure 1- Taxonomic distribution of acute and acclimation Q_{10} estimates across major habitats. **A)** Phylogenetic distribution of taxa contained within the data. The total number of acute and acclimation Q_{10} effect sizes are highlighted as well as whether the taxa are marine, freshwater or terrestrial.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

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

129 Relative variance in physiological rates ($\ln CVR_{Q_{10}}$) showed a decrease with increasing temperature across all
130 habitat types, which was especially pronounced in terrestrial and marine ectotherms. Overall, there was a
131 27.87% (95% CI: 10.77 to 40.91, $p_{MCMC} = 0.01$) reduction in relative physiological rate variance for
132 terrestrial ectotherms and a 14.94% (95% CI: 1.87 to 29.97, $p_{MCMC} = 0.07$) reduction in relative variation for
133 marine ectotherms when temperatures increased by 10°C. In contrast, freshwater ectotherms exhibited a
134 smaller reduction in relative physiological rate variance at high temperatures (8.62%, 95% CI: 0.41 to 21.78,
135 $p_{MCMC} = 0.33$).

136 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:
137 20.36 to 27.27), with most variation being driven by between-study and trait differences (see Supplement;
138 Figure S5). Each life-history stage exhibited the same pattern of variance change in each of the habitats
139 (Figure 2). Reduced relative variance was particularly prominent for resting metabolic rates and sprint speed
140 although traits differed in whether they exhibited a reduction in variation in physiological rates at high
141 temperatures (Figure S3).

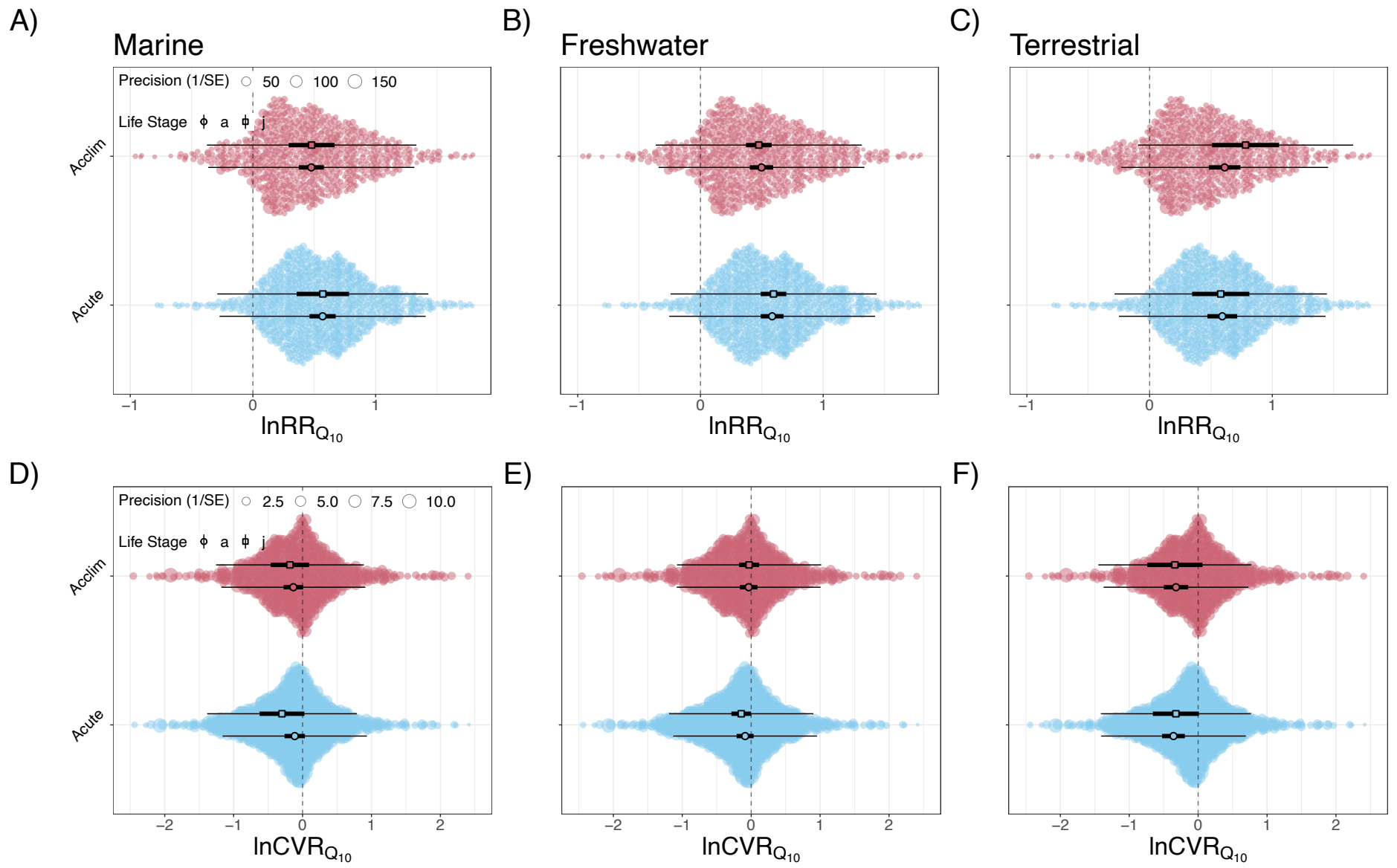


Figure 2- Estimated mean acclimation and acute $\ln RR_{Q_{10}}$ (A-C) and $\ln CVR_{Q_{10}}$ (D-F) for adult and juvenile life-history stages for Marine (A & D), Freshwater (B & E) and Terrestrial (C & F) ectotherms. k = total number of effect size estimates while the numbers in brackets indicate the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

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

145 Using the ERA5 climate model, we extracted a 72-year period (1950-2022) of either surface air temperature
146 (0.01°resolution) for both terrestrial and freshwater taxa, or sea surface temperature for the marine taxa (at
147 0.25°resolution). We used the historical temperature data for each geographical location to calculate a
148 measure of thermal variability and predictability (see *Methods*). Thermal variability (i.e., *CV*) and
149 predictability experienced by a population in the past did not explain acclimation capacity or changes in
150 physiological rate variance among terrestrial, marine or freshwater populations (Figure 3; Figure 4).

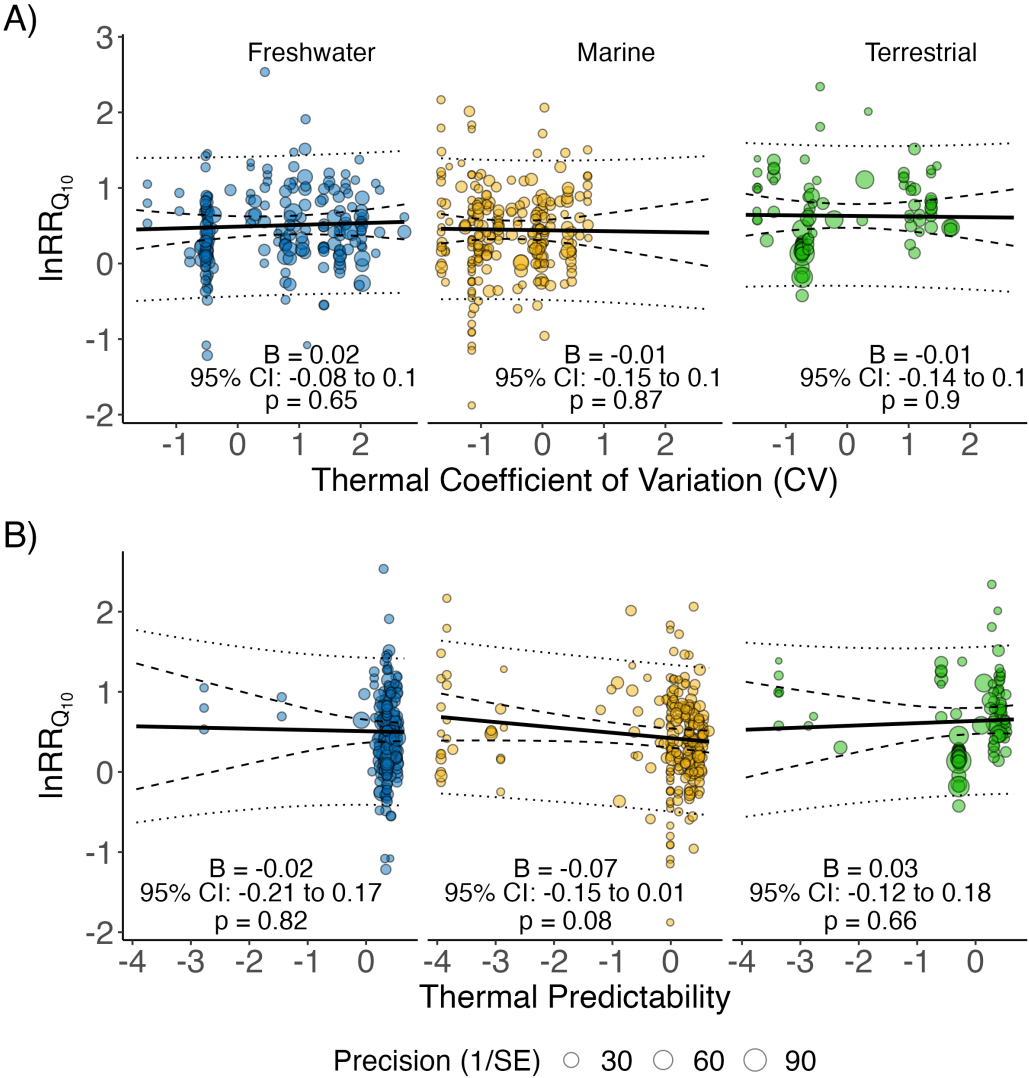


Figure 3- Predicted mean (thick black line) $\ln RR_{Q_{10}}$ as a function of the Thermal Coefficient of Variation (CV) (A) and thermal predictability (B) for wild populations across marine, freshwater and terrestrial habitats. Dashed lines indicate 95% confidence intervals and dotted lines indicate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

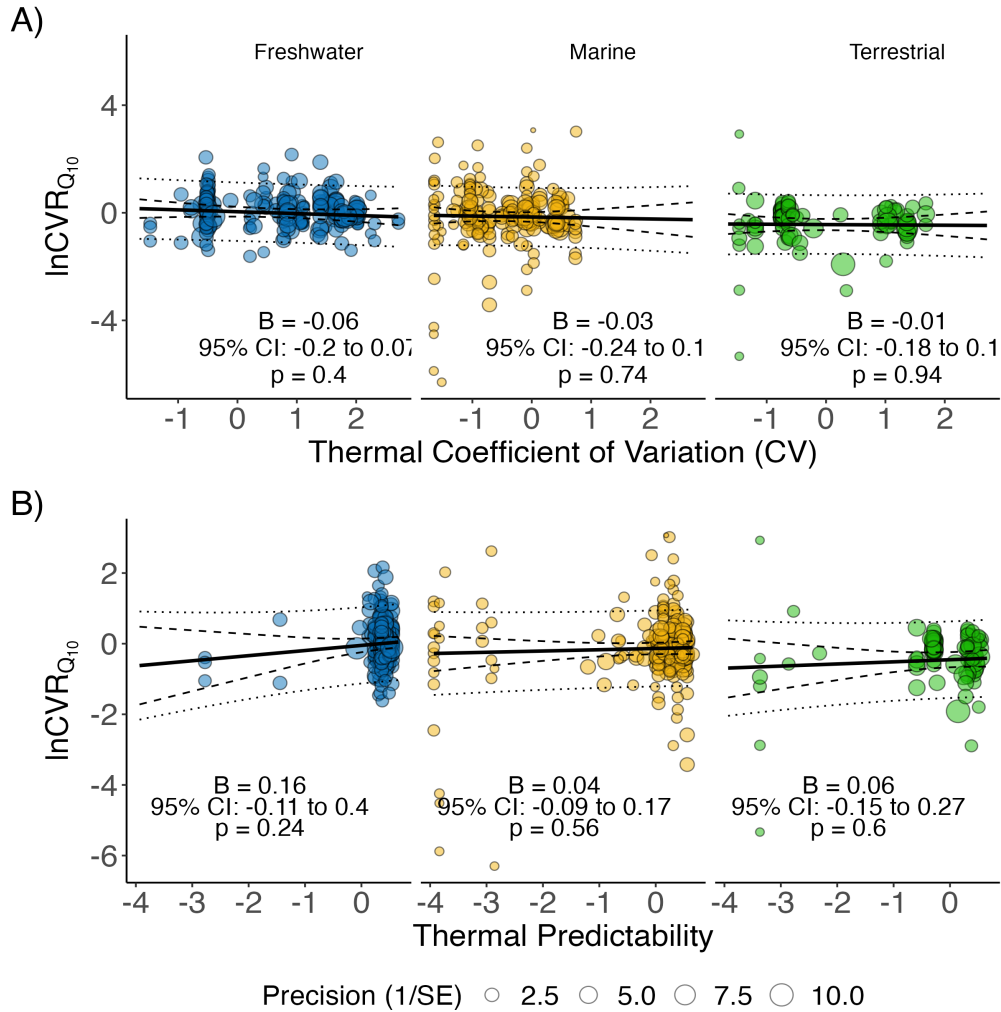


Figure 4- Predicted mean (thick black line) $\ln CVR_{Q_{10}}$ as a function of the Thermal Coefficient of Variation (CV) (A) and thermal predictability (B) for wild populations across marine, freshwater and terrestrial habitats. Dashed lines indicate 95% confidence intervals and dotted lines indicate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

Changes in physiological rate variance under climate change

Measurements of acute and acclimation responses from wild ectotherms were much less common than from captive populations ($N_{species} = 134$, from 188 wild populations). Globally, there was a clear bias towards species in the Northern Hemisphere (Figure 5 A-C). Projected changes in physiological rate variance were highly variable across the globe, with some regions showing a decrease in physiological rate variance, while others showing an increase (Figure 5 D). However, out of the 188 populations, relative variance was predicted to decrease in 97.87% of the locations.

159 Using the ERA5 climate model, predictions of current global changes in physiological rate variance were
 160 generally conservative with our model explaining $\sim 50\%$ of the variation in the observed data ($R^2 = 0.48$,
 161 95% CI: 0.31 to 0.6). Across habitat types climate change is predicted to result in a 1.02% change in relative
 162 variance for freshwater systems (95% CI: -5.49 to 7.1%, $p_{MCMC} = 0.65$), a 2.71% reduction in relative
 163 variance for marine systems (95% CI: -6.1 to 1.4%, $p_{MCMC} = 0.37$), and a 11.88% reduction in relative
 164 variance for terrestrial systems (95% CI: -18.95 to -5.98%, $p_{MCMC} = < 0.0001$) under a RCP8.5 climate
 165 scenerio.

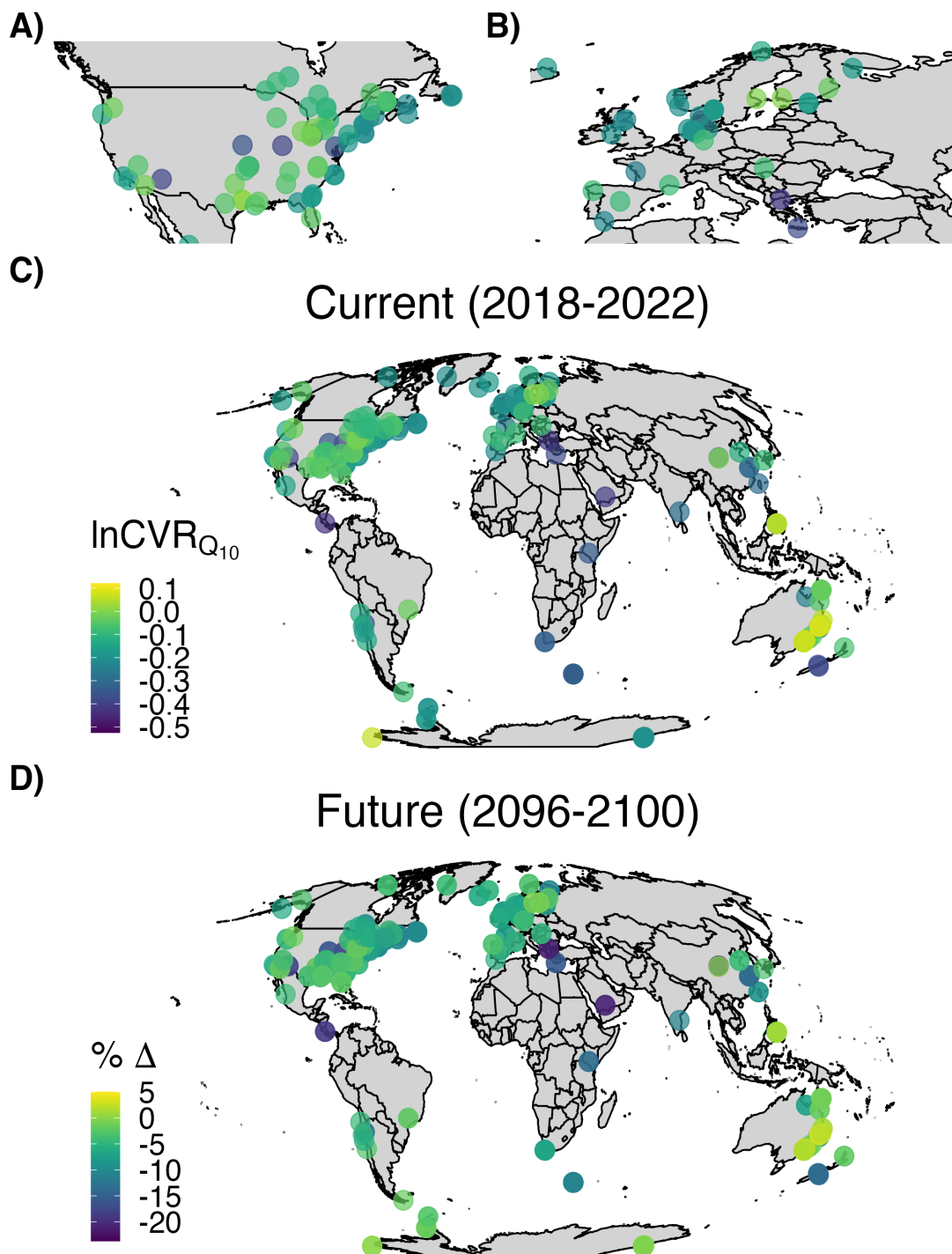


Figure 5- Model predictions for the expected change in acclimation $\ln CVR_{Q_{10}}$ across the globe for terrestrial, marine and freshwater ectotherms. Predictions consider the uncertainty in random effects (i.e., species, phylogeny, study). Predicted change in physiological rate variance (relative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

166 **Discussion**

167 Understanding acclimation capacity and how variation in physiological rates changes across populations and
168 species is important for predicting the ecological and evolutionary consequences of climate change^{7,8,10,26,39}.
169 Here, we show that the relative variance ($\ln CVR_{Q_{10}}$) in physiological rates of ectotherms decreased across
170 terrestrial, marine and freshwater ecosystems as temperatures increase, with the decrease being particularly
171 pronounced in terrestrial ectotherms (~28%). These effects are expected to result in a decrease in the
172 variability in physiological rates for marine and terrestrial ectotherms between ~4-13% under future climate
173 change projections. Our results uncover an hitherto unrecognised dynamic where the benefits of acclimation
174 may be counteracted by a decrease in trait variance.

175 ***Potential consequences of reduced plasticity and variance in physiological rates across*** 176 ***ectotherms***

177 Understanding the interplay between plasticity and genetic adaptation has important implications for
178 predicting population resilience to climate change^{8,10,11,39-42}. For example, incorporating phenotypic plasticity
179 and adaptation into species distribution models dampens the predicted contraction of distributions in the face
180 of climate change^{e.g., 39}. In addition, it may be expected that reductions in variance impact the ‘opportunity for
181 selection’ by reducing the strength of selection and/or the genetic variance exposed to selection, thereby
182 reducing the capacity to evolve under climate change^{40,41}. Quantifying the degree of plasticity and
183 genetic/phenotypic variation in key physiological responses is therefore recognised as being critical to
184 informing projections for organisms threatened by climate change¹¹.

185 We show that acclimation of physiological rates and changes relative variance differ across habitats. In
186 freshwater habitats, acclimation responses will likely be beneficial and this coincides with relatively little
187 reduction in the relative variance thereby maintaining the raw material for selection to operate. In contrast,
188 acclimation responses of marine organisms are associated with a nearly equal reduction in relative variance
189 so that the beneficial effects of acclimation trade-off against reduced potential for selection at high
190 temperatures. In terrestrial ectotherms, relative variance reductions are particularly pronounced, and this
191 coincides with a general inability to acclimate. Terrestrial ectotherms are therefore most vulnerable to climate
192 because both compensations for potentially negative effect of temperature via acclimation, and adaptation to
193 novel conditions are relatively ineffective. However, terrestrial species have greater opportunity for
194 behavioural microhabitat selection which will decrease the impacts of climate change at least in complex,
195 thermally heterogeneous environments⁴³.

196 Our findings highlight the potential vulnerability of terrestrial and marine ectotherms to climate change. Our
197 meta-analytic results provide percentage changes of relative variances and acclimation responses that can be
198 used to parameterise models (e.g., species distribution models)^{39,44} to predict species distributions or assess
199 population resilience in the face of climate warming. Our results also define the range of biological responses
200 observed across diverse taxa (e.g., through prediction intervals) providing opportunities to incorporate
201 realistic biological variation into the modelling process.

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

203 Life-history stages often occupy different ecological niches and exhibit different physiological responses,
204 levels of plasticity, and patterns of mortality in response to temperature. As such, it is becoming increasingly
205 important to understand how climate change will impact different life-history stages^{45,46}. Greater plasticity in

early life-stages of development is expected to be important to increase resilience to the effects of climate change because early life-stages are often particularly vulnerable periods in development^{47,48}. We show that there were generally similar patterns between early and late life stages across a diversity of taxa, both in terms of variance changes and the capacity for plasticity. On average, our results show that early life stages are not more vulnerable to the impacts of climate change. However, our general meta-analytic findings do not imply that early life stages are not always less plastic, but that such responses are likely context or trait dependent^{49,50}. For example, Moghadam *et al.*⁵⁰ showed that larval *Drosophila* were more plastic in their heat hardening responses compared to adults. In contrast, Carter *et al.*⁴⁹ showed greater thermal plasticity in metabolism for adults but little in pupae of *Onthophagus taurus*. Despite variation in the literature, very few studies measure multiple life-history stages within the same population. In future research, there needs to be more studies that explicitly compare differences in plasticity among life stages across multiple traits within the same population.

Ecological consequences of reduced variation in physiological rates

Variance reductions in metabolism and performance (e.g., sprint speed) were most strongly impacted by increased temperature. Changes in variability of traits governing energy demand could have important consequences on the flow of energy within and between populations, communities, and ecosystems^{10,37,51}. More variable populations, genetically and/or phenotypically, are predicted to be associated with broader niches, reduced intraspecific competition, increased growth rate, decreased vulnerability to environmental change and lower extinction risk^{26,33,51–53}. Maintaining intrapopulation variability in physiological rates in a warmer world may therefore be important for population resilience to climate change. For example, Kooijman *et al.*³¹ integrated individual variation in dynamic energy budget (DEB) models developed for *Daphnia magna*. They showed that greater between-individual variation in DEB parameters led to less extreme population fluctuations compared to scenarios with no variation³¹. Our results suggest that terrestrial ectotherms will likely face greater challenges to adapting to climate change^{22,24,34}, leading to greater rates of extinction and reduced productivity in terrestrial ecosystems. However, data testing the impacts of changes in variance on populations are limited to very few taxa. Future experimentation across a broader range of taxa should manipulate levels of variance to understand its ecological outcomes.

No signature of past climate on capacity for physiological plasticity

Theoretical evolutionary models predict that plasticity should evolve in populations experiencing greater environmental variability (spatial or temporal), particularly when oscillations are predictable over time to make environmental cues more reliable^{7–9,14,17,51,54}. Higher spatial and temporal heterogeneity in terrestrial ecosystems⁵⁵ suggests that plasticity should be more likely to evolve in terrestrial environments. However, we did not find evidence to this effect. Our finding is consistent with other meta-analyses^{22,56} with thermal tolerance (which we did not consider here). Modelling correct microenvironments for over 200 species across such diverse habitats is challenging. The lack of a relationship between physiological plasticity and environmental variability and predictability could be due the fact that ectotherms simply seek out microhabitats that make their environment quite stable⁴³. Therefore, it is possible that more fine-scale resolution of the habitats that organisms occupy will elucidate expected patterns. Randomly fluctuating environments have been suggested to select for reduced plasticity, particularly if plastic responses are costly and this has been demonstrated by a number of empirical studies^{18,57,58}. For example, using seed beetles (*Callosobruchus maculatus*), Hallsson *et al.*⁵⁹ showed that experimentally evolving populations under randomly fluctuating thermal conditions did not show any increase in plasticity, but had reduced plasticity. Leung *et al.*¹⁸ also showed reduced plasticity in morphological traits of experimentally evolving algae populations (*Dunaliella salina*) when environments were less predictable^{see also 58}. While it is unclear how these findings relate directly to acclimation because they integrate multiple forms of plasticity, they do suggest that there are costs to being plastic or that the environmental signals are insufficient to trigger endocrine and epigenetic mechanisms that lead to plasticity when environments are not predictable^{18,51}. The fact that aquatic ectotherms did show a capacity to acclimate suggests that environmental predictability,

254 which is expected to be higher in aquatic environments, may be more important than environmental
255 variability in driving the evolution of plasticity.

256 ***Conclusions and future directions***

257 Enhanced knowledge of how variation in physiological rates vary across populations and species and the
258 degree to which they can be adjusted in response to the environment may lead to more informed predictions
259 about the ecological and evolutionary dynamics of natural populations^{10,11,52}. While we show general patterns
260 across taxa and habitats it is important to recognise that this does not mean such patterns apply to all
261 populations. Substantial variation in acclimation responses and changes in variance exist among populations
262 as evidenced by wide prediction intervals. Nonetheless, changes in the relative variance in physiological rates
263 could be better incorporated into physiological and ecological models to provide more nuanced and possibly
264 more realistic predictions about the impacts of climate change on natural populations. While we do not yet
265 understand the relative contribution of environmental and genetic factors to variances changes, models could
266 better decouple how different levels of heritability with different total variance impact evolutionary and
267 ecological predictions. Our meta-analysis now provides the opportunity to parameterise models and ensure
268 they are better aligned with empirical findings. Nonetheless, many fascinating questions remain unanswered
269 that will require greater focus on the consequences of changes in variance (rather than just the mean).
270 Particularly interesting questions include: How does a reduction in physiological rate variance change energy
271 flow across tropic levels within communities? What are the biochemical, cellular, and physiological
272 mechanisms that underly reduced variance in physiological rates? Are reductions in variance in one trait
273 associated with reductions in correlated traits, or do some traits increase while others decrease? How much of
274 the reduction in variance is driven by lower levels of genetic variance? Answers to these questions will
275 require integrative approaches that combine empirical and theoretical work across multiple levels of
276 biological organisation but will likely provide useful advances in understanding the full consequences that
277 climate change will have on ectotherms across all major ecosystems.

278 **Methods & Protocols**

279 ***Literature collection***

280 We compiled literature on ectothermic animals that measured physiological rates (e.g., metabolic rate) at two
281 or more temperatures after having been acclimated (or acclimatized) at these temperatures. We used data
282 from a previous meta-analysis⁴ and updated⁴'s data by extracting data from suitable studies from our own
283 searches that followed the same search protocol. More specifically, we performed a literature search using
284 the Web of Science database for articles or proceedings papers published in English from 2013 to 2017 the
285 date after 4 searches were conducted using the following topic search string: “(acclimat AND (therm* OR
286 temp) NOT (plant OR tree* OR forest* OR fung* OR mammal* OR marsup* OR bird* OR human OR
287 exercis* OR train* OR hypoxi)) “. We further limited to the following research areas: Anatomy Morphology;
288 Biodiversity Conservation; Biology; Ecology; Endocrinology Metabolism; Entomology; Evolutionary
289 Biology; Marine Freshwater Biology; Physiology; Respiratory System, Reproductive Biology, Zoology.

290 Our search resulted in 1,321 papers for screening in Rayyan⁶⁰. We also cross-checked papers we found in our
291 searches with a recent paper by²³, which also updates the dataset of⁴'s. We included any papers that were
292 missed between our searches and those of²³.²³ added 7 new studies (mainly because they were focused on
293 metabolic rates), and our searches differed from theirs by only a single paper^{i.e., 61}. Given the physiological
294 traits we included were broader, we had a substantial increase in additional papers that we added to⁴'s
295 dataset. More specifically, in addition to the 191 papers we included from the⁴ dataset, we extracted data
296 from an extra 65 papers (with a total of 238 effects; a 34.03% increase in the number of published articles).
297 Note that⁴ included a total of 205 publications, however, not all these contained the necessary statistics we
298 needed to derive effect sizes and associated sampling variances (see below). While we may have missed
299 papers, our goal was to obtain a large representative (and unbiased) sample of acclimation research rather

300 than a comprehensive dataset. As such, our database represents the most up-to-date dataset used by⁴ to
301 answer questions on physiological rates across ectotherms.

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

313 ***Data Compilation***

314 We extracted means, standard deviations, and sample sizes for physiological rates at the two test
315 temperatures. If there were more than two test temperatures, we chose only the test temperatures that fell
316 within the most likely natural range of temperatures experienced by the species in question. We extracted
317 these data from text, tables or figures of a given paper. Data were extracted from figures using the R package
318 *metaDigitise*⁶². We also recorded the phylum, class, order, genus and species, and the latitude and longitude
319 from where the experimental animals were sourced. For studies that did not provide latitude and longitude for
320 the population, we searched for similar studies by the same lab group to identify where the population was
321 likely to have been sourced. If the experimental animals were derived from the wild, we recorded the nearest
322 latitude and longitude of the field collection site. If the animals were sourced from a commercial supplier, we
323 took the latitude and longitude of the supplier. When it was not possible to find latitude and longitude using
324 these methods, we looked up the distribution of the species in question and took the latitude and longitude of
325 the centroid of the species' distributional range.

326 ***Q₁₀ Based Effect Sizes and Sampling Variances for Means and Variances***

327 Following³⁸ we calculated a series of temperature-corrected effect sizes that compared mean physiological
328 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
329 are similar to the traditional temperature coefficient (Q_{10}), but with formal analytical approximations of their
330 sampling variances. Sampling variances for effect sizes allowed us to make use of traditional meta-analytic
331 modelling approaches.

332 ***Comparing changes in mean physiological rates***

333 To compare mean physiological rates, we calculated the log Q_{10} response ratio, $\ln RR_{Q_{10}}$ ³⁸ as follows:

$$334 \quad \ln RR_{Q_{10}} = \ln \left(\frac{R_2}{R_1} \right) \left(\frac{10^\circ C}{T_2 - T_1} \right) \quad (1)$$

335 Where, R_1 and R_2 are mean physiological rates and T_1 and T_2 are the temperatures at which these rates are
336 measured. Log transformation of this ratio makes the effect size normally distributed. Equation 1 is
337 essentially a temperature corrected equivalent to the log response ratio ($\ln RR$)^{63,64} when the numerator and
338 denominator are measured at different temperatures. This allows comparisons of the means from two
339 temperature treatments directly regardless of the absolute measurement temperatures. The sampling variance
340 for Equation 1 can be computed as follows (as described in³⁸):

341
$$s_{lnRR_{Q_{10}}} = \left(\frac{SD_2^2}{R_2^2 N_2} + \frac{SD_1^2}{R_1^2 N_1} \right) \left(\frac{10^\circ C}{T_2 - T_1} \right)^2 \quad (2)$$

342 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,
 343 respectively.

344 ***Comparing variance in physiological rates***

345 ⁶⁵ proposed analogous effect size estimates to $lnRR$ that allow for comparisons of changes in variance
 346 between two groups, the log variance ratio ($lnVR$) and the log coefficient of variation ($lnCVR$). $lnVR$ and
 347 $lnCVR$ are ratios that describe the relative difference in trait variability between two groups. We refer readers
 348 to⁶⁵ for the equations describing $lnVR$ and $lnCVR$, but these can easily be extended to their Q_{10} analogues
 349 (and associated sampling variance) as follows:

350
$$lnVR_{Q_{10}} = \ln \left(\frac{SD_2}{SD_1} \right) \left(\frac{10^\circ C}{T_2 - T_1} \right) \quad (3)$$

351
$$s_{lnVR_{Q_{10}}} = \left(\frac{1}{2(N_2 - 1)} + \frac{1}{2(N_1 - 1)} \right) \left(\frac{10^\circ C}{T_2 - T_1} \right)^2 \quad (4)$$

352 Equation 3 and Equation 4 describe the change in physiological rate variance (Equation 3) across a $10^\circ C$
 353 temperature change along with its sampling variance (Equation 4). While this is a useful metric, as discussed
 354 by⁶⁵ there is often a strong mean-variance relationship that needs to be accounted for in analysing changes in
 355 variance. As such, we calculated the coefficient of variation, which standardizes changes in variance for
 356 changes in means as follows:

357
$$lnCVR_{Q_{10}} = \ln \left(\frac{CV_2}{CV_1} \right) \left(\frac{10^\circ C}{T_2 - T_1} \right) \quad (5)$$

358
$$s_{lnCVR_{Q_{10}}} = \left[\frac{(SD_1)^2}{N_1(R_1)^2} + \frac{(SD_2)^2}{N_2(R_2)^2} + \frac{1}{2(N_1 - 1)} + \frac{1}{2(N_2 - 1)} \right] \left(\frac{10^\circ C}{T_2 - T_1} \right)^2 \quad (6)$$

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

361 ***Calculating acute and acclimation $lnRR_{Q_{10}}$, $lnVR_{Q_{10}}$ and $lnCVR_{Q_{10}}$ estimates***

362 Using the mean, standard deviation, and sample size for all acute and acclimation treatments of studies in our
 363 databases we derived acute and acclimation $lnRR_{Q_{10}}$, $lnVR_{Q_{10}}$ and $lnCVR_{Q_{10}}$ estimates. For all effect sizes
 364 the higher acute or acclimation temperature was in the numerator and the lower of the two temperatures in
 365 the denominator. As such, positive effect sizes suggest that the mean or variance is larger at the higher of the
 366 two temperatures, standardized to $10^\circ C$.

367 ***Moderator Variables***

368 We recorded or derived a series of moderator variables from each study that are expected to have an impact
 369 on our effect size estimates. These included the duration of acclimation in days and acclimation type
 370 (“acclimation” or “acclimatization”) given that acclimation responses are expected to depend on how long
 371 chronic temperature exposure occurs (longer exposure = better acclimation response)⁴. We also recorded if
 372 the sample of animals were derived from captive or wild stocks, the life-history stage of the animals used
 373 (“adult” or “juvenile”) and the habitat type (“freshwater”, “marine” or “terrestrial”) given that⁴ show that
 374 these factors can impact Q_{10} estimates. Physiological rate measures varied widely across the studies but
 375 could generally be grouped into discrete trait categories⁴. As such, using the detailed information on the trait

376 type, and its associated units from a given study, we categorized each effect size into one of 12 trait
377 categories. These categories included measures of whole organism performance measures including cardiac
378 (i.e., ‘cardiac’) and muscle (‘muscle’) function, sprint speed (‘sprint’) and endurance (‘endurance’) and
379 metabolic rates (i.e., maximal and resting metabolic rate; max MR’, ‘rest MR’, respectively). Studies also
380 quantified various enzymatic reaction rates, including enzymes involved in general metabolic responses
381 (categorized as ‘metabolic enzyme’), various parts of the electron transport chain, including ATPase activity
382 (‘ATPase’), mitochondrial leak (‘mito_leak’) and oxidation (‘mito_oxidation’) as well as antioxidant
383 enzymes (‘antiox’). All other traits not falling within these categories were placed into ‘other’.

384 ***Climate Data***

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

391 Monthly average temperature data were extracted from the ERA5 climate model, available from the
392 Copernicus climate data store⁶⁶. For each population and species in the dataset we extracted a 72-year period
393 (1950-2022) of either surface air temperature (0.01°resolution) for both terrestrial and freshwater taxa, or sea
394 surface temperature for the marine taxa (at 0.25°resolution) using the *ncdf4* R package^{vers. 1.22, 67}. We chose
395 surface temperature because we believed that it was more likely to reflect the micro-thermal environment
396 experienced by terrestrial and freshwater ectotherms at those locations. For terrestrial species we estimated
397 soil temperatures as this maybe more representative of microhabitat choice compared to air temperature. We
398 fit models using both air and soil temperature and found that the results were qualitatively similar. We
399 therefore only present results for air temperature.

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

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

409 ***Meta-Analysis***

410 We analysed our data using multilevel meta-analytic (MLMA) and meta-regression (MLMR) models in R
411 (vers. 4.3.1) using *brms*^{vers. 2.20.4 68,69,70} and *metafor*^{vers. 4.4.0 71}. We fit both Bayesian and frequentist approaches
412 to ensure that our results were consistent, and to create orchard plots more easily^{vers. 2.0, 72,73}. In addition,
413 Bayesian methods better protect against type I errors in the presence of complex sources of non-
414 independence⁷⁴⁻⁷⁶. For our Bayesian models, we ran 4 MCMC chains, each with a warm-up of 1000 followed
415 by 4000 sampling iterations keeping every 5 iterations for a total of 3200 samples from the posterior
416 distribution. We used flat Gaussian priors for ‘fixed’ effects (i.e., $N(0,10)$) and a student t-distribution for
417 ‘random’ effects (i.e., $student_t(3,0,10)$). We checked that all MCMC chains were mixing and had
418 converged (i.e., $R_{hat} = 1$). We compared any competing models using Akaike’s Information Criteria (AIC)
419 (if frequentist) or Wantabe Information Criteria (WIC) (if Bayesian). We deemed models with the lowest IC

420 value to be best supported if there was a ΔIC between the competing models of 2 or more. If two models
421 were within 2 ΔIC units we went with the most parsimonious model.

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

423 We first fit multi-level meta-analysis (MLMA) models (i.e., intercept-only models) for both $\ln RR_{Q_{10}}$ and
424 $\ln CVR_{Q_{10}}$, that included study, species, and phylogeny as random effects to account for non-independence.
425 We also included trait as a random effect to account for trait variation within the data. Our MLMA models
426 allowed us to partition the variation in $\ln RR_{Q_{10}}$ and $\ln CVR_{Q_{10}}$ among these key sources while accounting for
427 total sampling variance in each. This allowed us to calculate the proportion of total heterogeneity [i.e., I^2_{total} ;
428 *sensu*^{77,38}] along with various I^2 metrics describing the proportion of variance explained by each random
429 effect level⁷⁷. We also present 95% prediction intervals which describe the expected distribution of effects
430 from future studies^{38,72}.

431 A phylogeny was derived using the Open Tree of Life (OTL) with the *rotl* package in R (vers. 3.1.0)⁷⁸, and
432 plotted using *ggtree* (vers. 3.9.0)⁷⁹. We resolved all polytomies in the tree. Any missing taxa were replaced
433 with closely related species and branch lengths were computed using Grafen's method (using power = 0.7)⁸⁰.
434 We used the R packages *ape* (vers. 5.7.1)⁸¹ and *phytools* (vers. 1.9.16)⁸² to prune the tree for individual
435 analyses and calculate phylogenetic covariance (or correlation) matrices used in meta-analytic models.

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

437 After quantifying levels of heterogeneity, we fit a series of multi-level meta-regression (MLMR) models to
438 test our key questions. In all models, we included the same random effects as we used in our MLMA models.
439 Acclimation time varied from 4 to 408 days (mean (SD) = 37.98 ± 45.19 days), and terrestrial ectotherms
440 were acclimated for a much shorter duration (mean (SD) = 23.53 ± 15.56, n = 125) than both freshwater
441 (mean (SD) = 36.81 ± 28.71, n = 430) and marine species (mean (SD) = 46.18 ± 67.21, n = 313). Rates of
442 acclimation have been shown to be faster for many terrestrial groups compared to aquatic organisms [e.g.,
443 amphibians and reptiles have faster rates of acclimation than fishes; See⁸³], which would make it more likely
444 that terrestrial ectotherms would show lower post acclimation $\ln RR_{Q_{10}}$. To control for these possible
445 differences, acclimation time was mean-centered (mean = 0) and included in all our models. As such, all
446 estimates can be interpreted as values for an average level of acclimation time (i.e., 37.98 days).

447 We first tested the degree to which acute and acclimation $\ln RR_{Q_{10}}$ and $\ln CVR_{Q_{10}}$ effects varied by habitat
448 type (i.e., terrestrial, freshwater, and marine ecosystems). Models included an interaction between effect type
449 (i.e., acute or acclimation) and habitat. Reduced mean $\ln RR_{Q_{10}acclimation}$ relative to $\ln RR_{Q_{10}acute}$ indicates
450 that acclimation to thermal environments results in partial compensation of physiological rates (i.e.,
451 phenotypic plasticity), whereas no differences between $\ln RR_{Q_{10}acute}$ and $\ln RR_{Q_{10}acclimation}$ suggests
452 organisms are not capable of physiological plasticity^{4,23}. In contrast, a difference in $\ln CVR_{Q_{10}acclimation}$
453 relative to $\ln CVR_{Q_{10}acute}$ would imply that changes in between individual variation in physiological rates
454 across 10°C differ depending on whether acute or acclimation responses are measured. If the interaction
455 between effect type and habitat was not supported, then we fit a model that only contained additive effects of
456 effect type and habitat. Following on from these models, we subset each habitat type and explored how mean
457 $\ln RR_{Q_{10}}$ changed across traits. Within each habitat (marine, freshwater, and terrestrial) we fit a series of
458 models that included an interaction between effect type (acute / acclimation) and trait category (as defined
459 above). Variance in effects within trait categories appeared to vary depending on the trait type in question.
460 Comparison of a model with and without heteroscedastic residual variance favored a model with
461 heteroscedastic residual variance across trait categories (ΔAIC_C ; marine = 58, freshwater = 120, and
462 terrestrial = 12). To ensure models converged we limited to trait categories for each habitat with six or more
463 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., 50}, 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 $\ln\text{CVR}_{Q_{10}}$ 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 $\ln\text{CVR}_{Q_{10}}$ for each wild population in our dataset at the specific populations latitude and longitude. To do this, we first converted the predicted $\ln\text{CVR}_{Q_{10}}$ to a 1°C change as opposed to 10°C as follows:

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

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)⁸⁴. 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).

Funding

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

Data Availability

All data and code used to reproduce all analyses can be found on GitHub at: https://github.com/daniellnoble/Q10_meta_analysis.

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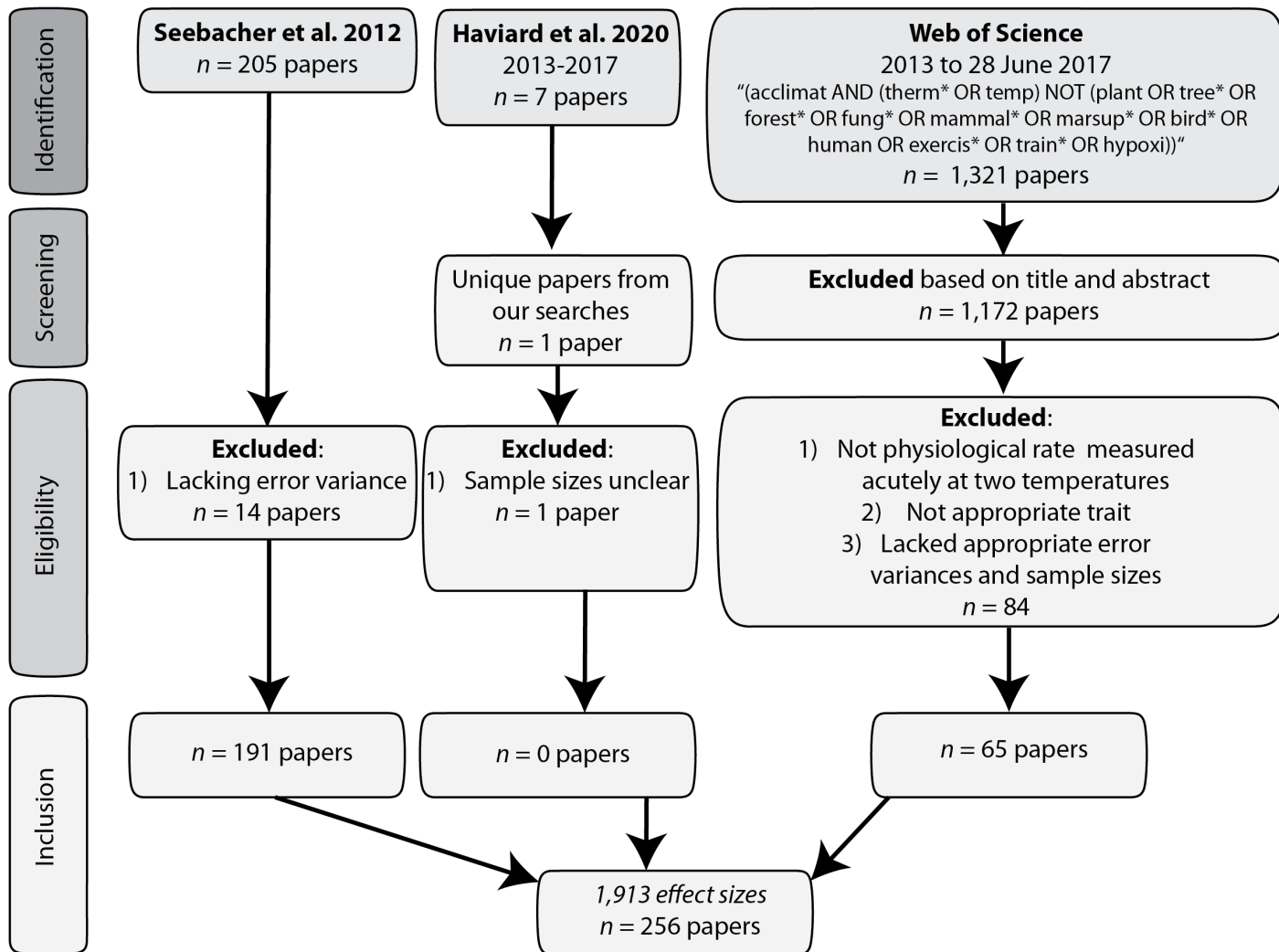


Figure S1- PRISMA flow diagram of the literature search and screening process.

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

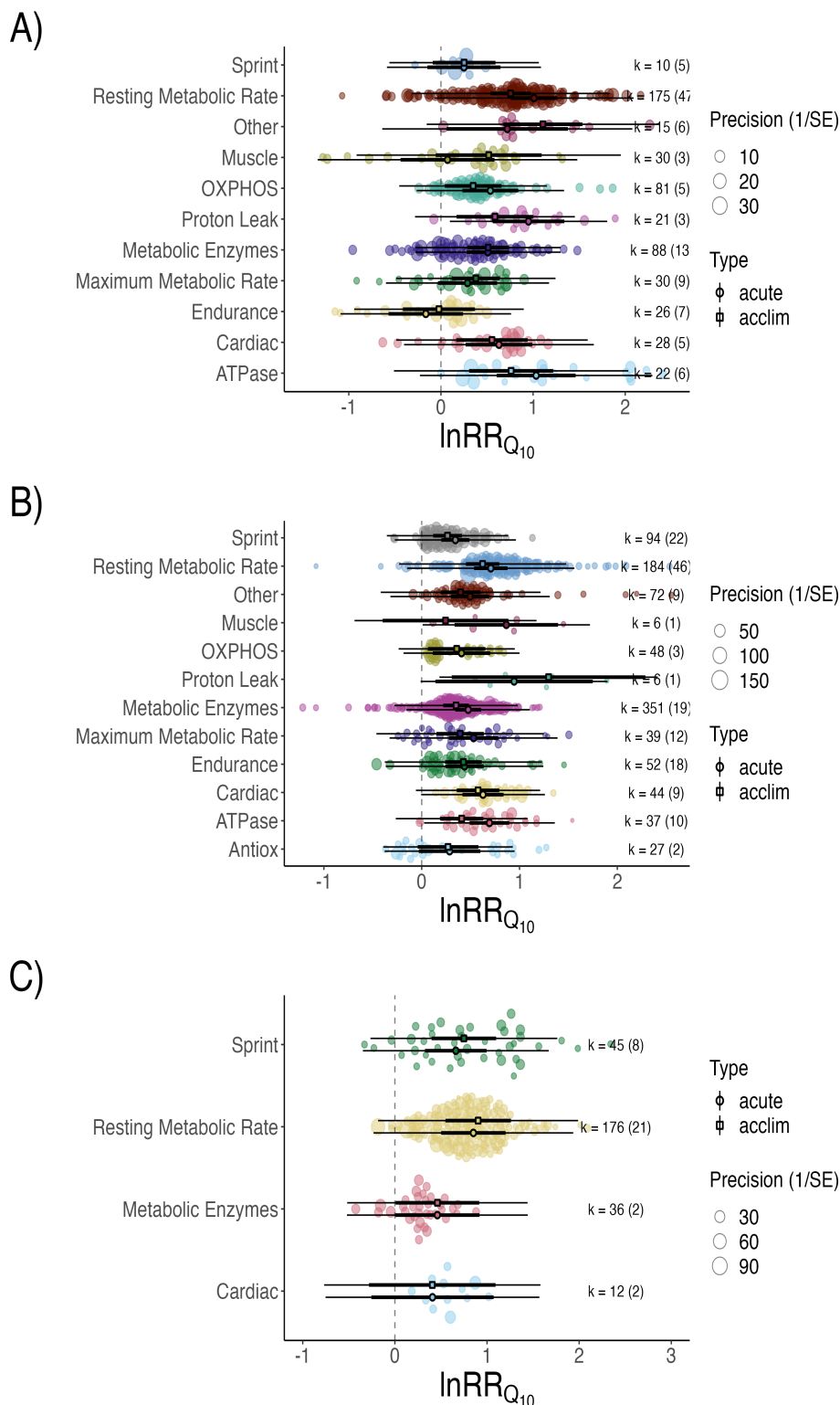


Figure S2- Acute and Acclimation $\ln RR_{Q_{10}}$ across traits for A) marine, B) freshwater and C) terrestrial systems. k = total number of effect size estimates while the numbers in brackets indicate the number of species. Thick bars indicate 95% confidence intervals and thin bars indicate 95% prediction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

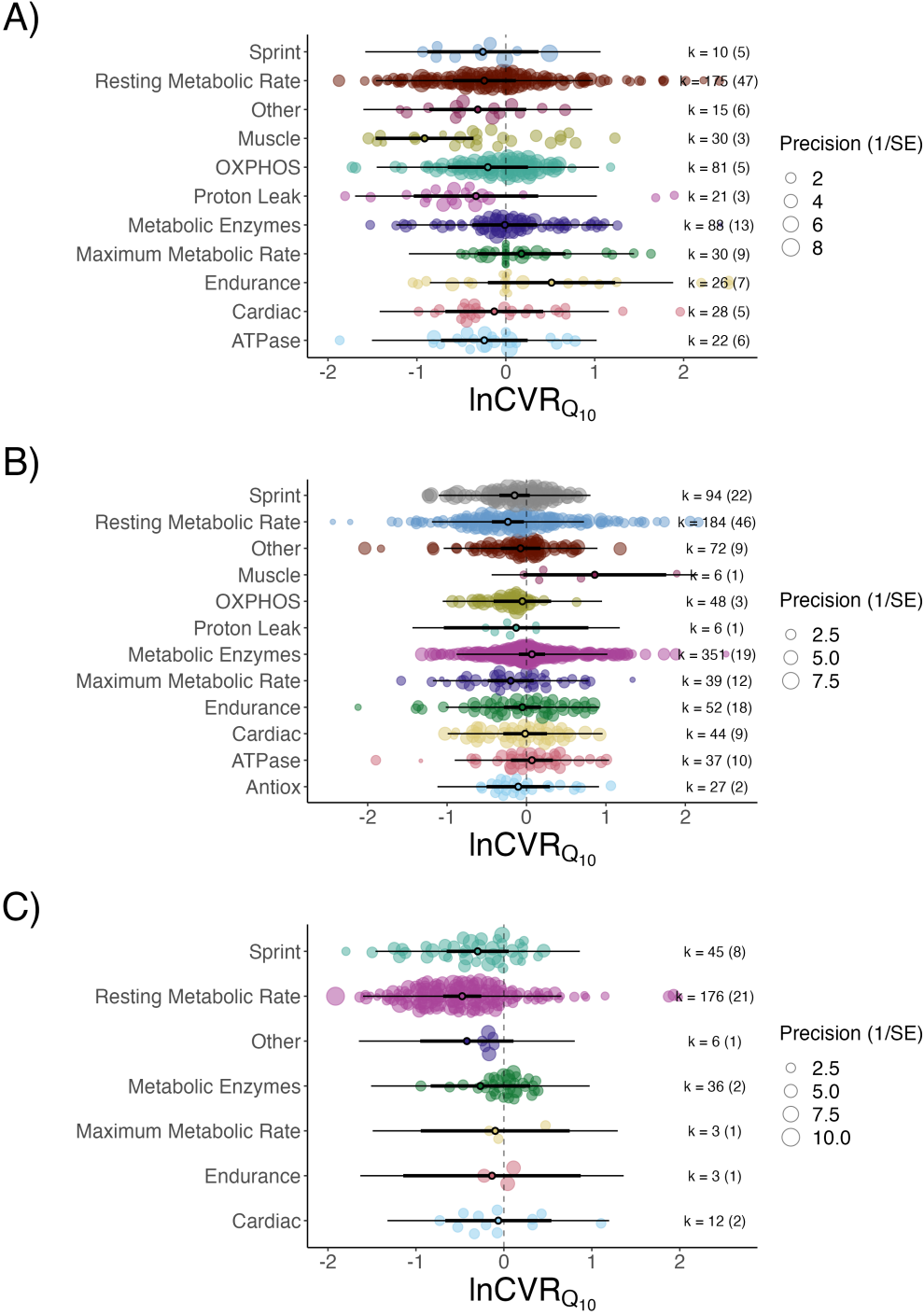


Figure S3- Acute and Acclimation $\ln\text{CVR}_{Q_{10}}$ across traits for A) marine, B) freshwater and C) terrestrial systems. k = total number of effect size estimates while the numbers in brackets indicate the number of species. Thick bars indicate 95% confidence intervals and thin bars indicate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

689 **Comparing raw variance changes using $\ln\text{VR}_{Q_{10}}$**

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

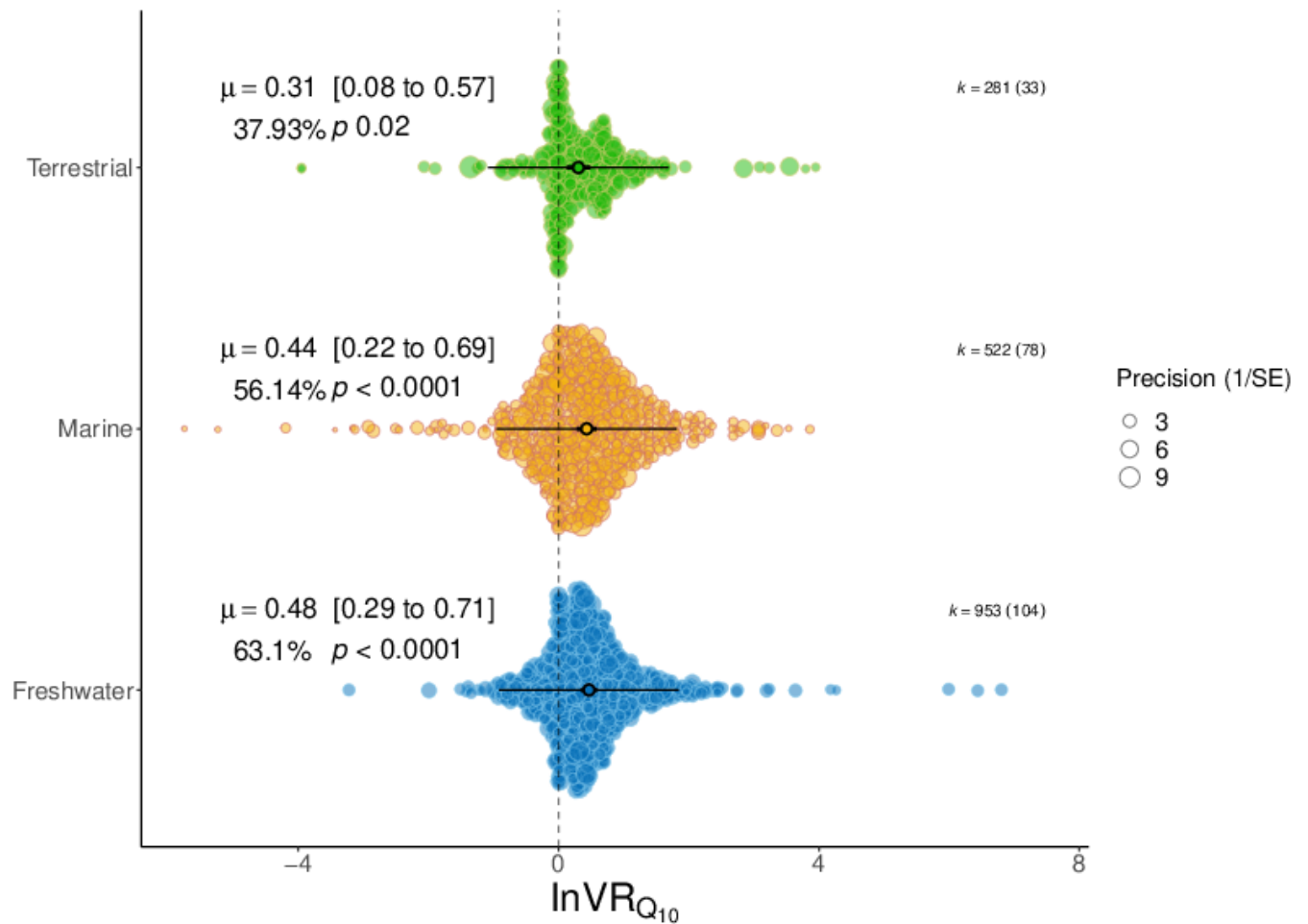


Figure S4- Estimated mean $\ln VR_{Q_{10}}$ for marine, freshwater and terrestrial systems. Note there were no differences between acute and acclimation Q_{10} types so they were averaged. Thick black bars are 95% confidence intervals (CI's) and thin bars 95% prediction intervals (PI's). The percentage 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	l-95% CI	u-95% CI
Fixed Effects				
Intercept	0.4932	0.10684	0.2984	0.7281
Acclimation Time (z scaled)	-0.0001	0.00071	-0.0015	0.0013
Acclimation Effect	-0.0247	0.04247	-0.1097	0.0593

Parameter	Estimate	Est.Error	I-95% CI	u-95% CI
Habitat (Marine)	-0.0024	0.09890	-0.1957	0.1968
Habitat (Terrestrial)	-0.2032	0.10196	-0.3956	-0.0049
Acclimation*Marine	-0.0857	0.07817	-0.2389	0.0700
Random Effects				
Study	0.3647	0.03944	0.2910	0.4434
Phylogeny	0.1194	0.09729	0.0043	0.3630
Species	0.0821	0.05471	0.0041	0.2017
Trait	0.3134	0.04159	0.2386	0.3975

692 **Plots of I^2 for multi-level models**

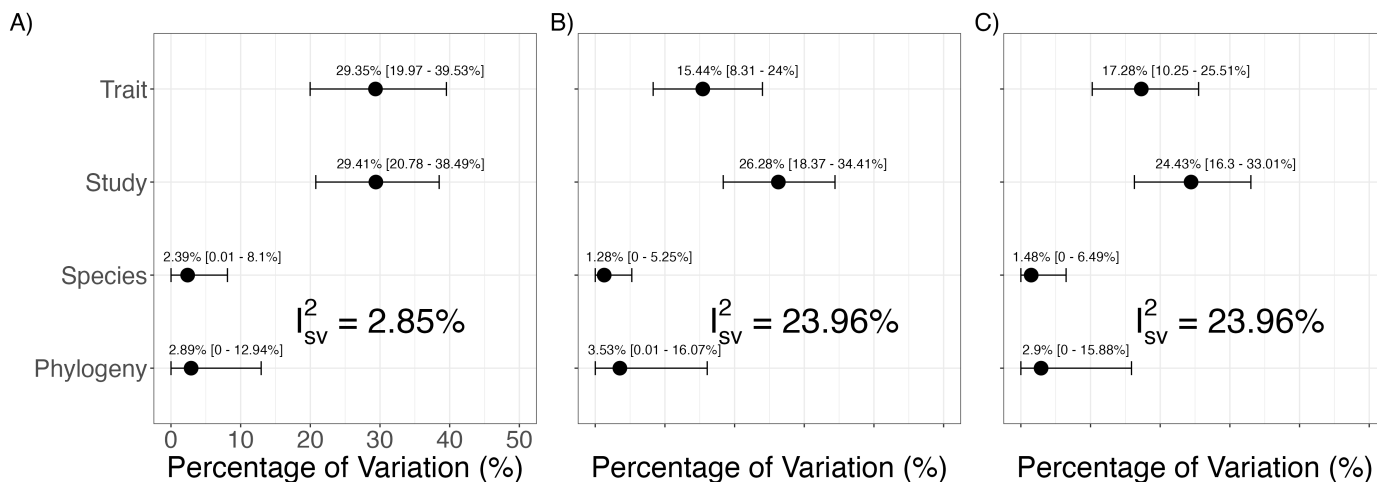


Figure S5- I^2 estimates. A) $\ln RR_{Q_{10}}$ B) $\ln CVR_{Q_{10}}$ and C) $\ln VR_{Q_{10}}$.

693 **Publication Bias Analysis**

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

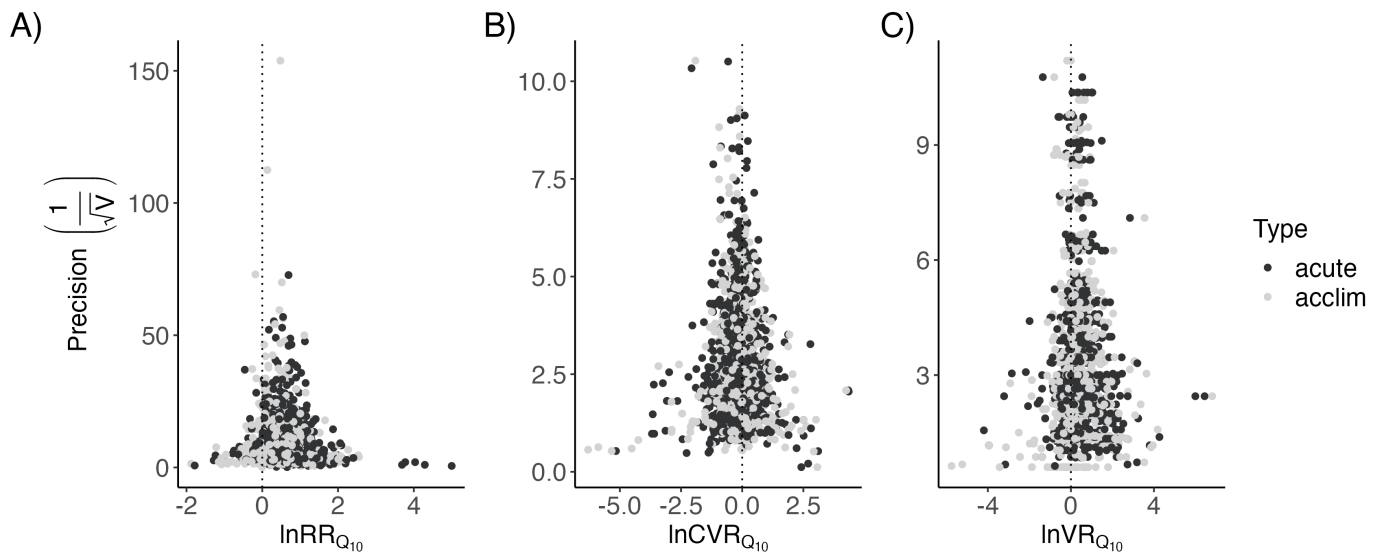


Figure S6- Funnel plot of precision (1/sampling standard error) against effect size for A) log response ratio Q_{10} ($\ln RR_{Q_{10}}$), B) log coefficient of variance ratio Q_{10} ($\ln CVR_{Q_{10}}$) and C) log variance ratio Q_{10} ($\ln VR_{Q_{10}}$). Both acute ('green') and acclimation ('orange')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