Life-history traits do not always evolve in response to changing thermal environments

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Abstract

Quantifying animals' capacity to evolve in response to changing environments is central to predicting ecological responses to climate change. However, empirical evidence for evolutionary responses to changing temperatures remains mixed, and we know little about how selection alters trait variance or generates trade-offs among traits. Here, we conducted a systematic review and meta-analysis of 44 experimental evolution studies to quantify how three key life-history traits—body size, fecundity, and survival—respond to multi-generational exposure to warm or cold temperature regimes. Contrary to our predictions, we found only weak evidence for directional evolution of these traits in changing environments, and no evidence for trade-offs. Across traits—particularly for body size—changes in trait means and variance were small, heterogeneous, and largely unexplained by moderators expected to influence the strength or detectability of evolutionary responses, including the magnitude of temperature change, and the number of generations of selection. Although responses to cooler temperatures were more consistent than responses to warming, this pattern was based on limited data and should be interpreted cautiously. Our results suggest that empirical support for directional evolutionary trait responses to changing temperatures is weak, making broad generalisations across species and contexts difficult. Considerable unexplained heterogeneity further indicates that evolutionary responses may be context-dependent, potentially shaped by the genetic background of source populations or uncaptured methodological variation. Our synthesis adds to growing evidence that many animal populations have limited capacity for rapid evolutionary adaptation and must instead rely predominantly on phenotypic plasticity to buffer the impacts of climate change.

Keywords

Global change, Climate warming, Thermal adaptation, Adaptive potential, Evolutionary rescue, Thermal performance, Fitness, Reproductive success, Trait evolution, Quantitative synthesis.

Introduction

Climate change is an increasing threat to biodiversity, with particularly strong consequences on ectothermic animals because their physiological processes are inherently dependent on temperature (Angilletta, 2009). Across taxa, climate change has been associated with shrinking body sizes (Gardner et al., 2011; Sheridan & Bickford, 2011), reductions in fecundity (Snook et al., 2026; Walsh et al., 2019), population declines (Both et al., 2006; Román-Palacios & Wiens, 2020), range shifts (Parmesan, 2006; Pecl et al., 2017), and an increased extinction risk (Thomas et al., 2004; Urban, 2015). With global mean temperatures projected to increase by approximately 2.7°C by the end of the century (SSP2-4.5; Arias et al., 2021), and extreme heat events increasing in frequency, duration, and intensity (Fischer et al., 2021; Meehl & Tebaldi, 2004), understanding the capacity of ectotherms to cope with rapid environmental change has become a central challenge in ecology and evolutionary biology.

Genetic adaptation is a key mechanism that can allow populations to persist under changing temperature regimes (Buckley & Kingsolver, 2021; Hoffmann et al., 2023; Hoffmann & Sgrò, 2011; Whiteley et al., 2015). Experimental evolution studies provide some evidence that populations can respond to selection imposed by changing temperatures (Hoffmann et al., 2023; Martin et al., 2023; Urban et al., 2024). For example, laboratory populations of various invertebrate taxa have shown evolutionary shifts in life-history traits under changing environments (Malusare et al., 2023; Partridge et al., 1994b, 1995; Plesnar-Bielak et al., 2013; Sales et al., 2024). However, evidence for adaptive responses remains mixed. Several studies report limited or no evolutionary change in response to thermal selection (Grainger & Levine, 2022). For example, gradual warming across generations leads to reproductive failure and population extinction in *Drosophila* species (van Heerwaarden & Sgrò, 2021), while other studies in vinegar flies and seed beetles found little divergence in key life-history traits after >20 generations of experimental evolution (Schou et al., 2014; Terada et al., 2019). On the other hand, more recent studies on seed beetles and *Drosophila* found evidence for pronounced life-history evolution to warming conditions (Antunes et al., 2025; Burc et al., 2025). These findings collectively suggest that adaptive responses to changing temperatures may be inconsistent, yet we still know little about what drives such large differences among study systems.

Meta-analyses provide powerful frameworks to reconcile mixed evidence by identifying general patterns and sources of heterogeneity among studies (Gurevitch et al., 2018). A previous meta-analysis reported little evidence for the evolution of development rate, body size, and fecundity under warming (Grainger & Levine, 2022), whereas a more recent study

found positive (albeit weak) evidence for directional changes in fitness after thermal experimental evolution (Malusare et al., 2023). In both syntheses, heterogeneity in responses across studies was high, emphasising the need to identify the drivers of variation in evolutionary trait responses.

Several important gaps remain. First, previous syntheses have largely focused on changes in trait means and have overlooked how selection affects trait variance. When populations are well adapted to their environment, they are expected to exhibit high "*adaptive precision*" (Hansen et al., 2006), whereby genotypes produce phenotypes with little between-individual variation. However, under changing environments, reduced adaptive precision (i.e., increased phenotypic variation) may be beneficial, as it can increase the likelihood that some individuals express advantageous phenotypes (Bódi et al., 2017; Ghalambor et al., 2007; Hansen et al., 2006). In this context, greater phenotypic variance can increase evolutionary potential by providing more raw material for selection to act upon. Conversely, selection under novel thermal regimes may instead erode standing genetic variation, and inbreeding depression in small populations may further reduce phenotypic variance, thereby constraining future evolutionary responses (Bijlsma & Loeschcke, 2012). In addition to changes in variance within populations, replicate populations may follow divergent evolutionary trajectories (non-parallel evolution Bolnick et al., 2018), which could further contribute to the large heterogeneity observed among experimental evolution studies. Second, the extent to which evolutionary responses in one trait trade off against changes in other traits remains unresolved (Griffiths et al., 2024). For example, adaptation to warming may involve correlated responses among fecundity, body size, and lifespan, reflecting trade-offs between reproduction, growth, and somatic maintenance. However, the direction and strength of these associations are likely to depend on species' life histories and developmental constraints (Audzijonyte & Richards, 2018; Berger et al., 2017). Quantifying the generality and magnitude of such correlated responses is essential for predicting life-history evolution and population trajectories under warming.

Here, we synthesised data from 44 experimental evolution studies in ectothermic animals and conducted a multivariate meta-analysis to quantify genetic responses in key life-history traits—body size, fecundity, and survival—to changing thermal environments. Specifically, we asked i) whether mean and variance in these traits respond consistently to warmer and cooler thermal regimes, ii) whether evolutionary responses in one trait are correlated with changes in other traits, and iii) which factors modulate evolutionary trait responses to changing temperatures. We hypothesised that experimental evolution under novel thermal environments would lead to adaptive divergence in key life-history traits. For body size, we

predicted that populations evolving under warmer conditions would exhibit larger body sizes than control populations when assayed under control and warm conditions. This pattern would reflect thermal compensation and countergradient variation, whereby evolved increases in body size offset the typically negative effect of warming on body size (Angilletta, 2009; Conover & Schultz, 1995). Alternatively, warming may favour smaller body sizes due to increased metabolic demand and oxygen limitation in larger individuals (Gardner et al., 2011; Partridge & French, 1996; Sheridan & Bickford, 2011; Verberk et al., 2021), or may not generate consistent evolutionary responses if observed body size changes are primarily driven by plasticity (Gotanda et al., 2015; Siepielski et al., 2019). We also predicted that populations evolving under warmer conditions would have higher survival under warm assay conditions. Higher mortality is often expected at warmer temperatures due to faster developmental, smaller body sizes at emergence, and accumulation of cellular damage (Hassall et al., 2006; Willi & Van Buskirk, 2022). Therefore, selection should favour genotypes with higher viability in novel environments. For fecundity, we predicted that populations would evolve higher fecundity under their selection regimes, such that warm-selected lines would outperform control lines under warm assay conditions, with the opposite pattern expected under control or cold conditions.

Based on these predictions, we expected evolutionary changes in body size, fecundity, and survival to be positively correlated if selection favours genotypes with higher overall performance in novel thermal regimes. However, negative correlations may arise if selection favours one fitness component over others, or if warming alters energy allocation among growth, reproduction, and maintenance (Audzijonyte & Richards, 2018; Berger et al., 2017). We further hypothesised that evolution to novel thermal environments (warming or cooling) would generally reduce trait variance through the depletion of standing genetic variation and inbreeding in small populations (Bijlsma & Loeschcke, 2012), but could also increase variance if adaptation exposes cryptic genetic variation (Hoffmann & Merilä, 1999; O'Dea et al., 2016; Paaby & Rockman, 2014). Finally, we predicted that the magnitude of evolutionary responses would increase with the number of generations of selection, population size (a proxy for standing genetic variance), and the deviation between selection and control temperatures (i.e., intensity of selection), but may decrease with the number of generations spent under common garden conditions prior to trait measurement. We also predicted broadly similar responses under cool and warm selection regimes, including increased performance at the respective assay temperatures and a tendency towards larger body sizes under cooler conditions (Partridge & French, 1996).

Materials and methods

Pre-registration and reporting

We pre-registered our predictions, methods, and analysis plan prior to extracting data (https://doi.org/10.17605/OSF.IO/4B38S; Pottier et al., 2023). All deviations from our pre-registered plans are reported in the supplementary material (see *Deviations from pre-registration*). We followed PRISMA-EcoEvo (*Preferred Reporting Items for Systematic Reviews and Meta-analyses in Ecology and Evolutionary biology*) guidelines for reporting this study (O'Dea et al., 2021), and report author contributions using the CRediT (Contributor Roles Taxonomy; McNutt et al., 2018) and MeRIT (Method Reporting with Initials for Transparency; Nakagawa et al., 2023) guidelines. In addition, we followed guidelines from (Pottier et al., 2025) to optimise the indexing of the title, abstract, and keywords in search engines and databases. All analyses were performed using R statistical software (v. 4.4.2; R Core Team, 2024), and statistical models were fitted using the high-performance computational cluster Katana, hosted by Research Technology Services at the University of New South Wales, Sydney. All data, code, and research materials are openly available at https://github.com/p-pottier/Exp_evol_temp.

Literature searches and study eligibility

We aimed to retrieve a representative sample of studies testing the evolution of fecundity, body size, and/or survival to changes in experimental temperatures. We considered both peer-reviewed publications and university dissertations for our systematic review. We searched ISI Web of Science (core collection; University of New South Wales library subscription), Scopus, and ProQuest (dissertations and theses) on 2022/10/21 without a time span limit. Our search strings are provided in *Supplementary Methods*.

We targeted studies measuring the fecundity, body size, or survival of ectothermic animals after multiple generations of experimental evolution to different temperature regimes (Fig. 1a). We included studies based on five eligibility criteria. First, we only included data from ectothermic animals, due to their expected vulnerability to changing thermal environments and to facilitate comparisons across species. Therefore, we excluded data on endothermic animals, single-celled eukaryotes, plants, fungi, and bacteria. Second, we only included studies that experimentally compared at least two average temperature conditions, either in the laboratory or in mesocosms. Third, we focused on studies that measured experimental evolution to different temperatures for at least three generations. We excluded studies that artificially selected individuals based on a given trait (e.g., heat tolerance, body size). We included studies exposing animals to constant temperature treatments and/or gradual

changes in temperatures (e.g., 0.5°C per generation), as long as the authors used ≥2 experimental temperatures differing in their mean. Fourth, we only included studies measuring fecundity (i.e., number of eggs or number of offspring produced following mating), body size (or a proxy for body size, e.g., wing size, body mass), or survival under common rearing conditions. We included studies measuring one, or a combination of these traits. We excluded studies applying stress to the animals prior to measuring survival (e.g., survival to heat shock). Fifth, we only included studies disentangling plastic responses and parental effects from evolutionary responses (de Villemereuil et al., 2016; Kawecki et al., 2012). Therefore, animals from each treatment must have been transferred to a common-garden temperature for at least one generation prior to assessing their fecundity, body size, or survival (de Villemereuil et al., 2016; Kawecki et al., 2012).

Our searches retrieved a total of 13,020 documents. Exact duplicates were removed using the packages litsearchr (v. 1.0.0) and synthesisr (v. 0.3.0) in R, leaving 9141 documents. All studies were screened manually in the literature review management website Rayyan QCRI (Ouzzani et al., 2016), which was also used to detect an additional 56 duplicates. In total, we scrutinised 9085 unique documents for eligibility. Our search strings were benchmarked on a sample of 20 relevant studies (Table S4) that we identified during pilot, non-systematic searches in Google Scholar, following recommendations of Foo et al., (2021). All 20 benchmark studies were retrieved by our literature search.

We used Rayyan QCRI (Ouzzani et al., 2016) to assess the title, abstracts, and keywords of the 9085 documents identified during our searches (see Fig. S1-2 and Table S2-3 for decision trees). We identified 585 potentially eligible documents that we then assessed for eligibility (see Fig. S1-2 and Table S2-3 for decision trees). The screening of titles, abstracts and keywords was done by PP (23.4%), CF (10.7%), LD (9.0%), MG (5.9%), AM (6.2%), CT (6.1%), PS (6.3%), MS (5.9%), BC (6.1%), EIS (6.0%), DB (6.1%), BCD (6.1%), RV (6.5%), SL (6.3%), SD (6.1%), NP (6.2%) and SR (1.3%) in Rayyan QCRI. The full-text screening was done by CF (5.3%), LD (6.2%), MG (6.2%), AM (6.2%), CT (6.0%), PS (6.0%), MS (6.2%), BC (6.2%), EIS (0.2%), DB (6.3%), BCD (6.2%), RV (7.4%), SL (6.2%), SD (6.3%), NP (6.2%), and SR (6.2%). A sample of 60 studies were cross validated by PP, and the two conflicts were discussed and resolved. A total of 44 studies (Fig. 1b) matched our inclusion criteria (Azevedo, 1997; Bakker et al., 2010; Barrie, 1993; Berger et al., 2014; Biale et al., 2020; Bochdanovits & Jong, 2003; Breckels et al., 2014; Cavalheri et al., 2019; Cavicchi et al., 1989; Condon et al., 2014; Ehiobu & Goddard, 1989; Esperk et al., 2016; Gibbin, Chakravarti, et al., 2017; Gibbin, Massamba N'Siala, et al., 2017; Gómez-Llano et al., 2021; Hallsson & Björklund, 2012; Kennington et al., 2003; Koch & Guillaume, 2020; Lind et al., 2020; Magiafoglou & Hoffmann, 2003; Pan et al., 2017; Partridge et al., 1994a, 1994b, 1995; Plesnar-Bielak et al., 2013; Rogell

et al., 2014; M. Santos et al., 2004, 2005, 2006; M. A. Santos et al., 2021; Schneider et al., 2020; Schou et al., 2014; Souissi et al., 2016, 2021; Stazione et al., 2021; Terada et al., 2019; Tobler et al., 2015; Van Doorslaer et al., 2007, 2009, 2010; van Heerwaarden & Sgrò, 2021; Walczyńska et al., 2017; Wootton et al., 2021; Zhang et al., 2019).

Data extraction and effect sizes

For each relevant study, we extracted the mean fecundity, body size, and/or survival at each experimental temperature, along with their associated standard deviations and sample sizes. Control temperatures were determined as the ones closest to the laboratory temperature prior to the experimental evolution if not directly mentioned by study authors. We extracted data from the main text, tables, figures, supplementary materials, and published data. We digitised data from figures using the metaDigitise package in R (v. 1.0.1; Pick et al., 2019). If the raw data associated with a study was published, we preferably used the raw data to calculate means, standard deviations and sample sizes instead of using the descriptive statistics presented in the manuscript or figures. When data were presented in different sources (e.g., figure and table), information was extracted at the finest resolution available. We imputed missing standard deviations (n = 13 effect sizes) based on relationships between means and standard deviations across the existing data set, as described in Nakagawa et al. (2022) ("missing cases" method). For each relevant study, we also extracted all data required to address our *a priori* hypotheses; that is, the selection temperature regime (i.e., cooler- or warmer-than-control), the number of generations of experimental evolution, the initial population size, the temperature of the control and selection treatment, the assay temperature at which traits were measured, and the number of generations in the common garden. Note that we only included comparisons in which selection lines were returned to a common garden temperature for at least one generation before traits were assayed, allowing us to focus on genetic rather than plastic responses to temperature (de Villemereuil et al., 2016; Kawecki et al., 2012). When studies included multiple assay or common garden temperatures, we retained all cases where traits from different lines could be compared at a shared assay temperature. When temperatures were increased progressively across generations, we calculated an average temperature across the duration of the experiment. The number of generations of selection was also sometimes inferred from generation time and the duration of the experiment. Taxonomic information about each species and non-independence of the data were also recorded (see *Statistical Analyses*). We also extracted additional details about the studies, such as the number of generations animals spent in the laboratory prior to the experimental evolution experiment, the genetic variance of the population prior to selection (i.e., standing genetic variance, or *de novo*), or details about each trait measurement. These data may be used in future studies. Data were extracted by CF (20.5% of studies), LD (9.1%),

MG (4.5%), AM (11.4%), PS (6.8%), MS (4.5%), BC (9.1%), BCD (6.8%), SL (11.4%), SD (9.1%), and PP (6.8%). PP cross-checked all extracted data and re-extracted some effect sizes from 17 (38.6%) studies to ensure consistency.

Effect sizes for analyses of means were calculated using the natural log-transformed response ratio (lnRR), which represents a standardised ratio of traits means between lines evolved under control and experimental conditions. A positive lnRR values indicates that trait means are higher in the experimental line relative to the control line. Equations 4 and 14 from Senior et al. (2020) were used to calculate lnRR and its associated sampling variance for independent samples. Effect sizes for analyses of variation were calculated using the natural log-transformed coefficient of variation ratio (lnCVR). Equations 6 and 16 from Senior et al. (2020) were used to calculate lnCVR and its associated sampling variance for independent samples. Because some studies may use more than two temperature treatments, it was possible to calculate effect sizes based on multiple control-treatment comparisons. However, such calculations generate a source of non-independence, where data from the control group are used for calculating multiple effect sizes. To account for this, we used Equations 19 and 24 from Senior et al. (2020) to calculate the sampling variance of dependent lnRR and lnCVR, respectively. Although not originally planned (see *Deviations from registration;* Supplementary material), we calculated the log variance ratio (lnVR), using equations 5 and 15 from Senior et al. (2020) for independent samples, and equations 8 and 22 for dependent samples. lnCVR represents the changes in variance relative to the mean, which provides important insights when mean-variance relationships are present, yet we argue that lnVR provides results that are more easily interpretable alongside changes in mean trait values (lnRR). Results for lnCVR are qualitatively and quantitatively similar to lnVR, and are provided in Table S17-22 and Fig. S6-8 (see also https://p-pottier.github.io/Exp_evol_temp/). Note that we calculated all our effect sizes using effective sample sizes (an estimate of the number of independent observations) rather than the number of assessed individuals to account for the large level of pseudo-replication within selection lines. We calculated effective sample sizes (Rutkowska et al., 2014) and used an intraclass correlation coefficient of 0.5 as a conservative measure. That is, the sample sizes used for effect size calculations were much closer to the number of technical replicates (i.e. replicate selection lines per selection temperature regime) than the number of individuals sampled. However, these calculations still assumed that effect sizes taken from studies with a larger number of individuals sampled within each replicate line would be weighed higher than effect sizes from replicate lines with a more limited number of individuals.

Meta-analysis and meta-regressions

We performed all statistical analyses in the R computing environment (v. 4.4.2; R Core Team, 2024). We used the package brms (v. 2.22.0; Bürkner, 2017) to run Bayesian meta-analytic multilevel multivariate models using three response variables (i.e., effect sizes for fecundity, body size, and survival) and three types of effect sizes (lnRR for analysis of mean traits, lnCVR for analysis of relative trait variance, lnVR for analysis of trait variance). Modelling multiple response variables allowed us not only to estimate the responses of each trait to thermal evolution, but also to estimate correlations (i.e., integration or trade-offs) between trait responses (Jackson et al., 2017; Pottier et al., 2024). Using a Bayesian approach allowed us to improve precision in the estimation of our parameters by accounting for the covariance among traits ("borrowing of strength"), and imputing missing data when effect sizes were not available for all three traits within a study (Jackson et al., 2017; Pottier et al., 2024). Our data had six main sources of non-independence. Multiple effect sizes were extracted from i) the same study, ii) the same sub-experiments within a study iii) the same species, iv) species with different degrees of phylogenetic relatedness, v) traits measured on the same cohort of animals (e.g., body length and body mass), and vi) control groups that were re-used in multiple effect size calculations. We accounted for non-independence in three ways. First, we included five random factors in our models: study ID, experiment ID, species ID, phylogenetic relatedness, and an effect size-level random effect (effect size ID) which is needed to correctly partition variance (Noble et al., 2022). Phylogenetic relatedness was accounted for by generating a phylogenetic tree from the Open Tree of Life database (Hinchliff et al., 2015) using the rotl package (v. 3.1.0; Michonneau et al., 2016). We used the ape package (v. 5.8-1; Paradis et al., 2004) to calculate branch lengths using Grafen's method (power = 1), and to generate a correlation matrix of species relatedness to be used in our models. One polytomy in the *Daphnia* genus was manually resolved according to the classification by (Cornetti et al., 2019). Second, we controlled for effect sizes from control groups involved in multiple control-treatment comparisons using a variance-covariance matrix to correlate errors of each control-treatment comparison (using the *fcor* argument in the models). We assigned a correlation among effect sizes sharing the same control treatment of $r = 0.5$ as a conservative measure (Noble et al., 2017). Third, we accounted for data measured sequentially on the same cohort of animals in our effect size calculations, using specific equations for dependent samples, as described above.

We fitted meta-analytic models to simultaneously quantify evolutionary responses to warming and cooling. We fitted models for each effect size (lnRR, lnVR, and lnCVR) independently. We ran each model using four chains, 4000 iterations, and 2000 iterations of warmup. We adjusted delta to 0.99 and the maximum tree depth to 15 to allow the sampler to take longer steps when

exploring the parameter space and facilitate model convergence. For each model, we allowed the type of trait (fecundity, survival, body size) to vary as a random "slope" among studies, as well as a moderator variable. In other words, each model estimated the variation in each trait independently, as well as their correlation across studies, which is akin to fitting a multivariate model. First, we fitted an overall model to estimate the overall effect for each trait type and estimate heterogeneity (I^2, the variation not explained by sampling variance) (Higgins et al., 2003; Senior et al., 2016) and decompose variance among the random terms. We then fitted all models with an interaction between trait type and selection temperature regime as a categorical factor (i.e., cooler-than-control vs. warmer-than-control) so that we can separate effects of warming or cooling on all traits. Because we predicted that effect sizes will vary depending on the temperature at which animals were assayed, we accounted for the variation in assay temperatures among experiments (Fig. 1a) in all models to account for this nuisance heterogeneity (Noble et al., 2017). Therefore, all our *a priori* moderators (intensity of selection, number of generations of selection, number of generations of common garden, initial population size) were fitted as an interaction with trait type, selection temperature regime, along with an interaction between trait type, selection temperature regime, and the difference between the assay temperature and the control temperature. That is, intercept estimates from our models were adjusted so they can be interpreted as the difference between selected lines and control lines, when assayed at the temperature of the control line. Finally, we fitted a model with all moderators (assay temperature difference, difference between the selection and control temperatures, number of generations of selection and common garden) to interpret effects after accounting for methodological variation across studies. In these multi-moderator models, we did not consider population size because this variable had 50 missing observations, which would have reduced the size of our working dataset by 11%. These multi-moderator models allowed us to interpret the predicted effects of experimental evolution to cooling and warming conditions, after standardising all methodological variation. In such case, we interpreted effects as a function of assay temperatures relative to the control temperatures, at an average (calculated from the dataset) intensity of selection ($\bar{x}$ = 5.65°C), generations of selection ($\bar{x}$ = 29.01 generations), and generations of common garden ($\bar{x}$ = 2.71 generations). We used the package emmeans (v. 1.11.0-001 Lenth, 2019) to generate predictions from all models. Outputs from all statistical models and additional data visualisations are available at https://p-pottier.github.io/Exp_evol_temp/.

Sensitivity and publication bias analyses

We assessed the robustness of our results using different types of sensitivity analyses. First, we performed a leave-one-out analysis to identify influential studies, where we fitted overall models after iteratively removing one study at a time. These models were fitted using 2000

iterations to reduce computational demands. Second, we assessed if our results differed between studies using constant selection temperatures (n = 37 studies and 389 effect sizes) and those using temperatures increasing at each generation (n = 7 studies and 87 effect sizes). Third, we fitted models without data with procedural concerns (i.e., unclear sample sizes or standard deviation measurement, no replicated lines, unusual fecundity or survival metric). To evaluate whether our data are influenced by publication bias against studies with small effective sample sizes, we ran multilevel models using the sampling variance of lnRR, lnVR, or lnCVR as moderator variables (Nakagawa et al., 2022). This shows whether the uncertainty in effect size estimates is associated with changes in effect size magnitude (Nakagawa et al., 2022). We also fitted publication year as a moderator variable to assess time-lag biases (Jennions & Møller, 2002). For all sensitivity and publication-bias analyses, we used the same primary modelling structure as in the main analyses, including the interaction between selection temperature regime (cooler- or warmer-than-control) and the difference between assay and control temperatures. However, we only used trait type as a moderator (i.e., overall model) for leave-one-out analyses to simplify the interpretation of estimates across models and reduce computational demands.

Results

Overview of the dataset

We extracted a total of 476 effect sizes from 44 studies across 25 ectothermic species (Fig. 2). A total of 31 studies (22 species) reported data on fecundity, while 27 studies (14 species) and 22 studies (13 species) reported data on body size and survival, respectively. Most studies (20/44) investigated a combination of two traits, while a smaller fraction investigated a single (16/44) or all three traits (8/44). The majority (80%) of effect sizes (381/476; 38 studies) focused on responses to warmer-than-control conditions, while the remaining 95 effect sizes (20%; 13 studies) focused on responses to cooler-than-control conditions. All species were invertebrates, except for two fish species, and nearly half of the effect sizes (46.4%) were taken from experiments on *Drosophila* species (Fig. 2). On average, studies used selection temperatures 5.35°C (median: 4; range: 0.7 - 16°C) above the control temperature for warming treatments, and 6.83°C (median: 8; range: 3 - 10°C) below the control temperature for cooling treatments. Studies selected animals for an average of 29.01 generations (median: 17; range: 2 - 365), and re-acclimated animals to common garden conditions for an average of 2.71 generations (median: 2; range: 1 - 163). In most cases, animals were assayed at the control temperature (32.3 and 54.7% of observations for cooler- and warmer-than-control selection treatments, respectively); though the average assay temperature difference was 3.34°C for warmer-than-control treatments (median: 2.4; range: -5.0 - 20°C), and -1.38°C for cooler-than-control treatments (median: 0; range: -8.5 - 5.0°C). The average starting population size was 1634 individuals (median: 750; range: 30 - 8000).

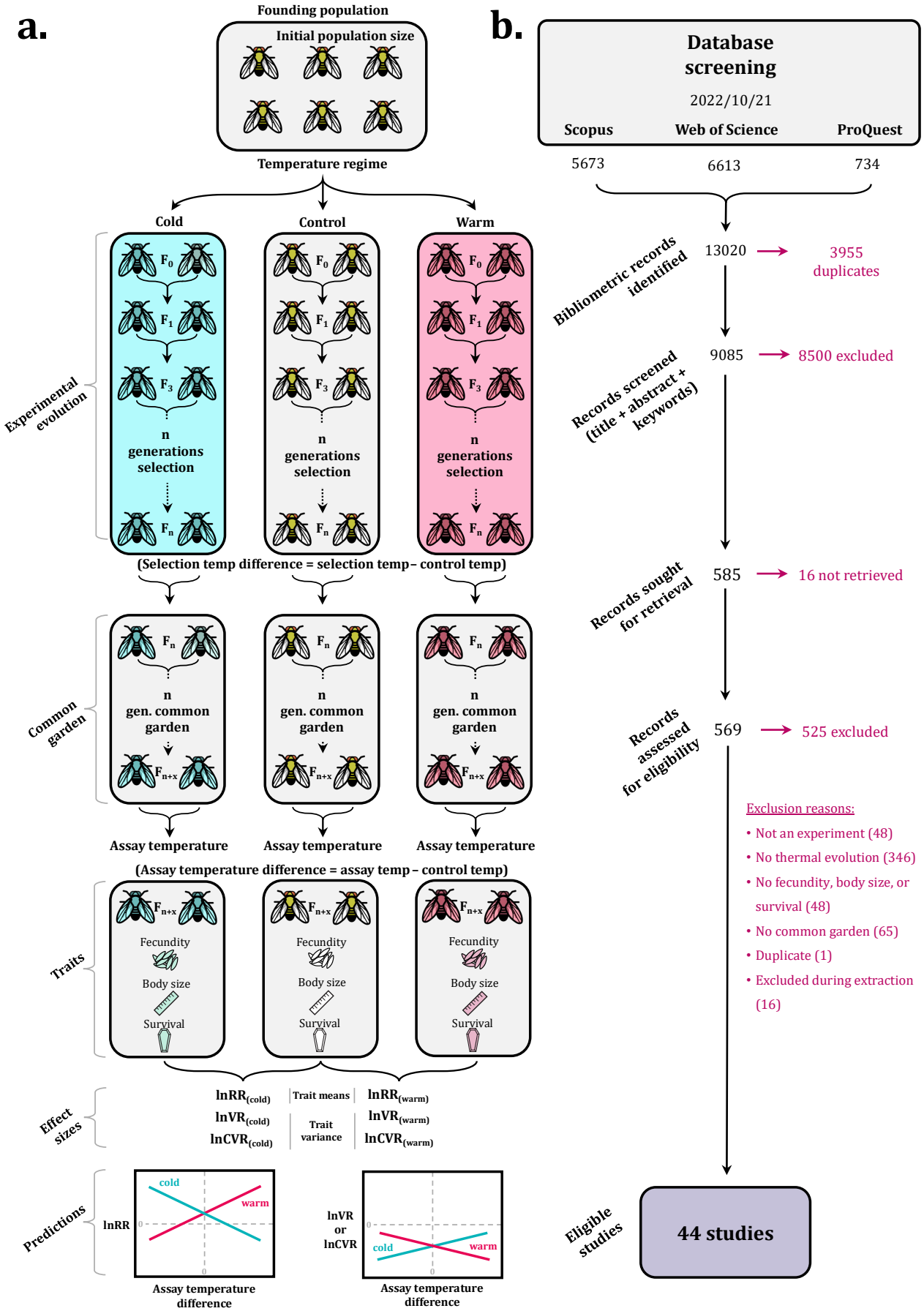

a.
Founding population
Initial population size
Temperature regime
Cold
Control
Warm
Experimental evolution
n generations selection
(Selection temp difference = selection temp – control temp)
Common garden
n gen. common garden
Assay temperature
(Assay temperature difference = assay temp – control temp)
Traits
Fecundity
Body size
Survival
Effect sizes
lnRR(cold)
lnVR(cold)
lnCVR(cold)
Trait means
Trait variance
lnRR(warm)
lnVR(warm)
lnCVR(warm)
Predictions
lnRR
cold
warm
Assay temperature difference
lnVR or lnCVR
Assay temperature difference
b.
Database screening
2022/10/21
Scopus
Web of Science
ProQuest
5673
6613
734
Bibliometric records identified
13020
3955 duplicates
Records screened (title + abstract + keywords)
9085
8500 excluded
Records sought for retrieval
585
16 not retrieved
Records assessed for eligibility
569
525 excluded
Exclusion reasons:
• Not an experiment (48)
• No thermal evolution (346)
• No fecundity, body size, or survival (48)
• No common garden (65)
• Duplicate (1)
• Excluded during extraction (16)
Eligible studies
44 studies

Figure 1: Graphical representation of the study selection. a) An example of experimental design synthesised in the present study. Cold and warm temperatures were defined as temperatures lower and higher than the control temperature, respectively. In this example, the common garden and assay temperatures were the same as the control temperature. However, note that some studies have measured traits at cooler- or warmer-than-control temperatures after experimental evolution. In addition, some studies have used assay temperatures that differed from the common garden temperature. temp: temperature; gen: generations; lnRR: log response ratio; lnVR: log variance ratio; lnCVR: log coefficient of variation ratio. b) PRISMA flowchart summarising the search methods and the number of studies screened for eligibility.

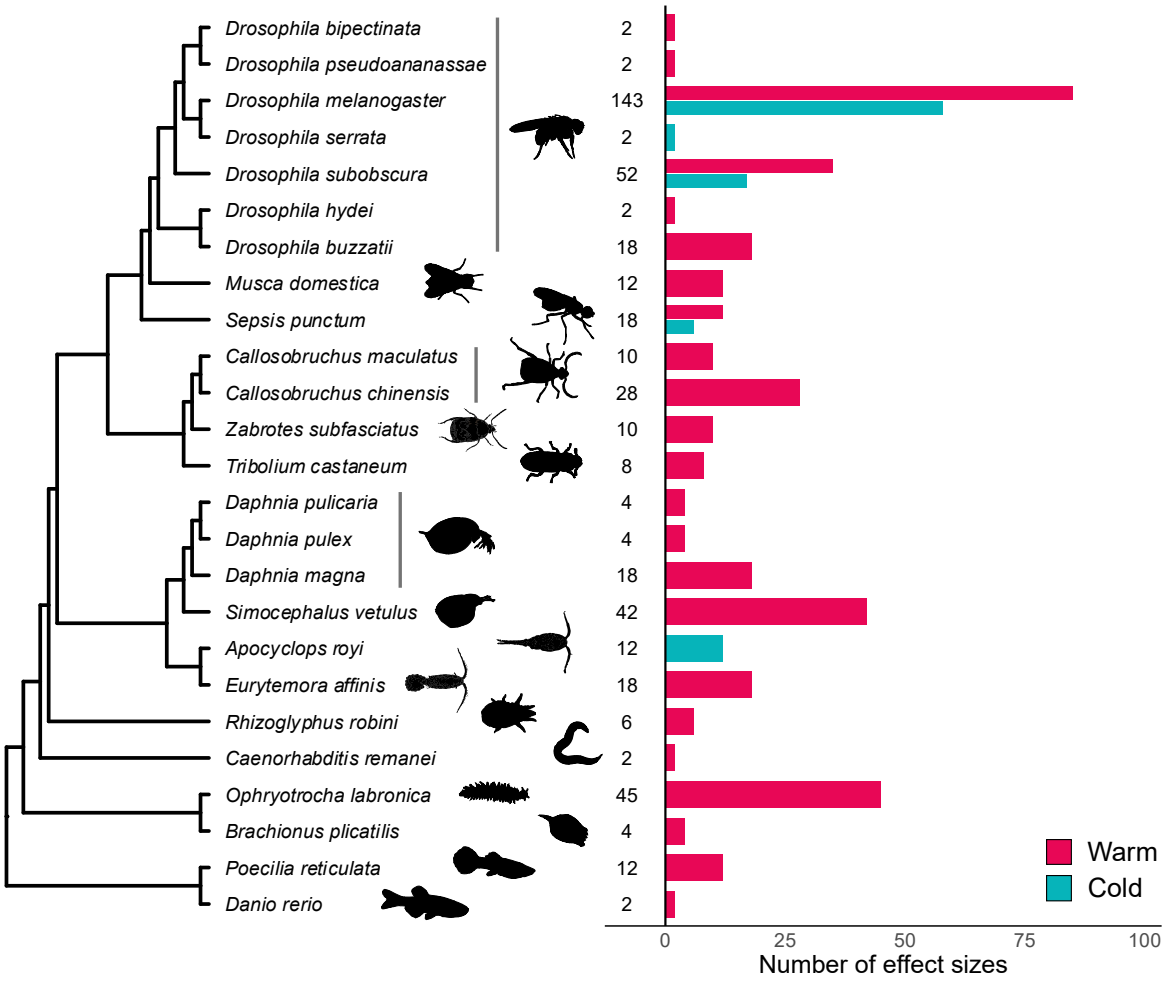


Figure 2: Number of effect sizes for each species represented in the dataset. The phylogenetic tree was constructed from the Open Tree of Life taxonomy *(Michonneau et al., 2016)*. The number of effect sizes is displayed separately for cooler-than-control ("Cold", blue bars), and warmer-than-control ("Warm", red bars) selection lines, with the total count on the left side of each histogram. Some silhouettes were taken from phylopic (https://phylopic.org).

Changes in mean trait responses

Heterogeneity and correlations among trait responses

We first fitted overall meta-analytic models to quantify heterogeneity in evolutionary trait responses and correlations among responses. The amount of variation not explained by sampling variance (i.e., heterogeneity) was extremely high (I^2_{total} = 99.97%, 95% higher posterior density intervals [HPD] = [99.97, 99.98]), with 65.40% of the variation explained by study differences, 9.96% by differences among experiments within the same study, 2.77% by differences among species, 4.42% by phylogenetic relatedness among species, and 17.43% by residual variation. We did not find strong evidence for trade-offs among traits, and these correlations were highly variable across studies ($cor_{(body\ size,\ fecundity)}$ = -0.14 [-0.90, 0.80]; $cor_{(body\ size,\ survival)}$ = 0.03 [-0.86, 0.89]; $cor_{(fecundity,\ survival)}$ = 0.08 [-0.84, 0.89]).

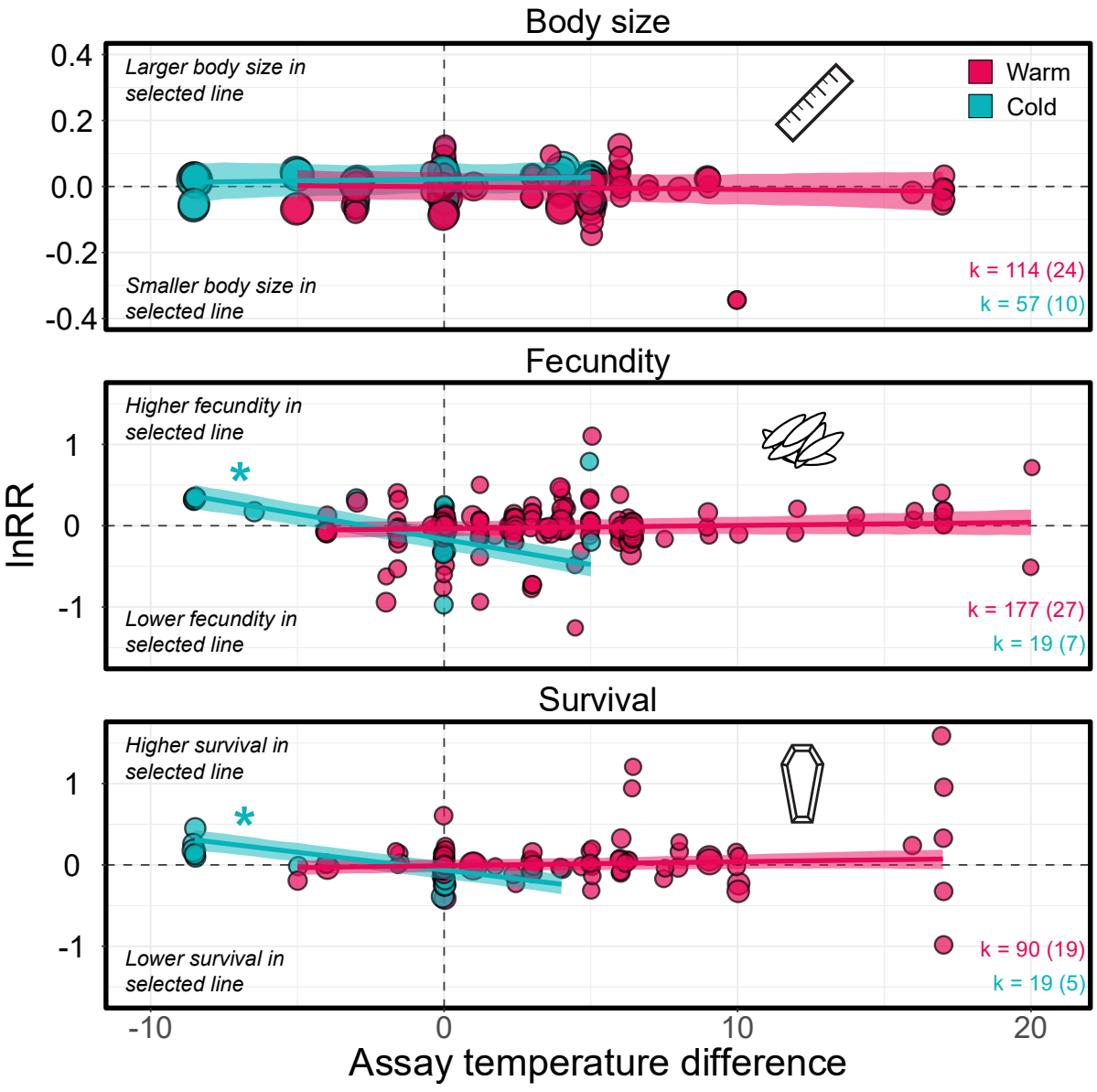


Figure 3: Association between changes in trait means (lnRR) and the difference between the assay temperature and the temperature of the control line. Effect sizes (lnRR) represent the relative difference between trait means of the warm- or cold-selected line relative to the control line. The assay temperature is the temperature at which traits were measured. Null values indicate that animals were assayed at the temperature of the control line, while positive and negative values indicate that animals were assayed at temperatures above or below the control temperature, respectively. Regression lines and shaded areas represent predicted mean and credible intervals from Bayesian multilevel linear models. Data points represent individual effect sizes, scaled by precision (1/SE). Estimates are displayed separately for each trait (body size, fecundity, survival), for cooler-than-control ("Cold", in blue), and warmer-than-control ("Warm", in red) selection lines. Note the different scale for the y axis of body size, and that 3 (2 fecundity, 1 survival) observations are not displayed for clarity. *: Statistically significant slope based on 95% credible intervals. k = number of effect sizes, with the number of studies in brackets.

Associations with moderator variables

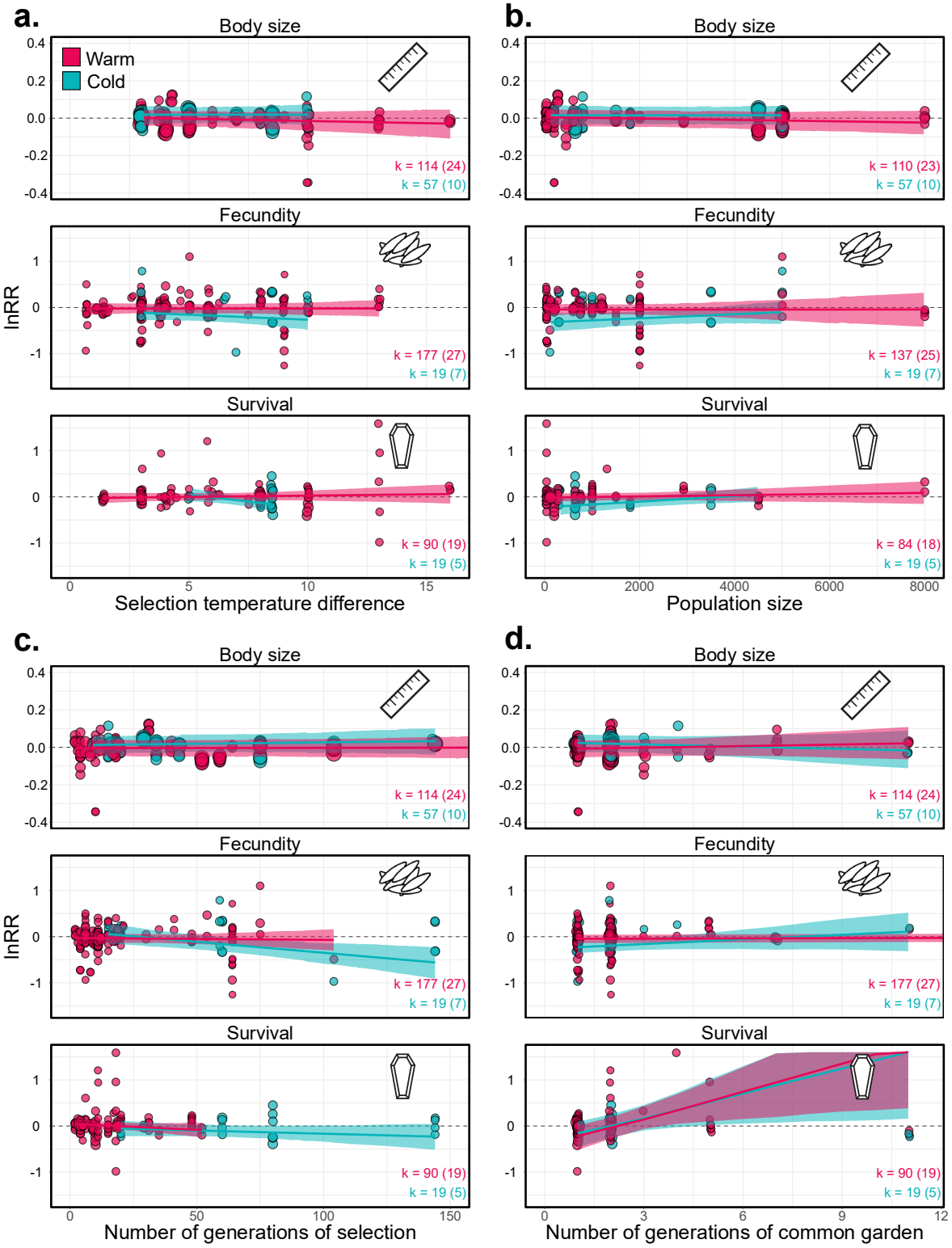
Because effect sizes are expected to vary with assay temperatures due to plasticity, we controlled for the assay temperature difference between control and selection regime (nuisance heterogeneity; *sensu* Noble et al., 2022) in all following models. That is, the model intercept (assay temperature difference = 0) corresponds to traits measured at the control temperature; while positive and negative assay temperature differences indicate that animals were assayed at temperatures above or below the control temperature, respectively.

We found no evidence for significant changes in fecundity, body size, or survival when animals were maintained at warmer-than-control temperatures for multiple generations, even after accounting for differences in assay temperatures (Table S5; Fig. 3). However, we found statistically significant variation in fecundity and survival with assay temperature in cold-selected lines ($slope_{fecundity(cold)}$ = -0.062 [-0.073, -0.052], n = 19; $slope_{survival(cold)}$ = -0.044 [-0.053, -0.034], n = 19; $R^2_{marginal}$ = 0.070 [0.049, 0.101]; Table S5; Fig. 3). When animals were assayed at control temperatures (assay temperature difference = 0), the cold-selected line were estimated to have on average 15.4% lower fecundity ($lnRR_{fecundity(cold)}$ = -0.167, [-0.295, -0.042]) than control animals, but we found no significant differences in survival between control and cold-selected lines ($lnRR_{survival(cold)}$ = -0.062, [-0.166, 0.052]; Fig. 3). In contrast, we found that cold-selected animals tended to have similar body sizes to control animals ($lnRR_{body\ size(cold)}$ = 0.022 [-0.017; 0.070], n = 57), and effect sizes did not vary significantly with assay temperatures ($slope_{body\ size(cold)}$ = 0.001 [-0.004, 0.006], n = 57; Table S5; Fig. 3).

Contrary to our predictions, we found no evidence that variation in fecundity, body size, and survival in warm-selected lines scaled with the intensity of selection, measured as the difference between the control and selected temperature ($slope_{body\ size(warm)}$ = -0.002 [-0.008, 0.004], n = 114; $slope_{fecundity(warm)}$ = 0.000 [-0.019, 0.019], n = 177; $slope_{survival(warm)}$ = 0.006 [-0.014, 0.025], n = 90; $R^2_{marginal}$ = 0.077 [0.053, 0.111]; Table S6; Fig. 4a). In cold-selected lines, survival relative to control lines decreased with the intensity of selection, but these effects were heterogeneous ($slope_{survival(cold)}$ = -0.060 [-0.116, -0.006], n = 19; Fig. 4a), and we

found no such evidence for body size and fecundity ($slope_{body\ size(cold)}$ = 0.000 [-0.009, 0.009], n = 57; $slope_{fecundity(cold)}$ = -0.022 [-0.064, 0.020], n = 19; Fig. 4a). We found little evidence for variation in any of the traits with the number of generations of selection ($R^2_{marginal}$ = 0.091 [0.059, 0.134]; Table S7; Fig. 4c). In fact, we only found a significant and negative relationship between the number of generations of selection and fecundity in cold-selected lines ($slope_{fecundity(cold)}$ = -0.163 [-0.283, -0.050]; Fig. 4c). We also found that the mean relative survival of both cold- and warm-selected lines tended to increase with the number of generations in a common garden environment ($slope_{survival(cold)}$ = 1.836 [0.292, 3.301]; $slope_{survival(warm)}$ = 2.069 [0.558, 3.455]; $R^2_{marginal}$ = 0.279 [0.106, 0.385]). However, these associations were associated with large uncertainty, and no such evidence was found for other traits and selection temperature regimes (Table S8; Fig. 4d). The initial population size tended to be positively correlated with the relative survival of cold-selected lines ($slope_{survival(cold)}$ = 0.119 [0.004, 0.244]), but not with other traits or in warm-selected lines ($R^2_{marginal}$ = 0.095 [0.065, 0.135]; Table S9; Fig. 4b).

Using multi-moderator models accounting for methodological variation among studies ($R^2_{marginal}$ = 0.344 [0.201, 0.428]), we found that results were mostly comparable to meta-regressions with single moderators (Supplementary results; Fig. S4; Table S10). However, note that, contrary to our single moderator meta-regressions, we did not find evidence for changes in fecundity between the control and cold-selected lines when re-acclimated at the control temperature ($lnRR_{fecundity(cold)}$ = -0.045 [-0.235, 0.150]). We also no longer found statistically significant evidence for evolutionary changes in survival in cold-selected lines across the range of assay temperatures ($lnRR_{survival(cold,\ -8.5°C)}$ = 0.315 [-0.258, 0.919]; $lnRR_{survival(cold,\ +4°C)}$ = -0.250 [-0.870, 0.298]), although we still found effects to vary with assay temperatures ($slope_{survival(cold)}$ = -0.045 [-0.055, -0.035]; Table S10).



531

532 **Figure 4:** Association between changes in trait means (lnRR) and the other moderators tested.
533 Variation across selection temperatures (a), initial population sizes (b), and generations of selection (c)
534 or in a common garden (d) are presented in different panels. Effect sizes (lnRR) represent the relative
535 difference between trait means of the warm- or cold-selected line relative to the control line. The
536 selection temperature difference is the difference between the temperature of warm- or cold-selected
537 and the temperature of the control line, in absolute values (i.e., intensity of selection). Regression lines
538 and shaded areas represent predicted mean and credible intervals from Bayesian multilevel linear
539 models. Data points represent individual effect sizes, scaled by precision (1/SE). Estimates are

displayed separately for each trait (body size, fecundity, survival), for cooler-than-control ("Cold", in blue), and warmer-than-control ("Warm", in red) selection lines. Note the different scale for the y axis of body size, and that up to 5 (1 body size, 4 fecundity, 1 survival) observations are not displayed for clarity. *: Statistically significant slope based on 95% credible intervals. k = number of effect sizes, with the number of studies in brackets.

Changes in trait variance

Heterogeneity and correlations among trait responses

We quantified the changes in trait variance using the log coefficient of variation ratio (lnCVR) and the log of variance ratio (lnVR). Here, we report the results for lnVR but note that the results for lnCVR are comparable (see Table S17-23 and Fig. S6-8).

Like our results about changes in trait means, we found no strong evidence for correlations among traits ($cor_{(body\ size,\ fecundity)}$ = 0.02 [-0.87, 0.88]; $cor_{(body\ size,\ survival)}$ = -0.02 [-0.88, 0.88]; $cor_{(fecundity,\ survival)}$ = -0.03 [-0.87, 0.86]. Heterogeneity was also high (I^2_{total} = 93.16% [91.17, 94.79]), with 25.53% of the variation associated with study differences, 6.51% of the variation explained by differences among experiments within the same study, 4.35% of the variation explained by differences among species, 6.57% of the variation explained by phylogenetic relatedness among species, and 50.19% associated with residual variation.

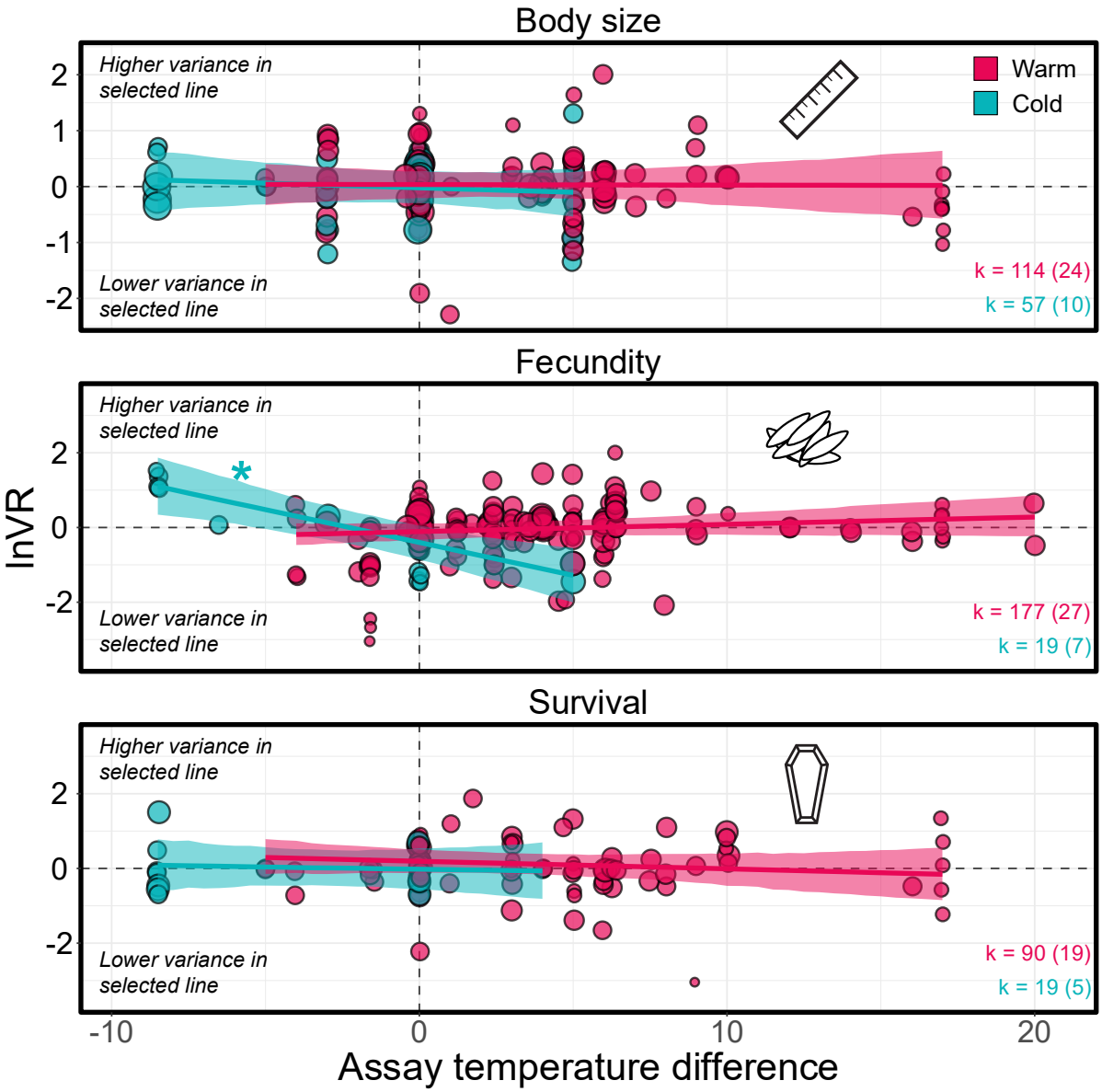
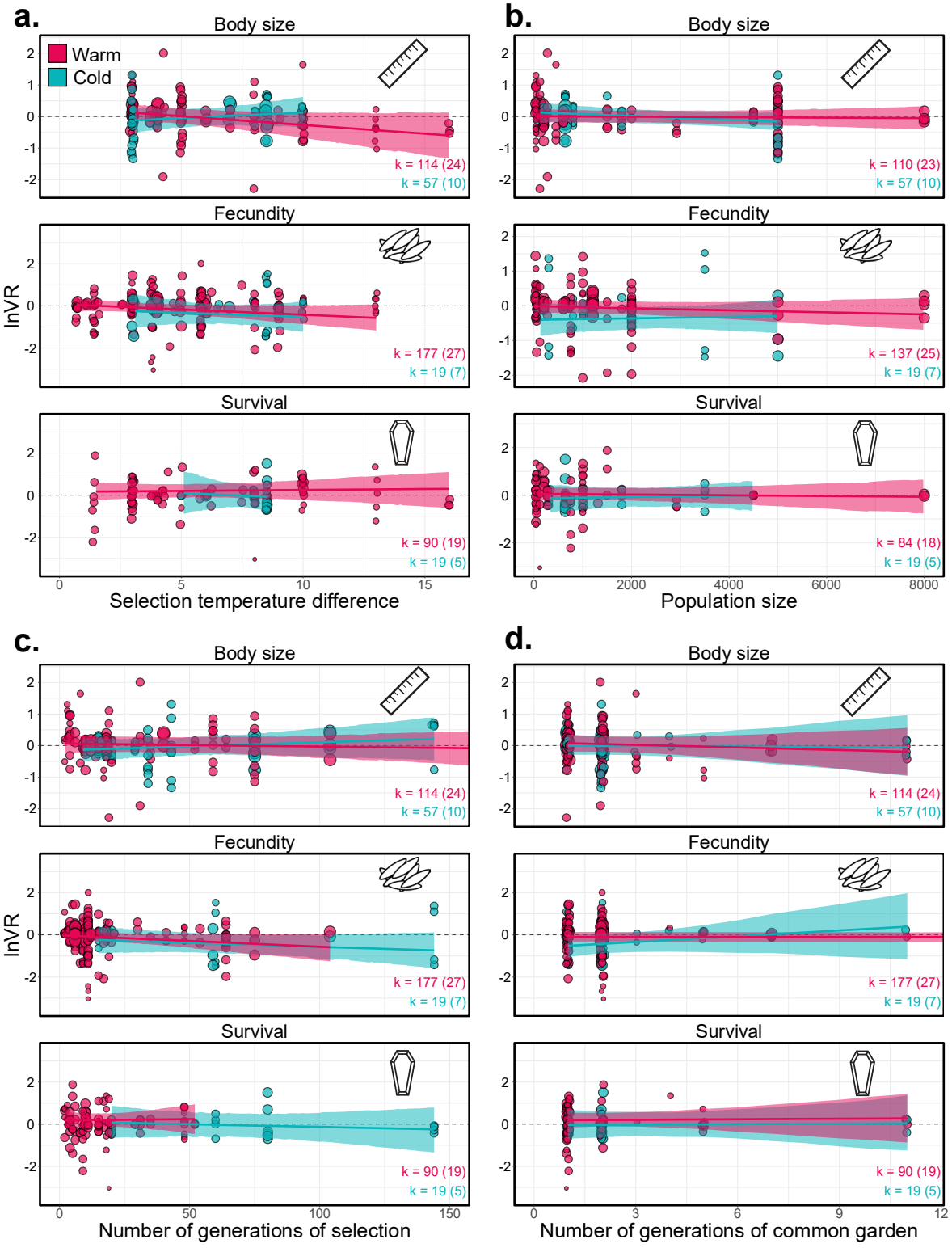


Figure 5: Association between changes in trait variance (lnVR) and the difference between the assay temperature and the temperature of the control line. Effect sizes (lnVR) represent the relative difference between trait variance of the warm- or cold-selected line relative to the control line. The assay temperature is the temperature at which animals were re-acclimated after selection. Null values indicate that animals were assayed at the temperature of the control line, while positive and negative values indicate that animals were assayed at temperatures above or below the control temperature, respectively. Regression lines and shaded areas represent predicted mean and credible intervals from Bayesian multilevel linear models. Data points represent individual effect sizes, scaled by precision (1/SE). Estimates are displayed separately for each trait (body size, fecundity, survival), for cooler-than-control ("Cold", in blue), and warmer-than-control ("Warm", in red) selection lines. Note that 4 survival observations were trimmed for clarity. *: Statistically significant slope based on 95% credible intervals. k = number of effect sizes, with the number of studies in brackets.

Associations with moderator variables

We found no support for changes in trait variance in cold- ($lnVR_{body\ size(cold)}$ = -0.020 [-0.298; 0.274]; $lnVR_{fecundity(cold)}$ = -0.401 [-0.854; 0.062]; $lnVR_{survival(cold)}$ = -0.022 [-0.567; 0.525]) or warm-selected lines ($lnVR_{body\ size(warm)}$ = 0.037 [-0.202; 0.282]; $lnVR_{fecundity(warm)}$ = -0.110 [-0.332; 0.106]; $lnVR_{survival(warm)}$ = 0.196 [-0.108; 0.517]) when animals were assayed at control temperatures (Table S11; Fig. 5). Contrary to our predictions, we found no evidence for changes in trait variance with assay temperature when animals evolved in warming environments ($slope_{body\ size(warm)}$ = -0.001 [-0.040, 0.039], n = 114; $slope_{fecundity(warm)}$ = 0.020 [-0.010, 0.050], n = 177; $slope_{survival(warm)}$ = -0.021 [-0.068, 0.026], n = 90; $R^2_{marginal}$ = 0.061 [0.027, 0.100]; Table S7; Fig. 5). However, we found evidence for a negative and significant relationship between variance in fecundity and assay temperature difference in cold-selected lines ($slope_{fecundity(cold)}$ = -0.176 [-0.266, -0.085], n = 19; Fig. 5), but no such trend with other traits ($slope_{body\ size(cold)}$ = -0.016 [-0.072, -0.042], n = 57; $slope_{survival(cold)}$ = -0.013 [-0.097, -0.073], n = 19; Table S10; Fig. 5). In fact, cold-selected animals had more variable fecundity than control animals when assayed at cooler-than-control temperatures, but reduced variance in fecundity when assayed to warmer temperatures (Fig. 5). Contrary to our predictions we did not find evidence that relative trait-variance between lines decreased with the intensity of selection (the temperature difference between control and selected lines), the number of generations of selection or in the common garden, or the initial population size, in either cold- or warm-selected lines (Fig. 6a-d; Table S12-15). Similar to our results for changes in trait means, results from our multi-moderator models were mostly comparable to models with single moderators (Table S15; Supplementary results).



593

594 **Figure 6:** Association between changes in trait variance (lnVR) and the other moderators tested.
595 Variation across selection temperatures (a), initial population sizes (b), and generations of selection (c)
596 or common garden (d) are presented in different panels. Effect sizes (lnVR) represent the relative
597 difference between trait variance of the warm- or cold-selected line to the control line. The selection
598 temperature difference is the difference between the temperature of warm- or cold-selected and the
599 temperature of the control line, in absolute values (i.e., intensity of selection). Regression lines and
600 shaded areas represent predicted mean and credible intervals from Bayesian multilevel linear models.
601 Data points represent individual effect sizes, scaled by precision (1/SE). Estimates are displayed

separately for each trait (body size, fecundity, survival), for cooler-than-control ("Cold", in blue), and warmer-than-control ("Warm", in red) selection lines. Note that up to six (1 body size, 1 fecundity, 4 survival) observations are not displayed for clarity. *: Statistically significant slope based on 95% credible intervals. k = number of effect sizes, with the number of studies in brackets.

Sensitivity analyses and publication bias

Our results were largely robust to the exclusion of data with procedural concerns (Table S32-34; Fig. S17-18) and to the iterative exclusion of one study at a time (Fig. S13-14). Our results were consistent between constant and increasing temperature treatments ($lnRR_{body\ size(constant - increasing)}$ = -0.032 [-0.106; 0.043]; $lnRR_{fecundity(constant - increasing)}$ = -0.006 [-0.236; 0.230]; $lnRR_{survival(constant - increasing)}$ = 0.011 [-0.160; 0.203]; $lnVR_{body\ size(constant - increasing)}$ = 0.156 [-0.541; 0.824]; $lnVR_{fecundity(constant - increasing)}$ = -0.157 [-0.620; 0.277]; $lnVR_{survival(constant - increasing)}$ = 0.205 [-0.610; 0.969]; Table S29-31; Fig. S15-16). We found some evidence for time-lag biases (i.e., changes in effect size magnitude over time) for changes in mean fecundity in cold-selected lines ($slope_{fecundity}$ = 0.157 [0.062; 0.256]; Fig. S11), and changes in the variance of survival in warm-selected lines ($slope_{survival}$ = -0.258 [-0.496; -0.012]; Fig. S12), but not for any of the other traits and effect sizes used (Table S26-28; Fig. S11-12). However, we found strong yet variable associations between mean changes in body size ($slope_{body\ size}$ = -37.45 [-69.801; -6.116]), fecundity ($slope_{fecundity}$ = 9.258 [2.897; 15.745]), and the sampling variance of lnRR in cold-selected lines (Table S23; Fig. S9). While these results suggest evidence for publication bias (small-study effects), these estimates were highly uncertain (wide credible intervals) due to small sample sizes and may not be generalisable. We did not find such evidence for publication bias for changes in trait variance (lnVR and lnCVR; Table S24-25; Fig. S10).

Discussion

Quantifying animals' capacity to adapt to changing temperatures is key to assessing population resilience to climate change. Here, we performed a meta-analysis of 44 studies to assess the extent to which the mean and variance in key determinants of fitness (i.e., body size, fecundity, and survival) vary among experimental animal populations raised for multiple generations under different temperature regimes.

Contrary to our predictions, we found weak and heterogeneous evidence that fecundity, body size, and survival evolve in warming environments, both in trait means and variances (Fig. 3-6). We found more predictable responses in cold-selected lines, although these results may be considered preliminary due to strong methodological heterogeneity and limited sample sizes. We also found that no moderator variables explained substantial variation in evolutionary responses to changing thermal environments, even for those expected to modulate the intensity of selective pressures (i.e., selection temperature deviation from the control temperature), or the ability to detect evolutionary changes (i.e., number of generations of selection). Taken together, our results suggest that genetic responses to thermal selection on life-history traits can occur, but such outcomes seem far from universal or predictable across experimental evolution studies. Therefore, adaptive responses to changing temperatures are likely to be weak and difficult to predict in nature.

Adaptation to cold temperatures may be more consistent than adaptation to warming

Although we did not find consistent evidence of evolutionary trait responses to warming, we found some evidence of selection on key life-history traits under cold-temperature regimes (Fig 3-6). Populations maintained for multiple generations in cooler environments tend to have higher fecundity than control lines when both are assayed under cool conditions (Fig. 3). Cold-selected lines also exhibited increased variance in fecundity relative to control lines under cold conditions (Fig. 5). This increase in variance contradicts our hypothesis that exposure to novel environments should decrease trait variance by depleting standing genetic variation (Bijlsma & Loeschcke, 2012). Instead, it suggests that adaptation to novel cold environments may have exposed cryptic genetic variation (Hoffmann & Merilä, 1999; O'Dea et al., 2016; Paaby & Rockman, 2014).

After controlling for methodological heterogeneity among studies, we found no evidence that cold-selected and control lines diverged when both were assayed at control temperatures (Fig. 3-6; Fig. S4-6). Increased mean and variance in the fecundity of cold-selected lines were only detectable when populations were assayed after re-acclimation to cooler- or warmer-than-control conditions (Fig. 3), or after an extended number of generations of selection (Fig. 4c). Selection on traits optimising performance in cooler environments also appeared to trade off

with performance at warmer temperatures. In fact, we found that cold-selected lines had reduced fecundity relative to control lines under warmer-than-control temperatures (Fig. 3). Therefore, cool environments have likely selected traits maximising the efficiency of physiological functions at cold temperatures—allowing populations to maintain high fecundity at cold temperatures, at the expense of performance at warmer temperatures. This is consistent with general theory invoking antagonistic pleiotropy as a central component in thermal adaptation (Angilletta, 2009) and conclusions from a similar meta-analysis on fitness responses to artificial selection (Malusare et al., 2023). A wide range of mechanisms is likely to drive adaptive responses and shape trade-offs across different temperatures (Tattersall et al., 2012). While we can hardly conclude on the exact mechanisms at play, deeper investigations into biochemical, cellular, and physiological changes occurring during experimental evolution may help shed light into the mechanisms driving adaptive responses to environmental change.

Evidence for evolutionary changes in cooler environments remains preliminary due to small sample sizes (n = 19 effect sizes from 7 studies). Moreover, effect size magnitude varied little with the intensity of selection (relative selection temperature; Fig. 4b), suggesting that the evolutionary responses we have detected may be largely species-, trait- and/or context-specific. Evidence for selection on survival in cooler environments also largely disappeared after accounting for methodological heterogeneity among studies (Fig. 4a), suggesting these responses may not be generalisable across contexts. In fact, a recent study on seed beetles instead found that life history adaptation to cold was much less pronounced and predictable across different genetic backgrounds compared to heat adaptation (Rêgo et al., 2025). Thus, evolutionary responses to cold environments are likely to be weak and heterogeneous in nature and it would be premature to claim broad generality of the current results.

Life history traits do not always evolve in response to changing temperatures

Previous comparative analyses have found mixed evidence for the evolution of fitness-related traits in changing thermal environments. For instance, a similar meta-analysis found very weak effects of warming on the evolution of fecundity and body size (Grainger & Levine, 2022). Consistent with our meta-analysis, responses were particularly weak for body size, and they found no correlation with study attributes expected to moderate evolutionary trait responses (i.e., temperature magnitude, number of generations of selection). However, in a recent meta-analysis, Malusare and colleagues (2023) found some evidence for positive responses to temperature selection, although the effects were weak. We suggest our results differ for two main reasons: i) study selection, and ii) analytical decisions. First, Malusare and colleagues (2023) included responses to artificial selection, which are likely to be stronger than those to

experimental evolution. In these experiments, selective pressures are artificially high, where only a limited proportion of individuals are selected to contribute to the next generation. In experimental evolution studies, trait responses are likely to take much longer to manifest because selection is not artificially imposed, and other buffering mechanisms such as physiological plasticity allow organisms to survive and contribute to the next generation, limiting the rate at which population-level changes occur (Chevin et al., 2010; Oostra et al., 2018; Price et al., 2003). Second, while we focused on life-history traits (i.e., body size, fecundity, survival), Malusare and colleagues (2023) integrated fecundity and population growth into estimates of fitness, which may result in more consistent or predictable responses than individual components of fitness. In addition, our taxonomic scope was restricted to animals, while they also included algae and bacteria, which comprised most of their dataset, and for which effects were generally stronger. These differences in analytical decisions and taxonomic scope are likely to have generated discrepancies between our studies. However, the fact that adaptive responses seem weak (Grainger & Levine, 2022; Malusare et al., 2023) suggests that life history traits do not often evolve in a predictable direction in response to changing thermal environments. This notion is further supported by a recent study finding that life history traits show weak and unpredictable genetic differentiation along latitudinal gradients compared to phenological traits in insects (Gotthard et al., 2026). Similarly, comparative studies in wild populations generally do not find strong evidence for selection on fitness-related traits such as body size in warming environments (Horne et al., 2015; Radchuk et al., 2019; Siepielski et al., 2017, 2019; Teplitsky & Millien, 2014). Therefore, widely reported changes in body size with warming are most likely attributable to (beneficial) plasticity rather than genetic adaptation.

Plasticity and genetic constraints likely explain the lack of adaptive responses

Weak evolutionary trait responses to changing thermal environments are likely driven by the expression of plasticity and genetic constraints. Phenotypic plasticity may buffer the effects of changing temperatures in selected lines, reducing the mismatch between phenotype and environment and weakening selection (Chevin et al., 2010; Martin et al., 2023; Oostra et al., 2018; Price et al., 2003). However, this is unlikely to explain most of our results. Plasticity is often insufficient to fully offset environmental changes (Gunderson & Stillman, 2015; Noble et al., 2025; Seebacher et al., 2015), thus we would expect stronger evolutionary responses with increasing selection intensity and across more generations of selection, which our results do not support (Fig. 4b,d; Fig. 6b,d). Moreover, theory predicts that because thermal performance curves are asymmetrical and typically left-skewed (Angilletta, 2009), temperatures above the thermal optimum should exert stronger selection than temperatures below it (Berger et al., 2021; Logan & Cox, 2020; Martin et al., 2008). However, we detected greater evolutionary

trait responses to cold environments. Our results may thus be more consistent with the hypothesis of "*plastic floors and concrete ceilings*" (Sandblom et al., 2016). That is, plasticity may facilitate adaptation in the cold by generating additional phenotypic variation for selection to act upon ("*plastic floors*"), which is supported by our results suggesting an increase in variance with cold- but not warm-selection. In contrast, adaptation to warmer environments may be constrained, because plasticity is limited by tighter physiological boundaries at high temperatures (e.g. in relation to enzyme function; Daniel, 1996) ("*concrete ceilings*"). This would be consistent with evidence showing greater ability to evolve thermal tolerance in cold rather than warm environments (Bennett et al., 2021; Morgan et al., 2020), and reductions in the rate of heat tolerance evolution as animals approach physiological ceilings (Morgan et al., 2020). In addition, "*hard limits*" (Hoffmann et al., 2023) may limit evolutionary responses to changing temperatures. These hard limits can reflect weak additive genetic variance available for selection to work upon, or traits that cannot easily be changed without rare mutations or substantial genomic reorganisation (Hoffmann et al., 2023). Most of our dataset spanned animal populations kept under controlled laboratory conditions for an extended number ($\bar{x}$ = 33.7) of generations prior to experimental evolution, which is expected to deplete standing genetic variance (Breckels et al., 2014; Moose et al., 2004; Ørsted et al., 2019). Some studies have also shown that traits tightly linked to fitness—such as fecundity and survival, captured in our study—tend to have lower heritability (Merilä & Sheldon, 1999), potentially because there is much underlying non-additive genetic variance (e.g., epistatic), thereby potentially limiting opportunities for genetic adaptation to occur. However, we did not find evidence that trait responses varied with initial population size, a proxy we considered for genetic variance, though it is possible that initial populations already had poor standing genetic variance before selection (Hoffmann et al., 2023; Hoffmann & Ross, 2018; Martin et al., 2023). Prolonged maintenance in laboratory conditions can also lead to genetic drift and/or relaxed selection on plastic responses, which can positively or negatively modulate the intensity of selection (Hoffmann & Ross, 2018). For instance, a recent study found that adaptation of zebrafish to laboratory conditions caused major reductions in physiological plasticity for various traits (Morgan et al. 2020). Investigating whether responses to experimental evolution are stronger in wild populations is thus an interesting avenue for future research.

Limitations and future directions

Our study provides compelling evidence that evolutionary trait responses to changing temperatures are weak and highly variable given the sample of studies. However, broad generalisation of our results across species and contexts must be done with caution. First, we documented extensive taxonomic biases in the literature, whereby most data on experimental evolution studies are restricted to invertebrates (with half of the data from the genus

Drosophila), and—when data on vertebrates was available (n = 2 fish species)—animals were only selected for a limited number ($\bar{x}$ = 5.8) of generations. This is not surprising since experimental evolution studies on long-lived vertebrates are logistically difficult. Interestingly, despite extremely high heterogeneity (>99%), we found that most of the variation in evolutionary trait responses was explained by differences in traits and selection temperature regimes among studies, rather than by ecological differences or phylogenetic relatedness among species. Therefore, our results are likely generalisable across species, though we caution against extrapolations beyond invertebrates given the strong taxonomic biases. Until we aggregate further evidence, it is unclear whether our results generalise across taxa.

Second, limited sample sizes challenge the generality of some of our results. Although we found some evidence for selection on fecundity and survival in cold environments, it is difficult to draw robust conclusions from the results of seven studies. For instance, survival responses largely disappeared after controlling for methodological heterogeneity (Fig. S4), and the associations between fecundity responses and the number of generations of selection were drawn from a limited number of data points that may not replicate with additional studies (Fig. 4c). In addition, our models could not reliably estimate trade-offs among the evolution of body size, fecundity, and survival, because of the weak evolutionary responses overall. We encourage further experimental evolution studies to tease apart evolutionary responses from weak statistical power.

Third, it is possible that we did not find evidence for evolutionary trait responses to warming environments because of the simplicity of laboratory conditions used. Temperature itself may not impose sufficiently strong selection to generate responses in experimental evolution studies, especially in constant environments (Buckley & Kingsolver, 2021). However, temperature, in combination with other variables, may generate stronger evolutionary trait responses. For example, biotic factors are likely to modulate the intensity of selection in warming environments because temperature has strong effects on interspecific interactions (Amarasekare, 2015; Jiang & Morin, 2004), movement and escape response to predators (Domenici et al., 2019; Grigaltchik et al., 2012), and immunity (Raffel et al., 2006; Wojda, 2017). Therefore, laboratory conditions during experimental evolution may not provide realistic conditions for evolution to occur or be detectable within study timeframes. Further investigating how animals evolve in changing environments with more ecological realism (e.g., multi-species mesocosms) may provide fruitful avenues to our understanding of climate change responses (Doorslaer et al., 2010).

Fourth, the absence of a general trend in animals' ability to adapt to changing temperatures does not imply that evolutionary responses do not occur in some contexts. We found

substantial heterogeneity in the results, and some authors reported strong responses to experimental evolution (e.g. Bakker et al., 2020; Zhang et al., 2019). However, the large spectrum of responses and the fact that none of our tested covariates significantly moderated the strength of responses suggest that such adaptive responses are likely driven by additional factors. For instance, there may be unintentional selection on other traits, such as fast development time being favoured at large densities (Engen et al., 2020; Hoffmann et al., 2023). The very nature of traits unintentionally selected are likely to vary across studies and explain a significant proportion of the large heterogeneity we observed. In addition, divergence in responses among replicate lines (non-parallel evolution; Bolnick et al., 2018) may mask overall signals of adaptation (Gotthard et al., 2026; Urban et al., 2024). Although we did not find large evidence for changes in trait variance after experimental evolution, evidence for non-parallel evolution would be difficult to detect in a meta-analytic framework because changes in trait variance may also not be predictable among replicate lines. Investigating responses to experimental evolution in a diverse range of traits, replicate lines, and in ecologically relevant settings will be important for dissecting evolutionary responses to environmental change.

Implications for ecological responses to environmental change

Weak directional evidence for adaptive responses to changing temperatures may pose challenges for the persistence of ectotherms under rapid environmental change. The limited and highly heterogeneous capacity of populations to evolve higher fitness at warmer temperatures suggests that predicting adaptive responses to climate change will be difficult and, in many cases, insufficient to buffer ongoing warming. Although we found some evidence that cold environments can facilitate adaptive responses, such conditions are becoming increasingly rare under progressively changing climates and are unlikely to provide consistent opportunities for evolutionary rescue. Instead, our results imply that many animal populations may need to rely predominantly on phenotypic plasticity to buffer the impacts of climate change. However, mounting evidence indicates that plasticity often provides only partial benefits (Gunderson & Stillman, 2015; Noble et al., 2025; Pottier et al., 2022; Seebacher et al., 2015) and may itself be constrained or eroded under sustained environmental change (Morgan et al., 2020). If plastic responses are insufficient and adaptive evolution remains limited, many ectothermic species are likely to experience reduced reproductive success, with potentially important demographic consequences under a changing climate.

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Artificial Intelligence use disclosure

The authors used OpenAI's ChatGPT 5.5 to make minor improvements to the clarity of the manuscript and to assist with code editing. All outputs were carefully reviewed and verified by the authors, who take full responsibility for the content and analyses presented.