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Coral adaptation to climate change: meta-analysis reveals high heritability across multiple traits

Running Title: Trait heritability in reef-building corals

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Abstract

Anthropogenic climate change is a rapidly intensifying selection pressure on biodiversity across the globe and, particularly, on the world's coral reefs. The rate of adaptation to climate change is proportional to the amount of phenotypic variation that can be inherited by subsequent generations (i.e., narrow-sense heritability, h^2). Thus, traits that have higher heritability (e.g., $h^2 > 0.5$) are likely to adapt to future conditions faster than traits with lower heritability (e.g., $h^2 < 0.1$). Here, we synthesize 95 heritability estimates across 19 species of reef-building corals. Our meta-analysis reveals low heritability ($h^2 < 0.25$) of gene expression metrics, intermediate heritability ($h^2 = 0.25$–0.50) of photochemistry, growth, and bleaching, and high heritability ($h^2 > 0.50$) for metrics related to survival and immune responses. Some of these values are higher than typically observed in other taxa, such as survival and growth, while others were more comparable, such as gene expression and photochemistry. There was no detectable effect of temperature on heritability, but narrow-sense heritability estimates were generally lower than broad-sense estimates, indicative of significant non-additive genetic variation across traits. Trait heritability also varied depending on coral life stage, with bleaching and growth in juveniles generally having lower heritability compared to bleaching and growth in larvae and adults. These differences may be the result of previous stabilizing selection on juveniles or may be due to constrained evolution resulting from genetic trade-offs or genetic correlations between growth and thermotolerance. While we find no evidence that heritability decreases under temperature stress, explicit tests of the heritability of thermal tolerance itself – such as coral thermal reaction norm shape – are lacking. Nevertheless, our findings overall reveal high trait heritability for the majority of coral traits, suggesting corals may have a greater potential to adapt to climate change than has been assumed in recent evolutionary models.

Keywords: adaptation, animal model, Breeder’s equation, climate change, evolution, natural selection, Scleractinia, thermal tolerance

Introduction

Anthropogenic climate change is one of the greatest selective pressures on organisms worldwide (Davis et al. 2005; Hughes et al. 2018b; Nolan et al. 2018). To avoid extinction, species need to either acclimatize, move to new habitats, or adapt to new conditions (Davis et al. 2005; Jump and Peñuelas 2005; Gienapp et al. 2008). Acclimatization on its own may initially increase the duration of time that a population can persist in an altered environment, but is bounded by physiological thresholds that limit tolerance of long-term environmental change, and for populations living close to their extremes already (Comte & Olden, 2017; Sasaki & Dam, 2019; van Heerwaarden, Kellermann, & Sgr, 2016). Migration to new environments is similarly limited (Jump & Peñuelas, 2005; Schloss, Nuñez, & Lawler, 2012; Walters & Berger, 2019), especially for predominantly sessile organisms for which range extension depends upon long-distance dispersal of offspring (Hughes et al. 2003; Archambault et al. 2018; c.f. Kremer et al. 2012). Consequently, understanding whether and how species are likely to adapt to future conditions is crucial in predicting species persistence in the context of climate change (C. A. Logan, Dunne, Eakin, & Donner, 2014).

Adaptive evolution to a changing environment occurs when population genotype frequencies change to express traits or phenotypes that provide increased fitness (Falconer & Mackay, 1996). However, adaptation of a trait can only occur at a rate proportional to the narrow-sense heritability coefficient, h^2, calculated as the ratio between population variance attributable to additive genetic effects, V_a, and the total observed phenotypic variance, V_p (Box 1). The narrow-sense heritability coefficient is a key parameter in the univariate 'Breeder's equation', which predicts the mean population response in trait values for a single trait undergoing selection.

Box 1. Heritability and the Breeder's equation

Heritability is the proportion of a trait's relative genetic variation compared to its total phenotypic variation (V_P). As a dimensionless quantity that describes population responses to selection, heritability is often calculated to compare across different traits, populations, or species (Visscher, Hill, & Wray, 2008). There are two types of heritability: broad-sense heritability (H^2) and narrow-sense heritability (h^2).

$$\text{Broad-sense: } H^2 = \frac{V_A+V_D+V_I}{V_P} \qquad \text{Narrow-sense: } h^2 = \frac{V_A}{V_P} \qquad (1)$$

The former is 'broad' in that it includes all sources of genetic variation (V_G), including additive genetic variation (V_A), as well as non-additive sources such as dominance (V_D) and epistasis (V_I), which are genetic effects not (necessarily) inherited by offspring produced through sexual reproduction (Falconer & Mackay, 1996), and thus broad-sense heritability is calculated using clones or genets. Narrow-sense heritability, h^2, is the proportion of phenotypic variance that is due to additive genetic variance (V_A) alone, and thus is the strictly 'heritable' genetic component of the trait of interest in sexually-reproducing individuals. Narrow-sense heritability is thus calculated using pedigree information from genetically distinct individuals. Important caveats when estimating either narrow or broad-sense heritability include controlling for common environment across individuals as well as considering potential genotype-by-environment interactions, parental effects that may alter offspring phenotype, and the potential for epigenetic inheritance (Falconer & Mackay, 1996; Visscher et al., 2008).

Narrow sense heritability can be used to predict and understand population responses to selection. Consider one population where the mean critical thermal maximum (CT_{max}) of the population is 30°C and CT_{max} is highly heritable, e.g. $h^2 =$

0.5. If a temperature anomaly occurs, resulting in the death of the more heat-susceptible individuals and shifting the mean population CT_{max} to 32°C, the univariate Breeder's equation predicts that the mean change in population response (R) in CT_{max} will be:

$$R = h^2 \cdot S = 0.5 \cdot (32°\text{C} - 30°\text{C}) = +1°\text{C} \qquad (2)$$

In other words, an increase in the mean selected population CT_{max} of +2°C (S, the 'selection differential') translates to an expected increase in the next generation's average CT_{max} of +1°C (Falconer & Mackay, 1996; Lande, 1979; Lush, 1937). Now consider a second population experiencing the same selection event, but with a relatively low heritability in CT_{max}, e.g. $h^2 = 0.1$. The predicted change in CT_{max} in the next generation would be: $R = 0.1 \cdot (32°\text{C}–30°\text{C}) = +0.2°\text{C}$, or a five-fold lower response to the same selection pressure. Thus, the relative response of a trait in a population under selection is proportional to the value of the narrow-sense heritability coefficient for said trait, h^2.

Different traits often have different heritability coefficients, and may also covary with one another (Wright et al. 2019). Counterintuitively, traits which are tied closely to biological fitness (e.g., life history traits, longevity/survival, fecundity) often have relatively low heritability compared to physiological and behavioural traits, and compared to morphological traits that often have higher heritability (Martins, Kruuk, Llewelyn, Moritz, & Phillips, 2019; Mousseau & Roff, 1987; Price & Schluter, 1991; Wheelwright, Keller, & Postma, 2014). For example, when populations have previously undergone strong stabilizing selection for a trait tied closely to fitness, the narrower range and variance of trait values observed in the population translates to a reduction in the relative contribution of additive genetic effects to total phenotypic variation, and a decrease in the heritability coefficient (Charmantier &

Garant, 2005; Teplitsky, Mills, Yarrall, & Merilä, 2009; Wheelwright et al., 2014). Understanding the potential rate and limits to adaptive evolution will therefore require an understanding of heritability across different traits (Wheelwright et al., 2014).

Selective pressures differ not only in terms of the trait being examined, but also across life stages/ages, growth forms, and environments (e.g., genotype-by-environment interactions). Thus, heritability should vary across these factors as well (Charmantier & Garant, 2005; Wheelwright et al., 2014; Wilson, Charmantier, & Hadfield, 2008). Early life stages/ages can experience strong stabilizing selection for traits associated with early life fitness, and thus exhibit reduced h^2 for these traits. Increasing importance of environmental effects and acclimation to local environments can also reduce the relative importance of additive genetic variation and thus h^2 at intermediate stages/ages (Charmantier, Perrins, McCleery, & Sheldon, 2006a). Finally, late-acting mutations can accumulate in older individuals to cause age-dependent increases in V_{A}, and thus h^2, for traits tied closely with fitness (Charmantier et al., 2006a; Charmantier, Perrins, McCleery, & Sheldon, 2006b; Wilson et al., 2008). Similar selective pressures can result in similar h^2 values for traits of species occupying similar ecological niches. For example, in reef-building corals, colony growth form directly influences individual growth rate, fecundity, and survival (Madin et al., 2020; Pratchett et al., 2015). Tabular coral species (which form large horizontal plates supported by a central stalk) exhibit increased adult mortality relative to other coral growth forms in the same habitat due to their increased mechanical vulnerability (Madin, Baird, Dornelas, & Connolly, 2014). However, it remains unknown whether and how heritability of traits varies among coral species with different growth forms.

In the context of climate change, decreasing environmental suitability and increasing selective pressure on traits tied closely to fitness can reduce trait heritability, resulting in a counter-intuitive reduction in the capacity for populations to evolve to environmental change

(Charmantier & Garant, 2005; Wheelwright et al., 2014; Wilson et al., 2006). Conversely, other studies have found no distinguishable relationship between h^2 and environmental favourability (Rowínski & Rogell, 2017), and others still identify positive correlations of h^2 with increasingly harsh environmental temperatures (Gunay, Alten, & Ozsoy, 2011). Clearly, further research is required to quantify how heritability may change across life stages and environments of the future, especially when attempting to project population outcomes in response to future conditions.

Reef-building scleractinian corals are particularly sensitive to climate stressors, as evidenced by coral bleaching during thermal anomalies. Reef diversity and coral cover have declined throughout the 21st century (T. P. Hughes, Kerry, et al., 2018; Pratchett, Hoey, Wilson, Messmer, & Graham, 2011; Wulff, 2006), with 75% of global reefs now being considered threatened (Burke, Reytar, Spalding, & Perry, 2011). Widespread bleaching of coral communities now occurs at temperatures approximately 0.5°C higher than a decade ago, suggesting strong selection for increased thermotolerance worldwide (Guest et al., 2012; Maynard, Anthony, Marshall, & Masiri, 2008; Sully, Burkepile, Donovan, Hodgson, & van Woesik, 2019). However, given the rapid warming of sea surface temperatures and the increase in the frequency and severity of mass bleaching events on coral reefs worldwide (T. P. Hughes, Anderson, et al., 2018; Lough, Anderson, & Hughes, 2018), it remains unclear whether corals can adapt to the prolonged thermal stress they now experience with increasing regularity (Hoegh-Guldberg, Poloczanska, Skirving, & Dove, 2017; Pandolfi, Connolly, Marshall, & Cohen, 2011). Models estimating long-term coral adaptation to climate change have assumed low to medium heritability of thermotolerance (e.g., $h^2 = 0.01–0.50$; Cropp and Norbury 2020; Matz et al. 2020; Logan et al. 2021), despite some evidence of model outcomes being sensitive to the rate of adaptation (Bay, Rose, Logan, & Palumbi, 2017; Cropp & Norbury, 2020), evidence of high heritability for coral survivorship in high temperatures (e.g., $h^2 = 0.75$: Kirk et al. 2018), and the potential for rapid symbiont evolution in response to thermal change (e.g., Chakravarti et al. 2017; Buerger et al. 2020). Therefore, our ability to project the future of coral populations in the context of climate change is critically dependent upon the estimates of trait heritability used in eco-evolutionary models (C. A. Logan et al., 2014; M. L. Logan, Cox, & Calsbeek, 2014; Visser, 2008).

Worldwide, reef-building corals are undergoing increasingly strong selection for temperature tolerance due to anthropogenic climate change. Here, we undertake a quantitative meta-analysis of published heritability estimates for reef-building corals to better understand which traits are likely to change most rapidly given increased environmental change. We examine the relative heritability of different trait types such as coral gene expression, bleaching, growth, symbiont community structure, and survival, and investigate potential interactions among life stages and, for experiments that manipulate temperature, to the magnitude of temperature stress to which corals are exposed. We also estimate the relative heterogeneity of heritability estimates, examine differences between narrow-sense vs. broad-sense heritability estimates, and identify how differences in coral growth forms influence estimates of h^2.

Literature Analysis

Literature search

We undertook an exhaustive literature review to find all possible heritability point estimates and associated measures of sampling variance (e.g., standard errors, confidence or credibility intervals) for scleractinian corals by canvassing two major research databases: Google Scholar and Web of Science. Keyword searches were conducted in October 2020 to identify all studies reporting heritability estimates for corals, and/or their associated symbionts. We searched for studies using the keywords and Booleans: “heritability” AND "coral" OR "familial effects" AND "coral". We found a total of 16 studies reporting heritability and one study with heritability estimates that could be extracted from the published data. We then mined the references cited within each paper from the initial search to identify two additional studies reporting heritability estimates. We contacted some study authors when text alluded to heritability estimates, but values were not reported in the final manuscript, all of whom kindly contributed those heritability estimates to our analysis. Where possible, we selected single heritability estimates calculated using a fixed effect of temperature or other treatment, rather than taking multiple heritability estimates calculated by splitting the data by each treatment. Many of the studies report multiple heritability estimates for the same or similar traits. For five studies (Kirk, Howells, Abrego, Burt, & Meyer, 2018; Lohr & Patterson, 2017; Manzello et al., 2019; Wright et al., 2019; Zhang, Million, Ruggeri, & Kenkel, 2019), we selected one representative heritability estimate when there were multiple and highly related h^2 estimates (e.g., Kaplan-Meier survival and percent survival; symbiont abundance and chlorophyll A content; total linear extension and net buoyant weight). Finally, we extracted both broad-sense (H^2) and narrow-sense (h^2) heritability estimates for the same trait where both were reported together in order to examine differences between H^2 vs. h^2; however, this occurred only for a single study (Carlon, Budd, Lippé, & Andrew, 2011).

The above resulted in a total of 103 unique heritability values estimated using a number of methods (see Supplementary Text S1 for a description of the different methods used). Of the 103 total estimates, eight were further excluded on the basis of statistical issues for one of two reasons: (1) there was insufficient variation in relatedness among individuals to properly assess heritability (one study with one estimate), or (2) there was insufficient or expected null variation in the phenotype being examined (two studies, with one and six estimates each). The latter was the case when studies estimated heritabilities associated with coral mortality or bleaching while in ambient conditions, which results in little to no phenotypic variation from which to calculate narrow-sense heritability (i.e., none of the corals bleached or died). This left 95 unique and valid heritability estimates from 19 studies.

Pre-processing

Heritability is calculated as a proportion of total phenotypic variation, and thus is constrained to fall between zero and one (Falconer & Mackay, 1996). Because most classical meta-analytical statistical models assume normally-distributed uncertainty, transformation of our estimates prior to meta-analysis was necessary (Lin & Xu, 2020; Wolfgang Viechtbauer, 2010). Thus, we converted point estimates of heritabilities and associated standard errors (SE) to 95% confidence intervals, then transformed both the point estimates as well as the upper and lower 95% confidence (or Bayesian credible) limits to the natural logarithmic scale using the transformation:

$$h_T^2 = ln[h^2 + 0.2] \tag{1}$$

with a horizontal displacement of + 0.2 to avoid excluding lower h^2 CIs that had slightly negative values when the point estimate was close to zero (see Supplementary Text S2 and Supplementary Code Documentation A for details).

There were four estimates from two studies that did not report any associated SE or CI values, and another three estimates whose lower CI values (when calculated from the SE) were less than -0.2, which prevented their transformation to the ln-scale. To include these data in the meta-analysis but down-weight their leverage on the overall analysis, we fit a quantile regression through the 95th quantile of transformed SE vs. transformed h^2 (Koenker, 2020; Koenker & Hallock, 2001) using only heritability estimates that were able to be transformed to the ln-scale. value of the heritability on the transformed scale (h^2_T) to predict SE_T values. We then used this fitted equation ($SE_T = 0.255 - 0.452 \cdot h^2_T$) to interpolate missing

SE_T values, making the conservative assumption that they would have values at the upper 95th quantile (i.e., among the most uncertain estimates).

Factors of interest

We identified five explanatory factors present in most studies: trait type, heritability type, life stage, growth form, and temperature manipulation (Table 1). Differences in heritability estimates among specific coral/symbiont species were also of interest; however, most studies examined only a single species and there was little overlap in species across studies, with the exception of a number of studies examining *Acropora millepora* heritability.

Table 1. Explanatory factors and covariates examined in the meta-analysis of coral heritability estimates

Factor/Covariate	Levels	Definition
Heritability type	Broad-sense heritability, H^2	The proportion of phenotypic variation explained by all genetic effects, which includes sources of variance associated with additive, dominance, and epistatic effects
	Narrow-sense heritability, h^2	the proportion of phenotypic variation explained by additive genetic effects
Trait type	Gene expression	Up- or down-regulation of various genes involved in intracellular stress pathways
	Photochemistry	Measures of symbiont photochemistry, chromoprotein content
	Growth	Coral or corallite growth measures including calcification rates, buoyant weight change, larval areal expansion, linear extension, and new growth branches
	Nutrient content	Total protein or carbohydrate content present in hosts or whole holobiont tissues
	Bleaching	Symbiont cell densities or change in cell densities, bleaching index scores (a proxy for symbiont cell density), and Chlorophyll A content (correlated to symbiont cell density)
	Morphology	Static intraspecific corallite measurements and larval volumes upon birth

	Symbiont community	Symbiont community indices (Leinster and Cobbald's *D*) and proportion of symbionts that are more the thermally-tolerant species (*Durusdinium* spp.)
	Immune response	Catalase and phenoloxidase activity within holobiont tissues
	Survival	Measures of survival/mortality/settlement success, including counts of settlement success or survival, percent survival/mortality at the end of a fixed period, larval survival through high temperatures, or differences in survival between control and temperature treatments
	Gamete compatibility	π-value, the percent larval contribution of various sires to various dams. Excluded from meta-analysis due to the presence of only a single estimate
Coral life stage	larvae	Estimates for free-swimming gamete or planula larvae stages up to successful settlement
	juvenile	Estimates from post-settlement to sexually mature adult
	adult	Estimates from colonies after sexual maturity or using coral nubbins
Coral growth forms	branching	Arborescent form; tree-like branching extensions
	corymbose	Finger-like extensions
	massive	Ball- or boulder-shaped corals
	encrusting	Low-spreading corals often occurring on hard, rocky substrates

	columnar	Upwards-growing cylindrical corals
Temperature difference	covariate	Difference (in +°C) between the study's reported control or ambient temperature and the heat treatment temperature

Reported heritability estimates

We collected a total of 95 valid heritability estimates from 19 independent studies of scleractinian corals (Fig. 1). Three studies (Császár, Ralph, Frankham, Berkelmans, & van Oppen, 2010; Quigley, Randall, van Oppen, & Bay, 2020; Wright et al., 2019) each involving multiple trait types, provide 59% of all heritability estimates (Fig. 1-left). There was an even split of studies (9:9 studies) examining narrow-sense (h^2) and broad-sense (H^2) heritability, with one study (Carlon et al., 2011) reporting both heritability types. However, the number of raw estimates produced by each study differed markedly, with more broad-sense estimates (n = 70) than narrow-sense (n = 25). The studies also differed in terms of which trait type was reported, with most studies reporting only a single estimate (12 studies), and the other seven studies reporting on two to six distinct trait types. Survival was the most frequently studied trait type (nine studies, 15 estimates), while bleaching (six studies, 10 estimates) and growth (six studies, 23 estimates) were also diversely studied. The latter often included comparisons of multiple species or symbionts within the same study, resulting in a large number of estimates. Most trait type estimates originated from least two independent studies estimates, save for immune response (four estimates from one study) and gamete contribution (one estimate). We therefore interpret the results for immune response with caution, given that they all belong to the same study, and excluded the single estimate for gamete compatibility from the subsequent meta-analysis. Notably, there were limited studies of the heritability of coral reproduction and fecundity, and there were no heritability estimates of thermal optimum (T_{opt}), measures of performance breadth (e.g., B80, B95), or critical thermal limits ($CT_{max/min}$). Only three studies reported the total phenotypic variation and/or the level of additive genetic variation, which would be particularly useful for calculating metrics of evolvability (Ma, Lü, Wang, & Wan, 2014; Visscher et al., 2008). We therefore recommend that future studies report these estimates of variation.

For life stage, there were 63 estimates (from eight studies) for adults, 18 estimates for juveniles (from seven studies), and 14 for larvae (from five studies), with every study reporting on only a single life stage save for two reporting on two different life stages (Carlon et al., 2011; Quigley, Willis, & Bay, 2017). There was similar lack of overlap across heritability types (70 broad-sense vs. 25 narrow-sense heritability estimates across 10 vs. 10 studies, respectively), with only one study having both valid broad-sense and narrow-sense heritabilities (Carlon et al., 2011). Across coral growth forms, there were 61 estimates of corymbose corals (from seven studies), 21 estimates for massive corals (from eight studies), nine estimates for branching/arborescent (from six studies), and three and one estimates for encrusting and columnar corals, respectively (each from a single study). Finally, 14/19 studies (83/95 estimates) recorded temperatures, and thus the effect of temperature manipulation on heritability could be examined for these studies. However, the difference between the manipulated vs. control/ambient temperatures varied substantially across each study, with all temperature manipulation differences being positive (i.e., control/ambient conditions were always less than the treatment temperatures) but positively skewed (a few experiments used temperatures that differed by 10°C between control and high temperature treatments, but most used smaller elevations of temperature). For example, 29 estimates of heritability originated from control/ambient conditions (from seven separate studies), while 54 estimates were obtained from above-ambient temperature treatments (from 12 studies). Additionally, there was limited overlap of control and heated temperature differences for some trait types, making it difficult to compare the effect of temperature for trait types such as symbiont community (two control estimates), morphology (one control estimate) and gene expression (nine temperature differences, but no control estimates).

Meta-analysis approach

We used the *R* package *metafor* (Wolfgang Viechtbauer, 2010) to fit mixed-effects meta-analytic models to $ln(h^2 + 0.2)$ transformed heritability estimates (h^2_T) and associated estimate sampling variance, while accounting for both fixed and random effects. Due to some missing combinations of explanatory factors within the dataset (e.g., not all traits were measured for all life stages, or for all coral growth forms), the complete dataset only allowed us to consider additive effects of trait type, heritability type, life stage, and growth form in an overall analysis. Temperature was not controlled for or measured in all studies, and thus was excluded as a covariate at this stage. To further assess the robustness of this model and examine interactions, we then analyzed subsets of the complete dataset to test for: (a) trait × life stage interactions, (b) trait × heritability interactions, and (c) main effects and interactions involving growth form. Finally, we examined a subset of the complete data that reported treatment temperature differences relative to ambient temperature, including trait × temperature difference interactions and additive effects of life stage, heritability type, and growth form. All models were fit using more conservative t-distribution approximations of confidence intervals in the case of multi-level random effect models, and final models fit using the more conservative Knapp and Hartung (2003) adjustment for single-level random effect meta-models when multi-level random effects structures were not selected during model selection (VanAert & Jackson, 2019; Wolfgang Viechtbauer, 2010).

We considered the top model for each analysis as the model with the lowest Akaike's Information Criterion, corrected for small sample sizes (AICc). We considered this model a substantial improvement over other candidate models when the difference in AICc scores (ΔAICc) was greater than two (Burnham & Anderson, 2004). We followed the four-step model selection strategy outlined in Zuur et al. (2007, 2009): (1) define the 'beyond optimal' fixed effects structure – that is, the most conceivably complex yet biologically relevant fixed effects possible, (2) select (via the lowest AICc value) the optimal random effects structure for models fit using restricted maximum likelihood (REML), (3) select (via the lowest AICc value) the optimal fixed effects structures for models fit using maximum likelihood, (4) re-fit the final model using REML. Study and species were highly confounded and precluded the inclusion of both as random effects within the same model. Thus, we fit models using one of the following random effects structures: estimate ID only (1|estimate ID), study ID only (1|study ID), species only (1|species), estimate ID nested within its respective study ID (1|study ID/estimate ID), estimate ID nested within species (1|species/estimate ID), or a random effect variance fixed at zero.

After fitting models for each analysis, we examined the level of among-study heterogeneity (τ^2) using the I^2 index (Higgins & Thompson, 2002), which provides an estimate of the among-study variance relative to the total variance not explained by the fixed effects. We used the Q_E statistic to test for significant residual heterogeneity after accounting for fixed effects (W. Viechtbauer, López-López, Sánchez-Meca, & Marín-Martínez, 2015). Higher proportions of heterogeneity indicate that variation in true effect size of heritability is a distribution of study effects (i.e. due to methodological or other study differences), whereas lower heterogeneity indicates that any among-study heterogeneity is likely small relative to measurement error, so studies are measuring a common heritability value (Ban, Graham, & Connolly, 2014; Higgins & Thompson, 2002). We report the pseudo-R^2 for meta-analytical models, computed by comparing the difference in $\hat{\tau}^2$ estimated using models including fixed effects ($\hat{\tau}^2_{ME}$) vs. a model with the same random-effects structure, but with no fixed effects ($\hat{\tau}^2_{RE}$): $R^2 = (\hat{\tau}^2_{RE} - \hat{\tau}^2_{ME})/\hat{\tau}^2_{RE}$ (Raudenbush, 2009). Where significant interactions were found between factors with more than two levels, we employed simultaneous tests for testing multiple general linear hypotheses determined by visual inspection of marginal estimates, and report p-values adjusted using the single-step method.

Model standardized residuals were plotted against fitted values to look for strong deviations from normality, and data were simulated using the fitted model and plotted with the true data to assess model performance. We assessed the presence of publication bias by plotting the model residuals by their precision (inverse of standard error) to produce a funnel plot (Møller & Jennions, 2001). We also calculated the Rosenberg fail-safe number, which indicates if model findings are robust to any apparent publication bias if the number is greater than five times the number of studies plus ten (Rosenberg, 2005; Rosenthal, 1991). Finally, we used Cook’s distances to determine highly influential points for each model (Cook & Weisberg, 1982).

High heritability of coral traits

The results of the overall analysis reveal that the heritability of coral traits has considerable heterogeneity that can be explained by trait type. The final selected model used trait type as the sole explanatory factor, and had substantial residual heterogeneity ($QE_{85} = 478$, $p < 0.0001$), with the total percent of variance not attributable to sampling error, $I^2_{total} = 91\%$, composed of predominantly between-study variance ($I^2_{study} = 57\%$ of total), but with substantial within-study variance ($I^2_{estimate} = 34\%$ of total) as well. In all models, random effects involving estimate ID, study ID, or estimate ID nested in study ID were always selected, with no support for random effects involving species.

Trait type was by far the most important predictor of heritability across all studies (Table S1), with traits such as gene expression having low heritability ($h^2 < 0.25$); photochemistry, growth, nutrient content, symbiont abundance, morphology, and symbiont community having moderate heritability ($h^2 = 0.25–0.5$); and immune response and survival/larval settlement success having the highest heritability estimates ($h^2 > 0.5$; Fig. 2). However, models that included additive effects of trait type + heritability type and trait type + life stage were supported by model selection (i.e., they fit almost as well as the model with trait type alone). However, the effect sizes of both were small relative to the effect of different trait types (Table S2; Fig. S2). For example, broad-sense heritabilities were 1.4–2.1 times higher than narrow-sense heritability and varied by a factor of 1.1 to 2.1 across different life stages (within the same trait type), whereas trait type differences were much larger, being up to 6.7 times larger in the case of survival vs. gene expression. Estimates for the mean heritability of different traits ranged from low to high, but most traits were moderately heritable (Fig. 2). Gene expression traits had the lowest estimated mean heritability (h^2=0.12), while survival had the highest (h^2=0.79), followed by immune response (h^2=0.62), with the other estimated trait mean heritabilities falling between 0.26–0.50 (Fig. 2). One estimate in particular, a value of 0.92 for *Acropora millepora* (Wright et al., 2019), drove the high heritability of immune response (Cook's distance = 5.2), while all other Cook's distances were relatively low (< 2). Thus, the estimated high heritability of immune response should be interpreted cautiously.

The final model's funnel plot exhibited no signs of publication bias (Fig. S1), and the fail-safe number (i.e. the number of null-result studies required to overturn a significant result) was an order of magnitude above five times the number of studies plus ten (1,285 >> 100), indicating that the model findings are robust to any underlying publication bias.

Heritability across trait types in other organisms

Heritability differences across trait types have been widely reported in other taxa (Flood et al., 2016; Mousseau & Roff, 1987; Polderman et al., 2015; Wheelwright et al., 2014). Life history traits closely tied to fitness (e.g., longevity, fecundity) are often maintained due to strong stabilizing selection and thus exhibit lower heritability compared to morphological, physiological, and behavioural traits (Mousseau & Roff, 1987; Price & Schluter, 1991; Teplitsky et al., 2009; Wheelwright et al., 2014). However, traits may also have low heritability due to a large contribution to total variance by non-additive genetic variation, environmental variation, or through maternal effects (the latter likely to be less pronounced in broadcast spawning corals than in organisms with higher levels of parental care). In our analysis, gene expression had the lowest heritability, which is consistent with many other studies noting the low heritability of mRNA (i.e., the 'missing heritability' problem, Zuk et al. 2012; Yang et al. 2014). While the exact cause of missing heritability for gene expression measures has yet to be determined, it may be due to highly variable gene expression both within (i.e. low repeatability) and among individuals, or to epistatic gene interactions, or some combination of both (Yang et al., 2014; Zuk et al., 2012). The heritability of symbiont community composition was much higher than heritabilities estimated for the diversity of human gut microbes ($h^2 = 0.019$), which is predominantly environmentally rather than genetically-determined (Rothschild et al., 2018). However, beneficial microbes that are related to metabolic health, such as gut bacteria of the family Christensenellaceae, and microbiomes of mice in controlled laboratory environments (Org et al. 2015), show much higher heritabilities of h^2=0.3–0.6, more consistent with our findings. Photochemical traits were estimated to have modest heritability in our analysis; however, only two studies which included only broad-sense estimates were available (H^2 = 0.26). In plants, broad-sense heritability of photosynthetic traits is variable but can be very high (e.g., H^2 = 0.87, 0.5 – 0.99, and 0.99; Geber and Dawson 1997, Flood et al. 2016, and Tuhina-Khatun et al. 2015, respectively). Moderate narrow-sense heritability estimates, similar to those reported here, have been reported for narrow-sense heritability of maximum quantum yield in plants (h^2 = 0.12–0.34) (Qu et al., 2017). Heritability associated with bleaching and symbiont abundance in corals (often using chlorophyll content as a proxy) was estimated overall as h^2 = 0.36, which is similar to estimates of broad-sense heritability of chlorophyll content in plants (e.g., h^2 = 0.44-0.49 in *Oryza sativa* L., Tuhina-Khatun et al. 2015).

Life stage and heritability type, but not growth form, mediate trait heritability

Using a data subset to examine trait type and life stage interactions, a model of trait type × life stage + heritability type with a random effect of estimate ID only was preferred under model selection (Table S3). Other analyses of trait type versus heritability type interaction and trait type and growth form interaction found further support for a trait type × life stage interaction (see Supplementary Text S3). The final meta-model had moderate levels of heterogeneity among estimates (QE_{55} = 96, p = 0.0005; I^2_{total} = 47%) and fixed effects helped explain much of the variation in heritability estimates (pseudo R^2 = 78%). Parameter estimates for all trait types were similar to the previous overall model estimates (Fig. 3; Fig. S3; Table S4), but there were significant interactions for growth and bleaching in juveniles relative to other life stages as well as for nutrient content in adults (Fig. 3; Table S4). Cook's distances for the trait type × life stage + heritability type model were low overall (≤ 2), but three points had moderate leverage on the analysis (Cook's distance = 2.9–3.9), but the growth:juvenile interaction term remained important when any or all were excluded from the analysis. Coral growth form was never an important predictor of heritability, and species was never selected as an important random effect, suggesting that taxonomic differences may be too small or variable to detect, given the data currently available.

Life stage had a strong effect for certain trait type–heritability type combinations (Fig. 3; Table S4). For example, the estimated narrow-sense h^2 for bleaching metrics in adults was 9.1 times the same h^2 for juveniles, and two times the bleaching H^2 value in adults versus larvae. Growth and nutrient content broad-sense heritability also differed across life stage, with adult growth H^2 being 3.1 times that of juveniles and nutrient content H^2 being 3.9 times greater in larvae vs. adults. In contrast, the effect of heritability type was relatively weak (1.4 to 2.5–fold higher for broad-sense heritabilities vs. narrow-sense when controlling for trait type and life stage) compared to the effect of trait type on heritability, which was up to 13.2 times higher heritability when comparing h^2 between juvenile bleaching vs. survival (Fig. 3; Table S4). However, this difference in broad- vs. narrow-sense heritability type indicates the presence of substantial but not overwhelming non-additive genetic variation as a portion of the total genetic variation present in broad-sense heritability.

Low adaptive potential of juvenile growth and bleaching

Juvenile growth was much less heritable relative to adult growth, while bleaching was less heritable in juveniles relative to both larvae and adults, highlighting the differential adaptive potential of coral life stage to selection for some trait types. This reduced bleaching heritability from larvae to juveniles may be the result of previous strong stabilizing selection on growth and bleaching traits in juveniles, thus driving reduced additive genetic variance through the fixation of alleles and resulting in lower heritabilities compared to other traits (Fisher, 1930; Teplitsky et al., 2009). Indeed, bleaching events likely represent a strong selective pressure for juvenile corals (Dajka et al., 2019; T. P. Hughes et al., 2019). Similarly, reductions in growth may result in increased mortality due to overgrowth competition and size-dependent predation (Doropoulos, Ward, Marshell, Diaz-Pulido, & Mumby, 2012; Madin et al., 2014; Vermeij & Sandin, 2008). There is also evidence that increases in additive genetic variance (V_A) may occur via mutation accumulation across an organism's lifetime (Wilson et al. 2008b). Moreover, reduced importance of local environment with age can result in reduced relative total variation, V_P (e.g., the Wilson effect, Bouchard Jr. 2013). Both of these processes can therefore result in older life stages having higher heritability estimates. Making the distinction between these processes requires examining changes in V_A and V_P across an organism's lifetime, which no coral studies have done to date.

Increased disturbances related to anthropogenic climate change are likely to select for different species traits and communities (Herben, Klimešová, & Chytrý, 2018; Pratchett, McWilliam, & Riegl, 2020), but little is known regarding selection on life stages within the same trait. With increased frequency of bleaching events resulting in more free space being made available to coral recruits, the adaptive potential of juvenile coral growth rates may determine which corals become predominant in future communities. However, negative trade-offs between bleaching and growth have been observed for coral symbionts (Berkelmans & Van Oppen, 2006; Cunning, Gillette, Capo, Galvez, & Baker, 2015; Little, Oppen, & Willis, 2004) and juvenile coral hosts (Carly D. Kenkel, Almanza, & Matz, 2015; Morikawa & Palumbi, 2019), such that more thermally-specialized holobionts may exhibit reduced growth rates in ambient conditions. If these phenotypic trade-offs are genetically based, the genetic correlation between the two may constrain their evolution to climate change and thus would explain why the estimated heritabilities for juvenile bleaching and growth are lower compared to other life stages. More study of genetic correlations in juveniles is required to understand how juveniles are likely to respond to selection due to climate change; however, one laboratory selection experiment on adult fragments from *Acropora millepora* did find a significant positive genetic correlation ($r_g = 0.19$) between bleaching and growth (Wright et al., 2019). With increased study of narrow-sense heritabilities and especially genetic correlations among traits and at different life stages, the constraints on corals' responses to environmental change will come into sharper focus.

Confounding sources of variation

Our review of the literature highlights some potential sources of bias in heritability estimates that are not well-controlled in coral studies to date. Studies that do not use shared common environments may overestimate heritability by confounding environment-driven phenotypic variation with additive genetic variation, such as when related individuals occur in the same environment and thus acclimatize similarly. Importantly, no studies examining adult corals raised corals to adulthood in a shared common environment, and thus do not control for preconditioning or canalization differences among colonies (Putnam & Gates, 2015). However, coral larvae and juveniles were almost always raised in shared common environments during spawning and fertilization, thus larvae and juvenile heritability estimates are less likely to be overestimated due to this phenomenon. Despite this, there are a number of traits with higher heritability for larvae and/or juveniles relative to adults, such as survival, gene expression, nutrient content, and morphology (Fig. 3). This suggests that, at least for these traits, the variation associated with preconditioning and plasticity is unlikely to be particularly large relative to the additive genetic variance. Moreover, visual inspection of residuals suggested no additional unexplained variation that might be associated with whether or not a shared common environment was used (Fig. S9 in Supplementary Code C).

Our results are also affected by other sources of phenotypic variation not accounted for in present studies, such as parental and epigenetic effects. Parental effects may have a larger influence on heritability than previously assumed (C. D. Kenkel, Setta, & Matz, 2015; Noble, Mcfarlane, Keogh, & Whiting, 2014), and may be especially important for brooding corals in which the offspring develops within the parent colony as well as for species inheriting their symbiont communities directly from parents (i.e. vertical transmission) (C. D. Kenkel et al., 2015; Quigley et al., 2017). Vertically-transmitting brooders and broadcast spawning species make up a minority of species examined (3/19 and 9/19, respectively), with the remaining being horizontally-transmitting spawners. Similarly, the number of heritability estimates from vertical transmitters made up only 9/95 and 16/95 heritability estimates, respectively, and thus parental effects via brooding and/or vertical transmission would have impacted a minority of estimates. Epigenetic effects may also inflate heritability estimates (Putnam & Gates, 2015). In studies of multicellular animals, there has been little support for epigenetic inheritance via CgP methylation (Torda et al., 2017), although at least one recent study in corals has found such evidence (Liew et al., 2020). Further evidence is needed to determine if epigenetic changes confer fitness benefits similar to additive genetic effects (Torda et al., 2017), thus future studies aiming to separate phenotypic variation specific to parental effects, symbiont composition, epigenome, and additive genetic effects would be especially valuable.

Manipulated temperature has negligible effect on heritability

When examining only studies that controlled for temperature, the magnitude of the experiment temperature difference relative to ambient or control conditions had only a marginal effect on the recorded heritability estimate (Fig. 4). The temperature difference values were all positive and positively skewed, thus we square-root transformed the temperature difference data in order to reduce the leverage of estimates obtained from studies using these large temperature differences. After subsetting the data to exclude studies that did not report the temperature treatment used relative to ambient conditions, we examined whether an interaction between trait type and temperature difference was supported. Model selection favored a model of trait + heritability type, with some support for alternative models of trait type only and trait type × temperature difference (Table S9; ΔAICc = 0.50 and 1.89, respectively) using random effects of estimate ID nested in study ID. The trait + heritability type model had similar effect sizes compared to those in our analyses presented above (Fig. S6; Table S10). The effect of trait type in the trait type × temperature model (3rd-optimal model) saw heritability differences up to a factor of 3.4–4.6 when the temperature was increased +1°C to +3°C above ambient. However, within the same trait type, temperature alone had a reduced effect, with heritability differences between a factor of 0–2.1 and 0–1.6 for +1°C and +3°C, respectively. More specifically, temperatures +1°C above ambient resulted in immune response heritability increasing by a factor of 2.1, while an increase of +3°C above ambient would increase heritability by a factor of 1.6. This interaction was primarily driven by a single estimate of immune response (Cook's distance = 7.6), and when removed, resulted in no strong interactions between trait type and temperature. Within other traits, the effect of temperature was even less pronounced. Bleaching traits were decreased by 28–33% for an increase in temperature of +1–3°C (though this was not significant). Other traits such as growth, photochemistry, and survival all showed marginal declines in heritability with increasing temperature difference (~3–5% decrease in heritability with +1–3°C). Separate analyses examining temperature as a categorial variable (ambient vs elevated), as well as analyses omitting ambient treatments all resulted in similar weak to non-existent effects of temperature on heritability (Fig. S7-8; Tables S11-14), suggesting a limited effect of manipulated temperature on heritability across studies. Since a model of trait type + heritability type was preferred over the model of trait type × temperature manipulation (Table S9), and with the inclusion of heritability type precluding the ability to model a trait × temperature interaction, we fit an additive model of trait type, heritability type, and temperature difference to estimate the marginal effect of temperature and found evidence for, at most, a very weak effect of temperature (Fig. 4).

Trait adaptation to warming temperatures

Our meta-analysis suggests that the capacity for corals to adapt to warming temperatures may be relatively consistent over short periods of moderately high temperature (e.g., +1–3°C, the temperature increases used in most of the studies we analyzed). However, this is contingent on the assumption that coral responses to temperature conditions in the lab are similar to their responses to temperatures in the field. Previous studies have found that many traits are expected to respond differently to climate change (Ahrens et al., 2020), that heritability measurements may change with temperature (Bubliy & Loeschcke, 2002), and that the rate of temperature increase employed in each study can also affect heritability (Chown, Jumbam, Sørensen, & Terblanche, 2009). Similarly, previous heritability studies in insects report trait-specific interactions with temperature (Bubliy & Loeschcke, 2002; Gunay et al., 2011). Current theory suggests that more extreme environments should produce increased selective pressures that may reduce heritability (Charmantier & Garant, 2005; Falconer & Mackay, 1996; Wilson et al., 2006). However, despite expectations based on theory and empirical results like those described above, differences in the temperature gradients used in each study did not predict the among-treatment differences in heritability estimates for corals. Specifically, temperature had negligible effect on the estimation of trait heritability, such that an increase of +1°C may increase high vs. low trait heritability by 4 to 9%, respectively, while an increase of +3°C results in an increase in heritability of 7 to 16% (changes that, if real, would be opposite of the predicted direction). These findings indicate that populations with sufficient genetic diversity are unlikely to experience a reduction in heritability associated with warmer temperatures, in turn suggesting substantial retention of the capacity to adapt in the face of ongoing temperature change.

Coral thermal performance and challenges to predicting future adaptation to climate change

The absence of an effect of temperature on trait heritability observed here could reflect differences among studies in the way temperature treatments were applied, and/or differences in how temperature effects were statistically modelled. Many traits of organisms are non-linearly related to temperature, and these relationships are captured by measuring thermal performance curves (TPCs). TPCs are quantified by subjecting individuals to increasing temperatures at a standardized rate while repeatedly measuring performance (Angiletta, 2009; Chown et al., 2009), to identify: (1) the value of maximal performance (P_{max}), (2) the temperature at which maximum performance occurs i.e., the thermal optimum (T_{opt}); (3) the performance breadth (e.g., B80, B95), and, somewhat related to the latter, (4) the limits of thermal performance (e.g., CT_{max}) (Angilletta, 2009; Bodensteiner et al., 2020; M. L. Logan et al., 2014). Measuring limits to thermal tolerance involves either static assays of survival time in a constant high temperature, such as heat knockdown time (Castañeda, Romero-Soriano, Mesas, Roff, & Santos, 2019; Ma et al., 2014), or dynamic assays involving gradually increasing temperature until failure, such as temperature-at-death and CT_{max} (Castañeda et al., 2019; Doyle, Leberg, & Klerks, 2011).

The way in which temperature was modelled in each of the studies analyzed herein – and consequently, which component of thermal performance was captured – is likely to affect the heritability estimated. For example, studies incorporating temperature treatment as a fixed effect and estimating heritability using a single model (Dixon et al., 2015; Lohr & Patterson, 2017; Manzello et al., 2019; Meyer et al., 2009), or studies that calculate heritability from the difference in trait values between low vs. high temperature treatments (Császár et al., 2010; Dziedzic, Elder, Tavalire, & Meyer, 2019; Yetsko et al., 2020) likely estimated the heritability of thermal sensitivity (i.e., how performance changes as temperature changes). Conversely, studies that used separate models for low-temperature and high-temperature treatments (Kirk et al., 2018; Quigley et al., 2020; Wright et al., 2019; Zhang et al., 2019) produced separate estimates of the heritability of performance under the two temperatures. One inherent problem with such an approach arises if there is little or no variation in the trait value for one of the treatment levels (e.g., no mortality of bleaching observed under control conditions or no observable growth when corals are placed in extreme heat). The absence of among-individual variation in performance in these cases means that the estimated heritability will always be near zero, regardless of any underlying additive genetic variation associated with the trait in question. For studies of thermotolerance, obtaining heritability estimates via differenced treatment values or as a fixed treatment effect (and thereby providing heritability estimates indicative of the trait's thermal sensitivity) is likely preferable, but ideally future studies would characterize responses based on many temperature points along the TPC to obtain CT_{max}, T_{opt}, and P_{max}.

In this review, we were unable to assess whether heritabilities associated with thermal sensitivity in performance were different from heritabilities of performance itself (Fig. S10). However, the evolution of both maximal performance and the thermal sensitivity are inherently linked by the shape of the TPC (e.g., a higher peak in the TPC would result in higher trait values and greater trait thermal sensitivity), and thus their relationship may be correlated (Janhunen et al., 2016). For example, with the evolution of higher upper thermotolerance (e.g., increasing CT_{max}), organisms may face reduced thermal performance breadth and thermal plasticity (Hoffmann et al. 2013; Comte and Olden 2017; Baker et al. 2018). Growth and the thermal sensitivity of growth are negatively correlated for one-year-old rainbow trout (*Oncorhynchus mykiss*) at low temperatures, but not at higher temperatures, thus while there is moderate heritability for both growth ($h^2 = 0.46$) and thermal sensitivity of growth ($h^2 = 0.24$), selection for higher growth is predicted to result in increased thermal sensitivity in future generations held at low temperatures, but unlikely to affect thermal sensitivity at higher temperatures (Janhunen et al., 2016). Similar trade-offs of growth vs. sensitivity have been observed as well in adult rainbow trout (Sae-Lim et al., 2015). Further complicating the matter, some genetic correlations among life history traits may be temperature-specific (reviewed in Sgrò and Hoffmann 2004), including cases where negative genetic correlations can become positive at higher temperatures and vice-versa. Thus, coral trait evolution may further be complicated by (currently unmeasured) genetic correlations across TPC metrics.

Conclusion

Our meta-analysis estimates relatively high heritability for some traits, such as survival and growth. This, coupled with the fact that heritability does not appreciably decline with increasing temperature manipulation, suggests the potential for coral adaptation to future conditions of weak to moderate climate change. Nevertheless, potential confounding factors that could bias some of our heritability estimates upwards remain to be explored, including the effects of preconditioning and canalization in adults, parental and symbiont effects, and transgenerational inheritance of CgP methylation. Recent evolutionary models of corals consider the heritability of the thermal optimum for corals, T_{opt}, to be anywhere from negligible (e.g., $h^2 = 0.01$) to low/medium (e.g., $h^2 = 0.16$–0.50) (Cropp & Norbury, 2020; C. A. Logan et al., 2021; Matz et al., 2020). However, there are no available estimates for coral thermal performance traits such as T_{opt}, CT_{min}, CT_{max}, and *B80*, and our knowledge of how TPC parameters co-evolve remains very limited. For example, the evolution of higher thermal optima (T_{opt}) may result in reduced maximal performance (P_{max}) or performance breadth (CT_{min}, CT_{max}, and *B80*). Other genetic trade-offs such as growth vs. thermotolerance for both corals and symbionts may exist, further constraining coral evolution to climate change. Future studies would ideally construct TPCs using multiple temperatures across a known pedigree of individuals in order to calculate heritabilities and associated trade-offs for TPC parameters across one or multiple traits. Combined with our current knowledge of trait heritabilities, this would allow better predictions regarding thermal evolution of corals in response to climate change. Nevertheless, our findings suggest that corals may be capable of adapting more rapidly to the thermal challenges imposed by climate change than previously thought.

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Data accessibility statement

All extracted heritability estimates and supplementary code are available at https://github.com/ecolology/heritability-meta.

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Figure Captions

Fig. 1. Heritability estimates ($N = 95$) of various traits across 19 studies of reef-building corals. Colour indicates the specific trait type (hue) and heritability type (broad-sense H^2 as lighter tint

circles, narrow-sense h^2 as darker shade). Left: Number of estimates reported in each study. Right: Point estimates of heritability and their associated 95% confidence/credible intervals (whiskers) on a logarithmic (*ln*) scale. Heritability estimates closer to one indicate higher heritability and thus the potential for higher rates of trait adaptation within the population. Dashed lines represent heritability estimates where standard errors/confidence intervals were imputed.

Fig. 2. Heritability estimates ± SE for the trait type-only model, not accounting for differences due to (i.e., pooled across) life stage and heritability type. Traits are sorted along the spectrum according to their overall relative heritability, with heritability closer to one indicating more heritable traits. The number of estimates included in the meta-analysis for each trait type are indicated below each error bar in grey. The gamete compatibility trait type is excluded due to its reliance on only a single study/estimate.

Fig. 3. Heritability estimates ± SE across trait types with multiple life stages (x-axis) and different heritability types (lighter points: broad-sense heritability; darker points: narrow-sense heritability). Associated sample sizes (number of original estimates) are adjacent to each point in grey.

Fig. 4. Heritability vs. study temperature difference (treatment temperature relative to ambient/control temperature) for each trait type and heritability type, with the size of each point represents its relative precision. Dashed lines indicate the estimated marginal mean effect of temperature difference, while accounting for trait type and heritability type effects. One square-root degree difference ($+1\sqrt{}°C$) translates to a mean increase in $ln[h^2+0.2]$ heritability of 0.03 ± 0.05 SE.