



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

Journal:	<i>Global Change Biology</i>
Manuscript ID	Draft
Wiley - Manuscript type:	Research Review
Date Submitted by the Author:	n/a
Complete List of Authors:	Bairos-Novak, Kevin; James Cook University, ARC Centre for Excellence in Coral Reef Studies & College of Science and Engineering Hoogenboom, Mia; James Cook University, College of Science and Engineering and ARCCOE for Coral Reef Studies van Oppen, Madeleine; University of Melbourne, School of BioSciences; Australian Institute of Marine Science, Connolly, Sean; Smithsonian Tropical Research Institute Washington DC Offices, School of Marine and Tropical Biology, and ARC Centre of Excellence for Coral Reef Studies; James Cook University, College of Science and Engineering and ARCCOE for Coral Reef Studies
Keywords:	adaptation, animal model, Breeder's equation, climate change, evolution, natural selection, Scleractinia, thermal tolerance
Abstract:	<p>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 97 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</p>

	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.

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

Running Title: Trait heritability in reef-building corals

Authors: Kevin R Bairos-Novak^{1*}, Mia O Hoogenboom¹, Madeleine JH van Oppen^{2,3}, Sean R Connolly^{1,4}

*Corresponding Author; ORCID iD: 0000-0002-0152-1452

Institutional Affiliations:

¹ College of Science and Engineering and ARCCOE for Coral Reef Studies, James Cook University, Townsville Queensland, Australia

² Australian Institute of Marine Science, Australia

³ School of BioSciences, University of Melbourne, Australia

⁴ Smithsonian Tropical Research Institute, Panama

Contact Information for Corresponding Author:

Phone: (+61) 1800 246 446

Email: kevin.bairosnovak@my.jcu.edu.au

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 97 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.

45 **Keywords:** adaptation, animal model, Breeder's equation, climate change, evolution, natural
46 selection, Scleractinia, thermal tolerance

For Review Only

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 (van Heerwaarden et al. 2016; Comte and Olden 2017; Sasaki and Dam 2019). Migration to new environments is similarly limited (Jump and Peñuelas 2005; Schloss et al. 2012; Walters and 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 (Logan et al. 2014a).

Adaptive evolution to a changing environment occurs when population genotype frequencies change to express traits or phenotypes that provide increased fitness (Falconer and 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 et al. 2008). There are two types of heritability: broad-sense heritability (H^2) and narrow-sense heritability (h^2).

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

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 and Mackay 1996). Narrow-sense heritability includes the strictly 'heritable' genetic component: additive genetic variation (V_A) of the trait of interest. Important caveats to the accurate calculation of either heritability type include the absence of any genotype-by-environment interactions, non-random environments among relatives, parental effects, or significant multigenerational epigenetic changes (Falconer and Mackay 1996; Visscher et al. 2008).

Narrow sense heritability can be used to predict and understand population trait 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:

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

In other words, an increase in the mean selected population CT_{max} of $+2^\circ\text{C}$ (S , the 'selection differential') translates to an expected increase in the next generation's average CT_{max} of $+1^\circ\text{C}$ (Lush 1937; Lande 1979; Falconer and Mackay 1996). 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: $R = 0.1 \cdot (32^\circ\text{C} - 30^\circ\text{C}) = +0.2^\circ\text{C}$, 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 (Mousseau and Roff 1987; Price and Schluter 1991; Wheelwright et al. 2014; Martins et al. 2019). 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 and Garant 2005; Teplitsky et al. 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 and Garant 2005; Wilson et al. 2008; Wheelwright et al. 2014). 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 et al. 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 et al. 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 (Pratchett et al. 2015; Madin et al. 2020). 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 et al. 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 and Garant 2005; Wilson et al. 2006; Wheelwright et al. 2014). Conversely, other studies have found no distinguishable relationship between h^2 and environmental

favourability (Rowinski and Rogell 2017), and others still identify positive correlations of h^2 with increasingly harsh environmental temperatures (Gunay et al. 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 (Wulff 2006; Pratchett et al. 2011; Hughes et al. 2018b), with 75% of global reefs now being considered threatened (Burke et al. 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 (Maynard et al. 2008; Guest et al. 2012; Sully et al. 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 (Hughes et al. 2018a; Lough et al. 2018), it remains unclear whether corals can adapt to the prolonged thermal stress they now experience with increasing regularity (Pandolfi et al. 2011; Hoegh-Guldberg et al. 2017). Models estimating long-term coral adaptation to climate change have assumed low to medium heritability of thermotolerance (e.g., $h^2 = 0.01\text{--}0.16$) (Matz et al. 2018; Cropp and Norbury 2020; Matz et al. 2020), despite some evidence of model outcomes being sensitive to the rate of adaptation (Bay et al. 2017; Cropp and Norbury 2020) and evidence of high heritability for coral survivorship in high temperatures (e.g., $h^2 = 0.75$: Kirk et al. 2018). 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 (Visser 2008; Logan et al. 2014a; Logan et al. 2014b).

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 (Lohr and Patterson 2017; Kirk et al. 2018; Wright et al. 2019; Zhang et al. 2019; Manzello et al. 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 et al. 2011).

The above resulted in a total of 103 unique heritability estimates. Of these, eight estimates 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 and Mackay 1996). Because most

classical meta-analytical statistical models assume normally-distributed uncertainty, transformation of our estimates prior to meta-analysis was necessary (Viechtbauer 2010; Lin and Xu 2020). 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:

$$h_T^2 = \ln[h^2 + 0.2] \quad (1)$$

with a horizontal displacement of + 0.2 to avoid excluding many lower h^2 CIs that had slightly negative values when the point estimate was close to zero (Supplementary Materials Text S1; Supplementary Code Documentation A). Additionally, the logarithmic transformation somewhat normalizes the asymmetric Bayesian posterior distributions that tended to characterize heritability estimates near the lower boundary. We tested seven other transformations of proportions, such as the logit transformation on SE as well as CI and the double arc-sine square root transformation of SE, all resulted in similar model selection outcomes (Supplementary Code Documentation A), suggesting that our results are robust to our choice of transformation.

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 first fit a quantile regression through the 95th quantile of transformed SE vs. transformed h^2 (Koenker and Hallock 2001; Koenker 2020) using only heritability estimates that were able to be transformed to the \ln -scale. value of the heritability on the transformed scale (h_T^2) to predict SE_T values. We then used this fitted equation ($SE_T = 0.255 - 0.452 \cdot h_T^2$) 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). By doing so, the data were able to be included in the analysis, but with reduced leverage on subsequent analyses.

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
<i>Heritability type</i>	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
<i>Trait type</i>	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 Cobbold's <i>D</i>) and proportion of symbionts that are more the thermally-tolerant species (<i>Durussdinium</i> 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
<i>Coral life stage</i>	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
<i>Coral growth forms</i>	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
<i>Temperature</i>	covariate	Difference (in +°C) between the study's reported control or ambient temperature and the heat treatment
<i>manipulation</i>		temperature

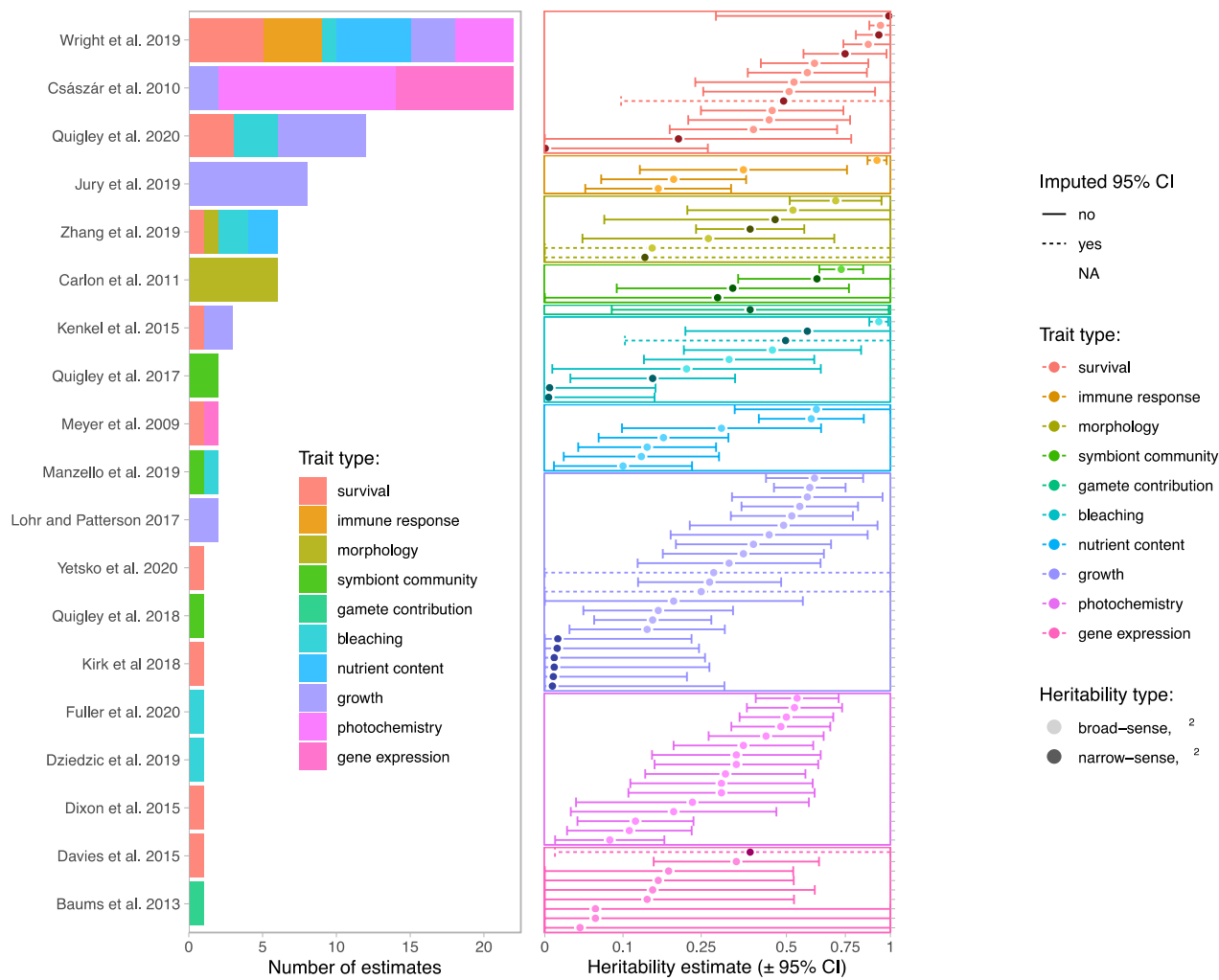
For Review Only

217 *Reported heritability estimates*

218 We collected a total of 95 valid heritability estimates from 19 independent studies of
 219 scleractinian corals (Fig. 1). Three studies (Császár et al. 2010; Wright et al. 2019; Quigley et al.
 220 2020) each involving multiple trait types, provide 59% of all heritability estimates (Fig. 1-left).
 221 There was an even split of studies (9:9 studies) examining narrow-sense (h^2) and broad-sense (H^2)
 222 heritability, with one study (Carlon et al. 2011) reporting both heritability types. However, the
 223 number of raw estimates produced by each study differed markedly, with more broad-sense
 224 estimates ($n = 70$) than narrow-sense ($n = 25$). The studies also differed in terms of which trait type
 225 was reported, with most studies reporting only a single estimate (12 studies), and the other seven
 226 studies reporting on two to six distinct trait types. Survival was the most frequently studied trait
 227 type (nine studies, 15 estimates), while bleaching (six studies, 10 estimates) and growth (six studies,
 228 23 estimates) were also diversely studied. The latter often included comparisons of multiple species
 229 or symbionts within the same study, resulting in a large number of estimates. Most trait type
 230 estimates originated from least two independent studies estimates, save for immune response (four
 231 estimates from one study) and gamete contribution (one estimate). We therefore interpret the results
 232 for immune response with caution, given that they all belong to the same study, and excluded the
 233 single estimate for gamete compatibility from the subsequent meta-analysis. Notably, there were
 234 limited studies of the heritability of coral reproduction and fecundity, and there were no heritability
 235 estimates of thermal optimum (T_{opt}), measures of performance breadth (e.g., B80, B95), or critical
 236 thermal limits ($CT_{max/min}$).

237 For life stage, there were 57 estimates (from eight studies) for adults, 24 estimates for
 238 juveniles (from seven studies), and 14 for larvae (from five studies), with every study reporting on
 239 only a single life stage save for one reporting on two different species at different life stages
 240 (Quigley et al. 2017). There was similar lack of overlap across heritability types (70 broad-sense vs.
 241 25 narrow-sense heritability estimates across 10 vs. 10 studies, respectively), with only one study
 242 having 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) and zero-inflated (due to an abundance of control/ambient treatments). For example, 29 estimates of heritability originated from control/ambient conditions (from seven separate studies), while 54 estimates were estimated in above-ambient temperature treatments (from 10 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).



260

261 **Fig. 1.** Heritability estimates ($N = 95$) of various traits across 19 studies of reef-building corals.
262 Colour indicates the specific trait type (hue) and heritability type (broad-sense H^2 as lighter tint
263 circles, narrow-sense h^2 as darker shade). Left: Number of estimates reported in each study. Right:
264 Point estimates of heritability and their associated 95% confidence/credible intervals (whiskers) on
265 a logarithmic (\ln) scale. Heritability estimates closer to one indicate higher heritability and thus the
266 potential for higher rates of trait adaptation within the population. Dashed lines represent
267 heritability estimates where standard errors/confidence intervals were imputed.

268

269 **Meta-analysis approach**

270 We used the *R* package *metafor* (Viechtbauer 2010) to fit mixed-effects meta-analytic
271 models to $\ln(h^2 + 0.2)$ transformed heritability estimates (h^2_T) and associated estimate sampling
272 variance, while accounting for both fixed and random effects. Due to some missing combinations of

273 explanatory factors within the dataset (e.g., not all traits were measured for all life stages, or for all
274 coral growth forms), the complete dataset only allowed us to consider additive effects of trait type,
275 heritability type, life stage, and growth form in an overall analysis. Temperature was not controlled
276 for or measured in all studies, and thus was excluded as a covariate at this stage. To further assess
277 the robustness of this model and examine interactions, we then analyzed subsets of the complete
278 dataset to test for: (a) trait \times life stage interactions, (b) trait \times heritability interactions, and (c) main
279 effects and interactions involving growth form. Finally, we examined a subset of the complete data
280 that reported treatment temperature differences relative to ambient temperature, including trait \times
281 temperature difference interactions and additive effects of life stage, heritability type, and growth
282 form. All models were fit using more conservative t-distribution approximations of confidence
283 intervals in the case of multi-level random effect models, and final models fit using the more
284 conservative Knapp and Hartung (2003) adjustment for single-level random effect meta-models
285 when multi-level random effects structures were not selected during model selection (Viechtbauer
286 2010; van Aert and Jackson 2019).

287 We considered the top model for each analysis as the model with the lowest Akaike's
288 Information Criterion, corrected for small sample sizes (AICc). We considered this model a
289 substantial improvement over other candidate models when the difference in AICc scores (ΔAICc)
290 was greater than two (Burnham and Anderson 2004). We followed the four-step model selection
291 strategy outlined in Zuur et al. (2007, 2009): (1) define the 'beyond optimal' fixed effects structure
292 – that is, the most conceivably complex yet biologically relevant fixed effects possible, (2) select
293 (via the lowest AICc value) the optimal random effects structure for models fit using restricted
294 maximum likelihood (REML), (3) select (via the lowest AICc value) the optimal fixed effects
295 structure for models fit using maximum likelihood, (4) re-fit the final model using REML. Study
296 and species were highly confounded and precluded the inclusion of both as random effects within
297 the same model. Thus, we fit models using one of the following random effects structures: estimate
298 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 and 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 (Viechtbauer et al. 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 (Higgins and Thompson 2002; Ban et al. 2014). 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 ($\hat{\tau}_{ME}^2$) vs. a model with the same random-effects structure, but with no fixed effects ($\hat{\tau}_{RE}^2$): $R^2 = (\hat{\tau}_{RE}^2 - \hat{\tau}_{ME}^2) / \hat{\tau}_{RE}^2$ (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 and 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 (Rosenthal 1991; Rosenberg 2005). Finally, we used Cook's distances to determine highly influential points for each model (Cook and Weisberg 1982).

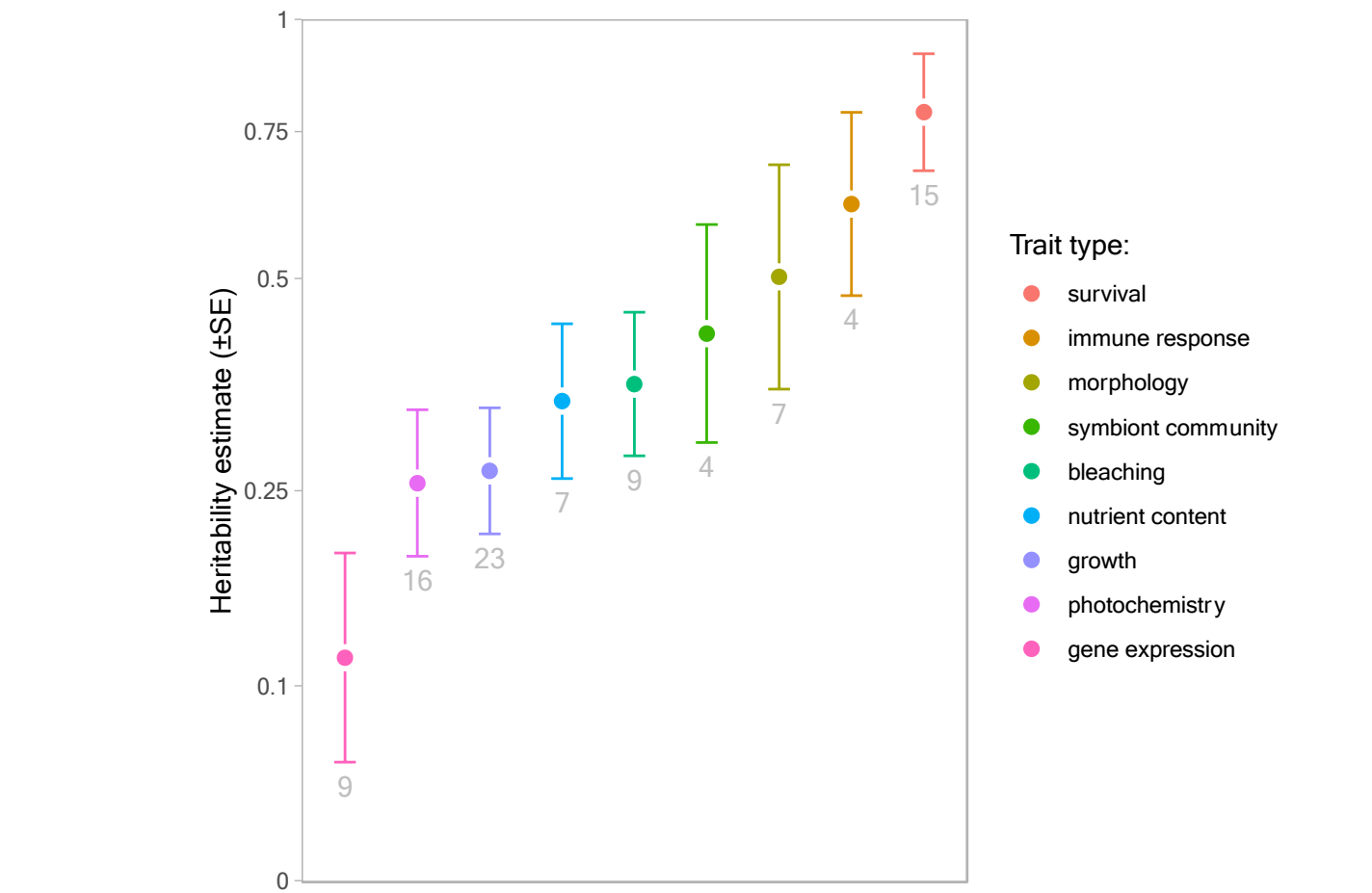
325 **High heritability of coral traits**

326 The results of the overall analysis reveal that the heritability of coral traits has considerable
 327 heterogeneity that can be explained by trait type. The final model using trait type as the sole
 328 explanatory factor had substantial residual heterogeneity ($QE_{85} = 459, p < 0.0001$), with the total
 329 percent of variance not attributable to sampling error, $I^2_{total} = 91\%$, composed of predominantly
 330 between-study variance ($I^2_{study} = 57\%$ of total), but with substantial within-study variance ($I^2_{estimate} =$
 331 34% of total) as well. In all models, random effects involving estimate ID, study ID, or estimate ID
 332 nested in study ID were always selected, with no support for random effects involving species.

333 Trait type was by far the most important predictor of heritability across all studies (Table
 334 S1), with traits such as gene expression having low heritability ($h^2 < 0.25$); photochemistry, growth,
 335 nutrient content, symbiont abundance, morphology, and symbiont community having moderate
 336 heritability ($h^2 = 0.25–0.5$); and immune response and survival/larval settlement success having the
 337 highest heritability estimates ($h^2 > 0.5$; Fig. 2). However, models that included additive effects of
 338 trait type + heritability type and trait type + life stage were supported by model selection (i.e., they
 339 fit almost as well as the model with trait type alone). However, the effect sizes of heritability type
 340 and life stage were weak relative to the effect of different trait types (Table S2; Fig. S2). For
 341 example, broad-sense heritabilities were 1.4–2.1 times higher than narrow-sense heritability and
 342 heritability varied by a factor of 1.5 to 2.4 across different life stages (within the same trait type),
 343 whereas trait type differences were much larger, being up to 6.7 times larger in the case of survival
 344 vs. gene expression. Estimates for the mean heritability of different traits ranged from low to high,
 345 but most traits were moderately heritable (Fig. 2). Gene expression traits had the lowest estimated
 346 mean heritability ($h^2=0.12$), while survival had the highest ($h^2=0.79$), followed by immune response
 347 ($h^2=0.61$), with the other estimated trait mean heritabilities falling between 0.26–0.50 (Fig. 2). One
 348 estimate in particular, a value of 0.92 for *Acropora millepora* (Wright et al. 2019), drove the high
 349 heritability of immune response (Cook's distance = 5.2), while all other Cook's distances were

350 relatively low (< 2). Thus, the estimated high heritability of immune response should be interpreted
351 cautiously.

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



356
357 **Fig. 2.** Heritability estimates \pm SE for the overall dataset model. Traits are sorted along the
358 spectrum according to their overall relative heritability, with values closer to 1 indicating more
359 heritable traits. The number of estimates included in the meta-analysis for each trait type are
360 indicated below each error bar in grey. The gamete compatibility trait type is excluded due to its
361 reliance on only a single study/estimate.

Heritability differences across trait types have been widely reported in other taxa (Mousseau and Roff 1987; Wheelwright et al. 2014; Polderman et al. 2015; Flood et al. 2016). 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 and Roff 1987; Price and 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; Lee et al. 2011; Polderman et al. 2015; Lloyd-Jones et al. 2017). 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 ($h^2 = 0.25$), 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 $h^2 = 0.37$, 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).

390

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

392 Using a data subset to examine trait type \times life stage interactions, a model of trait type \times life
 393 stage + heritability type and a random effect of estimate ID only was preferred under model
 394 selection (Table S3). Other analyses of trait type \times heritability type and trait type \times growth form
 395 found further support for a trait type \times life stage interaction (see Supplementary Materials Text S2).
 396 The final meta-model had moderate levels of heterogeneity among estimates ($QE_{56} = 94$, $p =$
 397 0.0007 ; $P_{total} = 45.9\%$) and fixed effects helped explain much of the variation in heritability
 398 estimates (pseudo $R^2 = 79\%$). Parameter estimates for all trait types were similar to the previous
 399 overall model estimates (Fig. 3; Fig. S3; Table S4), but there were significant interactions for
 400 growth and bleaching in juveniles relative to other life stages as well as a for nutrient content in
 401 adults (Fig. 3; Table S4). Cook's distances for the trait type \times life stage + heritability type model
 402 were low overall (≤ 2), but two points had moderate leverage on the analysis (Cook's distance = 4.0
 403 and 3.0), but the growth:juvenile interaction term remained important when either or both were
 404 excluded from the analysis. Coral growth form was never an important predictor of heritability, and
 405 species never was selected as an important random effect, suggesting that taxonomic differences
 406 may be too small or variable to detect, given the data currently available.

407 Life stage had a strong effect for certain trait type–heritability type combinations (Fig. 3;
 408 Table S4). For example, the estimated narrow-sense h^2 for bleaching metrics in adults was nine
 409 times the same h^2 for juveniles, and two times the bleaching H^2 value in adults versus larvae.
 410 Growth and nutrient content broad-sense heritability also differed across life stage, with adult
 411 growth H^2 being 3 times that of juveniles and nutrient content H^2 being 3.9 times greater in larvae
 412 vs. adults. In contrast, the effect of heritability type was relatively weak (1.4 to 2.5–fold higher for
 413 broad-sense heritabilities vs. narrow-sense when controlling for trait type and life stage) compared
 414 to the effect of trait type on heritability, which was up to 12.5 times higher heritability when
 415 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. The final model's funnel plot exhibited no signs of publication bias (see Supplementary Code Documentation B), and the fail-safe number was again large ($513 \gg 100$), indicating that the model findings are relatively robust to any underlying publication bias.

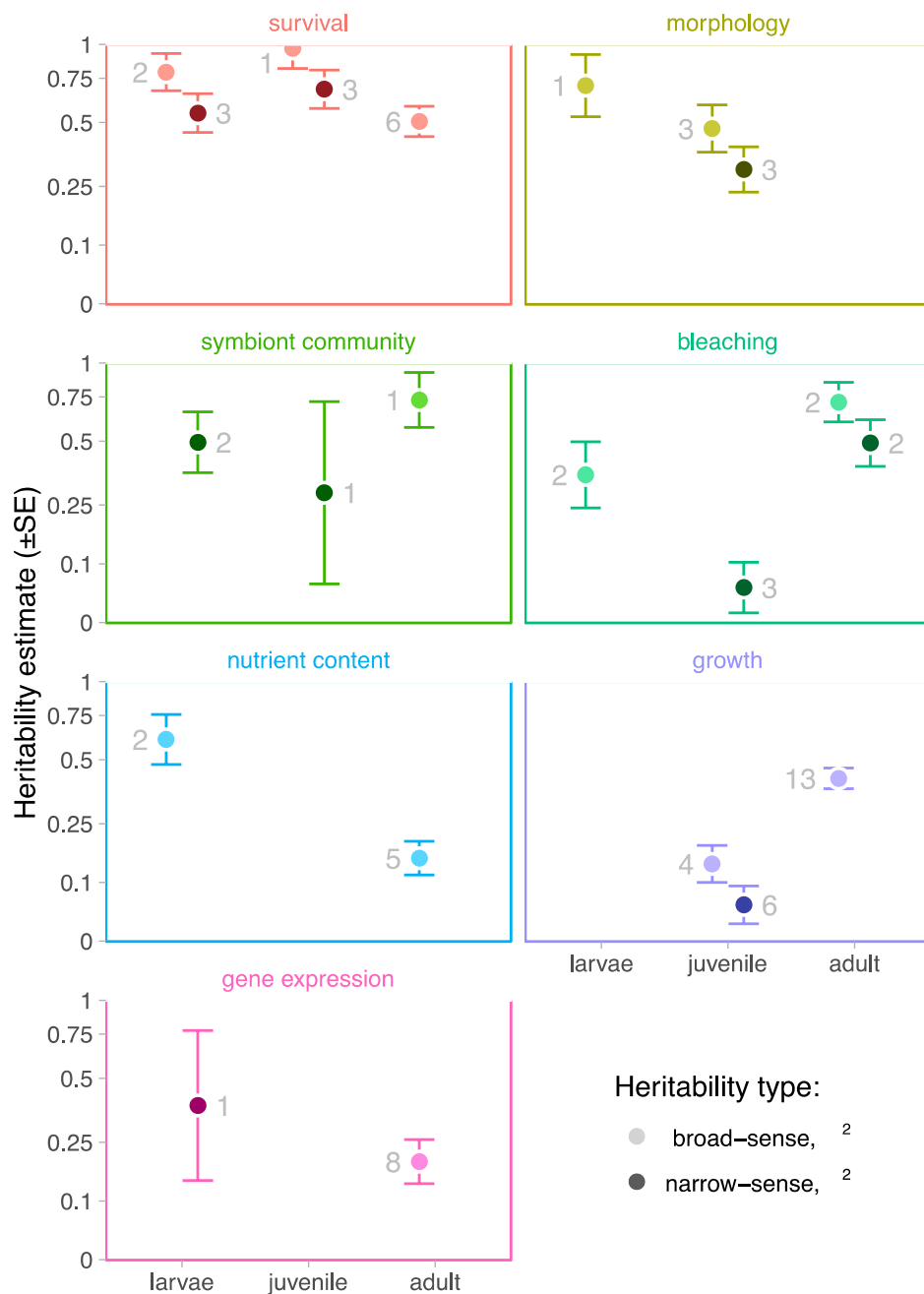


Fig. 3. Heritability estimates \pm SE across trait types with multiple life stages (x-axis) and different heritability types (lighter points: broad-sense heritability; darker points: narrow-sense heritability). Associated sample sizes (number of original estimates) are adjacent to each point in grey.

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 heritability 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; Hughes et al. 2019). Similarly, juvenile growth can determine long-term survivorship, with reductions in growth resulting in increased mortality due to overgrowth competition and size-dependent predation (Vermeij and Sandin 2008; Doropoulos et al. 2012; Madin et al. 2014).

Increased disturbances related to anthropogenic climate change are likely to select for different species traits and communities (Herben et al. 2018; Pratchett et al. 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 (Little et al. 2004; Berkelmans and Van Oppen 2006; Cunning et al. 2015) and juvenile coral hosts (Kenkel et al. 2015; Morikawa and 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.

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 an alternative model of trait type \times temperature difference (Table S9; $\Delta AIC_c = 1.89$) and random effects of estimate ID nested in study ID. Trait and heritability type had similar effect sizes compared to those in previous analyses (Fig. S6; Table S10). However, temperatures $+1^\circ\text{C}$ above ambient resulting in immune response heritability increasing by a factor of 2.1, while an increase of $+3^\circ\text{C}$ 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. The heritability of nutrient content was slightly increased with higher temperature ($\sim +5\text{--}7\%$ in heritability for $+1\text{--}3^\circ\text{C}$) while bleaching was decreased by 27–32% for an increase in temperature of $+1\text{--}3^\circ\text{C}$ (though this

was not significant). Other traits such as growth, photochemistry, and survival all showed marginal declines in heritability with increasing temperature difference (~1–4% decrease in heritability with +1–3°C). 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). Finally, separate analyses examining binary temperature data as well as non-zero temperature data 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.

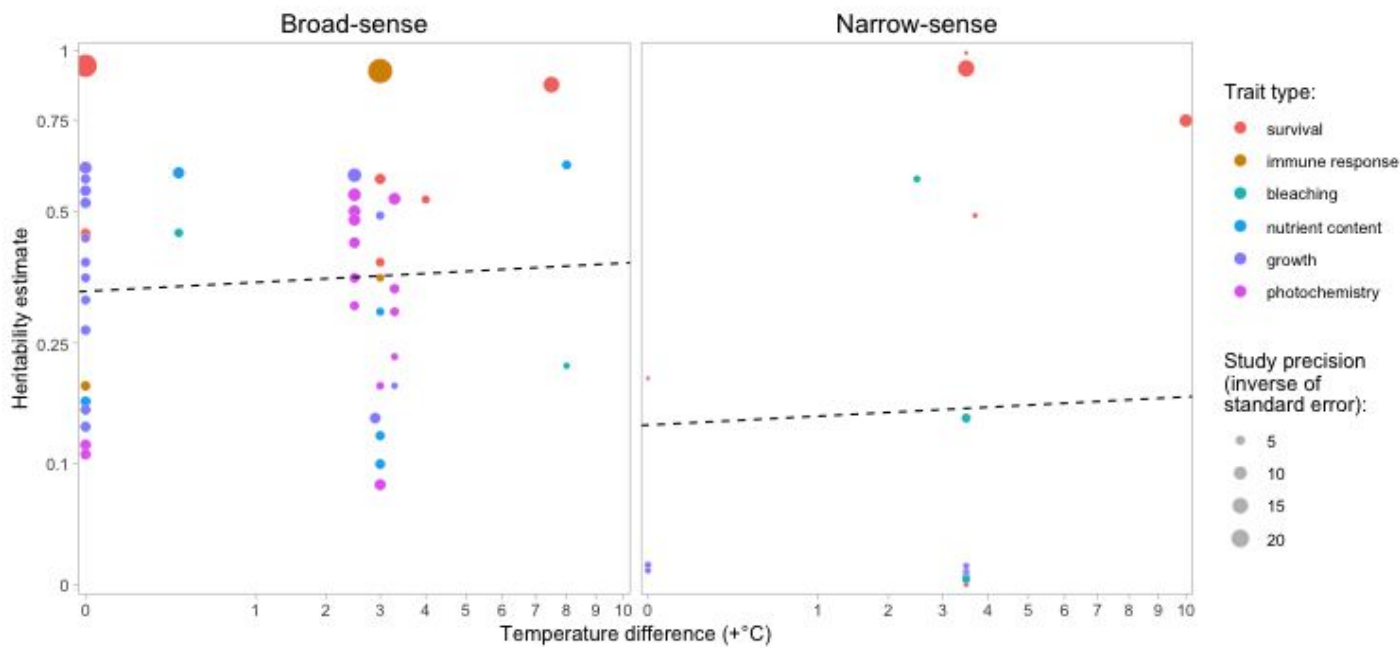


Fig. 4. Heritability vs. study temperature difference (treatment temperature relative to ambient/control temperature) for each trait type and heritability type, with the size of each point represents its relative precision. Dashed lines indicate the estimated marginal mean effect of temperature difference,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

493 *Trait adaptation to warming temperatures*

494 Our meta-analysis suggests that the capacity for corals to adapt to warming temperatures
495 may be relatively consistent over short periods of moderately high temperature (e.g., +1–3°C, the
496 temperature increases used in most of the studies we analyzed). However, this is contingent on the
497 assumption that coral responses to temperature conditions in the lab are similar to their responses to
498 temperatures in the field. Previous studies have found that many traits are expected to respond
499 differently to climate change (Ahrens et al. 2020), that heritability measurements may change with
500 temperature (Bubliy and Loeschke 2002), and that the rate of temperature increase employed in
501 each study can also affect heritability (Chown et al. 2009). Similarly, previous heritability studies in
502 insects report trait-specific interactions with temperature (Bubliy and Loeschke 2002; Gunay et al.
503 2011). Current theory suggests that more extreme environments should produce increased selective
504 pressures that may reduce heritability (Falconer and Mackay 1996; Charmantier and Garant 2005;
505 Wilson et al. 2006). However, despite expectations based on theory and empirical results like those
506 described above, differences in the temperature gradients used in each study did not predict the
507 among-treatment differences in heritability estimates for corals. Specifically, temperature had
508 negligible effect on the estimation of trait heritability, such that an increase of +1°C may increase
509 high vs. low trait heritability by 4 to 9%, respectively, while an increase of +3°C results in an
510 increase in heritability of 7 to 16% (changes that, if real, would be opposite of the predicted
511 direction). These findings indicate that populations with sufficient genetic diversity are unlikely to
512 experience a reduction in heritability associated with warmer temperatures, in turn suggesting
513 substantial retention of the capacity to adapt in the face of ongoing temperature change.

514

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

516 The absence of an effect of temperature on trait heritability observed here could reflect
517 differences among studies in the way temperature treatments were applied, and/or differences in
518 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 (Angilletta 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; Logan et al. 2014b; Bodensteiner et al. 2020). Measuring limits to thermal tolerance involves either static assays of survival time in a constant high temperature, such as heat knockdown time (Ma et al. 2014; Castañeda et al. 2019), or dynamic assays involving gradually increasing temperature until failure, such as temperature-at-death and CT_{max} (Doyle et al. 2011; Castañeda et al. 2019).

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 (Meyer et al. 2009; Dixon et al. 2015; Lohr and Patterson 2017; Manzello et al. 2019), or studies that calculate heritability from the difference in trait values between low vs. high temperature treatments (Császár et al. 2010; Dziedzic et al. 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; Wright et al. 2019; Zhang et al. 2019; Quigley et al. 2020) 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

545 associated with the trait in question. For studies of thermotolerance, obtaining heritability estimates
546 via differenced treatment values or as a fixed treatment effect (and thereby providing heritability
547 estimates indicative of the trait's thermal sensitivity) is likely preferable, but ideally future studies
548 would characterize responses based on many temperature points along the TPC to obtain CT_{max} ,
549 T_{opt} , and P_{max} .

550 In this review, we were unable to assess whether heritabilities associated with thermal
551 sensitivity in performance were different from heritabilities of performance itself (Fig. S9).
552 However, the evolution of both maximal performance and the thermal sensitivity are inherently
553 linked by the shape of the TPC (e.g., a higher peak in the TPC would result in higher trait values
554 and greater trait thermal sensitivity), and thus their relationship may be correlated (Janhunen et al.
555 2016). For example, with the evolution of higher upper thermotolerance (e.g., increasing CT_{max}),
556 organisms may face reduced thermal performance breadth and thermal plasticity (Hoffmann et al.
557 2013; Comte and Olden 2017; Baker et al. 2018). Growth and the thermal sensitivity of growth are
558 negatively correlated for one-year-old rainbow trout (*Oncorhynchus mykiss*) at low temperatures,
559 but not at higher temperatures, thus while there is moderate heritability for both growth ($h^2 = 0.46$)
560 and thermal sensitivity of growth ($h^2 = 0.24$), selection for higher growth is predicted to result in
561 increased thermal sensitivity in future generations held at low temperatures, but unlikely to affect
562 thermal sensitivity at higher temperatures (Janhunen et al. 2016). Similar trade-offs of growth vs.
563 sensitivity have been observed as well in adult rainbow trout (Sae-Lim et al. 2015). Further
564 complicating the matter, some genetic correlations among life history traits may be temperature-
565 specific (reviewed in Sgrò and Hoffmann 2004), including cases where negative genetic
566 correlations can become positive at higher temperatures and vice-versa. Thus, coral trait evolution
567 may further be complicated by (currently unmeasured) genetic correlations across TPC metrics.

568

569 Conclusion

Our analysis identifies relatively high heritability of some traits, such as survival and growth. This, coupled with the fact that heritability does not appreciably decline with increasing temperature manipulation, suggests potential for substantial coral adaptation to future conditions of weak to moderate climate change. In contrast, 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., $h^2 = 0.16$) (Matz et al. 2018; Cropp and Norbury 2020; 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 predicts regarding thermal evolution of corals in response to climate change. Nevertheless, our findings reveal that corals may be capable of adapting more rapidly to the thermal challenges imposed by climate change than previously thought.

587 **Acknowledgements**

588 We would like to thank Kate Quigley for helpful suggestions and discussions at various stages
589 throughout the project, as well as Holland Elder, Carly Kenkel, Mikhail Matz, Hanaka Mera,
590 Rachel Wright, and Yingqi Zhang for aiding in locating further heritability estimates from past and
591 current projects. KRB-N is supported by an Australian Government Research Training Program
592 Scholarship and MJHvO acknowledges Australian Research Council Laureate Fellowship
593 FL180100036. The authors have no conflicts of interest to declare.

594

595 **Data accessibility statement**

596 All extracted heritability estimates and supplementary code are available at
597 <https://github.com/ecology/heritabilitymeta> (pending article acceptance).

598 **References**

- 599 van Aert RCM, Jackson D. 2019. A new justification of the Hartung-Knapp method for random-
600 effects meta-analysis based on weighted least squares regression. *Research Synthesis*
601 *Methods*. 10(4):515–527. doi:10.1002/jrsm.1356.
- 602 Ahrens CW, Andrew ME, Mazanec RA, Ruthrof KX, Challis A, Hardy G, Byrne M, Tissue DT,
603 Rymer PD. 2020. Plant functional traits differ in adaptability and are predicted to be
604 differentially affected by climate change. *Ecol Evol*. 10(1):232–248. doi:10.1002/ece3.5890.
- 605 Angilletta M. 2009. *Thermal Adaptation: A Theoretical and Empirical Synthesis*. Oxford: Oxford
606 University Press.
- 607 Angilletta MJ. 2009. *Thermal Adaptation: A Theoretical and Empirical Synthesis*. Oxford
608 Scholarship Online.
- 609 Archambault JM, Cope WG, Kwak TJ. 2018. Chasing a changing climate: Reproductive and
610 dispersal traits predict how sessile species respond to global warming. *Diversity and*
611 *Distributions*. 24(7):880–891. doi:10.1111/ddi.12740.
- 612 Ban SS, Graham NAJ, Connolly SR. 2014. Evidence for multiple stressor interactions and effects
613 on coral reefs. *Glob Chang Biol*. 20(3):681–697. doi:10.1111/gcb.12453.
- 614 Bay RA, Rose NH, Logan CA, Palumbi SR. 2017. Genomic models predict successful coral
615 adaptation if future ocean warming rates are reduced. *Science Advances*. 3:e1701413.
- 616 Berkelmans R, Van Oppen MJH. 2006. The role of zooxanthellae in the thermal tolerance of corals:
617 A “nugget of hope” for coral reefs in an era of climate change. *Proc R Soc B*.
618 273(1599):2305–2312. doi:10.1098/rspb.2006.3567.
- 619 Bodensteiner BL, Agudelo-Cantero GA, Arietta AZA, Gunderson AR, Muñoz MM, Refsnider JM,
620 Gangloff EJ. 2020. Thermal adaptation revisited: How conserved are thermal traits of
621 reptiles and amphibians? *Journal of Experimental Zoology Part A: Ecological and*
622 *Integrative Physiology*. (April):1–22. doi:10.1002/jez.2414.
- 623 Bubliy OA, Loeschcke V. 2002. Effect of low stressful temperature on genetic variation of five

- quantitative traits in *Drosophila melanogaster*. *Heredity*. 89(1):70–75.
doi:10.1038/sj.hdy.6800104.
- Burke L, Reytar K, Spalding M, Perry A. 2011. Reefs at Risk Revisited.
- Burnham KP, Anderson DR. 2004. Multimodel inference: Understanding AIC and BIC in model selection. *Sociological Methods and Research*. 33(2):261–304.
doi:10.1177/0049124104268644.
- Carlson DB, Budd AF, Lippé C, Andrew RL. 2011. The quantitative genetics of incipient speciation: Heritability and genetic correlations of skeletal traits in populations of diverging *Favia fragum* ecomorphs. *Evolution*. 65(12):3428–3447. doi:10.1111/j.1558-5646.2011.01389.x.
- Castañeda LE, Romero-Soriano V, Mesas A, Roff DA, Santos M. 2019. Evolutionary potential of thermal preference and heat tolerance in *Drosophila subobscura*. *J Evol Biol*. 32(8):818–824. doi:10.1111/jeb.13483.
- Charmantier A, Garant D. 2005. Environmental quality and evolutionary potential : lessons from wild populations. (June):1415–1425. doi:10.1098/rspb.2005.3117.
- Charmantier A, Perrins C, McCleery RH, Sheldon BC. 2006a. Age-dependent genetic variance in a life-history trait in the mute swan. *Proc R Soc B*. 273(1583):225–232.
doi:10.1098/rspb.2005.3294.
- Charmantier A, Perrins C, McCleery RH, Sheldon BC. 2006b. Quantitative genetics of age at reproduction in wild swans: Support for antagonistic pleiotropy models of senescence. *Proceedings of the National Academy of Sciences of the United States of America*. 103(17):6587–6592. doi:10.1073/pnas.0511123103.
- Chown SL, Jumbam KR, Sørensen JG, Terblanche JS. 2009. Phenotypic variance, plasticity and heritability estimates of critical thermal limits depend on methodological context. *Funct Ecol*. 23(1):133–140. doi:10.1111/j.1365-2435.2008.01481.x.
- Comte L, Olden JD. 2017. Evolutionary and environmental determinants of freshwater fish thermal tolerance and plasticity. *Glob Chang Biol*. 23(2):728–736. doi:10.1111/gcb.13427.

- 650 Cook RD, Weisberg S. 1982. Residuals and influence in regression. London: Chapman and Hall.
- 651 Cropp R, Norbury J. 2020. The potential for coral reefs to adapt to a changing climate - an eco-
652 evolutionary modelling perspective. *Ecol Modell.* 426(March):109038.
653 doi:10.1016/j.ecolmodel.2020.109038. <https://doi.org/10.1016/j.ecolmodel.2020.109038>.
- 654 Császár NBM, Ralph PJ, Frankham R, Berkelmans R, van Oppen MJH. 2010. Estimating the
655 Potential for Adaptation of Corals to Climate Warming. *PLoS One.* 5(3):e9751.
656 doi:10.1371/journal.pone.0009751.
- 657 Cuning R, Gillette P, Capo T, Galvez K, Baker AC. 2015. Growth tradeoffs associated with
658 thermotolerant symbionts in the coral *Pocillopora damicornis* are lost in warmer oceans.
659 *Coral Reefs.* 34(1):155–160. doi:10.1007/s00338-014-1216-4.
- 660 Dajka JC, Wilson SK, Robinson JPW, Chong-Seng KM, Harris A, Graham NAJ. 2019. Uncovering
661 drivers of juvenile coral density following mass bleaching. *Coral Reefs.* 38(4):637–649.
662 doi:10.1007/s00338-019-01785-w. <https://doi.org/10.1007/s00338-019-01785-w>.
- 663 Dixon G, Davies S, Aglyamova G, Meyer E, Bay L, Matz M. 2015. Genomic determinants of coral
664 heat tolerance across latitudes. *Science.* 348(6242):2014–2016.
- 665 Doropoulos C, Ward S, Marshall A, Diaz-Pulido G, Mumby PJ. 2012. Interactions among chronic
666 and acute impacts on coral recruits: the importance of size-escape thresholds. *Ecology.*
667 93(10):2131–2138.
- 668 Doyle CM, Leberg PL, Klerks PL. 2011. Heritability of heat tolerance in a small livebearing fish,
669 *Heterandria formosa*. *Ecotoxicology.* 20(3):535–542. doi:10.1007/s10646-011-0624-2.
- 670 Dziedzic KE, Elder H, Tavalire H, Meyer E. 2019. Heritable variation in bleaching responses and
671 its functional genomic basis in reef-building corals (*Orbicella faveolata*). *Mol Ecol.*
672 28(9):2238–2253. doi:10.1111/mec.15081.
- 673 Falconer DS, Mackay TF. 1996. Introduction to Quantitative Genetics. Essex, UK: Longman.
- 674 Fisher R. 1930. The Genetical Theory of Natural Selection. Oxford: Clarendon.
- 675 Flood PJ, Kruijer W, Schnabel SK, Schoor R, Jalink H, Snel JFH, Harbinson J, Aarts MGM. 2016.

- 676 Phenomics for photosynthesis, growth and reflectance in *Arabidopsis thaliana* reveals
677 circadian and long-term fluctuations in heritability. *Plant Methods*. 12(1):1–14.
678 doi:10.1186/s13007-016-0113-y.
- 679 Geber MA, Dawson TE. 1997. Genetic variation in stomatal and biochemical limitations to
680 photosynthesis in the annual plant, *Polygonum arenastrum*. *Oecologia*. 109(4):535–546.
681 doi:10.1007/s004420050114.
- 682 Guest JR, Baird AH, Maynard JA, Muttaqin E, Edwards AJ, Campbell SJ, Yewdall K, Affendi YA,
683 Chou LM. 2012. Contrasting patterns of coral bleaching susceptibility in 2010 suggest an
684 adaptive response to thermal stress. *PLoS One*. 7(3):1–8. doi:10.1371/journal.pone.0033353.
- 685 Gunay F, Alten B, Ozsoy ED. 2011. Narrow-sense heritability of body size and its response to
686 different developmental temperatures in *Culex quinquefasciatus* (Say 1923). *Journal of*
687 *Vector Ecology*. 36(2):348–354. doi:10.1111/j.1948-7134.2011.00175.x.
- 688 van Heerwaarden B, Kellermann V, Sgr CM. 2016. Limited scope for plasticity to increase upper
689 thermal limits. *Funct Ecol*. 30:1947–1956. doi:10.1111/1365-2435.12687.
- 690 Herben T, Klimešová J, Chytrý M. 2018. Effects of disturbance frequency and severity on plant
691 traits: An assessment across a temperate flora. *Funct Ecol*. 32(3):799–808.
692 doi:10.1111/1365-2435.13011.
- 693 Higgins JPT, Thompson SG. 2002. Quantifying heterogeneity in a meta-analysis. *Stat Med*.
694 21(11):1539–1558. doi:10.1002/sim.1186.
- 695 Hoegh-Guldberg O, Poloczanska ES, Skirving W, Dove S. 2017. Coral reef ecosystems under
696 climate change and ocean acidification. *Frontiers in Marine Science*. 4(MAY).
697 doi:10.3389/fmars.2017.00158.
- 698 Hughes T, Baird A, Bellwood D, Card M, Connolly S, Folke C, Grosberg R, Hoegh-Guldberg O,
699 Jackson JBC, Kleypas J, et al. 2003. Climate change, human impacts, and the resilience of
700 coral reefs. *Science*. 301:877–1000.
- 701 Hughes TP, Anderson KD, Connolly SR, Heron SF, Kerry JT, Lough JM, Baird AH, Baum JK,

- 702 Berumen ML, Bridge TC, et al. 2018a. Spatial and temporal patterns of mass bleaching of
703 corals in the Anthropocene. *Science*. 359(6371):80–83. doi:10.1126/science.aan8048.
- 704 Hughes TP, Kerry JT, Baird AH, Connolly SR, Chase TJ, Dietzel A, Hill T, Hoey AS,
705 Hoogenboom MO, Jacobson M, et al. 2019. Global warming impairs stock–recruitment
706 dynamics of corals. *Nature*. doi:10.1038/s41586-019-1081-y.
707 <http://www.nature.com/articles/s41586-019-1081-y>.
- 708 Hughes TP, Kerry JT, Baird AH, Connolly SR, Dietzel A, Eakin CM, Heron SF, Hoey AS,
709 Hoogenboom MO, Liu G, et al. 2018b. Global warming transforms coral reef assemblages.
710 *Nature*. 556(7702):492–496. doi:10.1038/s41586-018-0041-2.
711 <http://dx.doi.org/10.1038/s41586-018-0041-2>.
- 712 Janhunnen M, Koskela J, Ninh NH, Vehviläinen H, Koskinen H, Nousiainen A, Thoa NP. 2016.
713 Thermal sensitivity of growth indicates heritable variation in 1-year-old rainbow trout
714 (*Oncorhynchus mykiss*). *Genet Sel Evol*. 48(1):1–11. doi:10.1186/s12711-016-0272-3.
- 715 Jump AS, Peñuelas J. 2005. Running to stand still: Adaptation and the response of plants to rapid
716 climate change. *Ecol Lett*. 8(9):1010–1020. doi:10.1111/j.1461-0248.2005.00796.x.
- 717 Kenkel CD, Almanza AT, Matz M V. 2015. Fine-scale environmental specialization of reef-
718 building corals might be limiting reef recovery in the Florida Keys. *Ecology*. 96(12):3197–
719 3212. doi:10.1890/14-2297.1.
- 720 Kirk NL, Howells EJ, Abrego D, Burt JA, Meyer E. 2018. Genomic and transcriptomic signals of
721 thermal tolerance in heat-tolerant corals (*Platygyra daedalea*) of the Arabian/Persian Gulf.
722 *Mol Ecol*. 27(24):5180–5194. doi:10.1111/mec.14934.
- 723 Knapp G, Hartung J. 2003. Improved tests for a random effects meta-regression with a single
724 covariate. *Stat Med*. 22(17):2693–2710. doi:10.1002/sim.1482.
- 725 Koenker R. 2020. quantreg: Quantile Regression. R package version 5.67.
- 726 Koenker R, Hallock KF. 2001. Quantile regression. *Journal of Economic Perspectives*. 15(4):143–
727 156.

- 728 Kremer A, Ronce O, Robledo-Arnuncio JJ, Guillaume F, Bohrer G, Nathan R, Bridle JR,
729 Gomulkiewicz R, Klein EK, Ritland K, et al. 2012. Long-distance gene flow and adaptation
730 of forest trees to rapid climate change. *Ecol Lett.* 15(4):378–392. doi:10.1111/j.1461-
731 0248.2012.01746.x.
- 732 Lande R. 1979. Quantitative genetic analysis of multivariate evolution, applied to brain: body size
733 allometry. *Evolution.* 33(1):402–416.
- 734 Lee SH, Wray NR, Goddard ME, Visscher PM. 2011. Estimating missing heritability for disease
735 from genome-wide association studies. *American Journal of Human Genetics.* 88(3):294–
736 305. doi:10.1016/j.ajhg.2011.02.002. <http://dx.doi.org/10.1016/j.ajhg.2011.02.002>.
- 737 Lin L, Xu C. 2020. Arcsine-based transformations for meta-analysis of proportions: Pros, cons, and
738 alternatives. *Health Science Reports.* 3(3):1–6. doi:10.1002/hsr2.178.
- 739 Little AF, Oppen MJH Van, Willis BL. 2004. Flexibility in Algal Endosymbioses Shapes Growth in
740 Reef Corals. 304(June):1492–1495.
- 741 Lloyd-Jones LR, Holloway A, McRae A, Yang J, Small K, Zhao J, Zeng B, Bakshi A, Metspalu A,
742 Dermitzakis M, et al. 2017. The Genetic Architecture of Gene Expression in Peripheral
743 Blood. *American Journal of Human Genetics.* 100(2):228–237.
744 doi:10.1016/j.ajhg.2016.12.008. <http://dx.doi.org/10.1016/j.ajhg.2016.12.008>.
- 745 Logan CA, Dunne JP, Eakin CM, Donner SD. 2014a. Incorporating adaptive responses into future
746 projections of coral bleaching. *Glob Chang Biol.* 20(1):125–139. doi:10.1111/gcb.12390.
- 747 Logan ML, Cox RM, Calsbeek R. 2014b. Natural selection on thermal performance in a novel
748 thermal environment. *Proceedings of the National Academy of Sciences of the United States*
749 *of America.* 111(39):14165–14169. doi:10.1073/pnas.1404885111.
- 750 Lohr KE, Patterson JT. 2017. Intraspecific variation in phenotype among nursery-reared staghorn
751 coral *Acropora cervicornis* (Lamarck, 1816). *J Exp Mar Bio Ecol.* 486:87–92.
752 doi:10.1016/j.jembe.2016.10.005. <http://dx.doi.org/10.1016/j.jembe.2016.10.005>.
- 753 Lough JM, Anderson KD, Hughes TP. 2018. Increasing thermal stress for tropical coral reefs: 1871-

2017. *Sci Rep.* 8(1):1–8. doi:10.1038/s41598-018-24530-9.
<http://dx.doi.org/10.1038/s41598-018-24530-9>.
- Lush JL. 1937. *Animal breeding plans*. Ames, Iowa: Iowa State College Press.
- Ma FZ, Lü ZC, Wang R, Wan FH. 2014. Heritability and evolutionary potential in thermal tolerance traits in the invasive Mediterranean cryptic species of *Bemisia tabaci* (Hemiptera: Aleyrodidae). *PLoS One.* 9(7):1–7. doi:10.1371/journal.pone.0103279.
- Madin JS, Baird AH, Baskett ML, Connolly SR, Dornelas MA, Madin JS. 2020. Partitioning colony size variation into growth and partial mortality.
- Madin JS, Baird AH, Dornelas M, Connolly SR. 2014. Mechanical vulnerability explains size-dependent mortality of reef corals. *Ecol Lett.* 17(8):1008–1015. doi:10.1111/ele.12306.
- Manzello DP, Matz M V., Enochs IC, Valentino L, Carlton RD, Kolodziej G, Serrano X, Towle EK, Jankulak M. 2019. Role of host genetics and heat-tolerant algal symbionts in sustaining populations of the endangered coral *Orbicella faveolata* in the Florida Keys with ocean warming. *Glob Chang Biol.*:0–2. doi:10.1111/gcb.14545.
- Martins F, Kruuk L, Llewelyn J, Moritz C, Phillips B. 2019. Heritability of climate-relevant traits in a rainforest skink. *Heredity.* 122(1):41–52. doi:10.1038/s41437-018-0085-y.
<http://dx.doi.org/10.1038/s41437-018-0085-y>.
- Matz M V., Treml E, Haller BC. 2020. Estimating the potential for coral adaptation to global warming across the Indo-West Pacific. *Glob Chang Biol.* 26:3473–3481.
doi:10.1111/gcb.15060.
- Matz M V., Treml EA, Aglyamova G V., Bay LK. 2018. Potential and limits for rapid genetic adaptation to warming in a Great Barrier Reef coral. *PLoS Genetics.* 14(4):1–20.
doi:10.1371/journal.pgen.1007220. <http://dx.doi.org/10.1371/journal.pgen.1007220>.
- Maynard JA, Anthony KRN, Marshall PA, Masiri I. 2008. Major bleaching events can lead to increased thermal tolerance in corals. *Marine Biology.* 155(2):173–182.
doi:10.1007/s00227-008-1015-y.

- 780 Meyer E, Davies S, Wang S, Willis BL, Abrego D, Juenger TE, Matz M V. 2009. Genetic variation
781 in responses to a settlement cue and elevated temperature in the reef-building coral *Acropora*
782 *millepora*. *Mar Ecol Prog Ser.* 392(Ipcc 2007):81–92. doi:10.3354/meps08208.
- 783 Møller AP, Jennions MD. 2001. Testing and adjusting for publication bias. *Trends Ecol Evol.*
784 16(10):580–586. doi:10.1016/S0169-5347(01)02235-2.
- 785 Morikawa MK, Palumbi SR. 2019. Using naturally occurring climate resilient corals to construct
786 bleaching-resistant nurseries. *Proceedings of the National Academy of Sciences of the*
787 *United States of America.* 116(21):10586–10591. doi:10.1073/pnas.1721415116.
- 788 Mousseau TA, Roff DA. 1987. Natural selection and the heritability of fitness components.
789 *Heredity.* 59(181–197):181–197.
- 790 Pandolfi JM, Connolly SR, Marshall DJ, Cohen AL. 2011. Projecting coral reef futures under global
791 warming and ocean acidification. *Science.* 333(6041):418–422.
792 doi:10.1126/science.1204794.
- 793 Polderman TJC, Benyamin B, Leeuw CA De, Sullivan PF, van Bochoven A, Visscher PM,
794 Posthuma D. 2015. Meta-analysis of the heritability of human traits based on fifty years of
795 twin studies. *Nature Genetics.* 47(7):702–709. doi:10.1038/ng.3285.
796 <http://dx.doi.org/10.1038/ng.3285>.
- 797 Pratchett MS, Anderson KD, Hoogenboom MO, Widman E, Baird AH, Pandolfi JM, Edmunds PJ,
798 Lough JM. 2015. Spatial, temporal and taxonomic variation in coral growth-implications for
799 the structure and function of coral reef ecosystems. *Oceanography and Marine Biology: An*
800 *Annual Review.* 53:215–295. doi:10.1201/b18733.
- 801 Pratchett MS, Hoey AS, Wilson SK, Messmer V, Graham NAJ. 2011. Changes in biodiversity and
802 functioning of reef fish assemblages following coral bleaching and coral loss. *Diversity.*
803 3(3):424–452. doi:10.3390/d3030424.
- 804 Pratchett MS, McWilliam MJ, Riegl B. 2020. Contrasting shifts in coral assemblages with
805 increasing disturbances. *Coral Reefs.* 39(3):783–793. doi:10.1007/s00338-020-01936-4.

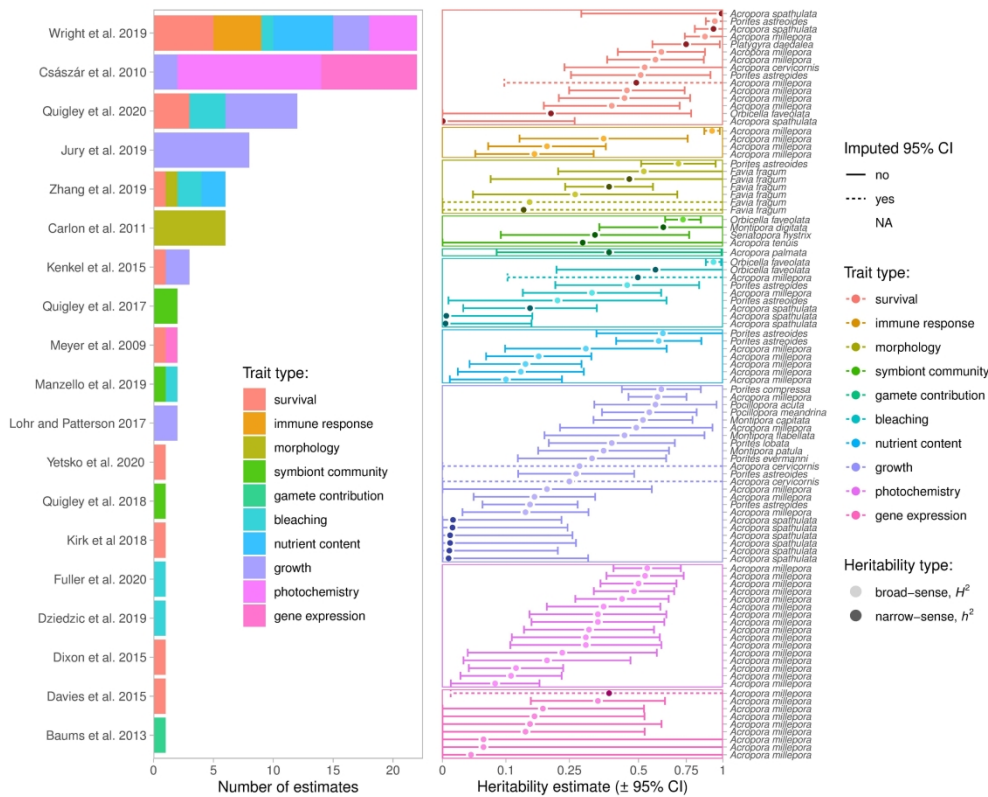
- 806 <https://doi.org/10.1007/s00338-020-01936-4>.
- 807 Price T, Schluter D. 1991. On the Low Heritability of Life-History Traits. *Evolution*. 45(4):853.
- 808 doi:10.2307/2409693.
- 809 Qu M, Zheng G, Hamdani S, Essemine J, Song Q, Wang H, Chu C, Sirault X, Zhu XG. 2017. Leaf
- 810 photosynthetic parameters related to biomass accumulation in a global rice diversity survey.
- 811 *Plant Physiology*. 175(1):248–258. doi:10.1104/pp.17.00332.
- 812 Quigley KM, Randall CJ, van Oppen MJ, Bay LK. 2020. Assessing the role of historical
- 813 temperature regime and algal symbionts on the heat tolerance of coral juveniles. *J Exp Biol*.
- 814 Quigley KM, Willis BL, Bay LK. 2017. Heritability of the Symbiodinium community in vertically-
- 815 and horizontally-transmitting broadcast spawning corals. *Sci Rep*. 7(1):1–14.
- 816 doi:10.1038/s41598-017-08179-4.
- 817 Raudenbush SW. 2009. Analyzing effect sizes: random effects models. In: Cooper H, Hedges L V.,
- 818 Valentine JC, editors. *The handbook of research synthesis and meta-analysis*. 2nd ed. New
- 819 York: Russell Sage Foundation. p. 295–315.
- 820 Rosenberg MS. 2005. The file-drawer problem revisited: a general weighted method for calculating
- 821 fail-safe numbers in meta-analysis. *Evolution*. 59:464–468.
- 822 Rosenthal R. 1991. *Meta-analytic Procedures for Social Research*. Newbury Park, CA: Sage
- 823 Publications, Inc.
- 824 Rothschild D, Weissbrod O, Barkan E, Kurilshikov A, Korem T, Zeevi D, Costea PI, Godneva A,
- 825 Kalka IN, Bar N, et al. 2018. Environment dominates over host genetics in shaping human
- 826 gut microbiota. *Nature*. 555(7695):210–215. doi:10.1038/nature25973.
- 827 <http://dx.doi.org/10.1038/nature25973>.
- 828 Rowínski PK, Rogell B. 2017. Environmental stress correlates with increases in both genetic and
- 829 residual variances: a meta-analysis of animal studies. *Evolution*. 17(5):1339–1351.
- 830 doi:10.1111/evo.13201.
- 831 Sae-Lim P, Mulder H, Gjerde B, Koskinen H, Lillehammer M, Kause A. 2015. Genetics of growth

- 832 reaction norms in farmed rainbow trout. *PLoS One*. 10(8):1–17.
833 doi:10.1371/journal.pone.0135133.
- 834 Sasaki MC, Dam HG. 2019. Integrating patterns of thermal tolerance and phenotypic plasticity with
835 population genetics to improve understanding of vulnerability to warming in a widespread
836 copepod. (August):4147–4164. doi:10.1111/gcb.14811.
- 837 Schloss CA, Nuñez TA, Lawler JJ. 2012. Dispersal will limit ability of mammals to track climate
838 change in the Western Hemisphere. *Proc Natl Acad Sci*. 109(22):8606–8611.
839 doi:10.1073/pnas.1116791109/-
840 /DCSupplemental.www.pnas.org/cgi/doi/10.1073/pnas.1116791109.
- 841 Sgrò CM, Hoffmann AA. 2004. Genetic correlations, tradeoffs and environmental variation.
842 *Heredity*. 93(3):241–248. doi:10.1038/sj.hdy.6800532.
- 843 Sully S, Burkepile DE, Donovan MK, Hodgson G, van Woesik R. 2019. A global analysis of coral
844 bleaching over the past two decades. *Nature Communications*. 10(1):1–5.
845 doi:10.1038/s41467-019-09238-2. <http://dx.doi.org/10.1038/s41467-019-09238-2>.
- 846 Teplitsky C, Mills JA, Yarrall JW, Merilä J. 2009. Heritability of fitness components in a wild bird
847 population. *Evolution*. 63(3):716–726. doi:10.1111/j.1558-5646.2008.00581.x.
- 848 Tuhina-Khatun M, Hanafi MM, Rafii Yusop M, Wong MY, Salleh FM, Ferdous J. 2015. Genetic
849 Variation, Heritability, and Diversity Analysis of Upland Rice (*Oryza sativa* L.) Genotypes
850 Based on Quantitative Traits. *BioMed Research International*. 2015:1–8.
851 doi:10.1155/2015/290861.
- 852 Vermeij MJA, Sandin SA. 2008. Density-dependent settlement and mortality structure the earliest
853 life phases of a coral population. *Ecology*. 89(7):1994–2004. doi:10.1890/07-1296.1.
- 854 Viechtbauer W. 2010. Conducting meta-analyses in R with the metafor package. *Journal of*
855 *Statistical Software*. 36(3):1–48.
- 856 Viechtbauer W, López-López JA, Sánchez-Meca J, Marín-Martínez F. 2015. A comparison of
857 procedures to test for moderators in mixed-effects meta-regression models. *Psychological*

- 858 Methods. 20:360–374.
- 859 Visscher PM, Hill WG, Wray NR. 2008. Heritability in the genomics area – concepts and
860 misconceptions. *Nature Reviews Genetics*. 9:255–267. doi:10.1038/nrg2322.
- 861 Visser ME. 2008. Keeping up with a warming world; assessing the rate of adaptation to climate
862 change. *Proc R Soc B*. 275(1635):649–659. doi:10.1098/rspb.2007.0997.
- 863 Walters RJ, Berger D. 2019. Implications of existing local (mal)adaptations for ecological
864 forecasting under environmental change. *Evolutionary Applications*. 12(7):1487–1502.
865 doi:10.1111/eva.12840.
- 866 Wheelwright NT, Keller LF, Postma E. 2014. The effect of trait type and strength of selection on
867 heritability and evolvability in an island bird population. *Evolution*. 68:3325–3336.
- 868 Wilson AJ, Charmantier A, Hadfield JD. 2008. Evolutionary genetics of ageing in the wild :
869 empirical patterns and future perspectives. *Funct Ecol*. 22:431–442. doi:10.1111/j.1365-
870 2435.2008.0.
- 871 Wilson AJ, Pemberton JM, Pilkington JG, Coltman DW, Mifsud D V., Clutton-Brock TH, Kruuk
872 LEB. 2006. Environmental coupling of selection and heritability limits evolution. *PLoS*
873 Biology. 4(7):1270–1275. doi:10.1371/journal.pbio.0040216.
- 874 Wright RM, Mera H, Kenkel CD, Nayfa M, Bay LK, Matz M V. 2019. Positive genetic associations
875 among fitness traits support evolvability of a reef-building coral under multiple stressors.
876 *Glob Chang Biol*. 25(10):3294–3304. doi:10.1111/gcb.14764.
- 877 Wulff JL. 2006. Rapid diversity and abundance decline in a Caribbean coral reef sponge
878 community. *Biological Conservation*. 127(2):167–176. doi:10.1016/j.biocon.2005.08.007.
- 879 Yetsko K, Ross M, Bellantuono A, Merselis D, Lanetty MR, Gilg MR. 2020. Genetic differences in
880 thermal tolerance among colonies of threatened coral *Acropora cervicornis*: Potential for
881 adaptation to increasing temperature. *Mar Ecol Prog Ser*. 646:45–68.
882 doi:10.3354/meps13407.
- 883 Zhang Y, Million WC, Ruggeri M, Kenkel CD. 2019. Family matters: Variation in the physiology

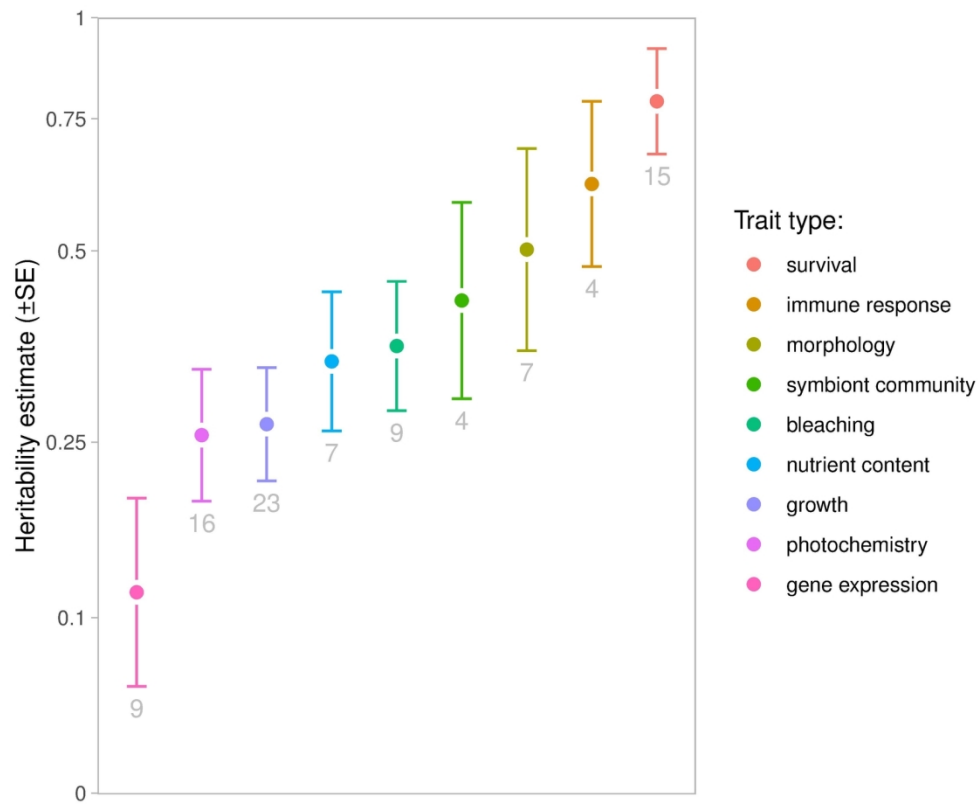
884 of brooded *Porites astreoides* larvae is driven by parent colony effects. *Comparative*
885 *Biochemistry and Physiology -Part A : Molecular and Integrative Physiology*.
886 238(August):110562. doi:10.1016/j.cbpa.2019.110562.
887 <https://doi.org/10.1016/j.cbpa.2019.110562>.
888 Zuur AF, Ieno EN, Smith GM. 2007. *Analysing Ecological Data*. New York: Springer Science +
889 Business Media, LCC.
890 Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM. 2009. *Mixed Effects Models and*
891 *Extensions in Ecology with R*. New York: Springer Science+Business Media, LLC.
892

For Review Only



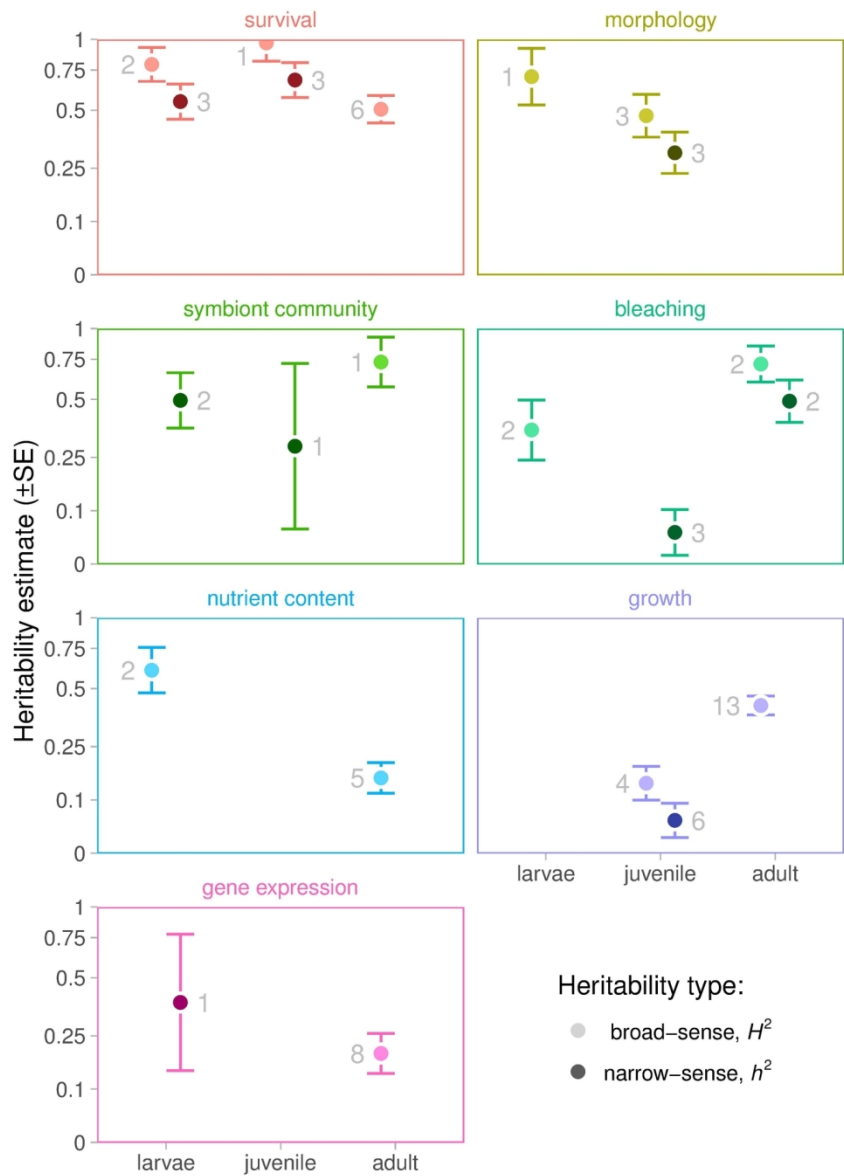
Heritability estimates (N = 95) of various traits across 19 studies of reef-building corals. Colour indicates the specific trait type (hue) and heritability type (broad-sense (H^2) as lighter tint circles, narrow-sense (h^2) as darker shade). Left: Number of estimates reported in each study. Right: Point 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.

254x203mm (300 x 300 DPI)



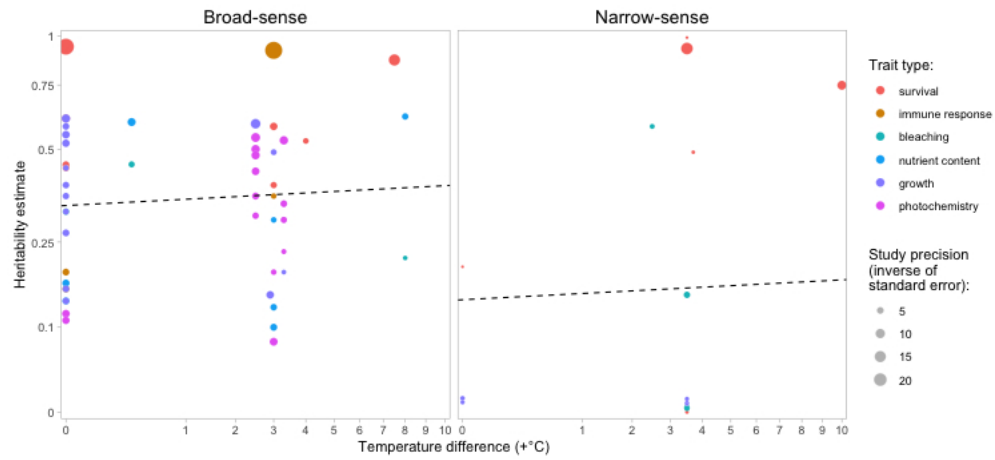
Heritability estimates \pm SE for the overall dataset model. Traits are sorted along the spectrum according to their overall relative heritability, with values closer to 1 indicating more heritable traits. The number of estimates included in the meta-analysis for each trait type are indicated below each error bar in grey. The gamete compatibility trait type is excluded due to its reliance on only a single study/estimate.

152x127mm (300 x 300 DPI)



Heritability estimates \pm 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.

127x177mm (300 x 300 DPI)



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 ($+1\sqrt{^\circ\text{C}}$) translates to a mean increase in $\ln[h^2+0.2]$ heritability of 0.03 ± 0.05 SE.

264x123mm (72 x 72 DPI)