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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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31

## 32 **Abstract**

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

56

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

## 59 **Introduction**

60 Anthropogenic climate change is one of the greatest selective pressures on organisms  
61 worldwide (Davis et al. 2005; Hughes et al. 2018b; Nolan et al. 2018). To avoid extinction,  
62 species need to either acclimatize, move to new habitats, or adapt to new conditions (Davis et  
63 al. 2005; Jump and Peñuelas 2005; Gienapp et al. 2008). Acclimatization on its own may

64 initially increase the duration of time that a population can persist in an altered environment,  
65 but is bounded by physiological thresholds that limit tolerance of long-term environmental  
66 change, and for populations living close to their extremes already (Comte & Olden, 2017;  
67 Sasaki & Dam, 2019; van Heerwaarden, Kellermann, & Sgr, 2016). Migration to new  
68 environments is similarly limited (Jump & Peñuelas, 2005; Schloss, Nuñez, & Lawler, 2012;  
69 Walters & Berger, 2019), especially for predominantly sessile organisms for which range  
70 extension depends upon long-distance dispersal of offspring (Hughes et al. 2003;  
71 Archambault et al. 2018; c.f. Kremer et al. 2012). Consequently, understanding whether and  
72 how species are likely to adapt to future conditions is crucial in predicting species persistence  
73 in the context of climate change (C. A. Logan, Dunne, Eakin, & Donner, 2014).

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

82  
83

**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:

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

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:  $R = 0.1 \cdot (32^\circ\text{C} - 30^\circ\text{C}) = +0.2^\circ\text{C}$ , 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,  $h^2$ .

84

85 Different traits often have different heritability coefficients, and may also covary with  
86 one another (Wright et al. 2019). Counterintuitively, traits which are tied closely to biological  
87 fitness (e.g., life history traits, longevity/survival, fecundity) often have relatively low  
88 heritability compared to physiological and behavioural traits, and compared to morphological  
89 traits that often have higher heritability (Martins, Kruuk, Llewelyn, Moritz, & Phillips, 2019;  
90 Mousseau & Roff, 1987; Price & Schluter, 1991; Wheelwright, Keller, & Postma, 2014). For  
91 example, when populations have previously undergone strong stabilizing selection for a trait  
92 tied closely to fitness, the narrower range and variance of trait values observed in the  
93 population translates to a reduction in the relative contribution of additive genetic effects to  
94 total phenotypic variation, and a decrease in the heritability coefficient (Charmantier &  
95 Garant, 2005; Teplitsky, Mills, Yarrall, & Merilä, 2009; Wheelwright et al., 2014).  
96 Understanding the potential rate and limits to adaptive evolution will therefore require an  
97 understanding of heritability across different traits (Wheelwright et al., 2014).

98 Selective pressures differ not only in terms of the trait being examined, but also across  
99 life stages/ages, growth forms, and environments (e.g., genotype-by-environment  
100 interactions). Thus, heritability should vary across these factors as well (Charmantier &  
101 Garant, 2005; Wheelwright et al., 2014; Wilson, Charmantier, & Hadfield, 2008). Early life  
102 stages/ages can experience strong stabilizing selection for traits associated with early life  
103 fitness, and thus exhibit reduced  $h^2$  for these traits. Increasing importance of environmental  
104 effects and acclimation to local environments can also reduce the relative importance of  
105 additive genetic variation and thus  $h^2$  at intermediate stages/ages (Charmantier, Perrins,  
106 McCleery, & Sheldon, 2006a). Finally, late-acting mutations can accumulate in older  
107 individuals to cause age-dependent increases in  $V_A$ , and thus  $h^2$ , for traits tied closely with  
108 fitness (Charmantier et al., 2006a; Charmantier, Perrins, McCleery, & Sheldon, 2006b;  
109 Wilson et al., 2008). Similar selective pressures can result in similar  $h^2$  values for traits of  
110 species occupying similar ecological niches. For example, in reef-building corals, colony  
111 growth form directly influences individual growth rate, fecundity, and survival (Madin et al.,  
112 2020; Pratchett et al., 2015). Tabular coral species (which form large horizontal plates  
113 supported by a central stalk) exhibit increased adult mortality relative to other coral growth  
114 forms in the same habitat due to their increased mechanical vulnerability (Madin, Baird,  
115 Dornelas, & Connolly, 2014). However, it remains unknown whether and how heritability of  
116 traits varies among coral species with different growth forms.

117 In the context of climate change, decreasing environmental suitability and increasing  
118 selective pressure on traits tied closely to fitness can reduce trait heritability, resulting in a  
119 counter-intuitive reduction in the capacity for populations to evolve to environmental change  
120 (Charmantier & Garant, 2005; Wheelwright et al., 2014; Wilson et al., 2006). Conversely,  
121 other studies have found no distinguishable relationship between  $h^2$  and environmental  
122 favourability (Rowinski & Rogell, 2017), and others still identify positive correlations of  $h^2$   
123 with increasingly harsh environmental temperatures (Gunay, Alten, & Ozsoy, 2011). Clearly,  
124 further research is required to quantify how heritability may change across life stages and  
125 environments of the future, especially when attempting to project population outcomes in  
126 response to future conditions.

127 Reef-building scleractinian corals are particularly sensitive to climate stressors, as  
128 evidenced by coral bleaching during thermal anomalies. Reef diversity and coral cover have  
129 declined throughout the 21<sup>st</sup> century (T. P. Hughes, Kerry, et al., 2018; Pratchett, Hoey,  
130 Wilson, Messmer, & Graham, 2011; Wulff, 2006), with 75% of global reefs now being  
131 considered threatened (Burke, Reytar, Spalding, & Perry, 2011). Widespread bleaching of

132 coral communities now occurs at temperatures approximately 0.5°C higher than a decade  
133 ago, suggesting strong selection for increased thermotolerance worldwide (Guest et al., 2012;  
134 Maynard, Anthony, Marshall, & Masiri, 2008; Sully, Burkepile, Donovan, Hodgson, & van  
135 Woesik, 2019). However, given the rapid warming of sea surface temperatures and the  
136 increase in the frequency and severity of mass bleaching events on coral reefs worldwide (T.  
137 P. Hughes, Anderson, et al., 2018; Lough, Anderson, & Hughes, 2018), it remains unclear  
138 whether corals can adapt to the prolonged thermal stress they now experience with increasing  
139 regularity (Hoegh-Guldberg, Poloczanska, Skirving, & Dove, 2017; Pandolfi, Connolly,  
140 Marshall, & Cohen, 2011). Models estimating long-term coral adaptation to climate change  
141 have assumed low to medium heritability of thermotolerance (e.g.,  $h^2 = 0.01\text{--}0.50$ ; Cropp and  
142 Norbury 2020; Matz et al. 2020; Logan et al. 2021), despite some evidence of model  
143 outcomes being sensitive to the rate of adaptation (Bay, Rose, Logan, & Palumbi, 2017;  
144 Cropp & Norbury, 2020), evidence of high heritability for coral survivorship in high  
145 temperatures (e.g.,  $h^2 = 0.75$ : Kirk et al. 2018), and the potential for rapid symbiont evolution  
146 in response to thermal change (e.g., Chakravarti et al. 2017; Buerger et al. 2020). Therefore,  
147 our ability to project the future of coral populations in the context of climate change is  
148 critically dependent upon the estimates of trait heritability used in eco-evolutionary models  
149 (C. A. Logan et al., 2014; M. L. Logan, Cox, & Calsbeek, 2014; Visser, 2008).

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

## 162 **Literature Analysis**

### 163 *Literature search*

164 We undertook an exhaustive literature review to find all possible heritability point  
165 estimates and associated measures of sampling variance (e.g., standard errors, confidence or

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

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

198  
199 *Pre-processing*

200 Heritability is calculated as a proportion of total phenotypic variation, and thus is  
201 constrained to fall between zero and one (Falconer & Mackay, 1996). Because most classical  
202 meta-analytical statistical models assume normally-distributed uncertainty, transformation of  
203 our estimates prior to meta-analysis was necessary (Lin & Xu, 2020; Wolfgang Viechtbauer,  
204 2010). Thus, we converted point estimates of heritabilities and associated standard errors  
205 (SE) to 95% confidence intervals, then transformed both the point estimates as well as the  
206 upper and lower 95% confidence (or Bayesian credible) limits to the natural logarithmic scale  
207 using the transformation:

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

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

211 There were four estimates from two studies that did not report any associated SE or  
212 CI values, and another three estimates whose lower CI values (when calculated from the SE)  
213 were less than -0.2, which prevented their transformation to the  $\ln$ -scale. To include these  
214 data in the meta-analysis but down-weight their leverage on the overall analysis, we fit a  
215 quantile regression through the 95<sup>th</sup> quantile of transformed SE vs. transformed  $h^2$  (Koenker,  
216 2020; Koenker & Hallock, 2001) using only heritability estimates that were able to be  
217 transformed to the  $\ln$ -scale. value of the heritability on the transformed scale ( $h_T^2$ ) to predict  
218  $SE_T$  values. We then used this fitted equation ( $SE_T = 0.255 - 0.452 \cdot h_T^2$ ) to interpolate missing  
219  $SE_T$  values, making the conservative assumption that they would have values at the upper  
220 95<sup>th</sup> quantile (i.e., among the most uncertain estimates).

221

### 222 *Factors of interest*

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

228

**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 $D$ ) and proportion of symbionts that are more the thermally-tolerant species ( <i>Durusdinium</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	$\pi$ -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 difference</i>	covariate	Difference (in +°C) between the study's reported control or ambient temperature and the heat treatment temperature

229 *Reported heritability estimates*

230 We collected a total of 95 valid heritability estimates from 19 independent studies of  
231 scleractinian corals (Fig. 1). Three studies (Császár, Ralph, Frankham, Berkelmans, & van Oppen,  
232 2010; Quigley, Randall, van Oppen, & Bay, 2020; Wright et al., 2019) each involving multiple trait  
233 types, provide 59% of all heritability estimates (Fig. 1-left). There was an even split of studies (9:9  
234 studies) examining narrow-sense ( $h^2$ ) and broad-sense ( $H^2$ ) heritability, with one study (Carlson et  
235 al., 2011) reporting both heritability types. However, the number of raw estimates produced by each  
236 study differed markedly, with more broad-sense estimates ( $n = 70$ ) than narrow-sense ( $n = 25$ ). The  
237 studies also differed in terms of which trait type was reported, with most studies reporting only a  
238 single estimate (12 studies), and the other seven studies reporting on two to six distinct trait types.  
239 Survival was the most frequently studied trait type (nine studies, 15 estimates), while bleaching (six  
240 studies, 10 estimates) and growth (six studies, 23 estimates) were also diversely studied. The latter  
241 often included comparisons of multiple species or symbionts within the same study, resulting in a  
242 large number of estimates. Most trait type estimates originated from least two independent studies  
243 estimates, save for immune response (four estimates from one study) and gamete contribution (one  
244 estimate). We therefore interpret the results for immune response with caution, given that they all  
245 belong to the same study, and excluded the single estimate for gamete compatibility from the  
246 subsequent meta-analysis. Notably, there were limited studies of the heritability of coral  
247 reproduction and fecundity, and there were no heritability estimates of thermal optimum ( $T_{opt}$ ),  
248 measures of performance breadth (e.g., B80, B95), or critical thermal limits ( $CT_{max/min}$ ). Only three  
249 studies reported the total phenotypic variation and/or the level of additive genetic variation, which  
250 would be particularly useful for calculating metrics of evolvability (Ma, Lü, Wang, & Wan, 2014;  
251 Visscher et al., 2008). We therefore recommend that future studies report these estimates of  
252 variation.

253 For life stage, there were 63 estimates (from eight studies) for adults, 18 estimates for  
254 juveniles (from seven studies), and 14 for larvae (from five studies), with every study reporting on  
255 only a single life stage save for two reporting on two different life stages (Carlson et al., 2011;  
256 Quigley, Willis, & Bay, 2017). There was similar lack of overlap across heritability types (70  
257 broad-sense vs. 25 narrow-sense heritability estimates across 10 vs. 10 studies, respectively), with  
258 only one study having both valid broad-sense and narrow-sense heritabilities (Carlson et al., 2011).  
259 Across coral growth forms, there were 61 estimates of corymbose corals (from seven studies), 21  
260 estimates for massive corals (from eight studies), nine estimates for branching/arborescent (from six  
261 studies), and three and one estimates for encrusting and columnar corals, respectively (each from a  
262 single study). Finally, 14/19 studies (83/95 estimates) recorded temperatures, and thus the effect of

263 temperature manipulation on heritability could be examined for these studies. However, the  
264 difference between the manipulated vs. control/ambient temperatures varied substantially across  
265 each study, with all temperature manipulation differences being positive (i.e., control/ambient  
266 conditions were always less than the treatment temperatures) but positively skewed (a few  
267 experiments used temperatures that differed by 10°C between control and high temperature  
268 treatments, but most used smaller elevations of temperature). For example, 29 estimates of  
269 heritability originated from control/ambient conditions (from seven separate studies), while 54  
270 estimates were obtained from above-ambient temperature treatments (from 12 studies).  
271 Additionally, there was limited overlap of control and heated temperature differences for some trait  
272 types, making it difficult to compare the effect of temperature for trait types such as symbiont  
273 community (two control estimates), morphology (one control estimate) and gene expression (nine  
274 temperature differences, but no control estimates).

275

### 276 **Meta-analysis approach**

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

294 We considered the top model for each analysis as the model with the lowest Akaike's  
295 Information Criterion, corrected for small sample sizes (AICc). We considered this model a  
296 substantial improvement over other candidate models when the difference in AICc scores ( $\Delta\text{AICc}$ )  
297 was greater than two (Burnham & Anderson, 2004). We followed the four-step model selection  
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298 strategy outlined in Zuur et al. (2007, 2009): (1) define the ‘beyond optimal’ fixed effects structure  
299 – that is, the most conceivably complex yet biologically relevant fixed effects possible, (2) select  
300 (via the lowest AICc value) the optimal random effects structure for models fit using restricted  
301 maximum likelihood (REML), (3) select (via the lowest AICc value) the optimal fixed effects  
302 structures for models fit using maximum likelihood, (4) re-fit the final model using REML. Study  
303 and species were highly confounded and precluded the inclusion of both as random effects within  
304 the same model. Thus, we fit models using one of the following random effects structures: estimate  
305 ID only (1|estimate ID), study ID only (1|study ID), species only (1|species), estimate ID nested  
306 within its respective study ID (1|study ID/estimate ID), estimate ID nested within species  
307 (1|species/estimate ID), or a random effect variance fixed at zero.

308 After fitting models for each analysis, we examined the level of among-study heterogeneity  
309 ( $\tau^2$ ) using the  $I^2$  index (Higgins & Thompson, 2002), which provides an estimate of the among-  
310 study variance relative to the total variance not explained by the fixed effects. We used the  $Q_E$   
311 statistic to test for significant residual heterogeneity after accounting for fixed effects (W.  
312 Viechtbauer, López-López, Sánchez-Meca, & Marín-Martínez, 2015). Higher proportions of  
313 heterogeneity indicate that variation in true effect size of heritability is a distribution of study  
314 effects (i.e. due to methodological or other study differences), whereas lower heterogeneity  
315 indicates that any among-study heterogeneity is likely small relative to measurement error, so  
316 studies are measuring a common heritability value (Ban, Graham, & Connolly, 2014; Higgins &  
317 Thompson, 2002). We report the pseudo- $R^2$  for meta-analytical models, computed by comparing the  
318 difference in  $\hat{\tau}^2$  estimated using models including fixed effects ( $\hat{\tau}_{ME}^2$ ) vs. a model with the same  
319 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,  
320 2009). Where significant interactions were found between factors with more than two levels, we  
321 employed simultaneous tests for testing multiple general linear hypotheses determined by visual  
322 inspection of marginal estimates, and report p-values adjusted using the single-step method.

323 Model standardized residuals were plotted against fitted values to look for strong deviations  
324 from normality, and data were simulated using the fitted model and plotted with the true data to  
325 assess model performance. We assessed the presence of publication bias by plotting the model  
326 residuals by their precision (inverse of standard error) to produce a funnel plot (Møller & Jennions,  
327 2001). We also calculated the Rosenberg fail-safe number, which indicates if model findings are  
328 robust to any apparent publication bias if the number is greater than five times the number of  
329 studies plus ten (Rosenberg, 2005; Rosenthal, 1991). Finally, we used Cook’s distances to  
330 determine highly influential points for each model (Cook & Weisberg, 1982).

331

332

### 333 **High heritability of coral traits**

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

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

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

364

365 *Heritability across trait types in other organisms*

366 Heritability differences across trait types have been widely reported in other taxa (Flood et  
367 al., 2016; Mousseau & Roff, 1987; Polderman et al., 2015; Wheelwright et al., 2014). Life history  
368 traits closely tied to fitness (e.g., longevity, fecundity) are often maintained due to strong stabilizing  
369 selection and thus exhibit lower heritability compared to morphological, physiological, and  
370 behavioural traits (Mousseau & Roff, 1987; Price & Schluter, 1991; Teplitsky et al., 2009;  
371 Wheelwright et al., 2014). However, traits may also have low heritability due to a large contribution  
372 to total variance by non-additive genetic variation, environmental variation, or through maternal  
373 effects (the latter likely to be less pronounced in broadcast spawning corals than in organisms with  
374 higher levels of parental care). In our analysis, gene expression had the lowest heritability, which is  
375 consistent with many other studies noting the low heritability of mRNA (i.e., the ‘missing  
376 heritability’ problem, Zuk et al. 2012; Yang et al. 2014). While the exact cause of missing  
377 heritability for gene expression measures has yet to be determined, it may be due to highly variable  
378 gene expression both within (i.e. low repeatability) and among individuals, or to epistatic gene  
379 interactions, or some combination of both (Yang et al., 2014; Zuk et al., 2012). The heritability of  
380 symbiont community composition was much higher than heritabilities estimated for the diversity of  
381 human gut microbes ( $h^2 = 0.019$ ), which is predominantly environmentally rather than genetically-  
382 determined (Rothschild et al., 2018). However, beneficial microbes that are related to metabolic  
383 health, such as gut bacteria of the family Christensenellaceae, and microbiomes of mice in  
384 controlled laboratory environments (Org et al. 2015), show much higher heritabilities of  $h^2=0.3-0.6$ ,  
385 more consistent with our findings. Photochemical traits were estimated to have modest heritability  
386 in our analysis; however, only two studies which included only broad-sense estimates were  
387 available ( $H^2 = 0.26$ ). In plants, broad-sense heritability of photosynthetic traits is variable but can  
388 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  
389 Tuhina-Khatun et al. 2015, respectively). Moderate narrow-sense heritability estimates, similar to  
390 those reported here, have been reported for narrow-sense heritability of maximum quantum yield in  
391 plants ( $h^2 = 0.12-0.34$ ) (Qu et al., 2017). Heritability associated with bleaching and symbiont  
392 abundance in corals (often using chlorophyll content as a proxy) was estimated overall as  $h^2 = 0.36$ ,  
393 which is similar to estimates of broad-sense heritability of chlorophyll content in plants (e.g.,  $h^2 =$   
394  $0.44-0.49$  in *Oryza sativa* L., Tuhina-Khatun et al. 2015).

395

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

397 Using a data subset to examine trait type and life stage interactions, a model of trait type  $\times$   
398 life stage + heritability type with a random effect of estimate ID only was preferred under model  
399 selection (Table S3). Other analyses of trait type versus heritability type interaction and trait type  
400 and growth form interaction found further support for a trait type  $\times$  life stage interaction (see

401 Supplementary Text S3). The final meta-model had moderate levels of heterogeneity among  
402 estimates ( $QE_{55} = 96, p = 0.0005; I^2_{total} = 47\%$ ) and fixed effects helped explain much of the  
403 variation in heritability estimates (pseudo  $R^2 = 78\%$ ). Parameter estimates for all trait types were  
404 similar to the previous overall model estimates (Fig. 3; Fig. S3; Table S4), but there were  
405 significant interactions for growth and bleaching in juveniles relative to other life stages as well as a  
406 for nutrient content in adults (Fig. 3; Table S4). Cook's distances for the trait type  $\times$  life stage +  
407 heritability type model were low overall ( $\leq 2$ ), but three points had moderate leverage on the  
408 analysis (Cook's distance = 2.9–3.9), but the growth:juvenile interaction term remained important  
409 when any or all were excluded from the analysis. Coral growth form was never an important  
410 predictor of heritability, and species was never selected as an important random effect, suggesting  
411 that taxonomic differences may be too small or variable to detect, given the data currently available.

412 Life stage had a strong effect for certain trait type–heritability type combinations (Fig. 3;  
413 Table S4). For example, the estimated narrow-sense  $h^2$  for bleaching metrics in adults was 9.1 times  
414 the same  $h^2$  for juveniles, and two times the bleaching  $H^2$  value in adults versus larvae. Growth and  
415 nutrient content broad-sense heritability also differed across life stage, with adult growth  $H^2$  being  
416 3.1 times that of juveniles and nutrient content  $H^2$  being 3.9 times greater in larvae vs. adults. In  
417 contrast, the effect of heritability type was relatively weak (1.4 to 2.5–fold higher for broad-sense  
418 heritabilities vs. narrow-sense when controlling for trait type and life stage) compared to the effect  
419 of trait type on heritability, which was up to 13.2 times higher heritability when comparing  $h^2$   
420 between juvenile bleaching vs. survival (Fig. 3; Table S4). However, this difference in broad- vs.  
421 narrow-sense heritability type indicates the presence of substantial but not overwhelming non-  
422 additive genetic variation as a portion of the total genetic variation present in broad-sense  
423 heritability.

424

#### 425 *Low adaptive potential of juvenile growth and bleaching*

426 Juvenile growth was much less heritable relative to adult growth, while bleaching was less  
427 heritable in juveniles relative to both larvae and adults, highlighting the differential adaptive  
428 potential of coral life stage to selection for some trait types. This reduced bleaching heritability  
429 from larvae to juveniles may be the result of previous strong stabilizing selection on growth and  
430 bleaching traits in juveniles, thus driving reduced additive genetic variance through the fixation of  
431 alleles and resulting in lower heritabilities compared to other traits (Fisher, 1930; Teplitsky et al.,  
432 2009). Indeed, bleaching events likely represent a strong selective pressure for juvenile corals  
433 (Dajka et al., 2019; T. P. Hughes et al., 2019). Similarly, reductions in growth may result in  
434 increased mortality due to overgrowth competition and size-dependent predation (Doropoulos,  
435 Ward, Marshall, Diaz-Pulido, & Mumby, 2012; Madin et al., 2014; Vermeij & Sandin, 2008). There  
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436 is also evidence that increases in additive genetic variance ( $V_A$ ) may occur via mutation  
437 accumulation across an organism's lifetime (Wilson et al. 2008b). Moreover, reduced importance of  
438 local environment with age can result in reduced relative total variation,  $V_P$  (e.g., the Wilson effect,  
439 Bouchard Jr. 2013). Both of these processes can therefore result in older life stages having higher  
440 heritability estimates. Making the distinction between these processes requires examining changes  
441 in  $V_A$  and  $V_P$  across an organism's lifetime, which no coral studies have done to date.

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

#### 462 *Confounding sources of variation*

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

478 Our results are also affected by other sources of phenotypic variation not accounted for in  
479 present studies, such as parental and epigenetic effects. Parental effects may have a larger influence  
480 on heritability than previously assumed (C. D. Kenkel, Setta, & Matz, 2015; Noble, Mcfarlane,  
481 Keogh, & Whiting, 2014), and may be especially important for brooding corals in which the  
482 offspring develops within the parent colony as well as for species inheriting their symbiont  
483 communities directly from parents (i.e. vertical transmission) (C. D. Kenkel et al., 2015; Quigley et  
484 al., 2017). Vertically-transmitting brooders and broadcast spawning species make up a minority of  
485 species examined (3/19 and 9/19, respectively), with the remaining being horizontally-transmitting  
486 spawners. Similarly, the number of heritability estimates from vertical transmitters made up only  
487 9/95 and 16/95 heritability estimates, respectively, and thus parental effects via brooding and/or  
488 vertical transmission would have impacted a minority of estimates. Epigenetic effects may also  
489 inflate heritability estimates (Putnam & Gates, 2015). In studies of multicellular animals, there has  
490 been little support for epigenetic inheritance via CgP methylation (Torda et al., 2017), although at  
491 least one recent study in corals has found such evidence (Liew et al., 2020). Further evidence is  
492 needed to determine if epigenetic changes confer fitness benefits similar to additive genetic effects  
493 (Torda et al., 2017), thus future studies aiming to separate phenotypic variation specific to parental  
494 effects, symbiont composition, epigenome, and additive genetic effects would be especially  
495 valuable.

#### 497 **Manipulated temperature has negligible effect on heritability**

498 When examining only studies that controlled for temperature, the magnitude of the  
499 experiment temperature difference relative to ambient or control conditions had only a marginal  
500 effect on the recorded heritability estimate (Fig. 4). The temperature difference values were all  
501 positive and positively skewed, thus we square-root transformed the temperature difference data in  
502 order to reduce the leverage of estimates obtained from studies using these large temperature  
503 differences. After subsetting the data to exclude studies that did not report the temperature treatment  
504 used relative to ambient conditions, we examined whether an interaction between trait type and  
505 temperature difference was supported. Model selection favored a model of trait + heritability type,  
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506 with some support for alternative models of trait type only and trait type  $\times$  temperature difference  
507 (Table S9;  $\Delta\text{AICc} = 0.50$  and  $1.89$ , respectively) using random effects of estimate ID nested in  
508 study ID. The trait + heritability type model had similar effect sizes compared to those in our  
509 analyses presented above (Fig. S6; Table S10). The effect of trait type in the trait type  $\times$   
510 temperature model (3<sup>rd</sup>-optimal model) saw heritability differences up to a factor of 3.4–4.6 when  
511 the temperature was increased  $+1^\circ\text{C}$  to  $+3^\circ\text{C}$  above ambient. However, within the same trait type,  
512 temperature alone had a reduced effect, with heritability differences between a factor of 0–2.1 and  
513 0–1.6 for  $+1^\circ\text{C}$  and  $+3^\circ\text{C}$ , respectively. More specifically, temperatures  $+1^\circ\text{C}$  above ambient  
514 resulted in immune response heritability increasing by a factor of 2.1, while an increase of  $+3^\circ\text{C}$   
515 above ambient would increase heritability by a factor of 1.6. This interaction was primarily driven  
516 by a single estimate of immune response (Cook's distance = 7.6), and when removed, resulted in no  
517 strong interactions between trait type and temperature. Within other traits, the effect of temperature  
518 was even less pronounced. Bleaching traits were decreased by 28–33% for an increase in  
519 temperature of  $+1$ – $3^\circ\text{C}$  (though this was not significant). Other traits such as growth,  
520 photochemistry, and survival all showed marginal declines in heritability with increasing  
521 temperature difference ( $\sim 3$ – $5\%$  decrease in heritability with  $+1$ – $3^\circ\text{C}$ ). Separate analyses examining  
522 temperature as a categorical variable (ambient vs elevated), as well as analyses omitting ambient  
523 treatments all resulted in similar weak to non-existent effects of temperature on heritability (Fig.  
524 S7-8; Tables S11-14), suggesting a limited effect of manipulated temperature on heritability across  
525 studies. Since a model of trait type + heritability type was preferred over the model of trait type  $\times$   
526 temperature manipulation (Table S9), and with the inclusion of heritability type precluding the  
527 ability to model a trait  $\times$  temperature interaction, we fit an additive model of trait type, heritability  
528 type, and temperature difference to estimate the marginal effect of temperature and found evidence  
529 for, at most, a very weak effect of temperature (Fig. 4).

530

### 531 *Trait adaptation to warming temperatures*

532 Our meta-analysis suggests that the capacity for corals to adapt to warming temperatures  
533 may be relatively consistent over short periods of moderately high temperature (e.g.,  $+1$ – $3^\circ\text{C}$ , the  
534 temperature increases used in most of the studies we analyzed). However, this is contingent on the  
535 assumption that coral responses to temperature conditions in the lab are similar to their responses to  
536 temperatures in the field. Previous studies have found that many traits are expected to respond  
537 differently to climate change (Ahrens et al., 2020), that heritability measurements may change with  
538 temperature (Bubliy & Loeschcke, 2002), and that the rate of temperature increase employed in  
539 each study can also affect heritability (Chown, Jumbam, Sørensen, & Terblanche, 2009). Similarly,  
540 previous heritability studies in insects report trait-specific interactions with temperature (Bubliy &  
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541 Loeschke, 2002; Gunay et al., 2011). Current theory suggests that more extreme environments  
542 should produce increased selective pressures that may reduce heritability (Charmantier & Garant,  
543 2005; Falconer & Mackay, 1996; Wilson et al., 2006). However, despite expectations based on  
544 theory and empirical results like those described above, differences in the temperature gradients  
545 used in each study did not predict the among-treatment differences in heritability estimates for  
546 corals. Specifically, temperature had negligible effect on the estimation of trait heritability, such  
547 that an increase of +1°C may increase high vs. low trait heritability by 4 to 9%, respectively, while  
548 an increase of +3°C results in an increase in heritability of 7 to 16% (changes that, if real, would be  
549 opposite of the predicted direction). These findings indicate that populations with sufficient genetic  
550 diversity are unlikely to experience a reduction in heritability associated with warmer temperatures,  
551 in turn suggesting substantial retention of the capacity to adapt in the face of ongoing temperature  
552 change.

553

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

555 The absence of an effect of temperature on trait heritability observed here could reflect  
556 differences among studies in the way temperature treatments were applied, and/or differences in  
557 how temperature effects were statistically modelled. Many traits of organisms are non-linearly  
558 related to temperature, and these relationships are captured by measuring thermal performance  
559 curves (TPCs). TPCs are quantified by subjecting individuals to increasing temperatures at a  
560 standardized rate while repeatedly measuring performance (Angilletta, 2009; Chown et al., 2009), to  
561 identify: (1) the value of maximal performance ( $P_{max}$ ), (2) the temperature at which maximum  
562 performance occurs i.e., the thermal optimum ( $T_{opt}$ ); (3) the performance breadth (e.g., B80, B95),  
563 and, somewhat related to the latter, (4) the limits of thermal performance (e.g.,  $CT_{max}$ ) (Angilletta,  
564 2009; Bodensteiner et al., 2020; M. L. Logan et al., 2014). Measuring limits to thermal tolerance  
565 involves either static assays of survival time in a constant high temperature, such as heat  
566 knockdown time (Castañeda, Romero-Soriano, Mesas, Roff, & Santos, 2019; Ma et al., 2014), or  
567 dynamic assays involving gradually increasing temperature until failure, such as temperature-at-  
568 death and  $CT_{max}$  (Castañeda et al., 2019; Doyle, Leberg, & Klerks, 2011).

569 The way in which temperature was modelled in each of the studies analyzed herein – and  
570 consequently, which component of thermal performance was captured – is likely to affect the  
571 heritability estimated. For example, studies incorporating temperature treatment as a fixed effect  
572 and estimating heritability using a single model (Dixon et al., 2015; Lohr & Patterson, 2017;  
573 Manzello et al., 2019; Meyer et al., 2009), or studies that calculate heritability from the difference  
574 in trait values between low vs. high temperature treatments (Császár et al., 2010; Dziedzic, Elder,  
575 Tavalire, & Meyer, 2019; Yetsko et al., 2020) likely estimated the heritability of thermal sensitivity

576 (i.e., how performance changes as temperature changes). Conversely, studies that used separate  
577 models for low-temperature and high-temperature treatments (Kirk et al., 2018; Quigley et al.,  
578 2020; Wright et al., 2019; Zhang et al., 2019) produced separate estimates of the heritability of  
579 performance under the two temperatures. One inherent problem with such an approach arises if  
580 there is little or no variation in the trait value for one of the treatment levels (e.g., no mortality of  
581 bleaching observed under control conditions or no observable growth when corals are placed in  
582 extreme heat). The absence of among-individual variation in performance in these cases means that  
583 the estimated heritability will always be near zero, regardless of any underlying additive genetic  
584 variation associated with the trait in question. For studies of thermotolerance, obtaining heritability  
585 estimates via differenced treatment values or as a fixed treatment effect (and thereby providing  
586 heritability estimates indicative of the trait's thermal sensitivity) is likely preferable, but ideally  
587 future studies would characterize responses based on many temperature points along the TPC to  
588 obtain  $CT_{max}$ ,  $T_{opt}$ , and  $P_{max}$ .

589 In this review, we were unable to assess whether heritabilities associated with thermal  
590 sensitivity in performance were different from heritabilities of performance itself (Fig. S10).  
591 However, the evolution of both maximal performance and the thermal sensitivity are inherently  
592 linked by the shape of the TPC (e.g., a higher peak in the TPC would result in higher trait values  
593 and greater trait thermal sensitivity), and thus their relationship may be correlated (Janhunen et al.,  
594 2016). For example, with the evolution of higher upper thermotolerance (e.g., increasing  $CT_{max}$ ),  
595 organisms may face reduced thermal performance breadth and thermal plasticity (Hoffmann et al.  
596 2013; Comte and Olden 2017; Baker et al. 2018). Growth and the thermal sensitivity of growth are  
597 negatively correlated for one-year-old rainbow trout (*Oncorhynchus mykiss*) at low temperatures,  
598 but not at higher temperatures, thus while there is moderate heritability for both growth ( $h^2 = 0.46$ )  
599 and thermal sensitivity of growth ( $h^2 = 0.24$ ), selection for higher growth is predicted to result in  
600 increased thermal sensitivity in future generations held at low temperatures, but unlikely to affect  
601 thermal sensitivity at higher temperatures (Janhunen et al., 2016). Similar trade-offs of growth vs.  
602 sensitivity have been observed as well in adult rainbow trout (Sae-Lim et al., 2015). Further  
603 complicating the matter, some genetic correlations among life history traits may be temperature-  
604 specific (reviewed in Sgrò and Hoffmann 2004), including cases where negative genetic  
605 correlations can become positive at higher temperatures and vice-versa. Thus, coral trait evolution  
606 may further be complicated by (currently unmeasured) genetic correlations across TPC metrics.

607

## 608 **Conclusion**

609 Our meta-analysis estimates relatively high heritability for some traits, such as survival and  
610 growth. This, coupled with the fact that heritability does not appreciably decline with increasing

611 temperature manipulation, suggests the potential for coral adaptation to future conditions of weak to  
612 moderate climate change. Nevertheless, potential confounding factors that could bias some of our  
613 heritability estimates upwards remain to be explored, including the effects of preconditioning and  
614 canalization in adults, parental and symbiont effects, and transgenerational inheritance of CgP  
615 methylation. Recent evolutionary models of corals consider the heritability of the thermal optimum  
616 for corals,  $T_{opt}$ , to be anywhere from negligible (e.g.,  $h^2 = 0.01$ ) to low/medium (e.g.,  $h^2 = 0.16$ –  
617 0.50) (Cropp & Norbury, 2020; C. A. Logan et al., 2021; Matz et al., 2020). However, there are no  
618 available estimates for coral thermal performance traits such as  $T_{opt}$ ,  $CT_{min}$ ,  $CT_{max}$ , and  $B80$ , and our  
619 knowledge of how TPC parameters co-evolve remains very limited. For example, the evolution of  
620 higher thermal optima ( $T_{opt}$ ) may result in reduced maximal performance ( $P_{max}$ ) or performance  
621 breadth ( $CT_{min}$ ,  $CT_{max}$ , and  $B80$ ). Other genetic trade-offs such as growth vs. thermotolerance for  
622 both corals and symbionts may exist, further constraining coral evolution to climate change. Future  
623 studies would ideally construct TPCs using multiple temperatures across a known pedigree of  
624 individuals in order to calculate heritabilities and associated trade-offs for TPC parameters across  
625 one or multiple traits. Combined with our current knowledge of trait heritabilities, this would allow  
626 better predictions regarding thermal evolution of corals in response to climate change. Nevertheless,  
627 our findings suggest that corals may be capable of adapting more rapidly to the thermal challenges  
628 imposed by climate change than previously thought.

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## 637 **Data accessibility statement**

638 All extracted heritability estimates and supplementary code are available at  
639 <https://github.com/ecology/heritability-meta>.

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999

## 1000 **Figure Captions**

1001

1002 **Fig. 1.** Heritability estimates ( $N = 95$ ) of various traits across 19 studies of reef-building corals.  
1003 Colour indicates the specific trait type (hue) and heritability type (broad-sense  $H^2$  as lighter tint  
1004 circles, narrow-sense  $h^2$  as darker shade). Left: Number of estimates reported in each study. Right:  
1005 Point estimates of heritability and their associated 95% confidence/credible intervals (whiskers) on  
1006 a logarithmic ( $\ln$ ) scale. Heritability estimates closer to one indicate higher heritability and thus the  
1007 potential for higher rates of trait adaptation within the population. Dashed lines represent  
1008 heritability estimates where standard errors/confidence intervals were imputed.

1009

1010 **Fig. 2.** Heritability estimates  $\pm$  SE for the trait type-only model, not accounting for differences due  
1011 to (i.e., pooled across) life stage and heritability type. Traits are sorted along the spectrum according  
1012 to their overall relative heritability, with heritability closer to one indicating more heritable traits.  
1013 The number of estimates included in the meta-analysis for each trait type are indicated below each  
1014 error bar in grey. The gamete compatibility trait type is excluded due to its reliance on only a single  
1015 study/estimate.

1016

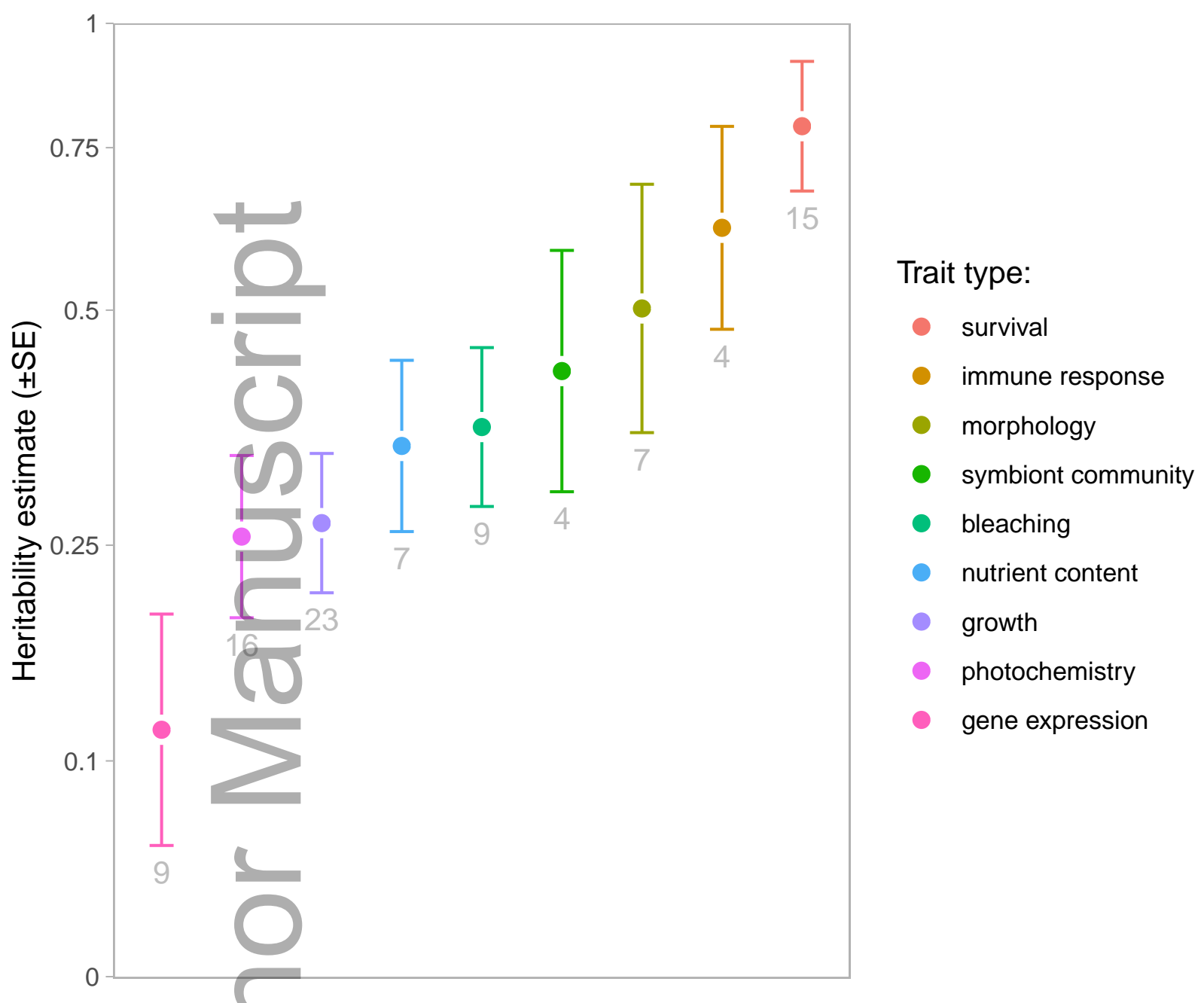
1017 **Fig. 3.** Heritability estimates  $\pm$  SE across trait types with multiple life stages (x-axis) and different  
1018 heritability types (lighter points: broad-sense heritability; darker points: narrow-sense heritability).  
1019 Associated sample sizes (number of original estimates) are adjacent to each point in grey.

1020

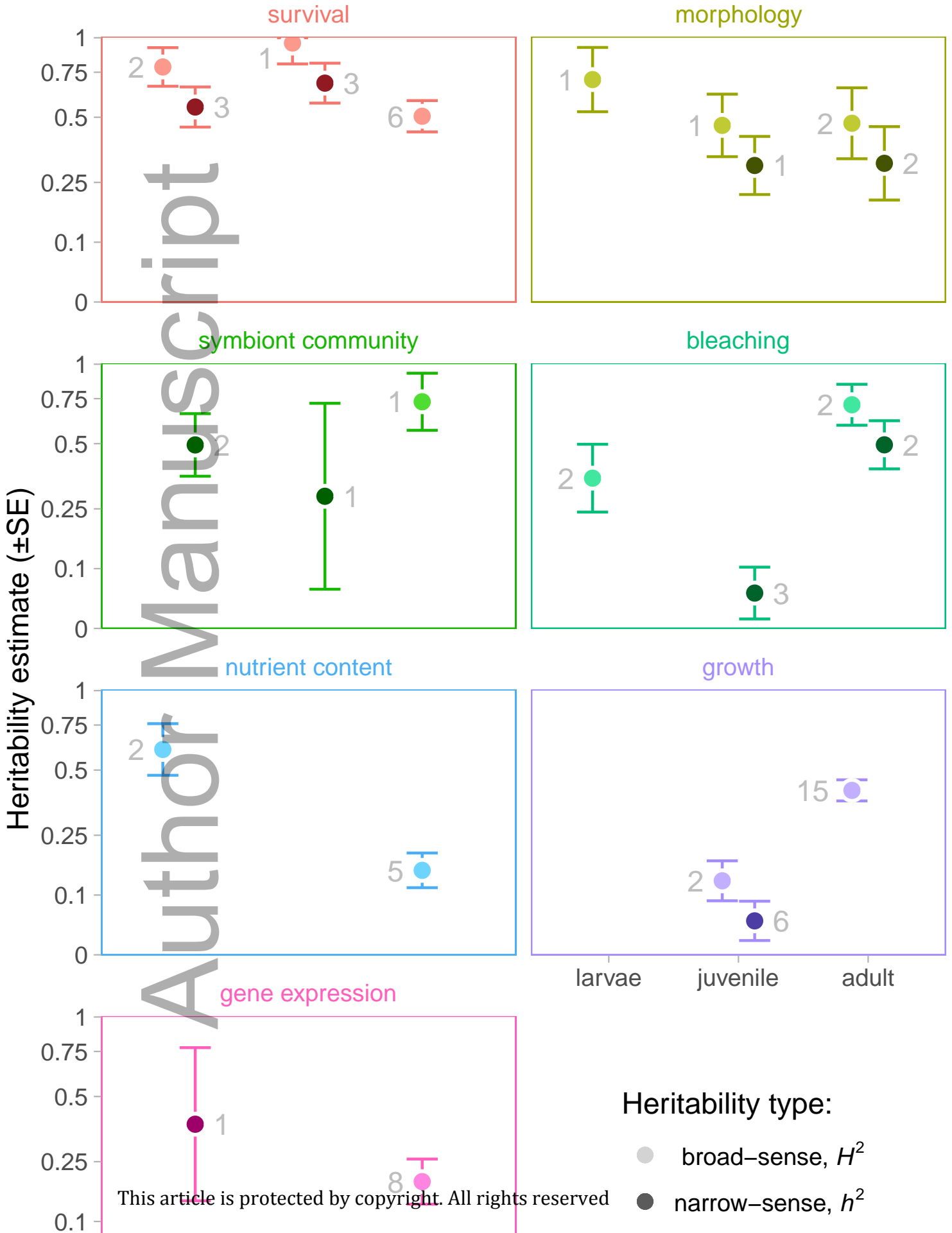
1021 **Fig. 4.** Heritability vs. study temperature difference (treatment temperature relative to  
1022 ambient/control temperature) for each trait type and heritability type, with the size of each point  
1023 represents its relative precision. Dashed lines indicate the estimated marginal mean effect of  
1024 temperature difference, while accounting for trait type and heritability type effects. One square-root  
1025 degree difference ( $+1\sqrt{\circ\text{C}}$ ) translates to a mean increase in  $\ln[h^2+0.2]$  heritability of  $0.03 \pm 0.05$  SE.



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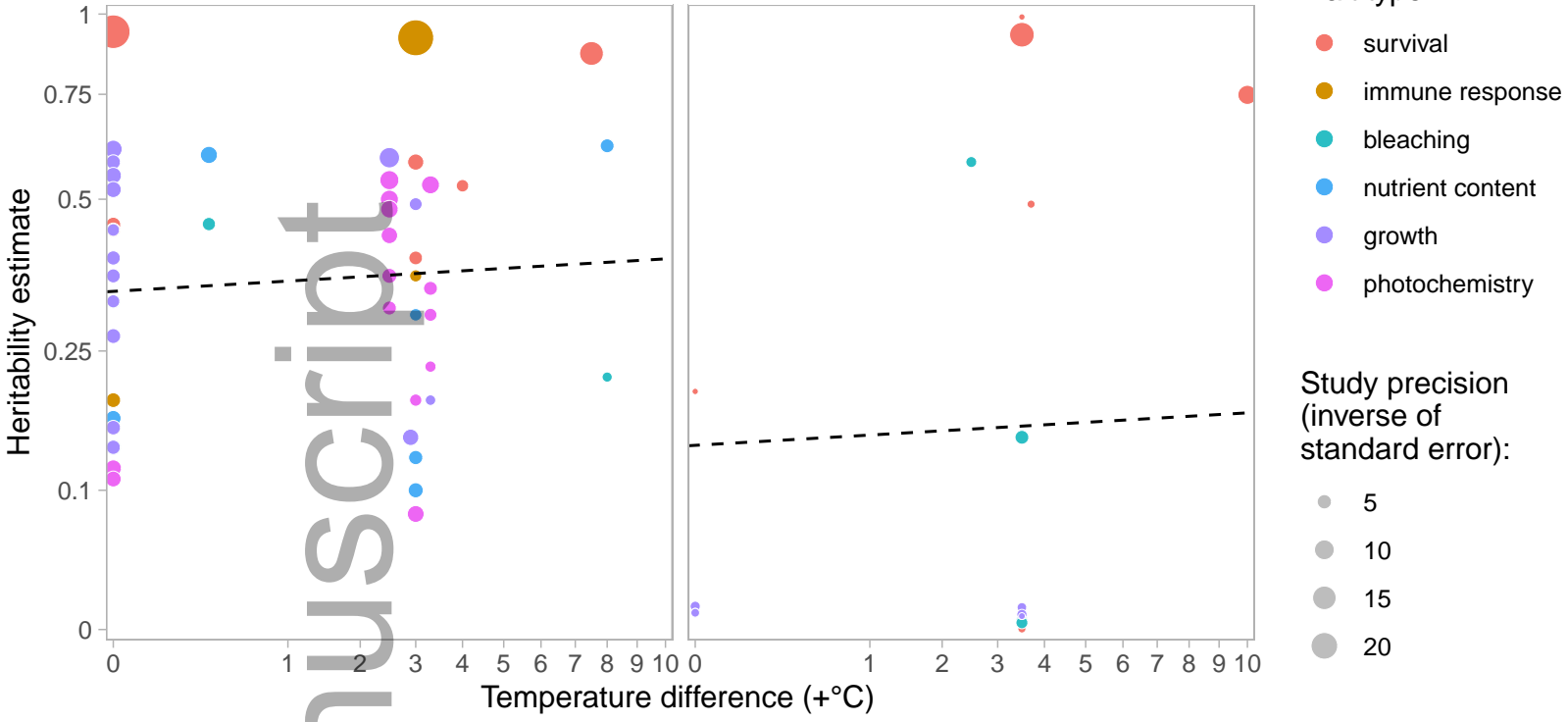
gcb\_15829\_f2.eps



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Broad-sense

Narrow-sense



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