

1 **Moving beyond heritability in the search for coral adaptive potential**

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## 32 **Abstract**

33 Global environmental change is happening at unprecedented rates. Coral reefs are among the  
34 ecosystems most threatened by global change. For wild populations to persist, they must  
35 adapt. Knowledge shortfalls about corals' complex ecological and evolutionary dynamics,  
36 however, stymie predictions about potential adaptation to future conditions. Here, we review  
37 adaptation through the lens of quantitative genetics. We argue that coral adaptation studies  
38 can benefit greatly from "wild" quantitative genetic methods, where traits are studied in wild  
39 populations undergoing natural selection, genomic relationship matrices can replace breeding  
40 experiments, and analyses can be extended to examine genetic constraints among traits.  
41 Individuals with advantageous genotypes for anticipated future conditions can be identified.  
42 Finally, genomic genotyping supports simultaneous consideration of how genetic diversity is  
43 arrayed across geographic and environmental distances, providing greater context for  
44 predictions of phenotypic evolution at a metapopulation scale.

## 45 **Introduction**

46 Anthropogenic change is pervasive, yet little is known about the complex ecological and  
47 evolutionary dynamics operating in wild populations, making biological predictions highly  
48 uncertain (Nosil et al., 2020; Urban et al., 2016). Such knowledge gaps are laid bare in  
49 marine systems, where the logistics of working underwater and the difficulties of rearing  
50 organisms and conducting manipulative experiments mean that key population parameters  
51 including survival, fecundity, and growth are often unavailable. Critically, coral reefs which  
52 already live close to their thermal limits (Berkelmans & Willis, 1999), are among the  
53 ecosystems most likely to be impacted by large-scale climate warming and have suffered  
54 extensive mortality due to heat-induced bleaching, where the cnidarian host expels their algal  
55 endosymbionts (Hoegh-Guldberg et al., 2007; Hughes et al., 2017; Walther et al., 2002).  
56 Greater knowledge regarding the ecological and evolutionary processes that underpin  
57 adaptation is urgently required if humans are to assume responsibility for mitigating or  
58 facilitating responses that promote coral reef resilience.

59 Current population models which predict long term changes to coral reefs fall into two  
60 categories. Ecology-focused models capture complex community dynamics and species  
61 interactions but treat species traits as fixed (e.g., Bozec et al., 2022). In contrast, evolution-  
62 focused models use demographic and population parameters to estimate genetic responses at

63 the population level but typically ignore species interactions (Bay et al., 2017; Kleypas et al.,  
64 2016; Logan et al., 2014; Matz et al., 2018; Matz et al., 2020; McManus et al., 2021). A  
65 limited number of studies have incorporated simple competition between two coral life  
66 histories (McManus et al., 2021; Walsworth et al., 2019) or focus on the interactions between  
67 the coral cnidarian hosts and their photosynthetic endosymbionts (Baskett et al., 2009; Day et  
68 al., 2008; Logan et al., 2021). Regardless of model details, evolutionary models consistently  
69 find that evolutionary adaptation, especially to elevated temperatures, is critical for long-term  
70 coral persistence.

71 While adaptation appears necessary for coral persistence in a changing climate, the number  
72 and effect of genes (the *genetic architecture*) determining thermal tolerance traits remains  
73 undiscovered for most coral species, and thus the potential for adaptive change is unknown.  
74 Some studies show that temperature related traits likely have a genetic basis (reviewed in  
75 Bairos-Novak et al., 2021; Howells et al., 2022), although these estimates might not  
76 accurately reflect adaptive potential under natural conditions (Humanes et al., 2022). Many  
77 studies have identified gene expression responses to acute heat stress (e.g., Barshis et al.,  
78 2013; Parkinson et al., 2018; Rose et al., 2018; Traylor-Knowles et al., 2017), but whether  
79 expression differences among individuals within species have a genetic basis is largely  
80 unresolved (Dixon et al., 2015; Kenkel & Matz, 2016; but see Dixon et al., 2018; Rose et al.,  
81 2018). Fuller *et al.* (2020) established that the bleaching tolerance in *Acropora millepora* is  
82 affected by many cnidarian host loci and by photosynthetic endosymbiont identity. While we  
83 acknowledge that symbionts play an important role in thermal tolerance of the coral  
84 holobiont, we focus this review on cnidarian host genetics, as methods evaluating relatedness  
85 between cnidarian individuals are more tractable.

86 Here, we aim to identify key genetic parameters that determine adaptive capacity in corals  
87 and highlight data gaps that hinder our ability to make robust predictions for coral futures.  
88 There are many complementary approaches to study functionally important genetic variation  
89 (Vasemägi & Primmer, 2005) such as DNA sequence variation including genotype-  
90 environment association analyses (Lasky et al., 2023), reciprocal transplantation (Kawecki &  
91 Ebert, 2004), and evolve-and-resequence experiments (Turner et al., 2011). The emerging  
92 consensus that adaptation depends on the combined contribution of many genes with small  
93 effects (i.e., that fitness traits are polygenic or complex, see Falconer & Mackay, 1996; Hill,  
94 2010; Lynch & Walsh, 1998) is supported by studies that: examine associations of alleles

95 between adult corals from contrasting environments (Bay & Palumbi, 2014; Howells et al.,  
96 2021; Rippe et al., 2021; Rose et al., 2018; van Oppen et al., 2018); monitor gene expression  
97 changes with reciprocal transplantation (Kenkel & Matz, 2016); or show allelic shifts induced  
98 by experimental manipulation of coral larvae (Dixon et al., 2015; Kirk et al., 2018). Because  
99 adaptive traits appear primarily polygenic, we focus primarily on quantitative genetic  
100 inference in this review. Quantitative genetic methods provide tools designed to study  
101 polygenic phenotypes and to decouple genetic from environmental contributions to  
102 phenotypic traits thereby providing insights into future adaptation. Throughout, we note  
103 where future experimental research should be directed, which genetic parameters to estimate,  
104 and how they might be estimated.

### 105 **Selection, heritability, and genetic variance in single traits**

106 Adaptive evolution begins when individuals in a population differ in fitness as a function of  
107 their trait values (Fig. 1). For complex traits, single trait phenotypes can be expressed as:

$$108 \quad P = G + E + G \times E \quad ,$$

109 where the phenotypic value ( $P$ ) results from the individual's genes ( $G$ ), its environment ( $E$ ),  
110 and how genes interact with and respond to environmental conditions ( $G \times E$ ). This treatment  
111 of the phenotype as the sum of underlying genetic and environmental effects defines the  
112 framework of quantitative genetics (Falconer & Mackay, 1996). At the population level, the  
113 relative contribution of genes to differences among individuals determines whether the  
114 population mean trait value evolves. If a population's phenotypic variation is predominantly  
115 due to  $G$  or  $G \times E$ , then selecting individuals by their phenotypes also selects a subset of the  
116 genetic variation controlling that phenotype, thereby increasing the frequency of selected  
117 alleles in the population.

118 The distribution of trait values in the population can also adjust in direct response to changes  
119 in environment, without any alteration of allele frequencies, namely *phenotypic plasticity*.  
120 Phenotypic plasticity may allow individual fitness to track shifts in changing environments,  
121 thereby maintaining population size. Plastic phenotypes can be adaptive when phenotypic  
122 change occurs in the direction favoured by natural selection - an example of this might  
123 include greater tolerance to heat stress where pre-warming events prepare the coral holobiont  
124 physiologically for the bleaching stress that follows (Ainsworth et al., 2016). However, the  
125 fitness benefits from plasticity can be fleeting due to the inherent flexibility of plastic

126 phenotypes and the absence of genetic changes influencing the trait (Ghalambor et al., 2007).  
127 Epigenetic mechanisms likely underpin plastic responses to the environment, but evidence for  
128 transgenerational persistence of epigenetic effects in corals is currently lacking (Torda et al.,  
129 2017). Intriguingly, growing evidence shows that plastic responses of a trait may align with  
130 the heritable genetic variation of the trait (Noble et al., 2019), suggesting that plasticity and  
131 adaptation may synergistically improve fitness. As a further complication, plasticity itself is a  
132 trait that can evolve where there is  $G \times E$ ; for example, inshore and offshore populations of  
133 *Porites astreoides* differ in plastic changes to gene expression, suggesting locally adapted  
134 plasticity in at least some coral species (Kenkel & Matz, 2016).

135 Despite the potential benefits of plasticity, evidence suggests that it may have limited  
136 potential to enhance thermal tolerance for species that live at their upper limit temperature  
137 range (Kingsolver & Buckley, 2018; van Heerwaarden et al., 2016). Therefore, plasticity  
138 may facilitate short term persistence for many corals which are already living close to their  
139 upper thermal threshold but might not be sufficient to bridge to new thermal optima.  
140 Furthermore, if plastic responses allow individuals with maladapted genotypes to persist, this  
141 may slow adaptive responses to selective pressure (Gilbert & Miles, 2019).

142 Adaptation to new fitness optima occurs via evolutionary processes that change allele  
143 frequencies, increasing the frequency of high fitness alleles. Thus, it is the genetic component  
144 of phenotypes that is the focus for studies of adaptive capacity (Hendry et al., 2018).

145 *Heritability* is a population specific metric that defines the proportion of phenotypic trait  
146 variance ( $V_P$ ) that can be attributed to genetic variation (Visscher et al., 2008). This genetic  
147 variation can be characterised in two ways: either *total* genetic variation ( $V_G$ : broad sense  
148 heritability,  $H^2 = V_G / V_P$ ) which defines all genetic effects on the trait of interest, or only the  
149 *additive* genetic variation ( $V_A$ : narrow sense heritability,  $h^2 = V_A / V_P$ ). Both estimates are  
150 widely used but differ in the conclusions that can be drawn from their estimation.

151 Additive genetic variance describes a subset of total genetic variance, excluding other, non-  
152 additive, sources of genetic variance such as dominance ( $V_D$ ) or epistasis ( $V_I$ ). Dominance  
153 refers to the interactions between alternative alleles at a *single* locus, while epistasis describes  
154 interactions *between* loci that affect the phenotype. Because these interactions are dependent  
155 on the specific combination of alleles present in the individual and these alleles are reshuffled  
156 when passed from generation to generation, non-additive sources of variation ( $V_D$ ,  $V_I$ ) are not  
157 inherited. Thus, broad-sense heritability may overestimate the potential for long-term

158 adaptive responses, although available evidence from wild populations suggests that  $V_A$  is a  
159 greater contributor to  $V_G$  than non-additive genetic variance (Class & Brommer, 2020). A  
160 common source of confusion arises from the fact that the relative magnitude of non-additive  
161 genetic variances does not relate to the prevalence of non-additive gene action: loci with  
162 dominant (and recessive) alleles can be common, even if  $V_D$  is small relative to  $V_A$  (Huang &  
163 Mackay, 2016).

164  $V_G$  can be estimated by partitioning phenotypic variation among a set of full-sibling families  
165 or clones, provided replicate offspring from each family (or clone) are maintained separately  
166 to avoid confounding relatedness and common experimental environment (where  $V_E$  could  
167 erroneously be ascribed to  $V_G$ ). Whereas evolutionary predictions based on additive genetic  
168 variance ( $V_A$ ) will be more precise than prediction based on total genetic variance ( $V_G$ ),  
169 methods for estimating  $V_A$  are also more involved. A greater range of relationships between  
170 individuals is required to isolate the relative contributions of additive, dominance, and  
171 epistatic variance. For example, to separate dominance from additive genetic effects requires  
172 crosses between different parental combinations (e.g., half siblings sharing one parent but not  
173 the other, see Falconer & Mackay, 1996; Lynch & Walsh, 1998; Walsh & Lynch, 2018;  
174 Wilson et al., 2010). These constraints are particularly relevant to experimental designs for  
175 corals, where obtaining large numbers of independent crosses and multiple independent  
176 samples per cross requires extensive infrastructure (i.e., aquaria systems with multiple tanks  
177 for replication), which can be logistically challenging.

178 Another challenge to estimating genetic variance ( $V_G$  or  $V_A$ ) reflects these metrics'  
179 dependence on allele frequencies. Therefore, the sample of individuals (genotypes) taken  
180 from the field for experimental breeding must accurately encompass the natural genetic  
181 diversity of the population. Small samples are unlikely to capture the breadth of genetic and  
182 phenotypic variation. Increasing sample sizes using fragmentation or clonal replication does  
183 not avoid this problem as fragments do not increase the number of genotypes sampled from  
184 the population and can result in pseudo replication if fragments are treated as unique  
185 individuals in statistical analyses. Box 1 details how experimental designs can be modified to  
186 increase power, accuracy, and precision in estimating genetic variance, which is essential for  
187 improved predictions of coral adaptive capacity.

188 A few studies have estimated heritability and genetic variation of coral traits (reviewed  
189 recently in Bairos-Novak et al., 2021; Howells et al., 2022) including survival, growth and

190 bleaching response. But, Bairos-Novak et al (2021) identified no studies that explicitly  
191 quantified the heritability of key thermal tolerance traits such as thermal optimum ( $T_{opt}$ ),  
192 critical thermal limits ( $CT_{max}$ ,  $CT_{min}$ ), or the shape of the thermal tolerance reaction norm.  
193 Reported broad sense heritability of traits associated with temperature effects on growth and  
194 survival ( $H^2 = 0.2 - 0.6$ ) suggest substantial capacity for thermal adaptation in these traits.  
195 These estimates, however, are drawn from limited studies, the majority of which were  
196 conducted under laboratory conditions (Bairos-Novak *et al.* 2021), potentially yielding higher  
197  $H^2$  estimates than when measured under natural conditions due to dampened environmental  
198 variance under controlled laboratory conditions (Lynch & Walsh, 1998; Weigensberg &  
199 Roff, 1996). Empirical estimates of narrow sense heritability ( $h^2$ ) are relatively uncommon  
200 and often lower than those for broad sense heritability ( $H^2$ ) (Figure 1 in Bairos-Novak et al.,  
201 2021; Howells et al., 2022), implying large non-additive contributions to total genetic  
202 variance for these traits. There is also large variation between same trait estimates from  
203 different studies that could arise from: i) small sample sizes; ii) differences in genetic  
204 architectures across experimental source populations; iii) non-standardized measurements or  
205 experimental assays; iv) differences in life-stages where many estimates of heritability are  
206 based on larvae or juveniles. Further studies, especially longitudinal studies that assess  
207 performance across the life-cycle (Aguirre et al., 2014), are needed to provide basic  
208 knowledge about the degree to which thermal tolerance in early life-cycle stage is correlated  
209 with thermal tolerance in subsequent life-cycle stages (Dziedzic et al., 2019), and to  
210 determine at which life-cycle stages selection on thermal tolerance strongest. In summary, to  
211 provide beneficial insights, manipulative experiments must be more precise in characterising  
212 additive genetic variation, use offspring from a larger number of field collected parents rather  
213 than clonal replication of genets, and simulate marine heat wave stress conditions realistically  
214 and consistently (where standardised phenotypic assays for evaluating coral thermal tolerance  
215 would increase confidence in making comparisons across populations and species: see  
216 Grottoli et al., 2021).

217 New approaches could increase precision of key genetic parameters necessary for predicting  
218 coral adaptive responses in nature. Following terrestrial research on wild populations,  
219 narrow-sense genetic variances and covariances can be estimated under field conditions using  
220 an individual based ‘*animal model*’ (Charmantier et al., 2014; Gienapp et al., 2017; Johnston  
221 et al., 2022; Wilson et al., 2010). Rather than relying on strict breeding designs to generate  
222 offspring of varying relatedness, the animal model uses all the relationship information

223 available for a group of field sampled individuals. A matrix describing these relationships can  
224 be obtained from observed breeding events or genetic inferences of parentage and sibship to  
225 form a pedigree. Alternatively, multilocus genomic data can be used to directly estimate  
226 relatedness, bypassing the need to construct a pedigree (Charmantier et al., 2014; Gienapp et  
227 al., 2017; Johnston et al., 2022). Employing this *genomic relationship matrix* has several  
228 benefits: first, it capitalises upon diverse relationships in wild populations to partition  
229 additive from non-additive genetic effects (Yang et al., 2011). Second, ‘experiments’ can be  
230 conducted in natural settings, with treatment effects and population parameters reflecting  
231 realistic conditions (Gienapp, 2020). Third, it eliminates the need for long-term,  
232 multigeneration, studies, by determining shared alleles without tracing the path of co-  
233 inheritance (i.e., pedigree). Coral studies have employed genomic relationship approaches  
234 under laboratory conditions, estimating substantial heritability of adult bleaching responses in  
235 the Caribbean coral, *Orbicella faveolata* (Dziedzic et al., 2019) and larval survival under high  
236 temperature for *Platygyra daedalea* from the Arabian/Persian Gulf and Indian Ocean (Kirk et  
237 al., 2018).

238 It is also possible to directly link genotypes to phenotypes, such that genotypes can explicitly  
239 predict the phenotype, and ultimately the fitness of individuals. One such approach is  
240 genome-wide association study (GWAS or GWA), which identifies individual loci that  
241 significantly contribute to phenotypic trait variation. However, GWAS is biased to find large  
242 effect loci and often cannot detect small effect loci that typify polygenic traits (Gienapp,  
243 2020) such as thermal tolerance and lifetime fitness (Boyle et al., 2017). Greater insights into  
244 adaptive potential and causes of phenotypic variation may be gained by simultaneously  
245 considering many markers that individually may not significantly predict a trait value but  
246 cumulatively can - a family of approaches known as *genomic prediction*. Genomic prediction  
247 has been used widely in agriculture and medical genetics (Wray et al., 2019) and enables the  
248 study of evolutionary genetics in wild populations (Ashraf et al., 2020; Gienapp et al., 2019;  
249 McGaugh et al., 2021). Power may be further improved by incorporating additional genetic  
250 information in the model (McGaugh et al., 2021). To date, only one study has used genomic  
251 prediction in wild corals, albeit employing a modified procedure using GWA derived locus  
252 effect sizes to generate polygenic scores. These scores significantly improved prediction of  
253 bleaching response in *Acropora millepora* (Fuller et al., 2020), although environment and  
254 symbiont identity were also found to be important contributors to the phenotypic response.



255 The sample size used by Fuller et al. (213 genomes with 44 sequenced at high coverage)  
256 could realistically be improved upon in future coral studies to yield greater power.

257 Genomic prediction has immense potential benefit for coral conservation. Stress responses  
258 such as coral bleaching may be predictable from genomic sampling without the need to  
259 measure individual phenotypes, streamlining the process of selecting optimal genotypes for  
260 breeding and restoration practices. In addition, genomic prediction can be used to select  
261 target reefs for conservation or restoration based on the spatial distribution of colonies with or  
262 without heat tolerance associated alleles.

263

### 264 **Beyond single traits - expanding adaptive genetics to consider multivariate phenotypes** 265 **and trade-offs between traits**

266 In wild populations, the relationship between individual traits and fitness is typically unclear  
267 (Barghi et al., 2020). For instance, thermal tolerance is undoubtedly a complex  
268 multidimensional phenotype, comprised of multiple individual traits (Angilletta Jr, 2009),  
269 and thermal traits will not be the only determinants of fitness. Thus, when considering  
270 adaptation, it is useful to move beyond single trait heritability and consider the multivariate  
271 genetic architecture, which ultimately determines how the whole phenotype may respond to  
272 selective pressures (Lande & Arnold, 1983; Svensson et al., 2021; Walsh & Blows, 2009).  
273 Methods utilising genomic relationship matrices and supporting genomic prediction are  
274 expandable to incorporate multiple traits, so they can calculate additive genetic variance for  
275 individual traits as well as genetic co-variances between traits. Multivariate approaches, as  
276 well as being essential to account for the complex functional basis of fitness, may also  
277 improve genomic prediction accuracy, and power to detect causal loci (Pitchers et al., 2019).

278 Multivariate genetic variation is best captured by the genetic variance-covariance matrix **G**  
279 (Lande, 1980; Lynch & Walsh, 1998), a matrix describing both the quantity of genetic  
280 variance underlying individual traits and the degree to which that variation is shared among  
281 traits: namely the genetic co-variance (shown in Fig. 2). A co-variance of zero indicates that  
282 evolution of those traits can proceed independently (Fig. 2b), whereas a non-zero value  
283 indicates that selection on trait one is predicted to also change trait two (Fig. 2a & 2c).  
284 Adaptive evolution is more rapid and predictable when selection aligns with the major axes  
285 of genetic variation (Fig. 2c), so called ‘evolution along genetic lines of least resistance’

286 (Schluter, 1996). In contrast, adaptation can be prevented altogether when genetic  
287 covariances limit the phenotype space available for selection to act (Lande & Arnold, 1983)  
288 (Fig. 2a). Thus, while individual traits may harbour genetic variance, the presence of genetic  
289 correlation means that some trait combinations have little to no genetic variance, ultimately  
290 resulting in no response to selection and no adaptation (Walsh & Blows, 2009).

291 Despite being a fundamental factor determining how populations may respond to selection,  
292 estimates of genetic covariances in wild populations remain relatively uncommon. For  
293 terrestrial organisms, several long-term multigenerational monitoring projects have been  
294 conducted in birds and mammals (summarised in Bonnet et al., 2022), which have produced  
295 estimates of  $\mathbf{G}$ , and find some instances where trait covariances are putatively limiting  
296 evolution (Teplitsky et al., 2014). Recent studies have shown how to use genomic prediction  
297 to partition the adaptive potential of traits from other, non-adaptive, contributions to genetic  
298 covariance (Reddiex & Chenoweth, 2021). For corals, one of the few available studies  
299 suggests few trade-offs exist between fitness related traits such as growth rates, colour  
300 change, and survival in corals under environmental stress (Wright et al., 2019), however,  
301 more investigations are required before we can understand how genetic correlations might  
302 typically influence adaptive trajectories.

303 Provided that experiments are carefully designed and confounding factors are appropriately  
304 managed, the linear mixed model framework used to examine genetic correlations among  
305 traits in a single environment can be applied to estimate genetic correlations between the  
306 same trait in different life-cycle stages, sexes or environments (Falconer & Mackay, 1996). In  
307 all these contexts, genetic correlations that oppose the direction of multivariate selection will  
308 result in genetic constraints. This flexibility allows coral biologists to use a single currency,  
309 additive genetic variation in the direction of selection, when trying to predict the trajectories  
310 of populations. For example, a negative genetic correlation between  $T_{\max}$  measured in  
311 ambient pH and  $T_{\max}$  in low pH implies that genetic variants that might facilitate a response  
312 to warming temperatures in ambient pH will oppose adaptation to warming temperatures in  
313 low pH environments. This framework offers great power to predict the response of coral  
314 populations to environmental change under realistic conditions where life-stage, sex, and  
315 environmental context can contribute to genetic correlations and constraints.

## 316 **Integrating quantitative and population genetics to study adaptation**

317 Quantitative genetics largely focuses on single populations in isolation; however, in nature,  
318 populations will be connected by migration (gene flow) that may vary in magnitude and  
319 direction. Similarly, population sizes, and therefore the potential influence of genetic drift,  
320 will differ over space and time. Both migration and genetic drift will thus influence the  
321 quantitative genetic variation locally available to selection, and the study of these dynamics is  
322 largely the remit of population genetics.

323 Theory that seeks to expand quantitative genetic inferences across linked populations has  
324 largely focused on idealised arrays of populations with equal and symmetric migration  
325 subjected to a linear environmental gradient exerting selection (a configuration reminiscent of  
326 a north to south oriented fringing reef). Even such simplified representations of multiple  
327 populations show that interactions between the steepness of the environmental gradient,  
328 migration rates, and the intrinsic rate of population growth can result in a wide variety of  
329 outcomes (Holt & Gomulkiewicz, 1997; Kirkpatrick & Barton, 1997; Pease et al., 1989).  
330 Such simplified scenarios suggest that local adaptation is possible under some parameter  
331 combinations, especially for centre of range populations, while in peripheral populations  
332 allele frequencies are affected by immigration from central populations such that their  
333 phenotypes are not able to fully match the optimum set by the local environment (i.e.,  
334 peripheral populations are *maladapted* to local conditions). Fig. 3a provides a conceptual  
335 illustration of these dynamics, where range edge populations arrayed across a thermal  
336 gradient are slightly maladapted. Under rapid climate change (Fig. 3b; following Davis &  
337 Shaw, 2001), the species-wide dynamics will be altered and lagging edge populations will be  
338 greatly maladapted as their new optima lie outside any historical phenotypic value for the  
339 species. In contrast, leading edge populations may receive immigrants carrying genetic  
340 variation that can shift local phenotypes to the new local optimum (*genetic rescue*). In reality,  
341 estimates of migration rates, population sizes, intrinsic rates of population growth, and  
342 genetic architectures are available for only a few wild species, let alone corals that produce  
343 microscopic dispersive planktonic larvae. However, just as genomic resources can lead to  
344 greater understanding about how  $V_A$  is linked to the phenotype (via the animal model), these  
345 same genetic data can be used to infer population sizes and migration rates, providing greater  
346 clarity on the demographic parameters which determine possible outcomes across the species  
347 range. Coral-focused evolutionary models that attempt to incorporate coral population

348 parameters support the broad-brush concepts summarised in Fig. 3, concluding that poleward  
349 flowing ocean currents can disperse warm adapted larvae into more temperate populations  
350 (Matz et al., 2018; Matz et al., 2020; McManus et al., 2021).

351 Additionally, molecular and population genetic methods can help reveal which loci are or  
352 have been subject to selection (see Introduction) and when combined with geographic  
353 surveys of genetic variation can map the spatial distributions of putative adaptive loci.  
354 Especially promising are genotype-environment association studies (Lasky et al., 2023),  
355 which attempt to associate measured components of complex environments with observed  
356 shifts in allele frequencies arising from natural selection. Thus, genotype-environment  
357 association studies potentially reveal the environmental factors to which species have adapted  
358 in the past and thereby complement the genotype-phenotype focus of quantitative genetics. A  
359 few such studies in corals have found correlations between selected loci and sea surface  
360 temperature (Selmoni et al., 2020; Thomas et al., 2017), consistent with the idea that warmer  
361 (low latitude) populations may harbour warm-adapted alleles that could conceivably shift  
362 phenotypes in historically cooler (higher latitude) populations (as in Fig. 3), assuming that  
363 gene flow is sufficiently high.

364 Ultimately, integrating genomics with quantitative and population genetics provides better  
365 understanding of the effects of: 1) the genetic architecture of adaptive traits and potential  
366 constraint arising from genetic correlations; 2) the demographic and historical patterns that  
367 have shaped genetic variation within and between coral populations; and 3) possible  
368 evolutionary trajectories under anthropogenic selective pressures. As coral reef conservation  
369 moves to more active management strategies to facilitate adaptation, incorporating  
370 knowledge about population size and migration with information about the genetics of  
371 adaptive traits can provide the opportunity for more effective targeted interventions.

### 372 **The hidden problem of cryptic genetic structure in corals**

373 Molecular genetic studies of corals commonly uncover distinct genetic groups that are  
374 sympatric, suggesting that cryptic species are common (reviewed by Riginos & Beger, 2022).  
375 While many cryptic genetic groups appear to segregate by depth (e.g., Rippe et al., 2021; van  
376 Oppen et al., 2018), they may associate with subtle thermal microenvironments on a reef flat  
377 (Rose et al., 2018), or not have known niche differences. Thus, when individual colonies are  
378 selected for phenotyping based on morphology alone, an implicit assumption is that samples  
379 constitute a single random breeding population. Reanalysing a previous study, Gomez-

380 Corrales and Prada (2020) demonstrated that thermal performance can differ by cryptic  
381 genetic groups and therefore substantially change parameter estimates and biological  
382 interpretation. This issue of cryptic coral species provides additional motivation for  
383 integrating population genetics with quantitative genetic studies for corals to confirm that  
384 study metrics correspond to individuals from the same species.

385

## 386 **Implications and recommendations**

387 Understanding and predicting adaptation in corals requires deeper knowledge of the genetic  
388 basis of adaptive traits and better characterisation of the phenotypes conferring fitness in the  
389 wild. Here we briefly outline some key principles for this integration:

### 390 *1) Incorporate quantitative genetics into ongoing experimental designs*

391 Quantitative genetic designs can be woven into ongoing experiments, producing data on the  
392 genetic basis of potentially adaptive traits. Many classic statistical methods, such as  
393 regression, originate from quantitative genetics (Fisher, 1919), so in many cases, quantitative  
394 genetic principles can be built into existing experimental frameworks. The key requirement is  
395 that study subjects comprise individuals with some known degree of relatedness. Large  
396 numbers of crosses may be impractical but inference of relatedness from genotypes can boost  
397 samples sizes (Charmantier et al., 2014; Gienapp et al., 2017; Johnston et al., 2022).  
398 Additionally, by genotyping individuals, investigators can identify cryptic species and adjust  
399 analyses accordingly.

400 Experimental power comes from the choice of replication level: within family (or clonal)  
401 replication will be less useful than between family replication for population level inference.  
402 Box 1 provides some indications of how experimental designs can be tweaked (see also  
403 Gienapp et al., 2017; Wilson et al., 2010), and general quantitative genetic references (such  
404 as Falconer & Mackay, 1996; Lynch & Walsh, 1998) can provide deeper insights on relevant  
405 experimental designs. Incorporating these principles during experimental planning and before  
406 field sampling will greatly improve the potential insights gained from manipulative  
407 experiments and may facilitate the use of wild populations as a surrogate for experimental  
408 treatments (Ashraf et al., 2020; Bay & Guerrero, 2020; Kruuk, 2004). Thus, integrating  
409 quantitative genetic principles should enhance the power, precision, and accuracy of existing  
410 studies, all while strengthening opportunities for interdisciplinary collaboration.

411 *2) Understand the trade-offs and genetic constraints of the multivariate phenotype*

412 A large body of quantitative genetic theory generally concludes that “trait-by-trait  
413 explanations of the natural world are doomed to fail” (Walsh & Blows, 2009). Thus, we  
414 suggest that moving beyond the current focus on estimating single trait heritability to  
415 quantifying additive genetic variance for combinations of traits will yield more useful  
416 insights. While individual traits may harbour genetic variance, it is ultimately the patterns of  
417 variance shared among traits that determines if and how organisms can adapt to  
418 environmental change.

419 Critically, the multivariate animal model can provide understanding of genetic trade-offs that  
420 may occur as thermal traits evolve, which is key to realistic predictions about coral future  
421 adaptive capacity (Hoffmann et al., 2021). While gaining insight into genetic trade-offs or  
422 constraints may take substantial effort, serious consideration must be given to whether  
423 selection on thermal tolerance affects other fitness attributes such as growth or reproduction.  
424 Furthermore, studies are needed to understand how potential trade-offs might have diverged  
425 among populations experiencing different selective pressures, various sources of immigrants,  
426 and various population sizes.

427 *3) Use quantitative and population genetics to incorporate evolutionary thinking into*  
428 *restoration and resilience building.*

429 The rapid decline of coral reef ecosystems has motivated discussion regarding possible active  
430 human interventions to maintain and restore function in coral reef ecosystems (Anthony et  
431 al., 2020; Baums et al., 2019; National Academies of Sciences, 2019; van Oppen et al.,  
432 2017). Additionally, there is growing sentiment that reef management should plan for future  
433 ecological conditions rather than reconstruct pre-disturbed states (Higgs et al., 2018; van  
434 Oppen et al., 2017).

435 Incorporating principles from evolutionary genetics into management planning can improve  
436 the accuracy of managing for future conditions. Application of genomic prediction in  
437 agriculture has shown that combining good quality phenotyping with genomic data can  
438 provide insight into the genetic architecture underlying a wide range of complex traits and  
439 allow more efficient selection of high fitness individuals (Meuwissen et al., 2001), where  
440 recent methodological developments demonstrate that genomic predictions can be extended

441 to multivariate phenotypes (Reddiex & Chenoweth, 2021) allowing selection of individuals  
442 with superior multivariate phenotypes.

443 Because natural migration may not redistribute adaptive genetic variation fast enough to track  
444 the changes associated with climate change, human-assisted migration could accelerate  
445 adaptation rates in wild populations and enable genetic rescue (Aitken & Whitlock, 2013;  
446 Coles & Riegl, 2013; van Oppen et al., 2017; Weeks et al., 2011). For polygenic traits such as  
447 thermal tolerance, geographically separated populations have often arrived at different  
448 combinations of alleles underlying similar phenotypes (Bolnick et al., 2018; Yeaman, 2022).  
449 This difference in genetic solutions to similar environmental challenges may mean that  
450 assisted migration could accelerate adaptation by leveraging the fact that populations can be  
451 at the same latitude, experiencing broadly similar environments, but contain very different  
452 genetic solutions to equivalent stresses. To date, pilot studies have focused on crossing  
453 individuals from warmer and cooler environments (e.g., Howells et al., 2021; Kirk et al.,  
454 2018). Substantial gains might also be feasible by interbreeding individuals from  
455 geographically separated warm environments to yield individuals with novel combinations of  
456 alleles and the possibility of extreme phenotypes.

457 Conversely, evidence for considerable local adaptation (presumably across multiple traits:  
458 Baums, 2008) and considerable genetic variation for thermal tolerance within a reef  
459 (Humanes et al., 2022), suggests that transplantation over short distances might provide  
460 benefits through increased genetic variation available to selection. Importantly, robust  
461 estimates of adaptive potential of wild populations may reveal cases where natural standing  
462 variation is sufficient to support adaptive changes without assisted migration.

463

## 464 **Conclusions**

465 Shifting emphasis from single trait heritability toward describing additive genetic variance  
466 across multivariate phenotypes is key to predicting how wild populations will fare under  
467 future climate warming. Significant recent investment in coral reef research has yielded high  
468 quality phenotypic and genetic resources that have removed some of the previous barriers to  
469 characterising natural adaptive capacity. Incorporating quantitative genetic analyses in coral  
470 studies can reduce uncertainty in predictions and enhance targeted and effective conservation  
471 interventions.

472

473

474 >>>>START BOX 1

475 **Box 1: Notes on sample sizes**

476 Too many factors influence quantitative genetic experiments for a single recommendation for  
477 what constitutes an adequate sample size. The critical determinant is the “noise” in trait  
478 measures, where high measurement error, high micro-environmental sensitivity, and lower  
479 ‘true’ heritability, all contribute to experimental noise. Thus, if noise is low, fewer samples  
480 may give a good estimation of genotypic value. In contrast, traits with low heritability (high  
481 noise) such as life history and physiology traits will require more replication.

482

483 Klein (1974) provides some instructive calculations of power for breeding designs: for  
484 moderate heritability (0.4), an experiment with 100 families and 2-4 offspring per family has  
485 a > 98% probability of detecting broad-sense heritability ( $H^2$ ) if it exists (using mid-parent-  
486 offspring regression or full sibling designs), but this design only has a 66% probability of  
487 detecting narrow-sense  $h^2$  (using the intraclass correlation of half-siblings). An experiment  
488 would need 200 families with 4 offspring per family to get to > 90% probability of detecting  
489 moderate narrow sense  $h^2$  and over twice that sample size if heritability is 0.2 (Klein, 1974).  
490 Different experimental designs resulting in the same number of families would also differ in  
491 their ability to detect additive genetic effects; for instance, a design including 50 sires each  
492 mated to two dams would have greater power but lower accuracy than a design including 25  
493 sires each mated to 4 dams. Similar overall numbers are suggested for pedigree structured  
494 populations: Quinn et al. (2006) recommend minimum of 100 observations per year for 3  
495 years to detect  $h^2$  as low as 0.2 (with different distributions of those 300 data points, e.g., 30  
496 observations over 10 years, having lower power to detect genetic effects than 100  
497 observations over 3 years). Bonnet et al. (2022) re-analysed data from 19 published bird and  
498 mammal studies, finding generally low levels of  $h^2$  in fitness related traits. This approach  
499 illustrates the value of increased pedigree depth (number of years/generations, Bonnet et al.,  
500 2022, Table S2) and completeness (number of observations, Bonnet et al., 2022, Table S1)  
501 available from large, long-term, data sets allows detection of low additive genetic variance in  
502 fitness traits.

503



504 Power of genomic relationship matrix approaches can be more difficult to generalise due to  
505 population dynamics in wild populations, although Müller et al. (2015) provide some  
506 indication of sample size through simulation. For a population of 200 unrelated individuals,  
507 using 2,500 markers (10 chromosomes, 18 Morgans total) reliability equalled 0.36 for  $h^2 =$   
508 0.25, increasing 0.78 for  $h^2 = 0.75$  (where reliability is calculated as the squared correlation  
509 coefficient between genetic estimated breeding values and the simulated true genetic values).  
510 While these sample sizes are unrealistic for many experimental budgets and timelines, they  
511 highlight that all current quantitative genetic studies are likely underpowered and are  
512 incapable of correctly rejecting the null hypothesis that the trait is not heritable. In Table 1,  
513 we provide some suggestions on how researchers can pragmatically allocate experimental  
514 efforts within the logistical constraints of their system to maximise power, precision, and  
515 accuracy in estimating additive genetic effects. In all cases, increasing the number of families  
516 (rather than offspring per family), replicated measurement of the same individual over time,  
517 increasing the pedigree depth or number of generations, and avoiding clonal replication will  
518 likely be the best approach for increasing the power to detect additive genetic variation  
519 associated with thermal tolerance traits.

520

521 INCLUDE TABLE 1 IN BOX 1

522 >>>>END BOX 1

523

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528

529

## 530 **Data Availability**

531 Supporting scripts will be available on Dryad and are attached as supplementary files for  
532 review.

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**Table 1. Key determinants of power, precision and accuracy in different quantitative genetic experimental designs.** Quantitative genetic experiments require substantial sample sizes. If effective sample sizes are beyond the logistical constraints of their experimental system, practitioners should prioritise experimental effort towards maximising the key principles of power, accuracy, and precision. For each of the three main experimental designs, the data required to increase power, accuracy, and precision are identified along with key references.

Method	Power	Accuracy	Precision	Key References
Structured breeding (includes nested, full-sibling, and half-sibling design)	Number of sires	The number of dams (the number of times a sire effect can be measured)	Number of offspring per cross	(Klein, 1974; Klein et al., 1973; Lynch & Walsh, 1998, pp 543)
Unstructured breeding (Pedigree ‘animal’ models)	Number of individuals in the base population	The number of genetic lineages from the base population represented in the pedigree. If only parent and offspring are measurable, then the number of generations should be maximised, but if complex relationships (relatives breeding across years) can be measured, then maximising the cohorts (or years) can increase the links in the pedigree.	Phenotypes per lineage	(Hanocq et al., 1996) (Bonnet et al., 2022; Clément et al., 2001; Morrissey et al., 2007; Quinn et al., 2006)
Genomic relationship matrix (GRM ‘animal’ models)	Number of unrelated individuals and number of SNP <sup>a</sup> markers	Accuracy and precision depend on the sample size of the reference population and its genetic structure. The optimal number of SNPs <sup>a</sup> required balances the ability to characterise genetic similarity between individuals while also maximising the proportion of genetic variance those markers explain. <sup>b</sup>		(Lee et al., 2017; Mancin et al., 2022; McGaugh et al., 2021; Müller et al., 2015)

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<sup>a</sup> SNP = single nucleotide polymorphism

<sup>b</sup> Beyond a certain number, more markers do not improve the resolution of genomic relationships. Linking too many markers to a phenotype negatively affects the ability to detect relationships between phenotype and small effect loci. Methods for selection are described in the key references.

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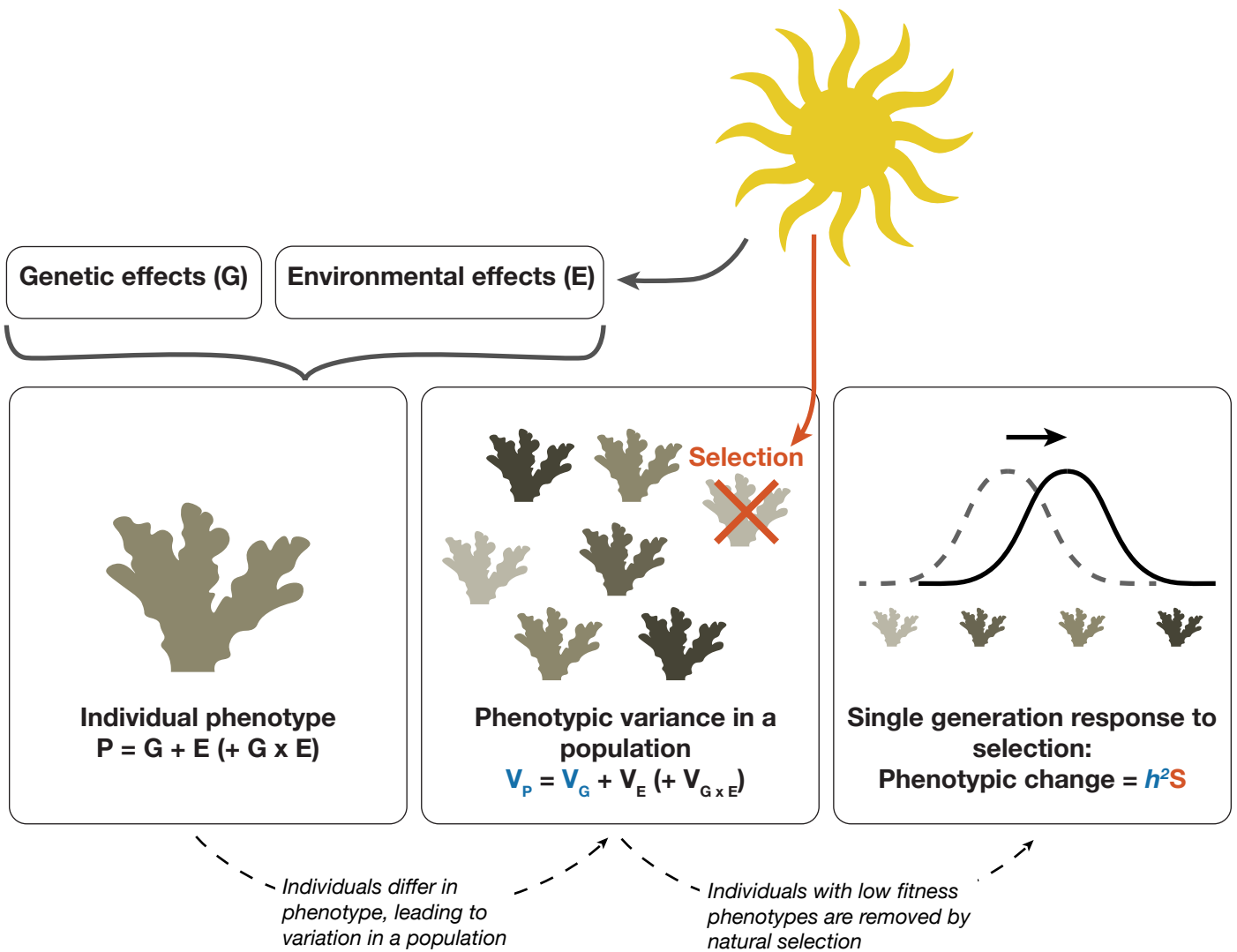
**Figure 1. Heritability and the partitioning of phenotypic variance.** Trait values in individuals are due to a combination of genetic and environmental effects. Individual phenotypes differ, leading to variation in a population. The environment also exerts selection against some phenotypes in the population. Heritability is the ratio of genetic variance ( $V_G$ ) to the phenotypic variance ( $V_P$ ). The rate of adaptation is dependent on heritability (narrow sense:  $h^2$ ) and the strength of selection.

**Figure 2: Simulations illustrate how genetic correlations among traits affect adaptation rates and outcomes.** The selective response is predicted by the *multivariate* breeder's equation ( $\Delta Z = \mathbf{GB}$ ) that describes the genetic variance and covariance between traits. In the two-trait examples shown here, genetic variance within traits ( $V_1, V_2$ ), and selection upon each trait ( $S_1, S_2$ ) are held constant in each example, but the covariance between traits (colour coded off-diagonal elements) differs, where: A)  $CV = -0.8$  (red) represents a strong negative correlation; B)  $CV = 0$  (blue) represents uncorrelated traits; C)  $CV = 0.8$  (yellow) is strongly positive. G matrices can also be visualised by an ellipse showing the distribution of individual breeding values (points) where the alignment of shared genetic variation with the direction of selection (shown by the arrow) defines the amount of genetic variation available for evolution. Adaptive walks (from simulations) show the process of phenotype evolution as selection acts upon both traits. When genetic correlation (covariance) is strong and *not* aligned with the direction needed for adaptation (red), the adaptive walk is slow, with populations moving over a wide range of values of both traits. When traits are genetically uncorrelated (blue) and each is heritable, evolution can proceed free from genetic constraint, relatively directly approaching the new optimum. When genetic variance is positively correlated (yellow), adaptation is fastest and follows a more direct path as alignment of genetic variance with the direction of selection facilitates simultaneous adaptation of each trait. The degree of correlation therefore determines whether traits evolve independently, in turn defining the rate of adaptation and the range of possible phenotypes available within a population. Simulations were performed in SLiM version 3.7.1 where each dot on the adaptive walk is trait value every 1000 generations.

**Figure 3: Conceptual models for source-sink dynamics and effects of migration under stable and rapidly warming climate scenarios.** Populations of varying sizes are arrayed across a thermal landscape under stable (historical) conditions and rapid wholesale warming.

Colour represents temperature, where the colour of environment (bar) determines the optimal trait value (triangles) and populations (circles) are colored by mean trait value. Perfectly adapted populations are found when the colour of the circle matches both the environment and optimal trait colours. Maladaptation is implied when colours do not match. Arrows indicate directional gene flow and are coloured by the source population's mean phenotype and arrow width indicates strength of gene flow. Self-recruitment to populations occurs but is not shown. A) For the *stable climate scenario*: this concept diagram follows an abundant centre model of a species range, where the central population is large, well adapted to ambient conditions, and exports many propagules. Populations towards left and right range margins are weakly maladapted to local conditions due to higher migration from, rather than to, the central population. B) Under the *rapidly warming climate scenario*, optimal phenotypes for all populations need to match warmer temperatures. Equatorial populations (right of centre) are on the lagging edge of the species range and are now maladapted due to migration load of cooler temperature alleles arriving from the centre source population. In contrast, populations on the poleward leading edge of the species range are "rescued" by warm alleles arriving from upstream populations.

**Figure S1: summary of published heritability estimates.** Manipulative laboratory based experiments are far more common than field experiments. There is large variation among heritability estimates for the same trait from different experiments (e.g. estimates of  $h^2 = 0$  and  $h^2 = 1$  available for growth in laboratory conditions). Narrow sense estimates are always lower than broad sense estimates for the same trait, suggesting substantial non-additive genetic variance is being included in broad sense estimates, and any prediction of adaptive capacity based on these estimates is likely to be overestimated. Similarly, the use of clones is widespread, also adding to potential overestimation of  $h^2$  and therefore adaptive capacity.



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