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

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29   Key words: adaptation, bleaching, coral, genetic constraint, genomic relationship matrix,

30   quantitative genetics, thermal tolerance

31   Running title: Coral adaptive potential

32 **Abstract**

33 Global environmental change is happening at unprecedented rates. Coral reefs are among the

34 ecosystems most threatened by global change and for wild populations to persist, they must

35 adapt. However, little is known about corals' complex ecological and evolutionary dynamics

36 making prediction about potential adaptation to future conditions precarious. Here, we review

37 the process of adaptation through the lens of quantitative genetics and make suggestions

38 about how incorporating genomic tools can help to both understand and predict adaptive

39 potential in corals. In many cases, small changes in experimental design may provide large

40 increases in the power, precision, and accuracy of information produced for predicting corals'

41 adaptation to environmental changes. We also outline where quantitative genetic principles

42 may be incorporated into current research programs that aim to bolster coral tolerance to

43 future warming conditions.

44

45 **Introduction**

46 Anthropogenic change is driving ecological change, yet little is known about the complex

47 ecological and evolutionary dynamics operating in wild populations making predictions

48 highly 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 fecundity, growth, connectivity 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 (Hoegh-Guldberg et

54 al., 2007; Hughes et al., 2017; Walther et al., 2002). Greater knowledge regarding the

55 ecological and evolutionary processes that underpin adaptation is urgently required if humans

56 are to assume responsibility for mitigating or facilitating responses that promote coral reef

57 resilience.

58 Current population models to predict long term changes to total coral cover typically fall into

59 two categories. Ecology-focused models capture complex coral population dynamics and

60 species interactions but typically treat species as fixed biological traits (e.g., Bozec et al.,

61 2022). In contrast, evolution-focused models use demographic and population parameters to

62 estimate genetic-based adaptation potential at the species level (Bay et al., 2017; Logan et al.,

63   2014; Matz et al., 2018; Matz et al., 2020; McManus et al., 2021). Some evolutionary models

64   include simple species interactions such as competition between two coral species with

65   different life histories (McManus et al., 2021; Walsworth et al., 2019) or focus on the

66   interaction between the coral cnidarian hosts and their photosynthetic endosymbionts

67   (Baskett et al., 2009; Day et al., 2008; Logan et al., 2021). Regardless of specific

68   assumptions, general conclusions are obscured by the discrepancy between ecological models

69   that generally assume traits do not change over time, and evolutionary models that

70   consistently find that evolutionary adaptation is a critical component for long-term coral

71   persistence (reviewed by Xuereb et al., 2021).

72   While adaptation appears vital for coral population persistence under a changing climate, the

73   number and effect of genes (the *genetic architecture*) determining tolerance traits remains

74   unknown for the vast majority of reef building coral species and therefore there is great

75   uncertainty regarding the scope and speed of possible adaptive change (reviewed by Howells

76   et al., 2022). Some studies show that temperature related traits likely have a genetic basis

77   (reviewed in Bairos-Novak et al., 2021), although these estimates might not accurately reflect

78   adaptive potential under natural conditions (Humanes et al., 2022). Many studies have

79   detailed gene expression responses to acute heat stress (Barshis et al., 2013; Parkinson et al.,

80   2018; Rose et al., 2018; Traylor-Knowles et al., 2017), but whether expression differences

81   among individuals within species have a genetic basis is largely unresolved (Dixon et al.,

82   2015; Kenkel & Matz, 2016). In a detailed examination of how genomic background affects

83   short-term heat tolerance, Fuller *et al*. (2020) established that the genomic basis for acute heat

84   tolerance in *Acropora millepora* is affected by many loci of the cnidarian host as well as their

85   photosynthetic endosymbionts. While acknowledging that symbionts play an important role

86   in thermal tolerance of the coral holobiont, we focus here on the genetics of the cnidarian

87   host, as methods evaluating relatedness between individuals are more tractable at this level.

88   Here, we aim to identify key genetic parameters that determine adaptive capacity in corals

89   and highlight data gaps that hinder our ability to make robust predictions for coral futures.

90   Such information is critical as empirical data on the genetic architecture of thermal tolerance

91   traits remains unknown for the vast majority of reef building coral species. As many of the

92   traits observed or predicted to confer adaptation are likely determined by the combined

93   contribution of many genes with small effect (alternatively termed quantitative, complex or

94   polygenic traits, see Falconer & Mackay, 1996; Hill, 2010; Lynch & Walsh, 1998), we

95   review the process of adaptive evolution with a focus on quantitative genetics. Finally, we

96 make some suggestions about where future experimental efforts should be directed, which
97 genetic parameters to estimate, and how they may be estimated.

98 **Selection, heritability, and genetic variance in single traits**

99 Adaptive evolution begins when individuals in a population differ in fitness relative to one
100 another as a function of their trait values (Fig. 1). For complex traits, single trait phenotypes
101 can be expressed in the form:

102 $P = G + E + G \times E$

103 Where the phenotypic value (P) is the result of the individual's genes (G), its environment
104 (E), and the way those genes interact with and respond to environmental conditions ($G \times E$).
105 This treatment of the phenotype as the sum of underlying genetic and environmental effects
106 defines the framework of quantitative genetics (Falconer & Mackay, 1996). When considered
107 at the population level, the relative contributions of genetic and environmental effects within
108 each individual have a defining role in determining how the population mean trait value
109 evolves. If the variation across phenotypes in a population is determined by genetic variation,
110 then selecting a subset of individuals based on their phenotype also selects a subset of the
111 genetic variation controlling that phenotype, thereby increasing the frequency of selected
112 alleles in the population. In contrast, if trait values are mainly due to differences in the
113 environments experienced by individuals, selection may change the mean trait value of the
114 population temporarily (i.e., phenotypic plasticity), but not changes to the allele frequencies.
115 An example of this might include greater tolerance to heat stress where pre-warming events
116 prepare an animal physiologically for the bleaching stress that follows (Ainsworth et al.,
117 2016).

118 Phenotypic plasticity may provide an avenue for individuals to track shifts in variable or
119 changing environments, even if responses do not persist over evolutionary time. Plastic
120 phenotypes can be adaptive when phenotypic change occurs in the direction favoured by
121 natural selection, but the fitness benefits of plasticity can be fleeting due to the inherent
122 flexibility of plastic phenotypes and the lack of changes in the underlying genetics of the trait
123 (Ghalambor et al., 2007). Similarly, epigenetic mechanisms may allow temporary increase in
124 heat tolerance, although evidence for a transgenerational persistence of epigenetic effects in
125 corals is currently lacking (Torda et al., 2017). Temporary and rapid phenotypic shifts can
126 maintain population size in the short term, as plastic responses allow individuals with

127   maladapted genotypes to persist, however, these responses are unlikely to allow population

128   persistence over the longer term and may slow adaptive responses to selective pressure

129   (Gilbert & Miles, 2019). There is also growing evidence that plastic responses of a trait under

130   selection may indicate the existence and possible alignment of heritable genetic variation in

131   that trait (Noble et al., 2019). Despite the potential benefits of plasticity, evidence suggests

132   plasticity may have limited potential to extend thermal tolerance for species living at the

133   upper end of their temperature limits (Kingsolver & Buckley, 2018; van Heerwaarden et al.,

134   2016). So, for many corals which are already living close to their upper thermal threshold,

135   plasticity may facilitate short term persistence, but may not be sufficient to bridge to new

136   thermal optima.

137   Adaptation to new fitness optima requires genetic changes in the direction of selection, as

138   only processes which change allele frequencies in a population can fuel evolutionary

139   adaptation. Thus, it is the genetic component of phenotypes that is the focus for studies of

140   adaptive capacity (Hendry et al., 2018). Heritability is the common way of defining the

141   genetic component of phenotypes and is a population specific metric that defines the

142   proportion of phenotypic trait variance (V_P) that can be attributed to genetic variation

143   (Visscher et al., 2008). This genetic variation can be characterised in two ways: either *total*

144   genetic variation (V_G: broad sense heritability, $H^2 = V_G/V_P$) which defines all genetic effects

145   on the trait of interest, or only the *additive* genetic variation (V_A: narrow sense heritability, h^2

146    $= V_A/V_P$). Both estimates are widely used but differ in terms of the conclusions which can be

147   drawn from their estimation.

148   Additive genetic variance describes a subset of total genetic variance, excluding other, non-

149   additive, sources of genetic variance such as dominance (V_D) or epistasis (V_I). Dominance

150   refers to the interactions between alternative alleles at a *single* locus, while epistasis describes

151   interactions *between* loci that effect the phenotype. As these interactions are dependent on the

152   specific combination of alleles present in the individual, and as this set is reshuffled when

153   those alleles are passed from generation to generation, non-additive sources of variation (V_D,

154   V_I) are not directly inherited. The relative magnitude of non-additive genetic variance in wild

155   populations remains unclear (Class & Brommer, 2020), however, broad-sense heritability

156   may overestimate the potential for long-term adaptive responses.

157   Whereas evolutionary predictions based on additive genetic variance (V_A) will be more

158   precise than prediction based on total genetic variance (V_G), methods for estimating V_A are

159   also more involved. An increased range of relatedness between individuals is required to

160   tease apart the relative contributions of additive, dominance, and epistatic effects on

161   phenotypic traits, which is difficult to achieve outside of laboratory conditions (Wilson et al.,

162   2010). For example, experiments might include large numbers of related siblings to reliably

163   estimate V_G, but statistical power to isolate dominance from additive genetic effects comes

164   not from the number of offspring produced, but from the number of crosses between different

165   parental combinations (e.g., half siblings sharing one parent but not the other, see Falconer &

166   Mackay, 1996; Lynch & Walsh, 1998; Walsh & Lynch, 2018; Wilson et al., 2010).

167   Some coral studies have attempted to produce multiple crosses per parent (e.g., Quigley et al.,

168   2017), however, future experiments should include more crosses between more parents for

169   reliable estimation of these partitioned variances (critically, V_A) alongside trait means.

170   Moreover, to isolate genetic and environmental influences on phenotypes, replicate clutches

171   of offspring from each family must be maintained separately to avoid confounding

172   relatedness and common experimental environment. Without clutches being replicated in

173   different experimental units (e.g., aquaria), differences in trait values among clutches driven

174   by common environment effects (V_E) may be erroneously ascribed to V_G. These constraints

175   are particularly relevant to experimental designs for reef-building corals, where obtaining

176   many independent samples requires extensive infrastructure (such as saltwater aquaria

177   systems with multiple tanks for replication) and generating crosses in large numbers can be

178   logistically challenging.

179   Genetic variance (V_G or V_A) is a population specific parameter, so estimates from field

180   sampled individuals provide estimates for the sample, not the wild population. The goal

181   therefore is to sample enough genotypes from the field to ensure the sample accurately

182   reflects the natural genetic diversity of the population. If the sample size is small, it is

183   unlikely to capture the breadth of genetic and phenotypic variance in the wild population and

184   evolutionary predictions will therefore be unreliable. Increasing sample sizes using

185   fragmentation or clonal replication does not avoid this problem as fragments do not increase

186   the sample size of genotypes and can result in pseudo replication if fragments are treated as

187   unique individuals in statistical analyses. Furthermore, clones share an identical genome,

188   which can bias estimates of heritability upward because non-additive genetic variance cannot

189   be partitioned from additive genetic variance. In short, estimating metrics such as heritability

190   to describe genetic variation is key to predicting the adaptive capacity of coral populations,

191   but the accuracy of these predictions may be compromised if experimental designs fail to

192 adequately partition variance into genetic and non-genetic components. Box 1 details how

193 experimental design can be modified to increase power, accuracy, and precision.

194 A few studies have estimated heritability and genetic variation of coral traits (reviewed

195 recently in Bairos-Novak et al., 2021). Broad sense heritability of traits associated with

196 temperature effects on growth and survival are reported in the moderate to high range ($H^2 =$

197 0.2 - 0.6), suggesting that there is substantial capacity to evolve. These estimates, however,

198 are drawn from a limited number of studies mostly conducted under laboratory conditions

199 (Bairos-Novak *et al.* 2021), which may yield higher H^2 estimates than when measured under

200 natural conditions due to dampened environmental variance under controlled laboratory

201 conditions (Lynch & Walsh, 1998; Weigensberg & Roff, 1996). Empirical estimates of

202 narrow sense heritability (h^2) are relatively uncommon, and with estimates substantially

203 lower as compared to those for broad sense heritability (H^2) (Figure 1 in Bairos-Novak et al.,

204 2021), implying that there are large non-additive contributions to total genetic variance for

205 these traits. There is also large variation between estimates for the same trait from different

206 studies. Differences across studies could arise from non-standardized measurements or

207 experimental assays including different life stages. Alternatively, responses could be sensitive

208 to source population, as expected with genetic differentiation among populations, or if natural

209 variation was not well captured by sampling efforts. While heritability has been estimated for

210 growth, survival, and select physiological attributes (Figure S1), Bairos-Novak et al (2021)

211 identified no studies that explicitly test the heritability of key thermal tolerance traits such as

212 thermal optimum (T_{opt}), critical thermal limits ($CT_{max–min}$), or thermal resistance in terms of

213 survivorship. Further studies are therefore needed to provide this basic knowledge about the

214 degree to which thermal tolerance will be passed to future generations. To provide beneficial

215 insight, manipulative experiments must focus on more realistic experimental conditions, be

216 more precise in characterising additive genetic variation in adaptive traits, and use offspring

217 from a larger number of field collected parents rather than clonal replication of genets.

218 To obtain more precise estimates of the key genetic parameters necessary for predicting

219 adaptive responses in the wild, new approaches to studying coral genetics will be required.

220 Following terrestrial researchers working in wild populations, the goal should be to estimate

221 narrow-sense genetic variances and covariances under field conditions using an individual

222 based '*animal model*' (Charmantier et al., 2014; Gienapp et al., 2017; Wilson et al., 2010).

223 Rather than relying on strict breeding designs to generate offspring of varying relatedness, the

224 animal model uses a relatedness matrix constructed of coefficients of relatedness among

individuals to inform estimates of quantitative genetic parameters. These coefficients of relatedness can be inferred from theoretical expectations based on known pedigrees (i.e., $r = 0.5$ for the relatedness between parents and offspring or between full-siblings or 0.25 for half siblings), from multilocus genotypes or a combination of both methods. Employing a genomic approach to estimate a *genomic relationship matrix* in quantitative genetic studies has several benefits: first, it takes advantage of the diversity of relationships in wild populations to partition additive from non-additive genetic effects. Second, 'experiments' can be conducted in natural settings, with treatment effects and population parameters reflecting realistic conditions (Gienapp, 2020). Additionally, the ability to directly link genotypes to phenotypes means that offspring phenotype can be predicted by genotyping parents (known as *genomic prediction*). Genomic prediction has been used widely in agriculture and medical genetics (Wray et al., 2019) and enables the study of evolutionary genetics in wild populations (Ashraf et al., 2020; McGaugh et al., 2021). To date, only one study has used genomic prediction in corals, where around 62% of the variation in bleaching tolerance in *Acropora millepora* could be predicted based on a model combining environmental variables, symbiont identity, and genomic sequence data as predictors (Fuller et al., 2020). The promise of genomic prediction is significant. We may be able to predict stress responses such as bleaching from genomic sampling without the need to measure individual phenotypes, streamlining the process of selecting optimal genotypes for breeding and restoration practices. In addition, genomic prediction can be used to select the target reefs for conservation or restoration priority based on the spatial distribution of tolerance associated alleles.

Beyond single traits - expanding adaptive genetics to consider multivariate phenotypes and trade-offs between traits

In wild populations, the relationship between individual traits and fitness is typically unclear (Barghi et al., 2020). The relationship could be causal where a variation in trait value causes variation in fitness, or the relationship could be correlated where association between one trait and fitness is due to effects of a second unmeasured trait on fitness. While it is tempting to think of heat tolerance as a trait in and of itself, in actuality thermal tolerance is likely a complex multidimensional phenotype comprised of multiple individual traits (Angilletta Jr, 2009; Lande & Arnold, 1983; Schluter, 1996; Svensson et al., 2021; Walsh & Blows, 2009).

257 Thus, when considering adaptation, it is useful to move beyond single trait heritability and

258 consider the multivariate genetic architecture, which ultimately determines how the whole

259 phenotype may respond to selective pressures.

260 Multivariate genetic variation is best captured by the genetic variance-covariance matrix **G**

261 (Lynch & Walsh, 1998), a matrix describing both the quantity of genetic variance underlying

262 individual traits and the degree to which that variation is shared among traits: namely the

263 genetic co-variance (shown in Fig. 2). A co-variance of zero indicates that evolution of those

264 traits can proceed independently (Fig. 2b), whereas a non-zero value indicates that selection

265 on trait one is predicted to also change trait two (Fig. 2a & 2c). Genetic correlations can

266 therefore limit or facilitate evolution depending on how genetic variation across multiple

267 traits is associated with overall fitness. Methods utilising genomic relatedness matrices and

268 supporting genomic prediction are expandable to incorporate multiple traits, so they can be

269 used to calculate additive genetic variance for individual traits as well as genetic co-variances

270 between traits (Kruuk, 2004).

271 Adaptive evolution is more rapid and predictable when selection aligns with the major axes

272 of genetic variation (Fig. 2c), so called 'evolution along genetic lines of least resistance'

273 (Schluter, 1996). In contrast, adaptation can be prevented altogether when genetic

274 covariances limit the phenotype space available for selection to act (Arnold et al., 2001) (Fig.

275 2a). It follows then, that while individual traits may harbour genetic variance, the presence of

276 genetic correlation means that some trait combinations have little to no genetic variance,

277 ultimately resulting in no response to selection and no adaptation (Walsh & Blows, 2009).

278 Despite being a fundamental factor determining how populations may respond to selection,

279 estimates of genetic covariances in wild populations remain relatively uncommon. For

280 terrestrial organisms, several long-term multigenerational monitoring projects have been

281 conducted in birds and mammals (summarised in Bonnet et al., 2022), which have produced

282 estimates of **G**, and find some instances where trait covariances are putatively limiting

283 evolution (Teplitsky et al., 2014). For corals, very little is known about patterns of genetic

284 covariance or genetic trade-offs. One of the few examples where genetic correlation has been

285 investigated suggests few trade-offs exist between fitness related traits such as growth rates,

286 coral colour, and survival in corals under environmental stress (Wright et al., 2019), however,

287 more investigations are required before we can be certain that adaptation will proceed

288 without constraint.

289

Integrating quantitative and population genetics to study adaptation

Quantitative genetics largely focuses on single populations in isolation; in nature, populations will be connected by migration (gene flow) that may vary in magnitude and direction. Similarly, population sizes will differ over space and time and therefore the influence of genetic drift will also vary across a species' range. Both migration and genetic drift will thus influence the quantitative genetic variation locally available for selection to act upon and the study of these dynamics is largely the remit of population genetics. For example, empirical estimates of migration and population size are readily obtained from DNA sequences or multilocus genotypes, so multiple research questions can be answered with genomic data.

Theory that seeks to expand quantitative genetic inferences across linked populations has largely focused on idealised arrays of populations with equal and symmetric migration subjected to a linear environmental gradient exerting selection (a configuration reminiscent of a north to south oriented fringing reef). Even such simplified representations of multiple populations show that interactions between the steepness of the environmental gradient, migration rates, and the intrinsic rate of population growth can result in a wide variety of outcomes (Holt & Gomulkiewicz, 1997; Kirkpatrick & Barton, 1997; Pease et al., 1989). Such simplified scenarios suggest that local adaptation is possible under some parameter combinations, especially for centre of range populations, while in peripheral populations allele frequencies are affected by immigration from central populations such that their phenotypes are not able to fully match the optimum set by the local environment (i.e., peripheral populations are maladapted). Fig. 3a provides a conceptual illustration of these dynamics, where range edge populations arrayed across a thermal gradient are slightly maladapted. Under rapid climate change (Fig. 2B; following Davis & Shaw, 2001), the species-wide dynamics will be altered and lagging edge populations will be greatly maladapted as their new optima lie outside any historical phenotypic value for the species. In contrast, leading edge populations may receive immigrants carrying genetic variation that can shift local phenotypes to the new local optimum (genetic rescue). In addition to environmentally mediated changes in fitness optima, populations can also move away from phenotypic optima through genetic drift, whether due to constant small population size (for example, a small reef patch) or bottlenecks resulting from extreme disturbances (cyclones or Crown-of-Thorn outbreaks, in the case of corals).

321   In reality, estimates of migration rates, population sizes, intrinsic rates of population increase,
322   and genetic architectures are available for few wild species, much less corals that produce
323   microscopic dispersive planktonic larvae. However, just as genomic resources can lead to
324   greater understanding about how V_A is linked to the phenotype (using the animal model, for
325   example), these same genetic data can also be used to infer population sizes and migration
326   rates, providing greater clarity on the demographic parameters which determine possible
327   outcomes for corals in a warming future. Indeed, coral-focused evolutionary models that
328   attempt to incorporate parameters relevant to coral biology support the broad brush concepts
329   summarised by Fig. 2, concluding that poleward flowing ocean currents can disperse warm
330   adapted larvae into more temperate populations, in effect rescuing them from the increase in
331   temperatures predicted under climate change (Matz et al., 2018; Matz et al., 2020; McManus
332   et al., 2021).

333   New insights regarding the possible range shifts resulting from climate change have provoked
334   considerable discussion on how management interventions might mitigate coral
335   maladaptation (Anthony et al., 2020; National Academies of Sciences, 2019). Because
336   natural migration may not redistribute adaptive genetic variation fast enough to track climate
337   change, human-assisted migration could accelerate adaptation rates in wild populations and
338   enable genetic rescue (Aitken & Whitlock, 2013; Coles & Riegl, 2013; van Oppen et al.,
339   2017; Weeks et al., 2011). Long-distance assisted migration might capture genetic variation
340   relevant to large-scale stressors such as warming temperature. For polygenic traits such as
341   thermal tolerance, geographically separated populations have often arrived at different
342   combinations of alleles underlying similar phenotypes (Bolnick et al., 2018; Yeaman, 2022).
343   This difference in genetic solutions to similar environmental challenges may mean that
344   assisted migration could accelerate adaptation by leveraging the fact that populations can be
345   at the same latitude, experiencing broadly similar environments, but contain very different
346   genetic solutions to equivalent stresses. Thus, long distance assisted migration could
347   introduce locally novel variants and might greatly expand the scope for phenotypic change.

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

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

362

363 **Implications and recommendations**

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

367 *1) Incorporate quantitative genetics into ongoing experimental design.*

368 Refinement of planned experiments in corals has the potential to shed light on the genetic
369 architecture of adaptive traits. Quantitative genetic designs can be woven into ongoing
370 experiments, producing data on the genetic basis of potentially adaptive traits. Many of the
371 classic statistical methods, such as regression, originate from quantitative genetics (Fisher,
372 1919), so in many cases, quantitative genetic principles can be built into existing
373 experimental frameworks designed around those analyses. The key requirement is that
374 populations are comprised of individuals with some known degree of relatedness. Large
375 numbers of crosses may be impractical under logistical constraints as mentioned above,
376 however this can be achieved through inference of relatedness from genotypes (Gervais et al.,
377 2019).

378 Experimental power then comes from the choice of replication level: within family (or
379 clonal) replication will be less useful than between family replication for population level
380 inference. Box 1 provides some indications of how experimental designs can be tweaked (see
381 also Gienapp et al., 2017; Wilson et al., 2010), and general quantitative genetic references
382 (such as Falconer & Mackay, 1996; Lynch & Walsh, 1998) can provide deeper insights on
383 relevant experimental designs. Incorporating these principles during experimental planning
384 and before field sampling will greatly improve the potential insights gained from

385 manipulative experiments and may facilitate the use of wild populations as a surrogate for

386 experimental treatments (Ashraf et al., 2020; Bay & Guerrero, 2020; Kruuk, 2004). Thus,

387 integrating both population and quantitative genetic principles should enhance the power,

388 precision, and accuracy of existing studies, all while strengthening opportunity for

389 interdisciplinary collaboration.

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

391 A large body of quantitative genetic theory generally concludes that "trait-by-trait

392 explanations of the natural world are doomed to fail" (Walsh & Blows, 2009). Thus, we

393 suggest that moving beyond the current focus on estimating single trait heritability to

394 quantifying additive genetic variance for combinations of traits will yield more useful

395 insights. While individual traits may harbour genetic variance, it is ultimately the patterns of

396 variance shared among traits that determines if and how organisms can adapt to

397 environmental change.

398 Using genomic data to infer relatedness allows characterisation of quantitative genetic

399 architecture of adaptation under natural conditions via the 'animal' model (Wolak & Reid,

400 2017). Critically, the multivariate animal model can provide understanding of genetic trade-

401 offs that may occur as thermal traits evolve, which is key to realistic predictions about coral

402 adaptive capacity in the future (Hoffmann et al., 2021). While gaining insight into genetic

403 trade-offs or constraints may take some time, serious consideration must be given to whether

404 selection on heat tolerance affects other fitness attributes such as growth or reproduction.

405 Furthermore, studies are needed to understand how potential trade-offs might have diverged

406 among populations experiencing different selective pressures, various sources of immigrants,

407 and various population sizes.

408 *3) Use quantitative and population genetics to incorporate evolutionary thinking into*

409 *restoration and resilience building.*

410 The rapid decline of coral reef ecosystems has motivated discussion regarding possible active

411 human interventions to maintain and restore function in coral reef ecosystems (Baums et al.,

412 2019; National Academies of Sciences, 2019; van Oppen et al., 2017). Additionally, there is

413 growing sentiment that reef management should plan for future ecological conditions rather

414 than reconstruct pre-disturbed states (Higgs et al., 2018; van Oppen et al., 2017). One way to

415 improve the accuracy of managing for future conditions is to incorporate principles from

416   evolutionary genetics into management planning. For instance, if natural adaptation cannot

417   keep pace with the speed of environmental change, genomic data can help select appropriate

418   interventions that aim to maintain or supplement adaptation. Recent methodological

419   developments demonstrate that genomic prediction is feasible outside model systems

420   (including corals: Fuller et al., 2020) and across multivariate phenotypes(Reddiex &

421   Chenoweth, 2021). Application of genomic prediction in agriculture has shown that

422   combining good quality phenotyping with genomic data can provide insight into the genetic

423   architecture underlying a wide range of complex traits and allow more efficient selection of

424   high fitness individuals (Meuwissen et al., 2001).

425   Shifting from estimation of metrics such as heritability in single traits toward characterisation

426   of additive genetic variance across a multivariate phenotype is key to predicting how wild

427   populations will fare under future climate scenarios. Significant recent investment in coral

428   reef research has yielded high quality phenotype and genetic resources that have removed

429   some of the previous barriers to the characterisation of natural adaptive capacity. Small shifts

430   in the way we study corals, including incorporating quantitative genetic analyses, can reduce

431   uncertainty in predictions and enhance targeted and effective conservation interventions.

432

433

434   >>>>START BOX 1

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

436   Too many factors influence quantitative genetic experiments for there to be one single

437   recommendation for what constitutes an adequate sample size. The critical determinant is the

438   "noise" in trait measures, where high measurement error, high micro-environmental

439   sensitivity, and lower 'true' heritability, all contribute to experimental noise. Thus, if noise is

440   low, fewer samples may give a good estimation of genotypic value. In contrast, traits with

441   low heritability (high noise) such as life history and physiology traits will require more

442   replication.

443

444   Klein (1974) provides some instructive calculations of power for breeding designs: for

445   moderate heritability (0.4), an experiment with 100 families and 2-4 offspring per family has

446   a > 98% probability of detecting broad-sense heritability (H^2) if it exists (using mid-parent-

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

Genomic relationship matrix approaches can be more difficult to generalise due to population dynamics in wild populations (discussed in *Integrating quantitative and population genetics to study adaptation*), although Müller et al. (2015) provide some indication of sample size through simulation. For a population of 200 unrelated individuals, using 2,500 markers (10 chromosomes, 18 Morgans total) the reliability (calculated as the squared correlation coefficient between genetic estimated breeding values and the simulated true genetic values, ρ^2) of $\rho^2 = 0.36$ for $h^2 = 0.25$, increasing to $\rho^2 = 0.78$ for high $h^2 = 0.75$. Larger sample sizes would be required for populations where inbreeding is common, such as for broadcast spawning marine invertebrates, as the number of genetic lineages would likely be fewer than the number of individuals.

While these sample sizes are unrealistic for most experimental budgets and timelines, they highlight the fact that all current quantitative genetic studies are likely underpowered and are incapable of correctly rejecting the null hypothesis that the trait is not heritable. In Table 1, we provide some suggestions on how researchers can pragmatically allocate experimental efforts within the logistical constraints of their system to maximise power, precision, and

481 accuracy in estimating additive genetic effects. In all cases, increasing the number of families

482 (rather than offspring per family), replicated measurement of the same individual over time,

483 increasing the pedigree depth or number of generations, and avoiding clonal replication will

484 likely be the best approach for increasing the power to detect additive genetic variation

485 associated with thermal tolerance traits.

486 >>>>END BOX 1

487

488 **Acknowledgements**

492 **Table 1. Key determinants of power, precision and accuracy in different quantiative genetics experimental design.** Quantitative genetic
493 experiments require substantial sample sizes. If effective sample sizes are beyond the logistical constraints of their experimental system,
494 practitioners should prioritise experimental effort towards maximising the key principles of power, accuracy, and precision. For each of the three
495 main experimental designs, the data required to increase power, accuracy, and precision are identified along with key references.
496
497

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) (Clément et al., 2001; Quinn et al., 2006) (Bonnet et al., 2022; Morrissey et al., 2007)
Genomic relatedness matrix (GRM 'animal' models)	Number of unrelated individuals and number of SNP[a] markers	Accuracy and precision depend on variant prioritisation. An intermediate optimum defines the number of SNPs required to balance the minimum sufficient numbers to characterise genetic variation, but low enough to maximise genetic similarity between individuals		(Lee et al., 2017; Mancin et al., 2022; Müller et al., 2015)

498
499 [a] SNP = single nucleotide polymorphism

Genetic effects (G) **Environmental effects (E)**

Selection

Individual phenotype
$P = G + E (+ G \times E)$

Phenotypic variance in a population
$V_P = V_G + V_E (+ V_{G \times E})$

Single generation response to selection:
Phenotypic change = $h^2 S$

Individuals differ in phenotype, leading to variation in a population

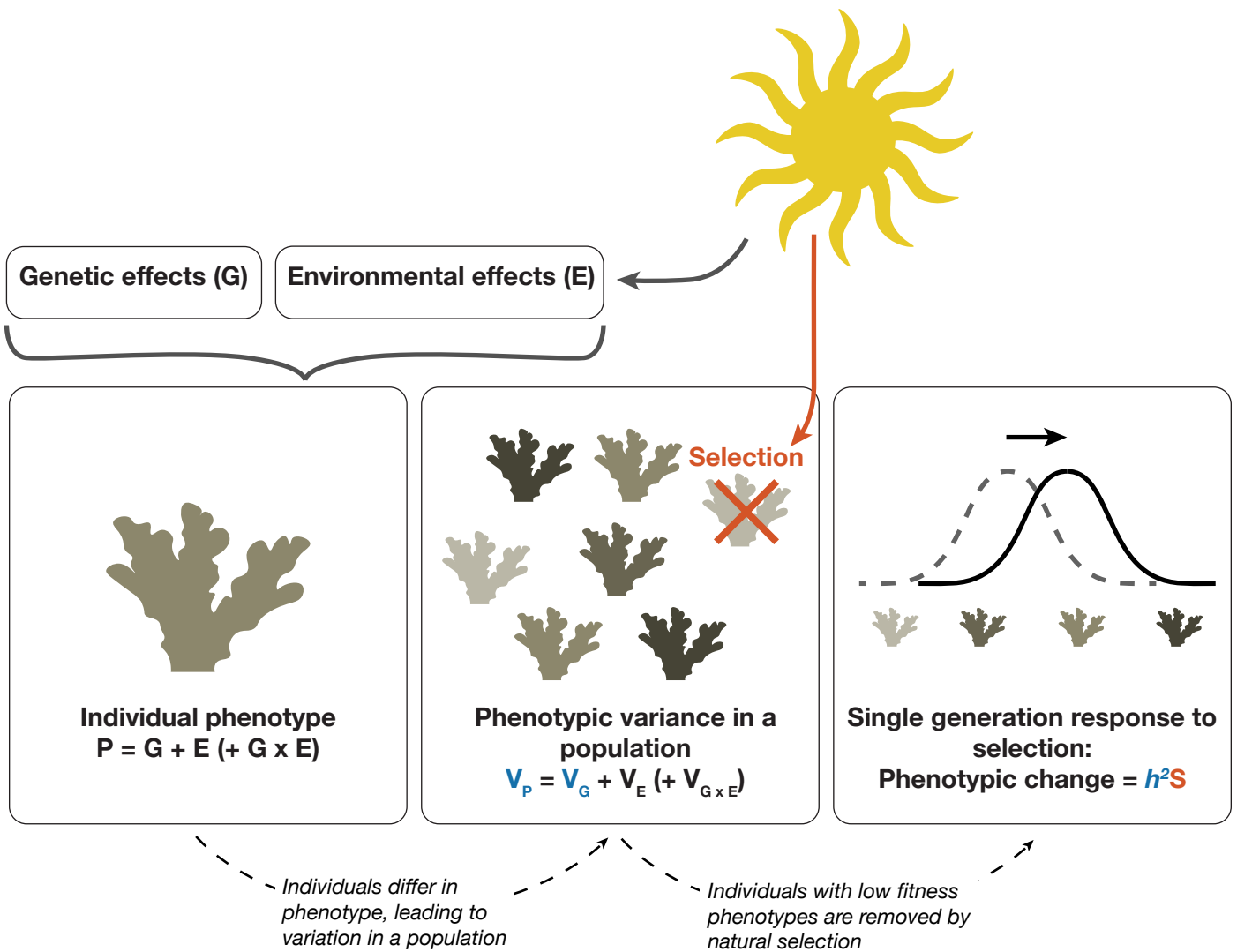*Individuals with low fitness phenotypes are removed by natural selection*

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 popualtion. 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 heritabilty (narrow sense: h^2) and the strength of selection.
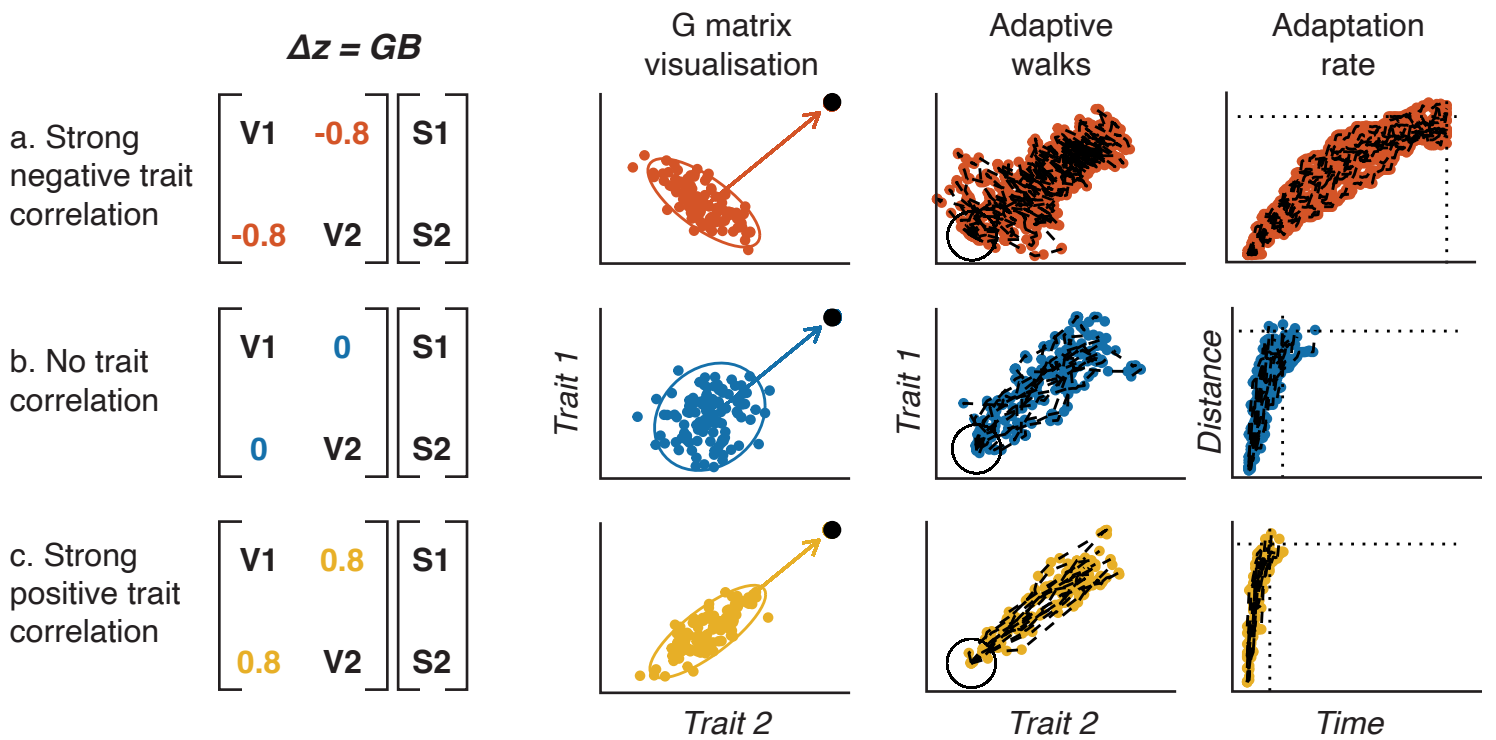
$\Delta z = GB$

G matrix visualisation

Adaptive walks

Adaptation rate

a. Strong negative trait correlation

$\begin{bmatrix} V1 & -0.8 \\ -0.8 & V2 \end{bmatrix} \begin{bmatrix} S1 \\ S2 \end{bmatrix}$

b. No trait correlation

$\begin{bmatrix} V1 & 0 \\ 0 & V2 \end{bmatrix} \begin{bmatrix} S1 \\ S2 \end{bmatrix}$

c. Strong positive trait correlation

$\begin{bmatrix} V1 & 0.8 \\ 0.8 & V2 \end{bmatrix} \begin{bmatrix} S1 \\ S2 \end{bmatrix}$

Trait 1

Trait 1

Distance

Trait 2

Trait 2

Time

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 ($\Delta z = GB$) that describes the genetic variance and covariance between traits. In the two-trait examples shown here, genetic variance within traits (V1, V2), and selection upon each trait (S1, S2) 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.)
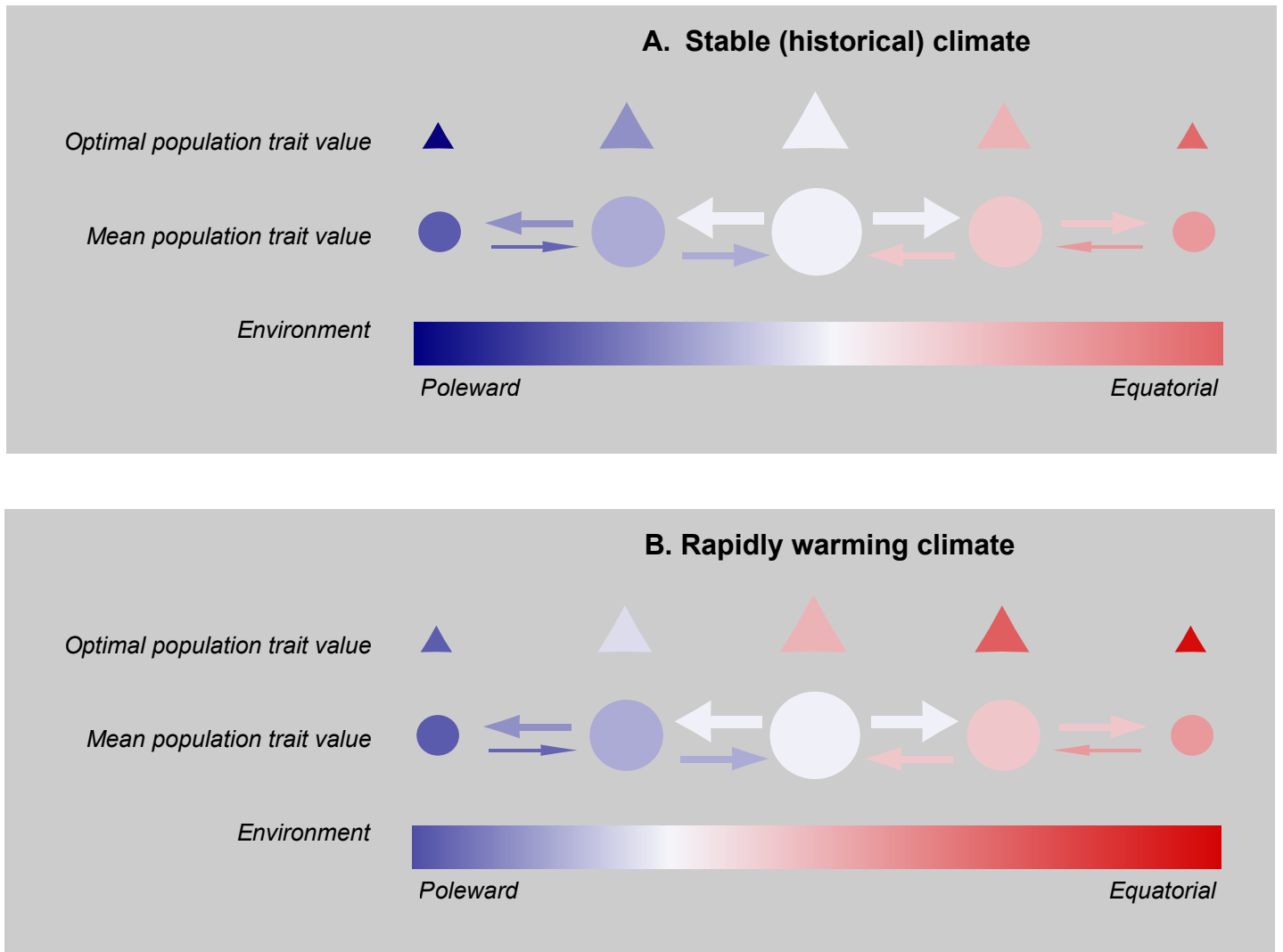
Figure 3: Conceptual models for source-sink dynamics and effects of migration under stable and rapidly warming climate scenarios. Populations of varying sizes are arrayed across a thermal landscape under stable (historical) conditions and rapid wholescale warming. Colour represents temperature, where 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 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.
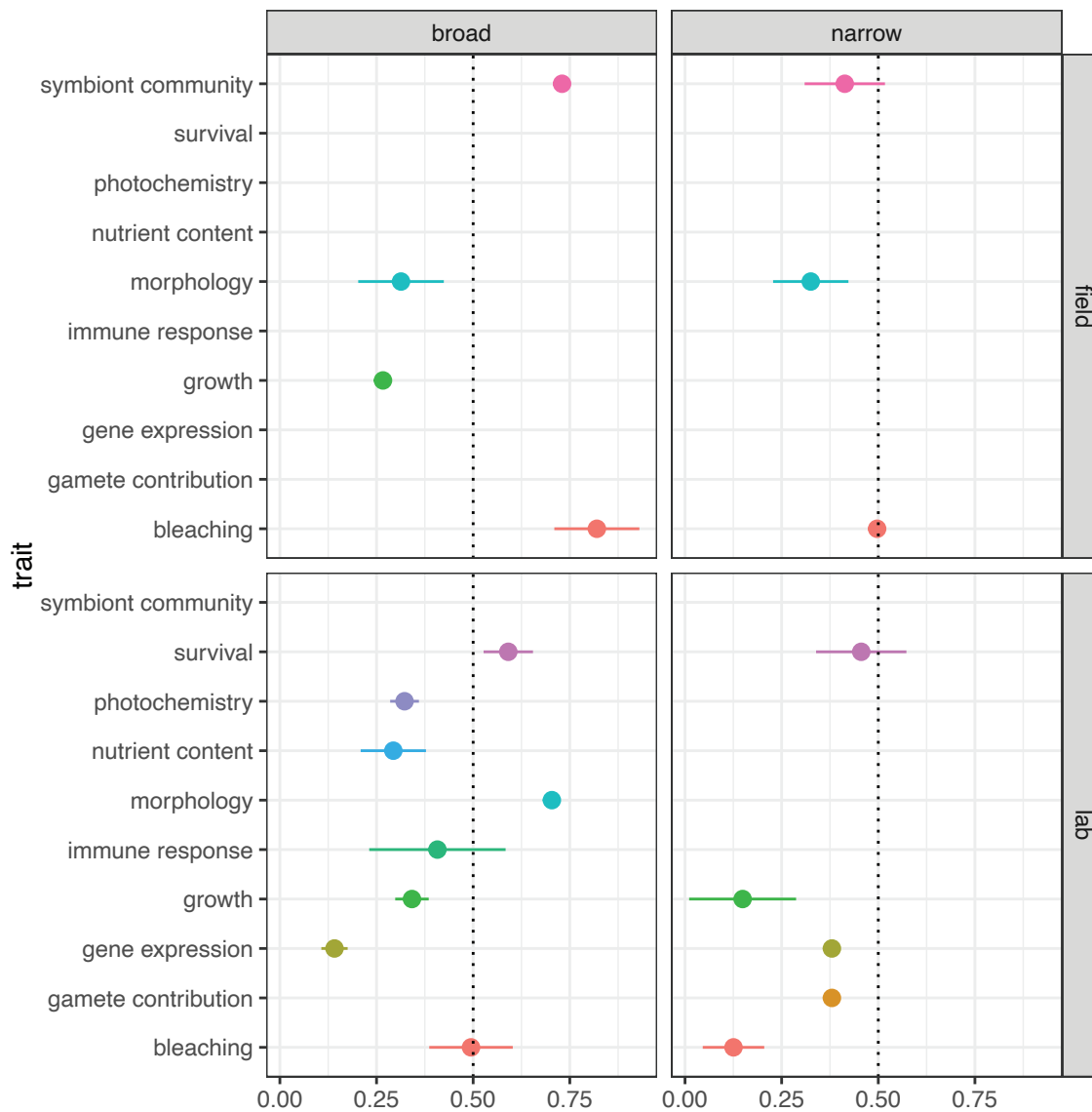
Figure S1: summary of published heritabilty estimates. Lab based experiments are far more common than field experiments. There is large variation among heritabilty estimates for the same trait from different experiments (e.g. estimates of h2 = 0 and h2 = 1 available for growth in lab conditions). Narrow sense estimates are always lower than the broad sense estimate for the same trait, suggesting substantial non-additive genetic variance is being included in broad sense estimates, and any prediction of adaptive capacity from these estimates is likely to be an overestimate. Similarly, the use of clones is common, also adding to potential overestimation of h2 and therefore adaptive capacity.

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