Moving beyond heritability in the search for coral adaptive potential

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Abstract

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

Introduction

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

Current population models which predict long term changes to coral reefs fall into two categories. Ecology-focused models capture complex community dynamics and species interactions but treat species traits as fixed (e.g., Bozec et al., 2022). In contrast, evolution-focused models use demographic and population parameters to estimate genetic responses at the population level but typically ignore species interactions (Bay et al., 2017; Kleypas et al., 2016; Logan et al., 2014; Matz et al., 2018; Matz et al., 2020; McManus et al., 2021). A limited number of studies have incorporated simple competition between two coral life histories (McManus et al., 2021; Walsworth et al., 2019) or focus on the interactions between the coral cnidarian hosts and their photosynthetic endosymbionts (Baskett et al., 2009; Day et al., 2008; Logan et al., 2021). Regardless of model details, evolutionary models consistently find that evolutionary adaptation, especially to elevated temperatures, is critical for long-term coral persistence.

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

Here, we aim to identify key genetic parameters that determine adaptive capacity in corals and highlight data gaps that hinder our ability to make robust predictions for coral futures. There are many complementary approaches to study functionally important genetic variation (Vasemägi & Primmer, 2005) such as DNA sequence variation including genotype-environment association analyses (Lasky et al., 2023), reciprocal transplantation (Kawecki & Ebert, 2004), and evolve-and-resequence experiments (Turner et al., 2011). The emerging consensus that adaptation depends on the combined contribution of many genes with small effects (i.e., that fitness traits are polygenic or complex, see Falconer & Mackay, 1996; Hill, 2010; Lynch & Walsh, 1998) is supported by studies that: examine associations of alleles between adult corals from contrasting environments (Bay & Palumbi, 2014; Howells et al., 2021; Rippe et al., 2021; Rose et al., 2018; van Oppen et al., 2018); monitor gene expression changes with reciprocal transplantation (Kenkel & Matz, 2016); or show allelic shifts induced by experimental manipulation of coral larvae (Dixon et al., 2015; Kirk et al., 2018). Because adaptive traits appear primarily polygenic, we focus primarily on quantitative genetic inference in this review. Quantitative genetic methods provide tools designed to study polygenic phenotypes and to decouple genetic from environmental contributions to phenotypic traits thereby providing insights into future adaptation. Throughout, we note where future experimental research should be directed, which genetic parameters to estimate, and how they might be estimated.

Selection, heritability, and genetic variance in single traits

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

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

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

The distribution of trait values in the population can also adjust in direct response to changes in environment, without any alteration of allele frequencies, namely *phenotypic plasticity*. Phenotypic plasticity may allow individual fitness to track shifts in changing environments, thereby maintaining population size. Plastic phenotypes can be adaptive when phenotypic change occurs in the direction favoured by natural selection - an example of this might include greater tolerance to heat stress where pre-warming events prepare the coral holobiont physiologically for the bleaching stress that follows (Ainsworth et al., 2016). However, the fitness benefits from plasticity can be fleeting due to the inherent flexibility of plastic phenotypes and the absence of genetic changes influencing the trait (Ghalambor et al., 2007). Epigenetic mechanisms likely underpin plastic responses to the environment, but evidence for transgenerational persistence of epigenetic effects in corals is currently lacking (Torda et al., 2017). Intriguingly, growing evidence shows that plastic responses of a trait may align with the heritable genetic variation of the trait (Noble et al., 2019), suggesting that plasticity and adaptation may synergistically improve fitness. As a further complication, plasticity itself is a trait that can evolve where there is G x E; for example, inshore and offshore populations of *Porites astreoides* differ in plastic changes to gene expression, suggesting locally adapted plasticity in at least some coral species (Kenkel & Matz, 2016).

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

Adaptation to new fitness optima occurs via evolutionary processes that change allele frequencies, increasing the frequency of high fitness alleles. Thus, it is the genetic component of phenotypes that is the focus for studies of adaptive capacity (Hendry et al., 2018). *Heritability* is a population specific metric that defines the proportion of phenotypic trait variance (V_P) that can be attributed to genetic variation (Visscher et al., 2008). This genetic variation can be characterised in two ways: either *total* genetic variation (V_G: broad sense heritability, $H^2 = V_G/ V_P$) which defines all genetic effects on the trait of interest, or only the *additive* genetic variation (V_A: narrow sense heritability, $h^2 = V_A/ V_P$). Both estimates are widely used but differ in the conclusions that can be drawn from their estimation.

Additive genetic variance describes a subset of total genetic variance, excluding other, non-additive, sources of genetic variance such as dominance (V_D) or epistasis (V_I). Dominance refers to the interactions between alternative alleles at a *single* locus, while epistasis describes interactions *between* loci that affect the phenotype. Because these interactions are dependent on the specific combination of alleles present in the individual and these alleles are reshuffled when passed from generation to generation, non-additive sources of variation (V_D, V_I) are not inherited. Thus, broad-sense heritability may overestimate the potential for long-term adaptive responses, although available evidence from wild populations suggests that V_A is a greater contributor to V_G than non-additive genetic variance (Class & Brommer, 2020). A common source of confusion arises from the fact that the relative magnitude of non-additive genetic variances does not relate to the prevalence of non-additive gene action: loci with dominant (and recessive) alleles can be common, even if V_D is small relative to V_A (Huang & Mackay, 2016).

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

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

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

New approaches could increase precision of key genetic parameters necessary for predicting coral adaptive responses in nature. Following terrestrial research on wild populations, narrow-sense genetic variances and covariances can be estimated under field conditions using an individual based '*animal model*' (Charmantier et al., 2014; Gienapp et al., 2017; Johnston et al., 2022; Wilson et al., 2010). Rather than relying on strict breeding designs to generate offspring of varying relatedness, the animal model uses all the relationship information available for a group of field sampled individuals. A matrix describing these relationships can be obtained from observed breeding events or genetic inferences of parentage and sibship to form a pedigree. Alternatively, multilocus genomic data can be used to directly estimate relatedness, bypassing the need to construct a pedigree (Charmantier et al., 2014; Gienapp et al., 2017; Johnston et al., 2022). Employing this *genomic relationship matrix* has several benefits: first, it capitalises upon diverse relationships in wild populations to partition additive from non-additive genetic effects (Yang et al., 2011). Second, 'experiments' can be conducted in natural settings, with treatment effects and population parameters reflecting realistic conditions (Gienapp, 2020). Third, it eliminates the need for long-term, multigeneration, studies, by determining shared alleles without tracing the path of co-inheritance (i.e., pedigree). Coral studies have employed genomic relationship approaches under laboratory conditions, estimating substantial heritability of adult bleaching responses in the Caribbean coral, *Orbicella faveolata* (Dziedzic et al., 2019) and larval survival under high temperature for *Platygyra daedalea* from the Arabian/Persian Gulf and Indian Ocean (Kirk et al., 2018).

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

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

Genomic prediction has immense potential benefit for coral conservation. Stress responses such as coral bleaching may be predictable 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 target reefs for conservation or restoration based on the spatial distribution of colonies with or without heat 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). For instance, thermal tolerance is undoubtedly a complex multidimensional phenotype, comprised of multiple individual traits (Angilletta Jr, 2009), and thermal traits will not be the only determinants of fitness. Thus, when considering adaptation, it is useful to move beyond single trait heritability and consider the multivariate genetic architecture, which ultimately determines how the whole phenotype may respond to selective pressures (Lande & Arnold, 1983; Svensson et al., 2021; Walsh & Blows, 2009). Methods utilising genomic relationship matrices and supporting genomic prediction are expandable to incorporate multiple traits, so they can calculate additive genetic variance for individual traits as well as genetic co-variances between traits. Multivariate approaches, as well as being essential to account for the complex functional basis of fitness, may also improve genomic prediction accuracy, and power to detect causal loci (Pitchers et al., 2019).

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

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

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

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

Integrating quantitative and population genetics to study adaptation

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

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* to local conditions). 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. 3b; 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 reality, estimates of migration rates, population sizes, intrinsic rates of population growth, and genetic architectures are available for only a few wild species, let alone corals that produce microscopic dispersive planktonic larvae. However, just as genomic resources can lead to greater understanding about how V_A is linked to the phenotype (via the animal model), these same genetic data can be used to infer population sizes and migration rates, providing greater clarity on the demographic parameters which determine possible outcomes across the species range. Coral-focused evolutionary models that attempt to incorporate coral population parameters support the broad-brush concepts summarised in Fig. 3, concluding that poleward flowing ocean currents can disperse warm adapted larvae into more temperate populations (Matz et al., 2018; Matz et al., 2020; McManus et al., 2021).

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

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

The hidden problem of cryptic genetic structure in corals

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

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

Implications and recommendations

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

1) Incorporate quantitative genetics into ongoing experimental designs

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

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

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

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

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

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

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

Incorporating principles from evolutionary genetics into management planning can improve the accuracy of managing for future conditions. Application of genomic prediction in agriculture has shown that combining good quality phenotyping with genomic data can provide insight into the genetic architecture underlying a wide range of complex traits and allow more efficient selection of high fitness individuals (Meuwissen et al., 2001), where recent methodological developments demonstrate that genomic predictions can be extended to multivariate phenotypes (Reddiex & Chenoweth, 2021) allowing selection of individuals with superior multivariate phenotypes.

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

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

Conclusions

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

>>>>START BOX 1

Box 1: Notes on sample sizes

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

Klein (1974) provides some instructive calculations of power for breeding designs: for moderate heritability (0.4), an experiment with 100 families and 2-4 offspring per family has 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-siblings). 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., 2022, Table S1) available from large, long-term, data sets allows detection of low additive genetic variance in fitness traits.

Power of genomic relationship matrix approaches can be more difficult to generalise due to population dynamics in wild populations, 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) reliability equalled 0.36 for $h^2 = 0.25$, increasing 0.78 for $h^2 = 0.75$ (where reliability is calculated as the squared correlation coefficient between genetic estimated breeding values and the simulated true genetic values). While these sample sizes are unrealistic for many experimental budgets and timelines, they highlight 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 accuracy in estimating additive genetic effects. In all cases, increasing the number of families (rather than offspring per family), replicated measurement of the same individual over time, increasing the pedigree depth or number of generations, and avoiding clonal replication will likely be the best approach for increasing the power to detect additive genetic variation associated with thermal tolerance traits.

INCLUDE TABLE 1 IN BOX 1

>>>>END BOX 1

Acknowledgements

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Data Availability

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

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 [a] markers	Accuracy and precision depend on the sample size of the reference population and its genetic structure. The optimal number of SNPs [a] required balances the ability to characterise genetic similarity between individuals while also maximising the proportion of genetic variance those markers explain. [b]		(Lee et al., 2017; Mancin et al., 2022; McGaugh et al., 2021; Müller et al., 2015)

[a] SNP = single nucleotide polymorphism

[b] 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.

References

Aguirre, J. D., Blows, M. W., & Marshall, D. J. (2014). The genetic covariance between life cycle stages separated by metamorphosis. *Proceedings of the Royal Society B, 281*(1788), 20141091. doi:10.1098/rspb.2014.1091

Ainsworth, T. D., Heron, S. F., Ortiz, J. C., Mumby, P. J., Grech, A., Ogawa, D., Eakin, C. M., & Leggat, W. (2016). Climate change disables coral bleaching protection on the Great Barrier Reef. *Science, 352*(6283), 338-342. doi:papers3://publication/doi/10.1126/science.aac7125

Aitken, S. N., & Whitlock, M. C. (2013). Assisted gene flow to facilitate local adaptation to climate change. *Annual Review of Ecology, Evolution, and Systematics, 44*(1), 367-388. doi:10.1146/annurev-ecolsys-110512-135747

Angilletta Jr, M. J. (2009). *Thermal Adaptation: A Theoretical and Empirical Synthesis*. Oxford: Oxford University Press.

Anthony, K. R. N., Helmstedt, K. J., Bay, L. K., Fidelman, P., Hussey, K. E., Lundgren, P., Mead, D., McLeod, I. M., Mumby, P. J., Newlands, M., Schaffelke, B., Wilson, K. A., & Hardisty, P. E. (2020). Interventions to help coral reefs under global change-A complex decision challenge. *PloS ONE, 15*(8), e0236399. doi:10.1371/journal.pone.0236399

Ashraf, B., Hunter, D. C., Bérénos, C., Ellis, P. A., Johnston, S. E., Pilkington, J. G., Pemberton, J. M., & Slate, J. (2020). Genomic prediction in the wild: A case study in Soay sheep. *Molecular Ecology, 31*, 6541-6555.

Bairos-Novak, K. R., Hoogenboom, M. O., van Oppen, M. J. H., & Connolly, S. R. (2021). Coral adaptation to climate change: Meta-analysis reveals high heritability across multiple traits. *Global Change Biology, 27*(22), 5694-5710. doi:10.1111/gcb.15829

Barghi, N., Hermisson, J., & Schlotterer, C. (2020). Polygenic adaptation: a unifying framework to understand positive selection. *Nature Reviews Genetics, 21*(12), 769-781. doi:10.1038/s41576-020-0250-z

Barshis, D. J., Ladner, J. T., Oliver, T. A., Seneca, F. O., Traylor-Knowles, N., & Palumbi, S. R. (2013). Genomic basis for coral resilience to climate change. *Proceedings of the National Academy of Sciences, 110*(4), 1387-1392. doi:papers3://publication/doi/10.1073/pnas.1210224110

Baskett, M. L., Gaines, S. D., & Nisbet, R. M. (2009). Symbiont diversity may help coral reefs survive moderate climate change. *Ecological Applications, 19*(1), 3-17. doi:papers3://publication/doi/10.1890/08-0139.1

Baums, I. B. (2008). A restoration genetics guide for coral reef conservation. *Molecular Ecology, 17*(12), 2796-2811. doi:10.1111/j.1365-294X.2008.03787.x

Baums, I. B., Baker, A. C., Davies, S. W., Grottoli, A. G., Kenkel, C. D., Kitchen, S. A., Kuffner, I. B., LaJeunesse, T. C., Matz, M. V., Miller, M. W., Parkinson, J. E., & Shanz, A. A. (2019). Considerations for maximizing the adaptive potential of restored coral populations in the western Atlantic. *Ecological Applications, 29*, e01978.

Bay, R. A., & Guerrero, L. (2020). Can coral genomes predict bleaching? *Science, 369*, 249-250.

Bay, R. A., & Palumbi, S. R. (2014). Multilocus adaptation associated with heat resistance in reef-building corals. *CURBIO, 24*(24), 2952-2956. doi:papers3://publication/doi/10.1016/j.cub.2014.10.044

Bay, R. A., Rose, N. H., Logan, C. A., & Palumbi, S. R. (2017). Genomic models predict successful coral adaptation if future ocean warming rates are reduced. *Science Advances, 3*(11), e1701413. doi:papers3://publication/doi/10.1126/sciadv.1701413

Berkelmans, R., & Willis, B. L. (1999). Seasonal and local spatial patterns in the upper thermal limits of corals on the inshore Central Great Barrier Reef. *Coral Reefs, 18*(3), 219-228. doi:10.1007/s003380050186

Bolnick, D. I., Barrett, R. D., Oke, K. B., Rennison, D. J., & Stuart, Y. E. (2018). (Non) parallel evolution. *Annual Review of Ecology, Evolution, and Systematics, Vol 49, 49*(1), 303-330.

Bonnet, T., Morrissey, M. B., de Villemereuil, P., Alberts, S. C., Arcese, P., Bailey, L. D., Boutin, S., Brekke, P., Brent, L. J. N., Camenisch, G., Charmantier, A., Clutton-Brock, T. H., Cockburn, A., Coltman, D. W., Courtiol, A., Davidian, E., Evans, S. R., Ewen, J. G., Festa-Bianchet, M., de Franceschi, C., Gustafsson, L., Höner, O. P., Houslay, T. M., Keller, L. F., Manser, M., McAdam, A. G., McLean, E., Nietlisbach, P., Osmond, H. L., Pemberton, J. M., Postma, E., Reid, J. M., Rutschmann, A., Santure, A. W., Sheldon, B. C., Slate, J., Teplitsky, C., Visser, M. E., Wachter, B., & Kruuk, L. E. B. (2022). Genetic variance in fitness indicates rapid contemporary adaptive evolution in wild animals. *Science, 376*(6596), 1012-1016. doi:10.1126/science.abk0853

Boyle, E. A., Li, Y. I., & Pritchard, J. K. (2017). An expanded view of complex traits: From polygenic to omnigenic. *Cell, 169*(7), 1177-1186. doi:papers3://publication/doi/10.1016/j.cell.2017.05.038

Bozec, Y.-M., Hock, K., Mason, R. A. B., Baird, M. E., Castro-Sanguino, C., Condie, S. A., Puotinen, M., Thompson, A., & Mumby, P. J. (2022). Cumulative impacts across Australia's Great Barrier Reef: a mechanistic evaluation. *Ecological Monographs, 92*(1), e01494. doi:10.1002/ecm.1494

Charmantier, A., Garant, D., & Kruuk, L. E. B. (2014). *Quantitative Genetics in the Wild*. Oxford: Oxford University Press.

Class, B., & Brommer, J. E. (2020). Can dominance genetic variance be ignored in evolutionary quantitative genetic analyses of wild populations? *Evolution, 74*(7), 1540-1550.

Clément, V., Bibé, B., Verrier, É., Elsen, J.-M., Manfredi, E., Bouix, J., & Hanocq, É. (2001). Simulation analysis to test the influence of model adequacy and data structure on the estimation of genetic parameters for traits with direct and maternal effects. *Genetics Selection Evolution, 33*(4), 369. doi:10.1186/1297-9686-33-4-369

Coles, S. L., & Riegl, B. M. (2013). Thermal tolerances of reef corals in the Gulf: A review of the potential for increasing coral survival and adaptation to climate change through assisted translocation. *Marine Pollution Bulletin, 72*(2), 323-332.

Davis, M. B., & Shaw, R. G. (2001). Range shifts and adaptive responses to quaternary climate change. *Science, 292*(673-679).

Day, T., Nagel, L., van Oppen, M. J., & Caley, M. J. (2008). Factors affecting the evolution of bleaching resistance in corals. *The American Naturalist, 171*(2), E72-88. doi:10.1086/524956

Dixon, G., Liao, Y., Bay, L. K., & Matz, M. V. (2018). Role of gene body methylation in acclimatization and adaptation in a basal metazoan. *Proc Natl Acad Sci U S A, 115*(52), 13342-13346. doi:10.1073/pnas.1813749115

Dixon, G. B., Davies, S. W., Aglyamova, G. A., Meyer, E., Bay, L. K., & Matz, M. V. (2015). Genomic determinants of coral heat tolerance across latitudes. *Science, 348*(6242), 1460-1462. doi:papers3://publication/doi/10.1126/science.1261224

Dziedzic, K. E., Elder, H., Tavalire, H., & Meyer, E. (2019). Heritable variation in bleaching responses and its functional genomic basis in reef-building corals (*Orbicella faveolata*). *Molecular Ecology, 28*(9), 2238-2253. doi:10.1111/mec.15081

Falconer, D. S., & Mackay, T. F. C. (1996). *Introduction to Quantitative Genetics* (fourth ed.). London, UK: Longman.

Fisher, R. A. (1919). XV.—The correlation between relatives on the supposition of Mendelian inheritance. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh, 52*(2), 399-433.

Fuller, Z. L., Mocellin, V. J. L., Morris, L. A., Cantin, N., Shepherd, J., Sarre, L., Peng, J., Liao, Y., Pickrell, J., Andolfatto, P., Matz, M., Bay, L. K., & Przeworski, M. (2020). Population genetics of the coral *Acropora millepora*: Toward genomic prediction of bleaching. *Science, 369*(6501), eaba4674. doi:10.1126/science.aba4674

Ghalambor, C. K., McKay, J. K., Carroll, S. P., & Reznick, D. N. (2007). Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. *Functional Ecology, 21*(3), 394-407. doi:papers3://publication/doi/10.1111/j.1365-2435.2007.01283.x

Gienapp, P. (2020). Opinion: Is gene mapping in wild populations useful for understanding and predicting adaptation to global change? *Global Change Biology, 26*(5), 2737-2749. doi:10.1111/gcb.15058

Gienapp, P., Calus, M. P. L., Laine, V. N., & Visser, M. E. (2019). Genomic selection on breeding time in a wild bird population. *Evolution Letters, 3*(2), 142-151. doi:papers3://publication/doi/10.1002/evl3.103

Gienapp, P., Fior, S., Guillaume, F., Lasky, J. R., Sork, V. L., & Csilléry, K. (2017). Genomic quantitative genetics to study evolution in the wild. *Trends in ecology & evolution, 32*(12), 897-908. doi:papers3://publication/doi/10.1016/j.tree.2017.09.004

Gilbert, A. L., & Miles, D. B. (2019). Antagonistic responses of exposure to sublethal temperatures: Adaptive phenotypic plasticity coincides with a reduction in organismal performance. *The American Naturalist, 194*(3), 344-355. doi:10.1086/704208

Gomez-Corrales, M., & Prada, C. (2020). Cryptic lineages respond differently to coral bleaching. *Molecular Ecology, 29*, 4265-4273. doi:10.1111/mec.15631

Grottoli, A. G., Toonen, R. J., van Woesik, R., Vega Thurber, R., Warner, M. E., McLachlan, R. H., Price, J. T., Bahr, K. D., Baums, I. B., Castillo, K. D., Coffroth, M. A., Cunning, R., Dobson, K. L., Donahue, M. J., Hench, J. L., Iglesias-Prieto, R., Kemp, D. W., Kenkel, C. D., Kline, D. I., Kuffner, I. B., Matthews, J. L., Mayfield, A. B., Padilla-Gamino, J. L., Palumbi, S., Voolstra, C. R., Weis, V. M., & Wu, H. C. (2021). Increasing comparability among coral bleaching experiments. *Ecological Applications, 31*(4), e02262. doi:10.1002/eap.2262

Hanocq, E., Boichard, D., & Foulley, J. L. (1996). A simulation study of the effect of connectedness on genetic trend. *Genetics Selection Evolution, 28*(1), 67-82.

Hendry, A. P., Schoen, D. J., Wolak, M. E., & Reid, J. M. (2018). The contemporary evolution of fitness. *Annual Review of Ecology, Evolution, and Systematics, 49*(1), 457-476. doi:papers3://publication/doi/10.1146/annurev-ecolsys-110617-062358

Higgs, E., Harris, J., Murphy, S., Bowers, K., Hobbs, R., Jenkins, W., Kidwell, J., Lopoukhine, N., Sollereder, B., Suding, K., Thompson, A., & Whisenant, S. (2018). On principles and standards in ecological restoration. *Restoration Ecology, 26*(3), 399-403. doi:10.1111/rec.12691

Hill, W. G. (2010). Understanding and using quantitative genetic variation. *Philosophical Transactions of the Royal Society B: Biological Sciences, 365*(1537), 73-85.

Hoegh-Guldberg, O., Mumby, P. J., Hooten, A. J., Steneck, R. S., Greenfield, P., Gomez, E., Harvell, C. D., Sale, P. F., Edwards, A. J., Caldeira, K., Knowlton, N., Eakin, C. M., Iglesias-Prieto, R., Muthiga, N., Bradbury, R. H., Dubi, A., & Hatziolos, M. E.

(2007). Coral reefs under rapid climate change and ocean acidification. *Science, 318*(5857), 1737-1742. doi:papers3://publication/doi/10.1126/science.1152509

Hoffmann, A. A., Weeks, A. R., & Sgro, C. M. (2021). Opportunities and challenges in assessing climate change vulnerability through genomics. *Cell, 184*(6), 1420-1425. doi:10.1016/j.cell.2021.02.006

Holt, R. D., & Gomulkiewicz, R. (1997). How does immigration influence local adaptation? A reexamination of a familiar paradigm. *The American Naturalist, 149*(3), 563-572. doi:papers3://publication/uuid/6DB537F1-8BD7-4C6F-905C-865C31EFAACF

Howells, E. J., Abrego, D., Liew, Y. J., Burt, J. A., Meyer, E., & Aranda, M. (2021). Enhancing the heat tolerance of reef-building corals to future warming. *Science Advances, 7*(34), eabg6070.

Howells, E. J., Bay, L. K., & Bay, R. A. (2022). Identifying, monitoring, and managing adaptive genetic variation in reef-building corals under climate change. In M. J. van Oppen & M. Aranda (Eds.), *Coral Reef Conservation And Restoration In The 'Omics' Age* (pp. 55-70).

Huang, W., & Mackay, T. F. (2016). The genetic architecture of quantitative traits cannot be inferred from variance component analysis. *PLoS Genetics, 12*(11), e1006421. doi:10.1371/journal.pgen.1006421

Hughes, T. P., Barnes, M. L., Bellwood, D. R., Cinner, J. E., Cumming, G. S., Jackson, J. B. C., Kleypas, J. A., van de Leemput, I. A., Lough, J. M., Morrison, T. H., Palumbi, S. R., van Nes, E. H., & Scheffer, M. (2017). Coral reefs in the Anthropocene. *Nature, 546*(7656), nature22901-22990. doi:papers3://publication/doi/10.1038/nature22901

Humanes, A., Lachs, L., Beauchamp, E. A., Bythell, J. C., Edwards, A. J., Golbuu, Y., Martinez, H. M., Palmowski, P., Treumann, A., van der Steeg, E., van Hooidonk, R., & Guest, J. R. (2022). Within-population variability in coral heat tolerance indicates climate adaptation potential. *Proceedings of the Royal Society B, 289*(1981), 20220872. doi:10.1098/rspb.2022.0872

Johnston, S. E., Chen, N., & Josephs, E. B. (2022). Taking quantitative genomics into the wild. *Proceedings of the Royal Society B, 289*(1989), 20221930. doi:10.1098/rspb.2022.1930

Kawecki, T. J., & Ebert, D. (2004). Conceptual issues in local adaptation. *Ecol Lett, 7*(12), 1225-1241. doi:10.1111/j.1461-0248.2004.00684.x

Kenkel, C. D., & Matz, M. V. (2016). Gene expression plasticity as a mechanism of coral adaptation to a variable environment. *Nature Ecology & Evolution, 1*(1), 0014. doi:papers3://publication/doi/10.1038/s41559-016-0014

Kingsolver, J. G., & Buckley, L. B. (2018). How do phenology, plasticity, and evolution determine the fitness consequences of climate change for montane butterflies? *Evolutionary Applications, 11*(8), 1231-1244.

Kirk, N. L., Howells, E. J., Abrego, D., Burt, J. A., & Meyer, E. (2018). Genomic and transcriptomic signals of thermal tolerance in heat-tolerant corals (*Platygyra daedalea*) of the Arabian/Persian Gulf. *Molecular Ecology, 27*(24), 5180-5194.

Kirkpatrick, M., & Barton, N. H. (1997). Evolution of a species' range. *The American Naturalist, 150*, 1-23.

Klein, T. W. (1974). Heritability and genetic correlation: Statistical power, population comparisons, and sample size. *Behavior Genetics, 4*(2), 171-189. doi:10.1007/BF01065758

Klein, T. W., DeFries, J. C., & Finkbeiner, C. T. (1973). Heritability and genetic correlation: Standard errors of estimates and sample size. *Behavior Genetics, 3*, 355-364.

Kleypas, J. A., Thompson, D. M., & Castruccio, F. S. (2016). Larval connectivity across temperature gradients and its potential effect on heat tolerance in coral populations. *Global Change Biology, 22*(11), 3539-3549. doi:papers3://publication/doi/10.1111/gcb.13347

Kruuk, L. E. (2004). Estimating genetic parameters in natural populations using the "animal model". *Philosophical Transactions of the Royal Society B: Biological Sciences, 359*(1446), 873-890. doi:10.1098/rstb.2003.1437

Lande, R. (1980). The genetic covariance between characters maintained by pleiotropic mutations. *Genetics, 94*, 203-215.

Lande, R., & Arnold, S. J. (1983). The measurement of selection on correlated characters. *Evolution, 37*(6), 1210-1226.

Lasky, J. R., Josephs, E. B., & Morris, G. P. (2023). Genotype-environment associations to reveal the molecular basis of environmental adaptation. *Plant Cell, 35*, 125-138. doi:10.1093/plcell/koac267

Lee, S. H., Clark, S., & Werf, v. d. J. H. J. (2017). Estimation of genomic prediction accuracy from reference populations with varying degrees of relationship. *PloS ONE, 12*(12), e0189775. doi:10.1371/journal.pone.0189775

Logan, C. A., Dunne, J. P., Eakin, C. M., & Donner, S. D. (2014). Incorporating adaptive responses into future projections of coral bleaching. *Global Change Biology, 20*(1), 125-139. doi:papers3://publication/doi/10.1111/gcb.12390

Logan, C. A., Dunne, J. P., Ryan, J. S., Baskett, M. L., & Donner, S. D. (2021). Quantifying global potential for coral evolutionary response to climate change. *Nat Clim Change, 11*(6), 537-542. doi:10.1038/s41558-021-01037-2

Lynch, M., & Walsh, B. (1998). *Genetics and Analysis of Quantitative Traits* (Vol. 1). Sunderland, MA: Sinauer.

Mancin, E., Mota, L. F. M., Tuliozi, B., Verdiglione, R., Mantovani, R., & Sartori, C. (2022). Improvement of genomic predictions in small breeds by construction of genomic relationship matrix through variable selection. *Frontiers in genetics, 13*.

Matz, M. V., Treml, E. A., Aglyamova, G. V., & Bay, L. K. (2018). Potential and limits for rapid genetic adaptation to warming in a Great Barrier Reef coral. *PLoS Genetics, 14*(4), e1007220-1007219. doi:papers3://publication/doi/10.1371/journal.pgen.1007220

Matz, M. V., Treml, E. A., & Haller, B. C. (2020). Estimating the potential for coral adaptation to global warming across the Indo-West Pacific. *Global Change Biology, 26*(6), 3473-3481. doi:10.1111/gcb.15060

McGaugh, S. E., Lorenz, A. J., & Flagel, L. E. (2021). The utility of genomic prediction models in evolutionary genetics. *Proceedings of the Royal Society B, 288*(1956), 20210693. doi:10.1098/rspb.2021.0693

McManus, L. C., Forrest, D. L., Tekwa, E. W., Schindler, D. E., Colton, M. A., Webster, M. M., Essington, T. E., Palumbi, S. R., Mumby, P. J., & Pinsky, M. L. (2021). Evolution and connectivity influence the persistence and recovery of coral reefs under climate change in the Caribbean, Southwest Pacific, and Coral Triangle. *Global Change Biology, 27*(18), 4307-4321. doi:10.1111/gcb.15725

Meuwissen, T. H. E., Hayes, B. J., & Goddard, M. E. (2001). Prediction of total genetic value using genome-wide dense marker maps. *Genetics, 157*(4), 1819-1829. doi:10.1093/genetics/157.4.1819

Morrissey, M. B., Wilson, A. J., Pemberton, J. M., & Ferguson, M. M. (2007). A framework for power and sensitivity analyses for quantitative genetic studies of natural populations, and case studies in Soay sheep (*Ovis aries*). *Journal of Evolutionary Biology, 20*(6), 2309-2321. doi:10.1111/j.1420-9101.2007.01412.x

Müller, D., Technow, F., & Melchinger, A. E. (2015). Shrinkage estimation of the genomic relationship matrix can improve genomic estimated breeding values in the training set. *Theoretical and Applied Genetics, 128*(4), 693-703. doi:10.1007/s00122-015-2464-6

National Academies of Sciences, E., and Medicine. (2019). *A decision framework for interventions to increase the persistence and resilience of coral reefs*. Washington, DC: The National Academies Press.

Noble, D. W., Radersma, R., & Uller, T. (2019). Plastic responses to novel environments are biased towards phenotype dimensions with high additive genetic variation. *Proceedings of the National Academy of Sciences, 116*(27), 13452-13461.

Nosil, P., Flaxman, S. M., Feder, J. L., & Gompert, Z. (2020). Increasing our ability to predict contemporary evolution. *Nature Communications, 11*(1), 5592. doi:10.1038/s41467-020-19437-x

Parkinson, J. E., Bartels, E., Devlin-Durante, M. K., Lustic, C., Nedimyer, K., Schopmeyer, S., Lirman, D., LaJeunesse, T. C., & Baums, I. B. (2018). Extensive transcriptional variation poses a challenge to thermal stress biomarker development for endangered corals. *Molecular Ecology, 27*(5), 1103-1119. doi:10.1111/mec.14517

Pease, C. M., Lande, R., & Bull, J. J. (1989). A model of population growth, dispersal and evolution in a changing environment. *Ecology, 70*(6), 1657-1664. doi:10.2307/1938100

Pitchers, W., Nye, J., Marquez, E. J., Kowalski, A., Dworkin, I., & Houle, D. (2019). A multivariate genome-wide association study of wing shape in *Drosophila melanogaster*. *Genetics, 211*(4), 1429-1447. doi:10.1534/genetics.118.301342

Quinn, J. L., Charmantier, A., Garant, D., & Sheldon, B. C. (2006). Data depth, data completeness, and their influence on quantitative genetic estimation in two contrasting bird populations. *Journal of Evolutionary Biology, 19*, 994-1002.

Reddiex, A. J., & Chenoweth, S. F. (2021). Integrating genomics and multivariate evolutionary quantitative genetics: a case study of constraints on sexual selection in *Drosophila serrata*. *Proceedings of the Royal Society B, 288*(1960), 20211785. doi:10.1098/rspb.2021.1785

Riginos, C., & Beger, M. (2022). Incorporating genetic measures of connectivity and adaptation in marine spatial planning for corals. In M. Van Oppen & M. Aranda (Eds.), *Coral reef conservation and restoration in the 'omics' age* (pp. 7-33).

Rippe, J. P., Dixon, G., Fuller, Z. L., Liao, Y., & Matz, M. (2021). Environmental specialization and cryptic genetic divergence in two massive coral species from the Florida Keys Reef Tract. *Molecular Ecology, 30*, 3468–3484.

Rose, N. H., Bay, R. A., Morikawa, M. K., & Palumbi, S. R. (2018). Polygenic evolution drives species divergence and climate adaptation in corals. *Evolution, 72*(1), 82-94. doi:papers3://publication/doi/10.1111/evo.13385

Schluter, D. (1996). Adaptive radiation along genetic lines of least resistance. *Evolution*, 1766-1774.

Selmoni, O., Lecellier, G., Vigliola, L., Berteaux-Lecellier, V., & Joost, S. (2020). Coral cover surveys corroborate predictions on reef adaptive potential to thermal stress. *Scientific reports, 10*(1), 19680. doi:10.1038/s41598-020-76604-2

Svensson, E. I., Arnold, S. J., Bürger, R., Csilléry, K., Draghi, J., Henshaw, J. M., Jones, A. G., De Lisle, S., Marques, D. A., McGuigan, K., Simon, M. N., & Runemark, A. (2021). Correlational selection in the age of genomics. *Nature Ecology & Evolution, 5*(5), 562-573. doi:10.1038/s41559-021-01413-3

Teplitsky, C., Tarka, M., Møller, A. P., Nakagawa, S., Balbontín, J., Burke, T. A., Doutrelant, C., Gregoire, A., Hansson, B., Hasselquist, D., Gustafsson, L., Lope, d. F., Marzal, A., Mills, J. A., Wheelwright, N. T., Yarrall, J. W., & Charmantier, A. (2014). Assessing multivariate constraints to evolution across ten long-term avian studies. *PloS ONE, 9*(3), e90444. doi:10.1371/journal.pone.0090444

Thomas, L., Kennington, W. J., Evans, R. D., Kendrick, G. A., & Stat, M. (2017). Restricted gene flow and local adaptation highlight the vulnerability of high-latitude reefs to rapid environmental change. *Global Change Biology, 23*(6), 2197-2205. doi:10.1111/gcb.13639

Torda, G., Donelson, J. M., Aranda, M., Barshis, D. J., Bay, L. K., Berumen, M. L., Bourne, D. G., Cantin, N., Foret, S., Matz, M. V., Miller, D. J., Moya, A., Putnam, H. M., Ravasi, T., van Oppen, M. J. H., Thurber, R. V., Vidal-Dupiol, J., Voolstra, C. R., Watson, S.-A., Whitelaw, E., Willis, B. L., & Munday, P. L. (2017). Rapid adaptive responses to climate change in corals. *Nat Clim Change, 7*(9), 627-636. doi:papers3://publication/doi/10.1038/nclimate3374

Traylor-Knowles, N., Rose, N. H., Sheets, E. A., & Palumbi, S. R. (2017). Early transcriptional responses during heat stress in the coral *Acropora hyacinthus*. *The Biological Bulletin, 232*, 91-100.

Turner, T. L., Stewart, A. D., Fields, A. T., Rice, W. R., & Tarone, A. M. (2011). Population-based resequencing of experimentally evolved populations reveals the genetic basis of body size variation in *Drosophila melanogaster*. *PLoS Genetics, 7*(3), e1001336. doi:10.1371/journal.pgen.1001336

Urban, M. C., Bocedi, G., Hendry, A. P., Mihoub, J. B., Peer, G., Singer, A., Bridle, J. R., Crozier, L. G., De Meester, L., Godsoe, W., Gonzalez, A., Hellmann, J. J., Holt, R. D., Huth, A., Johst, K., Krug, C. B., Leadley, P. W., Palmer, S. C. F., Pantel, J. H., Schmitz, A., Zollner, P. A., & Travis, J. M. J. (2016). Improving the forecast for biodiversity under climate change. *Science, 353*(6304), aad8466-aad8466. doi:papers3://publication/doi/10.1126/science.aad8466

van Heerwaarden, B., Kellermann, V., & Sgrò, C. M. (2016). Limited scope for plasticity to increase upper thermal limits. *Functional Ecology, 30*(12), 1947-1956.

van Oppen, M. J. H., Bongaerts, P., Frade, P. R., Peplow, L. M., Boyd, S. E., Nim, H. T., & Bay, L. K. (2018). Adaptation to reef habitats through selection on the coral animal and its associated microbiome. *Molecular Ecology, 27*(14), 2956-2971. doi:papers3://publication/doi/10.1111/mec.14763

van Oppen, M. J. H., Gates, R. D., Blackall, L. L., Cantin, N., Chakravarti, L. J., Chan, W. Y., Cormick, C., Crean, A., Damjanovic, K., Epstein, H., Harrison, P. L., Jones, T. A., Miller, M. W., Pears, R. J., Peplow, L. M., Raftos, D. A., Schaffelke, B., Stewart, K., Torda, G., Wachenfeld, D., Weeks, A. R., & Putnam, H. M. (2017). Shifting paradigms in restoration of the world's coral reefs. *Global Change Biology, 23*(9), 3437-3448. doi:papers3://publication/doi/10.1111/gcb.13647

Vasemägi, A., & Primmer, C. R. (2005). Challenges for identifying functionally important genetic variation: the promise of combining complementary research strategies. *Molecular Ecology, 14*(12), 3623-3642. doi:papers3://publication/doi/10.1111/j.1365-294X.2005.02690.x

Visscher, P. M., Hill, W. G., & Wray, N. R. (2008). Heritability in the genomics era—concepts and misconceptions. *Nature Reviews Genetics, 9*(4), 255-266.

Walsh, B., & Blows, M. W. (2009). Abundant genetic variation + strong selection = multivariate genetic constraints: A geometric view of adaptation. *Annual Review of*

Ecology, Evolution, and Systematics, 40(1), 41-59. doi:10.1146/annurev.ecolsys.110308.120232

Walsh, B., & Lynch, M. (2018). *Evolution And Selection of Quantitative Traits*: Oxford University Press.

Walsworth, T. E., Schindler, D. E., Colton, M. A., Webster, M. S., Palumbi, S. R., Mumby, P. J., Essington, T. E., & Pinsky, M. L. (2019). Management for network diversity speeds evolutionary adaptation to climate change. *Nat Clim Change, 9*(8), 632-636. doi:10.1038/s41558-019-0518-5

Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J., Fromentin, J.-M., Hoegh-Guldberg, O., & Bairlein, F. (2002). Ecological responses to recent climate change. *Nature, 416*(6879), 389-395.

Weeks, A. R., Sgrò, C. M., Young, A. G., Frankham, R., Mitchell, N. J., Miller, K. A., Byrne, M., Coates, D. J., Eldridge, M. D. B., Sunnucks, P., Breed, M. F., James, E. A., & Hoffmann, A. A. (2011). Assessing the benefits and risks of translocations in changing environments: a genetic perspective. *Evolutionary Applications, 4*(6), 709-725. doi:papers3://publication/doi/10.1111/j.1752-4571.2011.00192.x

Weigensberg, I., & Roff, D. A. (1996). Natural heritabilities: can they be reliably estimated in the laboratory? *Evolution, 50*(6), 2149-2157. doi:10.1111/j.1558-5646.1996.tb03605.x

Wilson, A. J., Reale, D., Clements, M. N., Morrissey, M. M., Postma, E., Walling, C. A., Kruuk, L. E., & Nussey, D. H. (2010). An ecologist's guide to the animal model. *Journal of Animal Ecology, 79*(1), 13-26. doi:10.1111/j.1365-2656.2009.01639.x

Wray, N. R., Kemper, K. E., Hayes, B. J., Goddard, M. E., & Visscher, P. M. (2019). Complex trait prediction from genome data: Contrasting EBV in livestock to PRS in humans: Genomic prediction. *Genetics, 211*(4), 1131-1141. doi:10.1534/genetics.119.301859

Wright, R. M., Mera, H., Kenkel, C. D., Nayfa, M., Bay, L. K., & Matz, M. V. (2019). Positive genetic associations among fitness traits support evolvability of a reef-building coral under multiple stressors. *Global Change Biology, 25*(10), 3294-3304. doi:10.1111/gcb.14764

Yang, J., Lee, S. H., Goddard, M. E., & Visscher, P. M. (2011). GCTA: A tool for genome-wide complex trait analysis. *The American Journal of Human Genetics, 88*(1), 76-82. doi:papers3://publication/doi/10.1016/j.ajhg.2010.11.011

Yeaman, S. (2022). Evolution of polygenic traits under global vs local adaptation. *Genetics, 220*(1), iyab134. doi:10.1093/genetics/iyab134

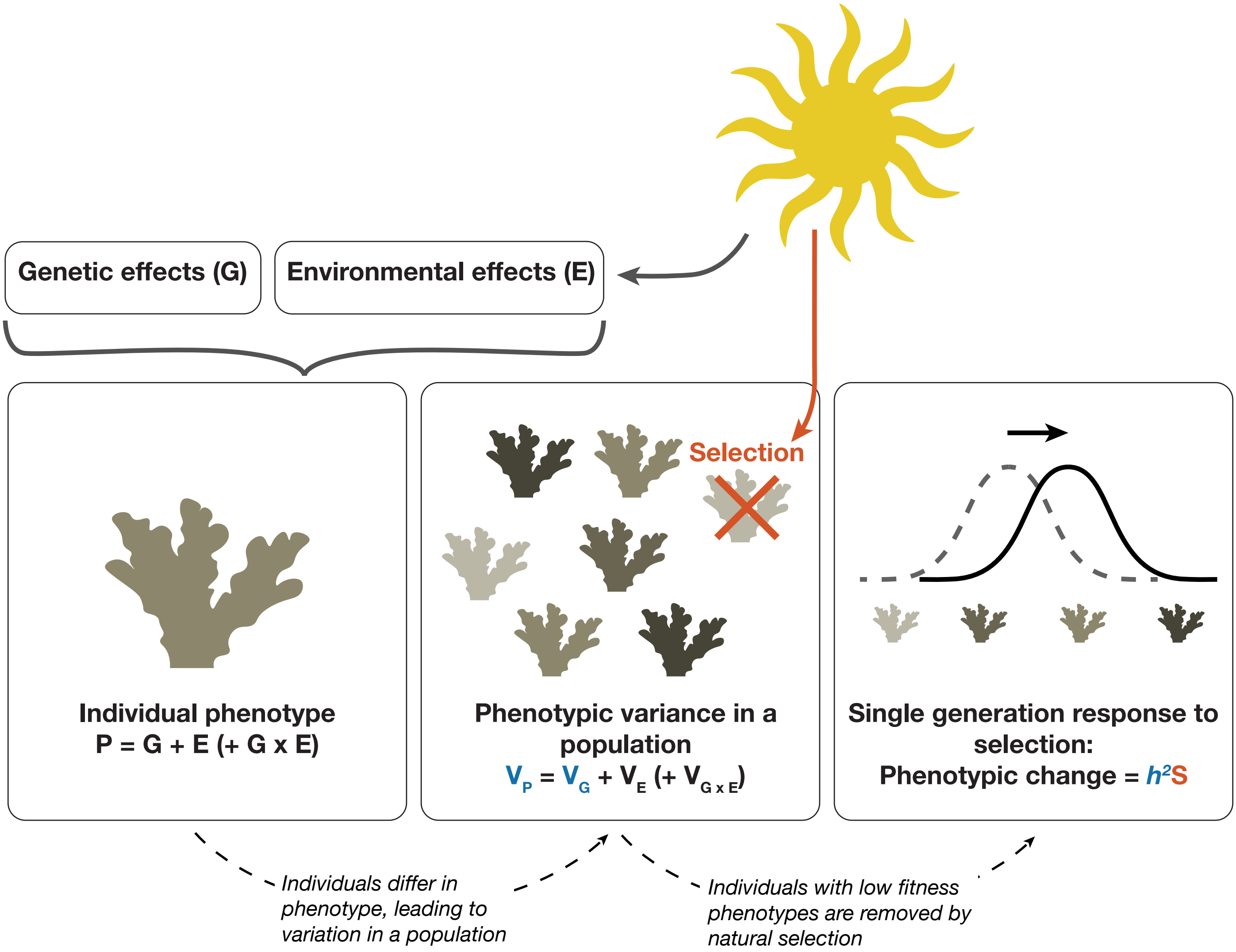
Figure 1. Heritability and the partitioning of phenotypic variance. Trait values in individuals are due to a combination of genetic and environmental effects. Individual phenotypes differ, leading to variation in a popualtion. The environment also exerts selection against some phenotypes in the population. 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.

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 ($\Delta z = \mathbf{G}B$) 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 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 heritabilty estimates. Manipulative laboratory 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 $h^2 = 0$ 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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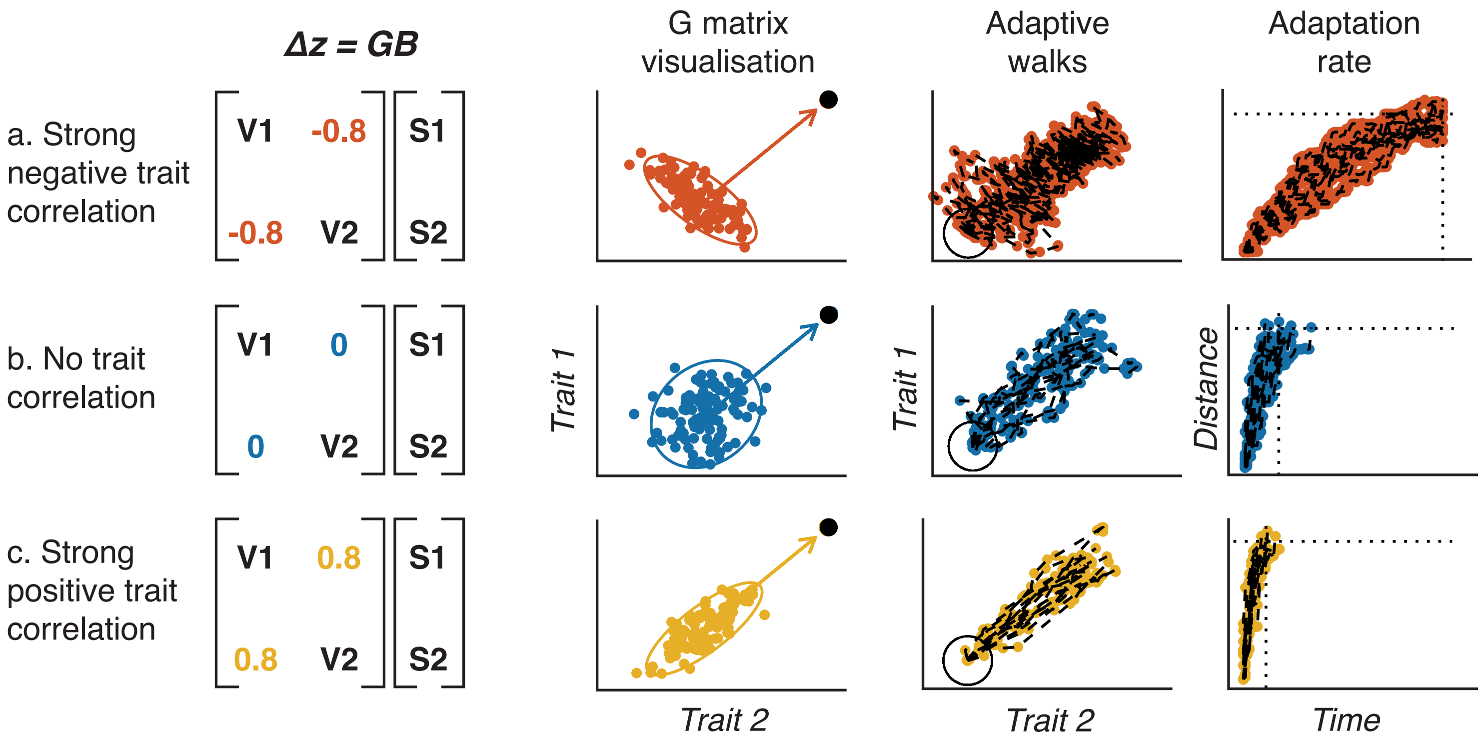

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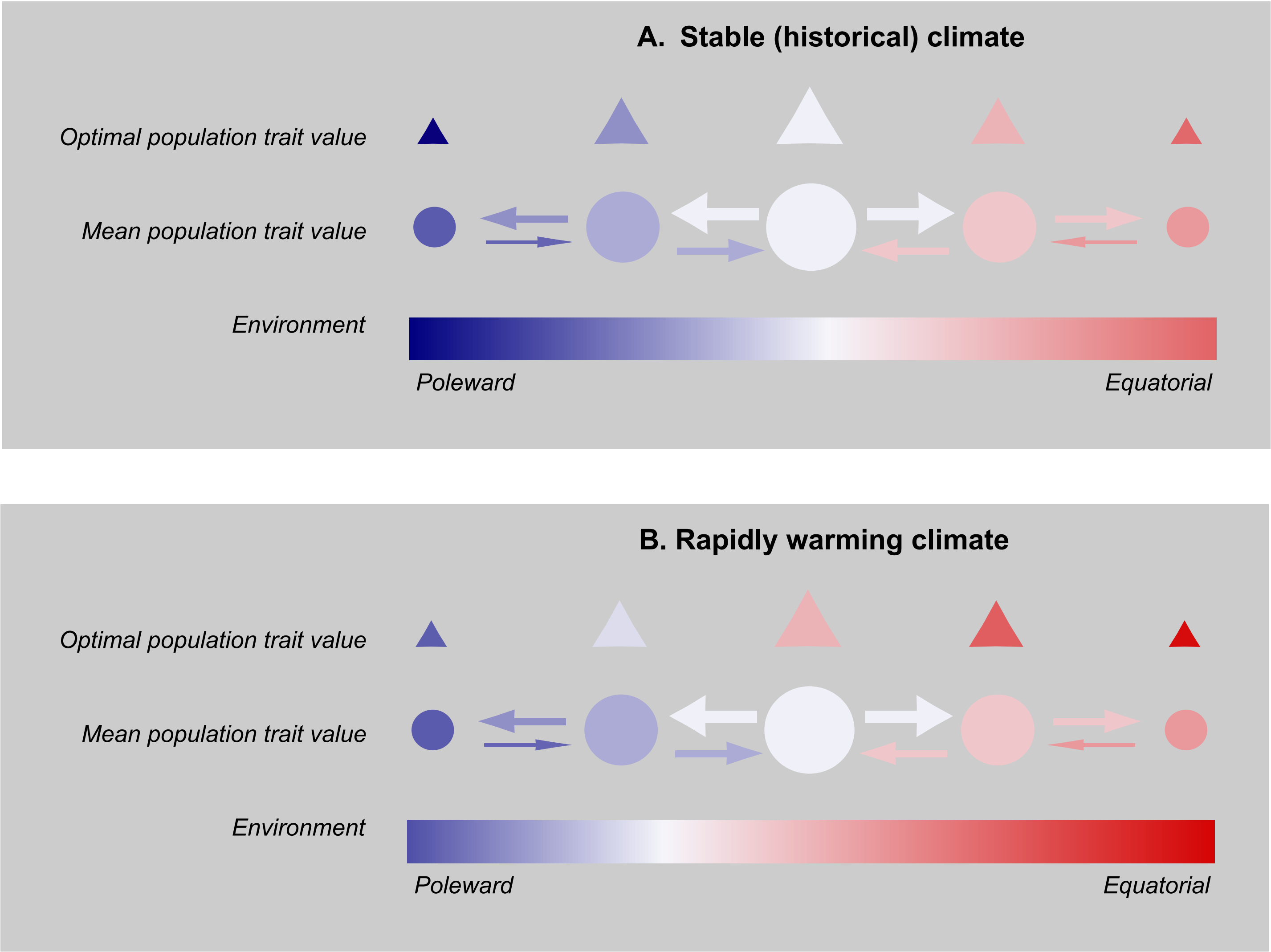

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