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Breeding and Selecting Corals Resilient to Global Warming

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Abstract

Selective breeding of resilient organisms is an emerging topic in marine conservation. It can help us predict how species will adapt in the future and how we can help restore struggling populations effectively in the present. Scleractinian corals represent a potential tractable model system given their widescale phenotypic plasticity across fitness-related traits and a reproductive life history based on mass synchronized spawning. Here, I explore the justification for breeding in corals, identify underutilized pathways of acclimation, and highlight avenues for quantitative targeted breeding from the coral host and symbiont perspective. Specifically, the facilitation of enhanced heat tolerance by targeted breeding of plasticity mechanisms is underutilized. Evidence from theoretical genetics identifies potential pitfalls, including inattention to physical and genetic characteristics of the receiving environment. Three criteria for breeding emerge from this synthesis: selection from warm, variable reefs that have survived disturbance. This information will be essential to protect what we have and restore what we can.

Thermal safety margins: temperature range (minimum to maximum) of habitat at which an organism can function, reproduce, and survive

1. INTRODUCTION

1.1. Our Climate Future: The Critical Difference Between Every 0.5°C

Global surface temperatures have already warmed by 1.2°C, on average, since the preindustrial era (1850–1900), and the likelihood of ocean temperatures exceeding 1.5°C, a commonly reported threshold, is high (1) (**Figure 1*a*–*c***). This rapid increase in warming has pushed up both the frequency and intensity of marine heatwaves. Different modeled warming scenarios are used to describe when these conditions are likely to occur given the various emissions scenarios (Intergovernmental Panel on Climate Change global greenhouse gas emission pathways). An intermediate pathway (SSP2–4.5) is becoming increasingly likely, where warming of 1.5°C or 2°C may occur within 9 to 31 years from the present (2). At +1°C, heatwaves are already predicted to occur 2.8× more frequently; at 1.5°C, they are 4.1× more likely, and conditions may be approximately 1.9°C hotter. Heatwaves may occur once every 5 years in some locations. At 2°C, heatwaves are 5.6× more likely, and conditions might get up to 2.6°C hotter (2). These temperature extremes will push already struggling ecosystems to their limits.

All organisms exist within a range of temperatures needed for optimal physiological functioning. The limits at which organisms can survive are described as their thermal safety margins (3). This has meant that ecosystems, and marine habitats in particular, have suffered rapid compositional changes in biodiversity (4). The impacts of warming can manifest in a variety of ecosystem impacts, including as large-scale die-offs in kelp and seagrass forests or as bleaching and mortality on coral reefs (5). As global climates change, organisms will be required to acclimate and adapt more quickly than ever to increasing extremes in temperature to survive.

These warming trends have already impacted the ability of some critical biomes, like coral reefs, to provide the ecosystem functions necessary to support biodiversity and livelihood values (6). Coral reefs are one of the most sensitive ecosystems globally (7). Most reef-building corals are holobionts, meaning they are a composite organism of host and multiple microbial partners, including dinoflagellate photosymbionts, bacteria, fungi, and viruses (reviewed in 8). The coral animal is made up of either single or multiple polyps to compose a clonal, modular organism. The physiological responses of corals can therefore be measured together or individually as constituent parts of the holobiont under different empirical conditions [i.e., genomics, transcriptomics of each partner, photophysiology of the dinoflagellate symbionts, or tissue extension/calcification (i.e., growth) of the host coral], among many other traits.

Corals' sensitivity in response to warming stems from the fact they already exist close to their upper thermal limits. Life in proximity of the upper thermal limits occurs in many ectotherms, especially in lower tropical latitudes, where growth form, life history, or phylogeny can also predict extinction risk based on thermal thresholds (9). Some estimates for coral reefs predict that an increase in 1.5°C is expected to cause a 70–90% loss of corals, and at 2.5°C, a 99% loss is expected (2). Warming on reefs globally is also occurring more rapidly than initially predicted, with Caribbean reefs warming at a linear rate of 0.2°C per decade (0.17–0.26°C) over the last 36 years, and is predicted to reach +1.6°C by 2100, equating to 5 heatwaves annually (10). This frequency would likely not leave time for recovery given limited reproductive cycles. The rate of warming in other reef regions, like the Red Sea (11), is also increasing. Clearly, coral reefs across latitudes will be impacted differently, with high northern latitudes projected to experience the largest increases (up to 6°C) compared to lower latitudes [4°C (9)]. It thus becomes clear from these future climate scenarios that each degree matters.

1.2. Exceeding the Thermal Safety Margins

When biological thermal safety margins are exceeded, organisms perish. This is because biological systems are constrained by physiology and can be pushed only so far before limits are met, leading to processes like protein denaturation (12). These margins appear more restricted in the tropics (3), exacerbating species diversity losses in these equatorial regions (13). The limits of organisms can be described using concepts like thermal tolerance, defined as the range of temperatures in which an organism can function. Thermal performance, which can be defined as a quantifiable trait, is

Thermal tolerance: range of temperatures in which an organism can optimally function and survive

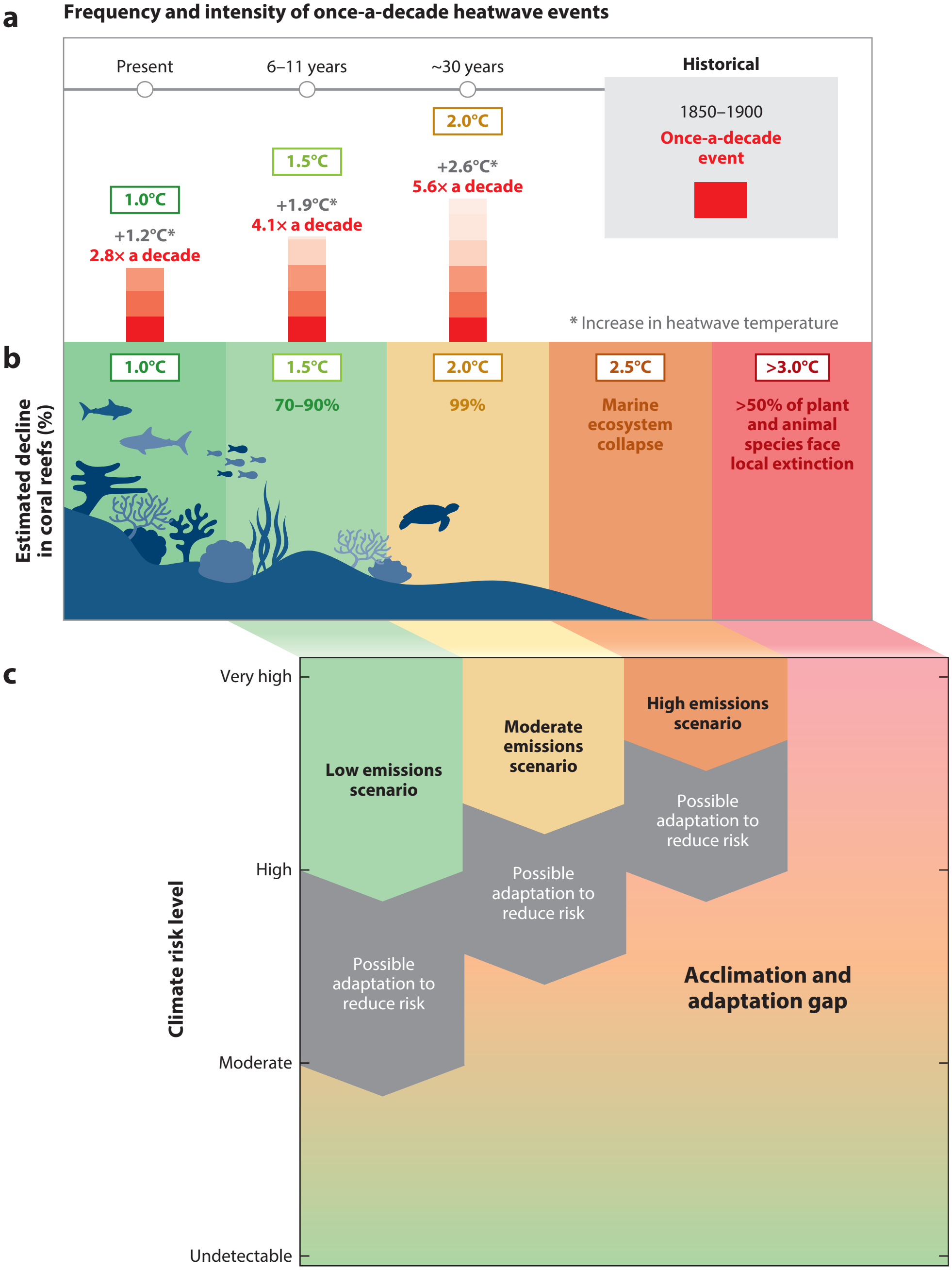

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Figure 1 (*Figure appears on preceding page*)

The impacts of marine heatwaves on coral reefs and the unknown acclimation and adaptation gap. Predictions of the impact of climate change on reefs are dire. (*a*) Previously once-a-decade events, heatwaves on earth are increasing in frequency and magnitude. Increases of +1°C, +1.5°C, and +2°C above present temperatures are projected to result in heatwaves that are +1.2°C, +1.9°C, and +2.6°C warmer and much (2.8–5.6×) more frequent. Data from IPCC, 2021: Summary for Policymakers using mean projections for SSP12.6, SSP5–8.5, and SSP2–4.5. Panel adapted from a public domain diagram by the Guardian. (*b*) If extreme enough, heatwaves on land may translate to marine heatwaves on reefs, resulting in coral bleaching and mortality. Each 0.5° increase (+1°C to >3°C) matters, and coral cover is expected to decline from 70% to 99% if not kept below +2.5°C of warming. (*c*) Higher temperatures are projected to result in mass extinctions. This sets up a gap that organisms, namely scleractinian corals, must overcome via four pathways: move, acclimate, adapt, or die. This gap grows as emissions increase and temperatures become warmer. The likelihood of acclimating or adapting fast enough also shrinks as evolutionary pathways and potentials run out. Figure adapted with permission from Reference 19, which gives permission that publications may be reproduced in whole or in part and in any form for educational or nonprofit services without specific permission from the copyright holder, provided acknowledgment of the source is made.

Thermal performance curves: function that describes the performance of an organism; this performance is a function of temperature, in which increasing temperatures can often lead to decreased function

CT_{max}: temperature of optimal performance of an organism at a maximal temperature; the maximal performance before declining, also described as the upper thermal tolerance limits

Selective breeding: reproductive mixing of gametes in specific combinations

Phenotype: organism's observable or expressed traits, determined by the interaction between the organism's genotype and environmental stressors

also constrained by underlying genetics, shaped by selective pressures, which can be measured using metrics like narrow- or broad-sense heritability (14). Importantly, this trait (tolerance) can be described mathematically using thermal performance curves, in which the performance of an organism is a function of temperature, where optimal performance is maximal thermal tolerance (CT_{max}) (15, 16).

These margins describe underlying, quantifiable mechanisms. Thermal safety margins as a function (i.e., the shape of the curve) then become key parameters to be determined, measured, and used as metrics for activities like conservation or active restoration (i.e., selective breeding). Selective breeding is the process of the directed reproductive mixing of individuals based on a trait of interest (phenotype) to produce offspring with an enhanced value for that trait(s) (17). The mean phenotypic value is determined by both the environment and additive genetic variance, and this information can be used in breeding designs. These include metrics like thermal range, CT_{max}, and temperature averages (e.g., temperatures at the warmest months). Importantly, these metrics can explain a vast majority of organismal responses and may vary by as much as 9.1°C (3). From these, other derived metrics can be calculated, including future warming risk, defined as the difference between the maximum trait temperature and predicted mean temperature of the warmest three months at a specific time of interest (e.g., 2050, 2070, 2100) (9). Taken together, physiological mechanisms can then be linked to environmental conditions. Hence, understanding these patterns will inform the thresholds and drivers of thermal tolerance limits, essential for forecasting species outcomes and for the development of applied conservation action like selecting and breeding corals resilient to warming.

1.3. The Pivotal Role of Acclimation and Adaptation for Coral Reef Futures

> *The rate of increase in fitness of any organism at any time is equal to its genetic variance in fitness at that time.*
>
> —Ronald Fisher, 1930, fundamental theorem of natural selection

Species may contend with environmental pressures via acclimation (plastic shifts, within generations) and/or adaptation (evolved shifts, between generations) through directional changes in populations to more tolerant phenotypes (16). Over geologic and global timescales, evolution via natural selection has favored variability in reef communities (18). Climate scenarios predict a range of temperature trajectories for reef futures (discussed above), which include uncertainties. What is certain is that reef corals likely will not be able to bridge the gaps caused by temperature extremes without some form of acclimation or adaptation (19) (**Figure 1*c***) and will likely change and/or decline even under "low" emission scenarios. For coral reefs to survive as we know them today, a strong and fast bend to the emissions curve, likely paired with rapid adaptation, will be needed. Adaptation can be supported in two general forms, through the protection and conservation of populations of high adaptive potential or, alternatively, through the active restoration of species or populations. One example of active restoration includes the use of selective breeding to generate corals that are more resilient to global warming. In this review, I present multiple pathways by which selective breeding methods can target corals' underlying acclimatory and adaptive potentials. I also outline the key considerations for future directions of research to connect the molecular underpinnings of adaptation to applied conservation outcomes.

1.4. What Is Coral Bleaching, and Why Is Understanding Bleaching Mechanisms Critical for Selective Breeding?

Rapid or extreme changes in environmental conditions, like warming temperatures, impact corals by disrupting the symbiosis between the coral animal (host) and their algae from the family Symbiodiniaceae (symbionts), termed bleaching. Symbiodiniaceae are made up of a diverse group of physiologically distinct dinoflagellate families (20), each with a varying propensity for symbiosis with their host corals; distinct biogeographic patterns *in hospite* and free-living; and tolerances to stress, especially heat tolerance. Hosts may have relatively low-diversity communities, made up of single or few distinct symbiont taxa, or more complex communities of multiple partners, influenced by the mode of symbiont transmission during corals' early life-history stages. This diversity in genetic and physiological backgrounds of the symbionts provides an opportunity for targeting breeding of corals for particular microbial backgrounds, given this is a heritable trait across many coral species (21).

This breakdown typically occurs approximately 3°C above the mean monthly maximum (MMM) sea surface temperature of the reef and if temperatures stay above the threshold for extended periods of time or if combined with other stressors (e.g., high light) (22–24). However, even lower temperatures over extended periods of heat exposure can lead to bleaching from the impairment of the photosynthetic apparatus of Symbiodiniaceae (25). Early experimental tests and field-based observations suggested that the causative agent was the dysregulation of the symbionts, caused by the disruption of different steps along the photosynthetic process (photoinhibition model) and the production of reactive oxygen species (26). This process was thought to lead the host to expel the cells. However, further analyses (27), and a series of elegant experiments (28), have revealed the relative contribution of four bleaching pathways: in situ degradation, expulsion, host-cell detachment, and host-cell death. Importantly, this information reveals more than just the underlying cellular mechanisms of bleaching; it also highlights that multiple levers can be modified to enhance heat tolerance (i.e., high survival under elevated temperatures). The relative contribution of enhanced tolerance for both the coral host and its range of symbiotic partners (combined, the holobiont) may differ for each of those levers. In practical terms, this means that for breeding, we have multiple targets of action and optimization.

Future warming risk: likelihood that a warming trend will increase in magnitude or frequency and lead to impacts on the performance of species, populations, or individuals

Acclimation: within-generation genetic or nongenetic changes that allow individuals, populations, and species content with environmental pressures through increased fitness

Adaptation: between-generation genetic changes that allow individuals, populations, and species content with environmental pressures through increased fitness

Heat tolerance: temperature tolerance of an organism within its upper thermal tolerance range; refers here to high survival under elevated temperatures

Mean monthly maximum (MMM): month of the year with the warmest, on-average, sea-surface temperatures for a particular location

1.4.1. Accelerating rapid acclimation and adaptation with selective breeding.

Theory, numerical modeling, and field studies suggest that rapid evolution is possible. Population genomic studies have revealed that adaptation in the wild can occur rapidly (29, 30) from predation pressure (~10 generations), artificial selection, or experimental evolution for benefits like pesticide resistance [3–10 generations (3)]. Indeed, Haldane's classic peppered moth experiments quantified how strong selection ($S = \sim 0.5$) can elicit rapid adaptive changes in populations. Although adaptive mutations can be very common, genetic drift paired with a fluctuation between very strong and nonadaptive selection can create genetic variation that occurs independently across many populations, resulting in a mosaic of adaptive evolutionary potentials (31). Unsurprisingly, strong selection coupled with unlimited mutation rates (θ) can result in the highest probability of adaptation (32). In light of this information, will underlying adaptive potentials be enough for the current projected warming rates? Given enough time (evolutionary timescales), the occurrence of heat-tolerant corals in very warm locations like the Red Sea (11) suggests the potential for adaptation in corals given enough time. Unfortunately, even if organisms like corals can adapt, adaptation may not be extensive enough due to processes like evolutionary load (i.e., imperfect adaptation), which result in incomplete adaptive responses (sensu 33). This mosaic of interacting processes may therefore impede organisms' ability to benefit from rapid adaptation. This opens the potential for interventions like selective breeding. In corals, this can be readily facilitated given their propensity for mass spawning and the simultaneous production of hundreds of thousands of individuals in a single breeding period event (34).

Assisted gene flow: intentional translocating of individuals within the natural range of a species to facilitate adaptation to anticipated local conditions

Assisted migration: intentional translocation of individual within (assisted gene flow) or outside (assisted colonization) the natural range of a species

1.4.2. Selective breeding using mass coral spawning.

The first records of coral spawning and early documented work in locations like the Caribbean and Indo-Pacific focused largely on spawning slicks (large aggregations of spawned bundles and fertilized and developing eggs). Breakthrough observations of mass coral spawning in locations like the Great Barrier Reef (GBR), led by pioneers in the field like Drs. Carden Wallace and Bette Willis, culminated in a joint Eureka Prize for their team in 1992 (35), and many of those observations are now cataloged in the Indo-Pacific Spawning Database (36). These early days of coral breeding used hermaphroditic spawning and coral reproduction (the release and subsequent separation of eggs/sperm bundles) to disentangle species boundaries and understand the adaptive benefits of inter- and intraspecies hybridization in coral evolution (37, 38). Only later did researchers apply these concepts to conservation and restoration contexts to take advantage of the mass (e.g., large-scale) nature of reproduction of many coral species to maximize conservation potential.

Selective breeding is one potential strategy to maximize applied conservation outcomes through the scalable potential of coral reproduction (39, 40). Breeding for conservation and restoration can take various forms, including assisted gene flow (movement of breeding adults or bred offspring within a species range) and assisted migration (movement between species ranges) (41). The end goal of these methods is to expedite the movement or spread of adaptive phenotypes from one location to another. These methods originated from observations showing that naturally interbreeding populations during range expansion can have distinct genetic impacts on genetic structure. These impacts stem from introgression of genes accompanied by increases in genetic fixation and drift from expanding populations at the range margins. Hence, this gene surfing at the range edge can increase fixation rates of positive or deleterious alleles. Importantly, fixation of specific genes may lead to decreases in fitness due to drift and expansion loads and is often seen at the range expansion edges of populations (42). This can also occur artificially through the directed breeding of different populations across a larger species range. Indeed, genetic mixing based on current or future distributions of climate or traits has been proposed (43, 44). For corals, this has included the movement of heat-tolerant corals within their ranges [GBR (45)] or research into the breeding of low-latitude thermal extremes (e.g., the Persian Gulf, which has average summer temperatures of 35°C) to reefs of more moderate temperatures (41, 46, 47).

Breeding for heat tolerance is feasible in corals because, at least in some species, thermal tolerance is heritable from parents to offspring and appears to persist across multiple life stages, at least to some degree [i.e., larvae and juveniles (48, 49)]. Trait heritability can be calculated by analyzing parent–offspring regressions or sibling relationships (see 21 for worked examples). Both methods have been applied to corals, and the production of offspring is needed for both methods. The mechanics of selective breeding via coral reproduction have been detailed extensively in recent reviews (39, 50). Generally, reproductive modes can be divided into broadcast spawners with the release of combined bundles of eggs and sperm or the release of brooded larvae (21, 51). Briefly, we focus on the use of broadcast spawners, which involves isolating eggs and sperm from individual corals by capturing gametes either in the field with a net or in the lab in isolation containers. After washing, the sperm and eggs can be mixed across a range of phenotypes for specifically selected combinations to achieve offspring within a desired phenotypic range (the full details of coral breeding are given in References 34, 39, 50).

Even with this propensity for mass reproduction through spawning, baseline gene flow between reefs may not be sufficient to rescue reefs affected by mass coral bleaching if the increased frequency and intensity of these events continue (45), suggesting targeted breeding may be a viable restoration option if risks are mitigated and minimized (52). In these targeted breeding experiments, reproductively mixing (crossing) parents from warmer to cooler reefs (of an average differential of ∼2°C) increased survival of larvae with one or both parents from warmer regions (49, 53, 54). This suggests that specific coral populations are locally adapted to higher ocean temperatures and can contribute enhanced thermal tolerance alleles to reefs that are under stress from recurrent periods of above-average ocean temperatures through breeding (55).

Phenotypic plasticity: environmentally induced changes to an organism's phenotype that are nongenetic; changes can be adaptive or have a neutral or negative impact

Phenotypic reaction norms: distributions that describe how values in a trait vary over the potential range of an environmental factor

2. UNDERSTANDING PHENOTYPIC VARIABILITY THROUGH PLASTICITY

2.1. What Are Plastic Responses?

Species, populations, and individuals exhibit a range of phenotypes, from a narrow to a more variable range of responses. Phenotypic plasticity (hereafter, plasticity) can be defined as the adaptive or nonadaptive range of variation in a phenotype in response to environmental clines, not attributable to underlying genetic changes (sensu 56). This underlying natural variation is represented here in corals and their symbionts, quantified via manipulation and experimentation (**Figure 2*a*,*b*, subpanel *i***). Plasticity is critical for organisms because it allows for the maximization of fitness in ever-changing environments (57). For individual traits, plasticity occurs when fitness is enhanced with increased variation in a trait (**Figures 2*b*, subpanel *ii*** and **3*a***) and is recognized by an increase in variation of a fitness-related trait (e.g., survival) relative to an experimental control treatment or a proxy environment in the wild. A well-studied example includes the variation in wing patterns in some butterfly species (58), where adaptive selection can lead to the increased frequency of that phenotype under a range of environmental conditions (**Figure 2*b*, subpanel *ii***), underpinned by causing adaptive changes in the genome (**Figure 2*b*, subpanel *iii***). Concepts like phenotypic reaction norms, which describe how trait values change across varying environmental clines, are especially helpful to describe this variation and how different organismal units (species, populations, individuals) respond differently to their environments. Importantly, this can be described quantitatively, using a range of functions [e.g., linear, quadratic, threshold; see **Figures 2** and **3** (59)]. Reaction norms and trait performance curves are useful when selecting for plastic responses. Operationally, this can include breeding successive generations of individuals with wider-than-average trait responses, theoretically resulting in wider population distributions in that trait over time or more rapid convergence on a fitness-enhancing trait value. This is especially true given that plasticity likely has a heritable genetic component via the generational transmission of mechanisms determining the range of phenotypic plasticity (56, 60). However, maximal plasticity comes at a cost (e.g., energetic costs) and is therefore limited but has selective advantages where more plastic populations evolve more quickly. Aside from the genetic underpinnings of plasticity, there is also a likely understudied epigenetic influence via methylation or histone modification (see 61, 62). It has long been thought that organisms with higher-than-average plasticity should have a greater ability to maintain that plasticity in changing environments, effectively buying time for populations to adapt (61). This may be true to a certain extent, but given that trait plasticity is constrained by underlying genetics, this also sets the limits, and therefore the shape, of the fitness functions (**Figure 3*a***). In the case of thermal tolerance, it would set the limits of thermal performance curves and therefore tolerance levels (63) (bounded as CT_{min} and CT_{max}) but not breadth

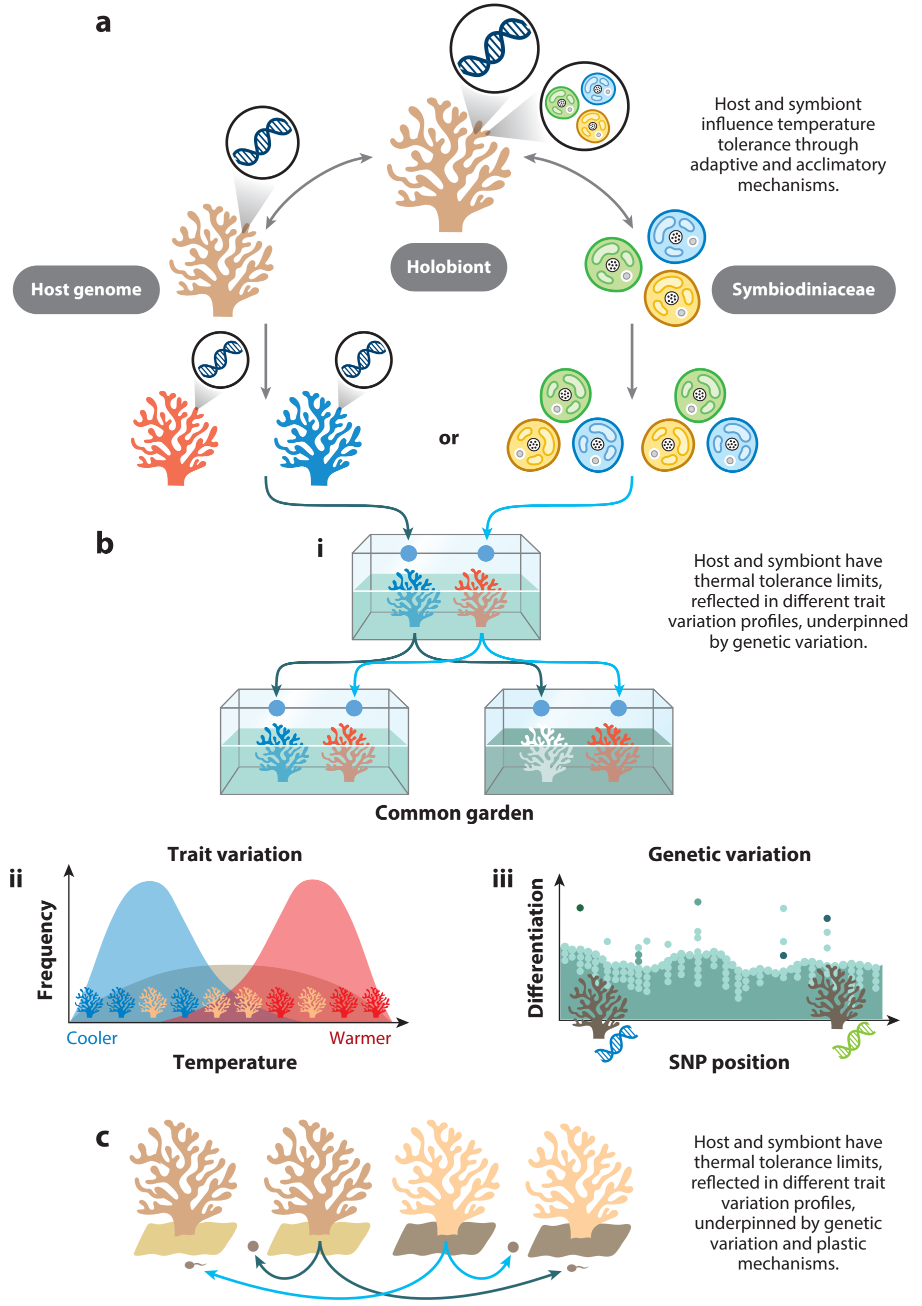

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Figure 2 (*Figure appears on preceding page*)

Leveraging plasticity for the selective breeding of resilient corals. (*a*) The coral holobiont phenotype is made up of the coral host and a range of partners, including dinoflagellate photoautotrophs from the family Symbiodiniaceae. Different taxa of these symbionts themselves display a wide range of phenotypes, represented here in different colors. Various corals and symbiont species and individuals within those species may contend with environmental pressures via acclimation (plastic shifts, within generations) and/or adaptation (evolved shifts, between generations) through directional changes in populations to more tolerant phenotypes. (*b*) Phenotypic variation of either the host or the symbiont can be selected for breeding, which can be best tested in an experimental factorial tank setup. An experimental setting can confirm which individuals have a resilient phenotype under stress (*red coral in dark green tank*) compared with less-resilient individuals (*white coral in dark green tank*). These tests render information about the scope of trait variation across clines, as well as the mechanisms underpinning them [like genomic architecture, shown here using single-nucleotide polymorphisms (SNPs)]. (*c*) Selective breeding can then be performed via directed mixing of eggs and sperm from donor colonies using a range of criteria, including corals from reefs of high and variable temperature and those that have survived disturbance and moved to a suitable wild environment (*yellow or brown*). Figure adapted with permission from Reference 30.

(64). Finally, and importantly, phenotypes can encompass multiple fitness functions across multiple environmental parameters of an organism (multi-trait space envelopes), which together encompass that organism's or population's niche. Taken together, this information is critical to facilitate enhanced heat tolerance through targeted breeding in the wild. It also highlights underutilized knowledge around acclimation and plasticity that will also be helpful to facilitate enhanced heat tolerance (**Figure 2*c***), which I focus on below.

Fitness function: distribution describing the varying level of individuals' fitness relative to the range of an environmental factor

2.2. How Far Can They Go? Investigating the Extent of Thermal Range and Phenotypic Plasticity

There are limits to plastic responses (57, 61, 65). In relation to thermal tolerance, the range of temperatures an organism can withstand is a fundamental biological principle dictated by biochemical processes. This property then scales from individuals' metabolism (e.g., stability of

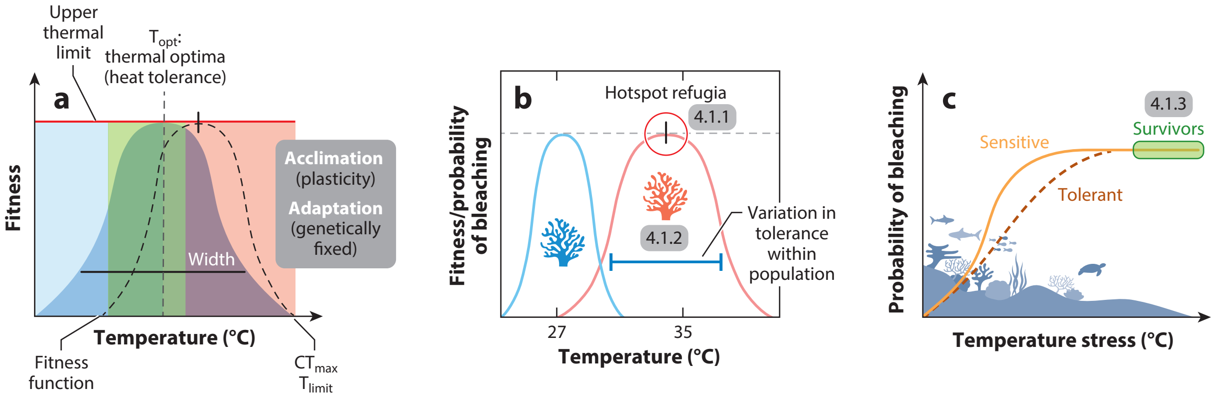

Figure 3

Conceptual illustration of how we can use quantitative functions to facilitate enhanced thermal tolerance through plasticity mechanisms of both coral hosts and their algal symbionts. Quantitative functions like thermal performance curves (*a*) allow us to extract specific parameters like the widths of curves to predict the breadth of possible adaptation in nature for conservation or via restoration practices like selective breeding. To best optimize breeding across a range of traits, and to manage risks associated with these practices, a range of mechanisms should be combined, including targeting individuals that fit three criteria: those sourced from hotspot refugia (4.1.1, genetically fixed adaptation) (*b*), individuals from highly variable reefs resulting in wide phenotypic ranges (4.1.2, plastic acclimation) (*b*), and survivors from disturbed reefs that are therefore likely to again have wide phenotypic ranges (4.1.3, plastic acclimation) (*c*).

Developmental cost theory: theory that describes the constraints to thermal tolerance and predicts a tight linkage between environmental temperature ranges and the range of predicted optimal temperatures of an organism

Evolutionary cap: maximum range limit of a trait at which a population can evolve up to

lipid membranes) up through to ecosystems (66). Hence, each species has a range of temperatures at which it can function optimally, which can be defined quantitatively by the width of the fitness function (**Figure 3*a***). Determining the upper thermal tolerance limits for organisms is essential given the immense pressure climate change–induced warming is putting on ecosystems worldwide. In the context of thermal tolerance, the upper thermal limits are set by the measurable ability of cells to physiologically contend with high temperatures and oxygen transportation. At the population and ecosystem level, this control of temperature sets fundamental limits on several ecological processes, including dispersal, reproduction, and ontogeny (67).

Developmental cost theory predicts a tight linkage between environmental temperature and optimal physiological temperature (68) that, in turn, sets strict biological constraints on heat tolerance. Hence, there may be a limited capacity to constantly evolve upward (e.g., an evolutionary cap), with evidence suggesting that tolerance may not go beyond 39–50°C (69, 70). This is possible through the reconstruction of evolutionary patterns and calculation of adaptive tempos after historical disturbance events, ultimately inferring the limits to tolerance acquisition across the tree of life (plants, ectotherms, endotherms) in aquatic and terrestrial systems. These limits, of course, will depend on local adaptation, reflected in species distributions, and are thought of as developmentally "costly" (63). Although ocean temperature is one, if not the, dominant driver of adaptive genomic variation in the ocean (reviewed in 71), environmental tolerance limits and the upper limits of marine organisms are driven by multiple pressures (e.g., hypoxia tolerance/O_2 supply) (69) as well as parental and developmental influence (63) (**Figure 3*a***). In particular, early life-history stages appear to have lower plasticity relative to adults, with 4.2–7.5°C, on average, needed during development to induce a 1°C increase in tolerance (63). These various competing and constraining influences shape the high variability documented across species in their ability to respond to stress and the speed at which temperature tolerance evolves (70). They also give a strong fundamental theoretical basis to understand how selection can be used in an applied conservation context.

2.3. Link Between Plasticity and Adaptation Potential

In the oceans, the central question is whether species, like corals, can acclimate or adapt fast enough to a warming world. With ocean temperatures increasing (72), both increased thermal acclimation (plasticity) and an evolutionarily conditioned underlying genomic architecture of tolerance (adaptation) should increase fitness and be selected for (73). Therefore, both are potential routes for enhanced thermal tolerance (73). Plasticity can take a somewhat mystical feel, whereas adaptation may appear a more tangible process given selection for underlying genetic changes over generations. Plasticity can be demystified via a more mechanistic definition—that it smooths the quantitative genetics fitness function (phenotype by fitness) (60). To illustrate, one can imagine a single trait with two fitness peaks (see T_{opt} in **Figure 3*a*** for an example of a peak). Increased phenotypic variance (the range of plasticity of the trait) increases the potential to transverse between these two fitness peaks, although increased plasticity tends to accelerate only the initial phases of adaptation by speeding up the search and selection of an optimal genotype (60).

However, it is important to distinguish between mechanisms of genetic adaptation and those of plastic acclimation in traits like heat tolerance. Firstly, in the acquisition of heat tolerance, plastic versus evolved responses are likely independent (16), meaning that the within-generation enhancements of tolerance may not result in increased between-generation enhancements. The contribution of plasticity to adaptation may vary generationally [e.g., decrease from the initial generation (F_0) to later generations (F_n) (74)] and spatially [increase plasticity and adaptation in new environments—the Baldwin effect (75)]. This occurs when the initially plastic response is optimized in the new environment, leading to enhanced fitness in that novel context (76).

Secondly, when examined across a range of taxa and locations, plastic responses alone will be insufficient to keep pace with warming trends, potentially due to the on-average lower levels of plasticity potential relative to adaptation (16, 77). Encouragingly, ancestral plasticity can lead to rapid selection and then adaptation [fewer than 1,000 generations (78)]. A good example of this is coloration in lizards, which can vary their color based on length of occupancy on lava flows (78). Genetic crosses of different-colored lizards revealed that the genetic underpinnings of this trait were attributed to de novo mutations under strong selection for coloration. This ultimately led to rapid phenotypic changes given the short generation time for these lizards (1–3 years). Generally, genetic adaptation follows the potential for plasticity (78). The role that evolved and/or plastic adaptive responses have in helping species escape extinction is (*a*) interactive; (*b*) dependent on selection; and (*c*) influenced by the rate, variance, and autocorrection of environmental change (56). Plasticity may also accelerate [Baldwin effect (74)] or slow [Bogert effect (52, 56)] adaptation and itself may be adaptive [i.e., have an underlying genetic component (56)]. Interestingly, the relative contribution of heritable variation will likely have a stronger effect if plasticity is low (63), and if both mechanisms are low, a more rapid pathway to extinction is likely. Therefore, both acclimatory and adaptive mechanisms are necessary given their interactive effect, and their interplay in driving thermal tolerance is of critical interest for predicting future species longevity.

Linking adaptive potential to phenotype, plasticity of environmental tolerance, and underlying genetics is a central theme of evolutionary research. Tractable systems like coloration in lizards have become a key model (78). Genetic crosses of different-colored lizards have revealed the genetic underpinnings of adaptive coloration (79) from genetic differences attributed to de novo mutations on two genes under strong selection ($S = 0.007$–0.008) (78). Other systems, like corals, have also received significant attention, especially for understanding the underpinnings of genetic thermal adaptation, including variation between individuals and species in bleaching and mortality responses (sensitive versus tolerant; **Figure 3*b***). Studies have also mapped seascape variability (80) and heritability (48, 49) and quantified the mechanisms driving them at both the genetic and transcriptomic level (49, 81, 82). Given that ocean temperatures are increasing (72) on reefs that already exhibit high daily temperature variability, high thermal plasticity should be adaptive (62, 83). From a breeding perspective, plasticity has received relatively less empirical scrutiny in corals. Indeed, corals are highly plastic in their responses across a range of critical traits, including temperature changes, coral metabolism, symbiont photosynthetic rates, gene expression, and calcification (84). Coral tolerance to temperature ranges includes both lower and upper thermal limits that cause bleaching (85–87). The lack of empirical study and manipulation is surprising given the importance of the breadth and variation in plasticity in corals. The importance of plasticity for coral survival is also underscored by modeling results showing that breadth of tolerance was the most important parameter for predicating their long-term survival (88). Selective breeding therefore should take advantage of the underlying phenotypic plasticity inherent in corals to facilitate enhanced thermal tolerance (52) (**Figure 3*c***).

3. LEVERAGING PLASTICITY IN CORALS FOR SELECTIVE BREEDING

3.1. Antagonistic, Synergistic, or Cumulative?

High plasticity increases the speed of and potential for adaptation (57). Within the conservation literature, successful rescue of populations has occurred when the abundance of individuals is paired with the widening of fitness distributions, reflected in reaction norms (89). This knowledge has direct implications for the feasibility of selective breeding in corals, where high and increasing plasticity in both the host and the symbiont should be leveraged. The initial evidence, summarized below, suggests that a widening, not shifting, of fitness functions (**Figure 3*a*,*c***) is beneficial, is likely occurring, and may be a persistent feature of heat tolerance acquisition. Evolutionary constraints of a widening, versus shifting, of tolerance must also be considered. The literature on thermal niche evolution of functional traits suggests that higher fitness is achieved with a narrower envelope and higher thermal optimum, but that this requires greater nutrient requirements (90). Therefore, a more generalist physiology may be easier to maintain during high-temperature stress, providing a reason for its pervasiveness in both the coral and dinoflagellate symbiont systems. Finally, using natural, underlying plasticity also provides an insurance against further changes in future environments because individuals or populations should be better able to maintain higher fitness across a greater breadth of environments (91). How long this buffer can hold out will depend on the thermal safety margins, the cumulative impact of multiple stressors, and the range of change in the environment. How might these theories be operationalized?

3.2. Accounting for Plasticity in Both Partners

Variation in phenotypic plasticity is widespread across scleractinian corals, which is demonstrated mainly by their variable growth forms but also in other traits, like their responses to environmental stimuli. Of particular interest is the wide range of phenotypic responses of different species in relation to heat stress. This is often described as the "winners and losers" of marine heatwaves, which may help to explain the highly patchy distribution of temperature tolerances across individual genotypes and populations observed in many species across the globe (24, 92, 93). Mechanistically, variability across coral taxa may be due to differences in mass transfer rates across growth forms that influence the ability to eliminate radical oxygen species produced during stress. For example, growth forms with higher volume-to-surface-area ratios may reduce heat exposure through thicker tissue, leading to a greater shading of symbiont cells and allowing for the maintenance of photosynthesis (24). Investigation has also revealed substantial individual genotypic variation (94–96), which further contributes to explaining these broader patterns. Whatever the mechanism(s) at play (62), this variation is critical to selective breeding, as it may reflect the underlying genetic diversity. Increased genetic diversity provides the needed variation on which natural selection may act. This in turn increases adaptive potentials, through which either natural or artificial mechanisms, like breeding, may act.

3.3. Plasticity of the Host

Breeding has focused mainly on targeting species or individuals at the extreme end of the phenotypic range for thermal tolerance, i.e., those that are highly tolerant to heat—the "survivors" (39, 47, 49, 54, 55, 81, 97, 98, 99). Breeding has resulted in initial gains in heat tolerance, including boosts of 2.6–3.08°C (mean 2.9°C ± 0.08) above the expected summertime maximum temperatures for specific reef locations (39, 54, 55). Importantly, there have been calls for a more nuanced approach to selection that includes other critical fitness-related traits, like growth (100, 101). Determining the key traits or combination of traits to focus on for breeding is essential. This is because an increase in the hard upper thermal limit of corals likely will not be as helpful as initially thought, and instead, an emphasis on widening the phenotypic scope may be best. Firstly, it is unlikely that specific individuals will be the best performers in every transplanted environment (see 95). Furthermore, the phenotypic margins (i.e., the extremes or edges) of thermal limits often hold the lowest potential for evolutionary rescue (74), because tolerance may initially peak in the middle of a species range before decreasing asymmetrically outward (e.g., by 25%), likely due to hitting the hard upper limits of tolerance dictated by the physiological constraints discussed in Section 1.2 (e.g., protein denaturation) (74).

Given this information, facilitating enhanced heat tolerance via targeted breeding of plasticity mechanisms should be examined. This would include a greater emphasis on widening fitness functions, including selecting individuals with wider-than-average fitness functions, instead of only increasing the upper limits, when assessing selective breeding. This may be especially true for corals returned to the wild after breeding. After being selectively bred in the laboratory using a crossing design for heat tolerance, coral offspring were returned to the ocean to assess their trait performance in the wild (i.e., outside of the selective regime of a laboratory-based setting). These results demonstrated that selectively bred corals showed no reduced fitness in growth or survival during non-warming years, relative to purebred corals native to that specific reef. This work also showed that breeding for specific crosses could widen rather than shift the mean fitness function and therefore environmental tolerance (100).

Extended genotype: increased optimal range of a trait in a host organism due to presence of certain symbiotic partnerships owing to addition of those symbionts' genetic material

3.4. Symbiont Plasticity

The interplay between coral metabolism and Symbiodiniaceae photosynthesis fuels the physiology of the coral holobiont [see the concept of the extended genotype (20, 102)]. This interdependence is evidenced by the obligate nature of the symbiosis across coral taxa (103). Dynamic processes regulate the symbiont community composition inside corals, including recognition, engulfment, proliferation, and dynamic stability (reviewed in 104). These symbiont communities, regulated through host mechanisms, are heritable (105) and likely driven by ligand proteins of both partners (reviewed in 104). In particular, the initial gateway—recognition—is one of the underlying mechanistic limitations for symbiont infection driving specificity.

Patterns in specificity are evident across distinct host–symbiont pairings across corals (106), underscoring the finely tuned and dynamic nature of the symbiosis (107). The diversity of Symbiodiniaceae taxa in the Indo-Pacific is generally high (20), with many taxa present at low abundances (108, 109) and some evidence for single-taxa domination, especially in the Caribbean (110) (but see 111 for full discussion). Stable symbiosis with a complex community is possible under conditions of resource partitioning (112). Therefore, the total community of symbionts makes up a symbiont phenotype, which goes on to influence the host phenotype and can therefore be selected, and manipulated, via breeding (113). For example, if an ideal symbiont phenotype is known (rescue genotype, *sensu* 113)—for instance, one that is stress or heat tolerant—that information can be used for targeted breeding. This is achieved by calculating the difference between the phenotypic mean of the offspring and the current phenotypic mean of the breeding adults to determine R, the response to selection, needed to achieve a desired phenotype after breeding. Simulations show breeding interventions targeted at selecting tolerant symbiont phenotypes are achievable across multiple coral species after only relatively few generations (see figure 2 in 113).

Importantly, this underlying, natural variation in symbiont phenotypes represents the opportunity in which the holobiont phenotype can be enhanced, outlined numerically using quantitative genetic models (113). Phenotypic changes under experimental settings show the potential for manipulating hosts and symbionts simultaneously (49). For example, tightly linked experiments between hosts and symbionts manipulated at high and low temperatures also demonstrate that host phenotypic changes were followed by corresponding phenotypic changes in the symbionts (114). Hence, plasticity in the composition of the symbiont community, not just in the symbiont phenotypes themselves (115), determines the holobiont response to environmental stress. This response is underpinned by the vast diversity of symbionts that can be found within corals, which can span across at least seven described and phenotypically distinct genera from the family Symbiodiniaceae, including *Cladocopium*, *Durusdinium*, *Symbiodinium*, and *Breviolum* (20). Representatives from some or all of these taxa can be found simultaneously in the tissues of different coral species. Plasticity in the trait of symbiont community therefore manifests in the wild, when these communities undergo dynamic regulation of diversity to modify community abundances from the reservoir of Symbiodiniaceae within their tissues (shuffling), and then potentially shuffle back to similar communities pre-bleaching (116). The replacement of community members (switching) may also occur and parallels other systems [e.g., plants that eject microbes through the forceful, host-directed, wave expansion of hair cells (117)]. Shuffling, in particular, contributes to rapid acclimation and adaptation (118).

Given their mathematically tractable properties, the quantification of the symbiont community becomes possible to parameterize, including how various aspects of tolerance can be manipulated. Interestingly, the breadth of symbiont thermal tolerance appears to be the critical parameter in determining long-term survival of coral reefs, generally, in a modeling context (88, 118). If applied to the quantification of plasticity of individual taxa, selection influencing the width (again, not directionality) of the fitness function was predicted as critical to enhancement (115). So, as discussed theoretically above, the natural capacity for tolerance via plasticity will reach a limit, as shown experimentally in the host coral. Specifically, although the onset of the shuffling response is rapid (multiple seasons or 5–10 years), its capacity to ameliorate heat stress will likely run out by 2040, when all "possible" heat-tolerant symbionts are projected to dominate in abundance (118). Moreover, complete transitions to heat-tolerant communities in corals are unlikely (see 119) due to the heritable constraints on symbiont communities (21). This highlights the possible use, but also limits, for plasticity in selective breeding. Looking forward, these symbiont manipulations (as described above) can also be used to amplify tolerance past what is possible if focusing only on the coral host.

4. USING PLASTICITY FOR BREEDING

The patterns discussed above in phenotypic plasticity in host and symbiont tolerance have led researchers to search for populations of corals that naturally exhibit a wide range of tolerances to temperatures, as a proxy for the ability to adapt rapidly (see 120–122). Recent reviews (34, 39, 50) have set out the more technical aspects and critical husbandry steps in the process of selectively breeding corals, and the reader is referred to those texts for details. Further important technical aspects include the limitations or unknown information around coral breeding and rearing, especially for gonochoristic corals and those with unknown reproductive timings (51). There is also a need to expand methods to new species, perform in-depth risk assessments of trait trade-offs, and characterize the underlying mechanisms of heat tolerance. In the short term, three lines of information concerning plasticity can be used for breeding as criteria to locate select resilient coral genotypes with the ability to survive warming and simultaneously transmit heat tolerance to future generations. In this way, the thermal history of adult coral can be used to build predictive models to guide conservation management or intervention science using a "climate predictive strategy" outlook (123). This strategy can be further operationalized to finding resilient coral genotypes once criteria are chosen (55). Other criteria for selection have been reviewed elsewhere, including proxy measures like rapid heat stress tests (124). Therefore, the targeted breeding of genetic backgrounds associated with plasticity (plasticity alleles) should be incorporated into coral selective breeding moving forward. This highlights that where possible, experimental evidence should bridge the gap with theoretical genetics in design.

Various experiments can be performed to examine the extent of host and symbiont plasticity. In host corals, this is readily tested via crosses of parental corals from distinct ends of a physiological trait's spectrum of phenotypes (74) (**Figure 2**). Given that most impacts from climate change stem from warming, the predominant traits of interest for breeding have been survival under warming stress, bleaching tolerance (measured as a change in coloration or symbiont cell density), and photosynthetic health of the symbiont. Accompanying data include photographs that can track coral color, growth through skeletal deposition, survival, or tissue necrosis. In the symbiont partners in which sexual reproduction remains somewhat elusive (20), asexual propagation of cell lines under selection in the laboratory over multiple generations is an ideal setting for studies of plasticity and adaptation (115). As with the host corals, various stressors (often heat or nutrients) can be applied to replicate cell lines of symbiont cells and then compare those to cell lines grown under control ambient conditions. Various traits can be measured, including photosynthetic health, pigment content, cell division rate, host cell infectivity, and a range of other metabolic parameters.

Climate refugia: habitat locations that will escape the future pressures of climate change due to biophysical characteristics and may house individuals or populations with adaptive genotypes for those specific conditions of the organisms present; here we focus on locations with adaptive genotypes

Hotspots: habitat locations that are already similar to future projected pressures from climate change due to their biophysical characteristics; have likely resulted in adaptive genotypes for those specific conditions of the organisms present

4.1. Selecting Resilient Broodstock

It is now clear that the thermal history of corals shapes their future responses as being more sensitive or tolerant to predicted heatwave conditions (125). Adult corals used for breeding, termed broodstock, should be selected from specific refugia reefs that include short-term exposure (acclimation, i.e., a post-bleaching event) and local conditions with long-term high temperature variability (adaptation of populations) (122). Indeed, the term climate refugia has been used to describe locations that will escape warming largely due to local oceanography (126) or locations that already demonstrate a greater likelihood of adaptation to future conditions, exemplified by the back reefs of American Samoa (83). The latter type of climate refugia are ideal locations for broodstock selection, given that these refugia encompass signatures of both acclimation and adaptation to warmer temperatures. This corresponds to theory predicting that in stressful environments, the variance—not only the mean effect—should increase resilience (127). Hence, stress begets plasticity. The importance of finding the optimal broodstock is outlined as one of the "10 Golden Rules for reef restoration" (119) to facilitate conservation and restoration action including adaptation (8, 128). This information is critical because, absent genetic information, trait and habitat diversity are likely to be useful proxies (129). In summary, various lines of evidence now exist in our understanding of what makes some corals more resilient to stress compared to others, including (*a*) long-term exposure to high temperatures (Persian Gulf), (*b*) exposure to more variable compared to more stable thermal environments (55, 122, 130–133), and (*c*) past exposure to heat stress (119, 134, 135). These are outlined individually below. Importantly, each can be used in a targeted breeding approach.

4.1.1. Long-term exposure to high temperatures.

Corals are generally thought to exist close to their thermal optima (T_{opt}) (**Figure 3*a***), generally approximately 1°C above their summer MMM (136), with the exact value depending on local adaptation, driven by the evolutionary history of that region. The search for hardy corals and the survivors that can exist well above MMM during mass-bleaching events is being explored (97, 121, 137), and experimental validation of these colonies is underway (54). For example, corals from the Red Sea are thought to be some of the most heat tolerant given their thermal history and responses to warming (hotspots concept), where metabolism can be maintained to potentially 8–15 degree heating weeks (136). This range corresponds to temperatures around 31.9–33°C (138). This may equate to lower MMM in other locations, like the GBR [26.7°C (55)] or Palau (139). Selecting corals from these hotspot reefs for breeding should render resilient broodstock but would be the equivalent to targeting the extreme end of the spectrum in terms of phenotypic tolerance (**Figure 3*a*,*b***).

4.1.2. Exposure to more variable thermal environments.

Aside from high temperatures, temperature variability, and in particular daily variability, has also created pockets of heat tolerance. This includes the GBR (daily range conditions of ~0.51°C) (55), Palau (e.g., pockets with 85% higher mean diurnal range of ~0.59°C) (139), and other locations globally (0.5–5°C) (131).

As discussed above, these patterns should be unsurprising given evidence that environmental variation leads to increased plasticity (56), thereby facilitating adaptation. The evidence from rapidly deteriorating environments leading to faster evolution supports this, compared to stable environments (140), including evidence of changing breeding patterns in birds and mammals in response to increased environmental variability (56). These highly variable reefs (locations within Palau, American Samoa, and GBR) represent environmental conditions that are ideal to target individuals with variable (wide) phenotypic responses (**Figure 3*b*,*c***), and corals selected there will more likely exhibit high plasticity. Aside from selecting broodstock directly from the wild, another option would be to subject adults or offspring to ecologically relevant thermal variation to select for increased plasticity (39, 40). As discussed above, it is not completely clear what mechanism(s) these highly variable conditions create (e.g., physiological underpinnings that make them more resilient to stress). These environments may select for corals with gene expression mechanisms primed for heat (81); those that are highly flexible; or those that have adaptively rapid, robust, and reactive responses (frontloading) when stress is applied (82).

4.1.3. Past exposure to heat stress.

Reefs should also be selected considering those that have survived disturbance and past exposure to stress (39, 141). As suggested above, this not only must include selection for coral genotypes of surviving corals but also should select for their communities of symbionts as well as a phenotype (**Figure 3*b*,*c***). Global meta-analyses using remote sensing have revealed that bleaching-resistant reefs are often associated with temperature metrics like high variability in seawater temperatures (130) or specific signatures of symbiont communities (119, 135). This again suggests the importance of temperature variability (Section 4.1.2). The ability to shuffle or switch symbionts is essential (116) for maintaining those changes under repeated bouts of stress (142). Environmental data related to stress, combined with genetic (gene flow) and ecological processes (dispersal) (45, 143), will help to resolve the underlying patterns in survival across large reef expanses to identify these locations. Indeed, studies are already describing the upper thermal limits of “winning” and “surviving” corals and where protective heat tolerance mechanisms “run out.” For corals, this may occur at +4.4°C (141) or up to +7°C, at temperatures as high as 37°C (133).

4.2. Selecting the Receiving Environment

A long-standing worry in conservation and restoration is the impact of the interaction between genetics and the environment [G × E (41)]. This interaction manifests when the “new” genotypes exhibit unexpected phenotypes in their new environment. These new genotypes are produced either from the directed movement of collected individuals from the wild or from breeding of preadapted genotypes. Many studies have attempted to quantify the impact of G × E but have done so in experimental plots that are, by design, as homogeneous as possible (44), potentially underestimating G × E impacts. Recent meta-analysis suggests an overestimation of impacts of trait trade-offs, which are a manifestation of G × E impacts (144). Given the highly heterologous environments of reefs, critical information is needed to better understand how selectively bred phenotypes perform in novel environments (100). Importantly, we can look to natural systems to understand this, for example, the large impact that parental population history has on the success of population mixing during range expansions (42).

In the coral context, the receiving environment is critical. If climate change emissions are not addressed, the receiving environment will not be adequate for these individuals if thermal tolerance limits are exceeded (limits discussed above). Next, the biophysical considerations of the environment are essential, including the spacing of reefs and connectivity (reviewed in 145). The amplitude of climate change variability is also important, where the selective advantage of bred corals diminishes in cold years, and the timing of arrival and frequency of those cold years impact the retention of heat-tolerant alleles in the receiving populations (52). This is likely caused by changes in fluctuating selection driven by differences in climate amplitude and predictability (146). Finally, gene flow, selection, and demographics are all critical to population persistence (147) and must be quantified and modeled within any scenario of selectively bred release into a particular environment. Systems that are particularly tractable to experimentation and molecular studies of evolution (i.e., model systems) are essential to answering these questions. These may include organisms with short life cycles and amenability to laboratory rearing, manipulation, and molecular techniques. Indeed, the importance of the receiving environment can be highlighted in classic evolutionary model systems like *Heliconius* butterflies, which demonstrate the interplay between pressure exerted by admixture and divergence driven by selection and isolation, underscoring that divergence does not necessarily occur in a linear manner (148).

In summary, selective breeding holds high potential for understanding both fundamental information about the potential for acclimation and adaptation in marine species and can be used as an applied conservation tool. However, the unpredictability of evolutionary change poses a challenge. Climate change will also bring instability in weather, likely increasing the cumulative impact of other stressors with warming, including changes in salinity or nutrient inputs. Our current challenge is to develop predictably heat-tolerant corals that can withstand a range of other stressors simultaneously. A focus on leveraging phenotypic plasticity at the same time as adaptive potentials (i.e., genetic main effects) is the paradigm shift needed now. Ultimately, the use of such methods must be balanced between investing in resources that use adaptive principles to conserve and other strategic resourcing around restoration (149). As an applied tool, breeding will likely only buy limited time. Emphasis should thus be on mitigating the impacts of warming. Indeed, this is the difference between proactive (conservation) versus reactive (restoration) approaches (4). Eventually, corals' natural adaptive capacity will run out, no matter the resiliency of the source population selected, underscoring the need for rapid action on climate change.

SUMMARY POINTS

1. Given the extreme trajectory of warming the oceans are on, coral reefs as we know them today are unlikely to persist without significant acclimation or adaptation.
2. Facilitating enhanced thermal tolerance via targeted breeding of plasticity mechanisms is underutilized. Breeding from the perspective of heat-tolerance plasticity, compared to maximal heat tolerance, has received comparatively less attention.
3. Breeding with a focus on the underlying symbiont community compared to the genetics of the host is also lacking. Both plasticity and breeding for the symbiont community should be undertaken.
4. Various methods have revealed that high monthly mean temperatures, high daily variability, and past signatures of bleaching are all predictive of corals with high tolerance and, importantly, an enhanced ability to transfer that tolerance. This information must be used to find resilient, highly plastic reefs for breeding of the host or symbionts and to identify vulnerable populations, assisting managers in protecting "high-value" reefs.
5. Given the unpredictability of future climates, selective breeding must use genetic main effects and phenotypic plasticity to produce corals able to withstand cumulative stressors.

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