

Building coral reef resilience through assisted evolution

Madeleine J. H. van Oppen^{a,1}, James K. Oliver^a, Hollie M. Putnam^b, and Ruth D. Gates^b

^aAustralian Institute of Marine Science, Townsville MC, QLD 4810, Australia; and ^bHawaii Institute of Marine Biology, Kaneohe, HI 96744

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The genetic enhancement of wild animals and plants for characteristics that benefit human populations has been practiced for thousands of years, resulting in impressive improvements in commercially valuable species. Despite these benefits, genetic manipulations are rarely considered for noncommercial purposes, such as conservation and restoration initiatives. Over the last century, humans have driven global climate change through industrialization and the release of increasing amounts of CO₂, resulting in shifts in ocean temperature, ocean chemistry, and sea level, as well as increasing frequency of storms, all of which can profoundly impact marine ecosystems. Coral reefs are highly diverse ecosystems that have suffered massive declines in health and abundance as a result of these and other direct anthropogenic disturbances. There is great concern that the high rates, magnitudes, and complexity of environmental change are overwhelming the intrinsic capacity of corals to adapt and survive. Although it is important to address the root causes of changing climate, it is also prudent to explore the potential to augment the capacity of reef organisms to tolerate stress and to facilitate recovery after disturbances. Here, we review the risks and benefits of the improvement of natural and commercial stocks in noncoral reef systems and advocate a series of experiments to determine the feasibility of developing coral stocks with enhanced stress tolerance through the acceleration of naturally occurring processes, an approach known as (human)-assisted evolution, while at the same time initiating a public dialogue on the risks and benefits of this approach.

adaptation | climate change | microbial symbionts | selective breeding | transgenerational acclimatization

Contemporary coral reefs worldwide have suffered and continue to face large declines in coral cover and shifts in community composition as a consequence of global and local disturbance regimes that include warmer than usual summer sea surface temperatures, cyclones, crown-of-thorn starfish assaults, destructive fishing, and terrestrial run-off (1, 2). A growing body of experimental data further suggests that the negative effects of elevated temperature may be compounded by increasing ocean acidification (3, 4). This deterioration raises concern regarding the resilience of coral reefs and their ability to retain their vital role as engineers of structures that support important ecosystem services. Recent scientific reviews and commentary on the future of reefs contend that corals may not be able to adapt in time to avoid major changes, or even loss of reef systems at a global scale. Although it is critical to increase efforts to reduce these threats, the possibility that these efforts might be too little and/or too late provides a clear need to consider alternative strategies that involve more direct intervention. One approach to direct mitigation that has attracted some controversial exchanges is environmental engineering (5) to increase atmospheric reflectivity using aerosols or to increase oceanic carbon assimilation by fertilizing the oceans. Another approach, which we explore here, is to enhance the ability of key reef organisms to tolerate stressful environments and to accelerate recovery after acute impacts. In this context,

terrestrial restoration ecology provides examples relevant to reef scientists and managers in the use of genetically resilient or modified stocks or species that can restore or maintain key ecosystem attributes and processes (6). However, this approach raises important theoretical and ethical questions regarding the feasibility and desirability of creating anthropogenically enhanced systems. Introduction of genetically superior corals may enable reefs to persist in the future, but there is a risk of unanticipated and unintended ecological consequences. Against the backdrop of the serious decline of coral reefs worldwide, we assert that there is an urgent need for research to evaluate the potential for developing resilient varieties of key reef organisms, an assessment of the ecological risks associated with assisted evolution, and the initiation of a public dialogue around the risks and benefits of such interventions. The application of assisted evolution approaches to coral reefs is discussed here from the perspective of our growing understanding of evolutionary mechanisms and knowledge gleaned from breeding programs for commercial and noncommercial stocks.

Fears and Facts

The genetic manipulation of biota through the translocation of species and populations and the release of captive bred or genetically modified (GM) organisms into the wild is sometimes criticized because of its potential to benefit some facets of an ecosystem,

while simultaneously harming others. A major concern is that artificially enhanced organisms might possess novel traits that give them a competitive advantage over the native population. From this perspective, artificially enhanced organisms are sometimes viewed as exotics (7), which can be invasive. For instance, of the 44 freshwater fish species that have been introduced into South Africa, 37% are considered invasive (8). Alternatively, exotics may hybridize with native species or other introduced species to produce invasive hybrids. Interspecific hybridization commonly facilitates invasiveness in plants (9). For example, invasive cordgrass species in the genus *Spartina* all originate from hybridization among introduced *Spartina* species (10). In this context, it is important to note that the approaches discussed for reef corals later in this Perspective article are restricted to explanting manipulated coral stock within the distribution range of its wild conspecifics, and only species that are sympatric in nature will be used for hybridization.

Other concerns are that translocated plants and animals may carry pathogens or parasites

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¹To whom correspondence should be addressed. Email: m.vanoppen@aims.gov.au.

affecting the health of the native populations, or that they may cause a change in genetic composition or population structure (i.e., genetic pollution) of native organisms, a loss of genetic diversity, or a break-down of coadapted gene complexes (11). These concerns have been debated in relation to commercially important species (11) as well as plants and animals whose phenotypes have been altered by the insertion of foreign genetic material [i.e., genetically engineered (GE) organisms or genetically modified organisms (GMOs)] (7, 12, 13). Although the development of GMO corals might be contemplated in extremis at a future time, we advocate less drastic approaches (discussed in *Assisted Evolution Approaches to Build Coral Reef Resilience*) that use widely accepted techniques to accelerate naturally occurring evolutionary processes (e.g., random mutations, natural selection, acclimatization, and changes in microbial symbiont communities). Nevertheless, there still is a possibility of adverse outcomes (11). Our proposal is, therefore, to develop a biological tool box for enhancing coral resilience and stress tolerance in step with an ecological risk–benefit analysis, with implementation being dependent on the outcomes of this analysis, the health status of coral reefs in years to come, and the likelihood of natural recovery of severely damaged reefs over ecological time scales. Therefore, there is an urgent need for an informed discussion among environmental managers, policy makers, scientists, and the general public on the value, feasibility, and risk associated with assisted evolution in corals. Well-established protocols exist for the risk assessment and approval process for the use of GMOs (7), which can guide this process for coral reefs.

Acclimatization, Adaptation, and Evolution

The response of organisms to environmental change can occur through both genetic (i.e., adaptation) and nongenetic (i.e., acclimatization) processes (Fig. 1). Genetic adaptation is defined as a change in the phenotype from one generation to the next through natural selection and involves a genetic change in the form of allele frequency changes between generations. It is sometimes referred to as hard inheritance. Acclimatization is a phenotypic response to variation in the natural environment that alters performance and possibly enhances fitness but does not involve a genetic change. Until recently, acclimatization has been considered to occur only within the life span of an organism providing no trait evolution from one generation to the next. It is, however, becoming evident that some environmentally induced nongenetic changes are heritable (14). This process is called transgenerational acclimatization or soft or nongenetic inheritance (15) and occurs through epigenetic processes. Epigenetics *sensu stricto* refers to the external modification of genes (without a change in the actual gene sequence) that causes a change in expression level of those genes. Well-documented epigenetic mechanisms are DNA methylation, histone tail modification, chromatin remodeling, and biogenesis of small noncoding RNAs (16). Some authors extend the definition of epigenetics to include the community of microbes associated with an organism (e.g., bacteria, algal endosymbionts, and viruses) (17) because microbial symbionts are able to influence the host phenotype. Specifically, a change in community composition can cause a change in the host phenotype, and, in some organisms, the microbes are passed on from one generation to the next.

We accept this extension because microbial symbionts play key roles in stress tolerance and health in many organisms (18) and in corals specifically (19–22). Although genetic adaptation and epigenetic acclimatization contribute to an organism’s response, human-assisted acceleration of these mechanisms has historically been targeted to commercially relevant species and applications.

Genetic and Epigenetic Modification of Stock for Commercial Applications

Natural mechanisms of adaptation can be harnessed in various ways to produce organisms with characteristics that benefit human populations. Humans have been improving wild animal and plants for thousands of years through selection of superior phenotypes resulting from intra- or interspecific crosses: i.e., selective breeding (23, 24). With a growing understanding of genetics over the past century, breeding methods have become more sophisticated, and advances in biotechnology have led to the creation of novel alleles and traits that do not exist in natural populations; these innovations have been achieved through mutagenesis or the insertion of foreign genetic material (i.e., the development of GMOs). The selective breeding and genetic modification of plants and animals to improve traits for commercial purposes is now commonplace (25, 26). Targeted traits include nutrient content, environmental stress tolerance, and herbicide/pest resistance in crops (27), growth rate and wood quality in forest trees (28), and meat yield in aquaculture species or farm animals (29, 30). Positive side effects of selection for a certain trait are occasionally observed. For instance, Sydney rock oysters artificially selected for faster growth exhibit a smaller reduction in shell growth under elevated pCO₂ conditions compared with wild populations (31). Conversely, trait evolution may be constrained due to tradeoffs between competing functions (32), and a lack of trait improvement despite artificial selection has been recorded in various breeding programs (33, 34). In the Nile tilapia, for example, two rounds of mass selection for growth did not result in a significant increase in growth, which was attributed to loss of genetic diversity due to inbreeding or drift (35).

More recently, epigenetic modifications have been used to generate commercially advantageous phenotypic effects through controlled stress exposure. Some of these epigenetic marks are mitotically stable (i.e., within a sexual generation) and therefore relevant in terms of sustained changes in perennial and strictly clonally reproducing species that can pass on these modifications to new ramets produced over extended

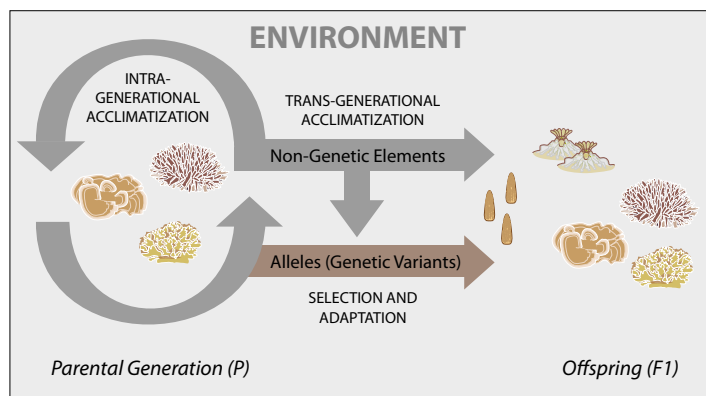


Fig. 1. Diagram showing within-generation acclimatization through nongenetic processes, as well as transgenerational nongenetic and genetic inheritance.

periods of time. For instance, exposure to mild stress conditions is known to lead to an increase in tolerance to more severe stress later in life in a range of plant species (i.e., hardening or priming) (36, 37). Vernalization, where plants require a prolonged period of exposure to cold to initiate the development of reproductive organs, is another example of a mitotically stable, environmentally induced epigenetic change (38). Exposing plants to mild stress can in some instances result in enhanced stress tolerance beyond the sexual generation that was exposed to the stress event (39). Epigenetic mechanisms also provide one possible explanation for the substantial amount of heritable variation that cannot be explained by genomic DNA sequence variation alone (24). Further, natural variation in DNA methylation and small RNAs among individuals of several plant species has been documented, and such variants can be stable for hundreds of years (24). As a consequence, the notion of exploiting epigenetic mechanisms for stock improvement is gaining traction (24, 39).

A growing body of evidence supports a critical role for microbes in the health and functioning of most if not all eukaryotic organisms. Well-studied examples are the human gut microbiome, the insect gut microbiome, *Vibrio fisheri* in the bobtail squid's light organ, nitrogen-fixing bacteria in legumes, and mycorrhizal fungi that enhance nutrient uptake in plants (18, 40, 41). A disruption of or change in the composition of these microbial communities can have far-reaching effects on the host phenotype. Recent research has shown that inoculation of plants with microbes from other species can increase their stress tolerance and growth dramatically and that the modification of microbial communities has a range of commercial applications (42, 43). For instance, salt, drought, and cold tolerance of two commercial rice varieties is enhanced by colonizing them with fungal endophytes isolated from other plant species (44). A range of soil bacteria, in particular plant growth-promoting rhizobacteria (PGPR), are also known to improve plant growth under stressful conditions (45). The combined application of fungi and PGPR may be extremely beneficial for sustainable agriculture (39, 45).

Enhancement of Stock for Noncommercial Purposes

In comparison with commercial applications, the development of genetically enhanced stocks that can boost resilience of natural populations and be used in restoration of natural ecosystems is rare. Terrestrial landscape ecologists are pioneering this field and

advocate manipulations that accelerate naturally occurring evolutionary processes for wildland restoration in heavily disturbed ecosystems (6). For example, a new green needlegrass variety, called Fowler Germplasm, was developed through artificial selection of five natural plant populations. The expectation is that Fowler will be used in landscape restoration projects (46). In the animal realm, at least one attempt to restore wildlife populations via selective breeding has been reported; selected animals of the plains zebra, *Equus quagga*, were successfully bred for three generations to reduce the degree of body striping and to resemble the extinct quagga phenotype (47). A more indirect and less controlled form of genetic enhancement through selective breeding is the translocation of individuals between conspecific populations within the current distribution range of the species (i.e., assisted migration or assisted translocation). Assisted migration is generally done to facilitate mixing of stocks and increase genetic diversity, resilience, and adaptability in the receiving population (i.e., augmentation) (48–51).

Other enhancement approaches have taken more extreme measures and have developed GMOs to be used in landscape restoration because selective breeding did not yield the desired outcomes. Four billion American chestnut trees (*Castanea dentata*) dominated the North American landscape until a fungus introduced from Asia wiped out most trees by the early 1900s. Recent field trials with transgenic trees have confirmed that the insertion of a wheat gene has resulted in heritable fungus resistance. Pending regulatory approval, these genetically modified (GM) trees will be planted in the wild for reestablishing this species in America's woodlands (52–54).

Finally, the manipulation of soil microbial communities is a well-documented strategy for crop improvement, and, recently, inoculation of the rhizosphere with fungi and/or PGPR has been proposed as a strategy to improve the success of landscape-restoration initiatives (55). The reconstruction of pre-disturbance soil bacterial diversity may be used to guide such landscape-restoration efforts (56).

State of Coral Reef Restoration Approaches

Coral reef restoration efforts have mostly been based on the use of asexually produced coral fragments (57). These fragments are generally sourced from healthy coral colonies that are still present either on the disturbed reefs or on less damaged nearby reefs, or represent “corals of opportunity”:

i.e., colonies dislodged through natural processes or coral fragments produced through natural processes and collected from the substratum (58). In the early days of coral reef restoration, fragments were directly explanted into the reef environment. However, a two-step protocol in which fragments are first grown in in situ or ex situ nurseries (“gardening”), followed by explanting them onto denuded reefs, has proven far more successful, in particular when floating in situ nurseries are used (59). The primary purpose of coral nurseries is to grow coral colonies to a size that reduces mortality after transplantation onto damaged or degraded reefs. Coral transplants have a greater chance of survival the larger they are (60). The nurseries offer the advantage of decreased competition for resources (space, light), decreased predation, and suspension above sea-floor sediments. Coral nurseries can also be used to capture and harvest coral larvae, as genetic repositories (61), or to grow mature breeding corals for larval production and seeding of surrounding reefs (62). Explanting of nursery-grown gravid colonies is another possibility but has received little attention so far (63).

The midwater floating nurseries have proven a successful tool for coral reef restoration, with close to 90 coral species successfully farmed around the world showing enhanced growth rates and low mortalities (59). In all of these efforts, natural, mostly local, coral stocks are used. The use of local stocks preserves the preexisting genetic identity and restores prior patterns of genetic variation (64). However, when an environment is severely altered or expected to change rapidly in the near future (as is the case under climate change scenarios), the original stock may be ill-suited for restoration (65). As a consequence, use of the original stock will likely result in high levels of mortality and a loss of ecosystem function.

Assisted Evolution Approaches to Build Coral Reef Resilience

The management and conservation of coral reefs has focused exclusively on the preservation of natural biodiversity, and any proposals to use corals enhanced via assisted evolution to promote resilience is a radical departure from this approach and thus likely to be controversial and stimulate heated debate. This debate may, however, be somewhat tempered by the broad acknowledgment that reefs are continuing to decline at an alarming rate in the face of intensifying climate change and increasing direct human impacts, a trajectory that infers that traditional methods

are insufficient to secure a future for coral reefs. In this context, we advocate that approaches for trait enhancement analogous to those listed above should be seriously considered for keystone organisms of coral reef systems, such as the reef-building corals. Four approaches that accelerate the rate of naturally occurring evolutionary processes warrant detailed research focus (Fig. 2): (i) stress exposure of natural stock to induce preconditioning acclimatization (i.e., within generations) and transgenerational acclimatization (i.e., between generations) through epigenetic mechanisms *sensu stricto* (66–69); (ii) the active modification of the community composition of coral-associated microbes (eukaryotic and prokaryotic); (iii) selective breeding to generate certain genotypes exhibiting desirable phenotypic traits; and (iv) laboratory evolution of the algal endosymbionts (*Symbiodinium* spp.) of corals through mutagenesis (70) and/or selection (i.e., evolution after the generation of variability) (71). In the next several paragraphs, we discuss these approaches, as well as the range of life-history traits that make corals amenable to assisted-evolution manipulations. The four approaches are incremental in the level of human intervention involved.

Exposure to nonlethal light or temperature stress is common on reefs; in natural populations and experimental settings, such conditions have sometimes resulted in enhanced tolerance to coral bleaching (the breakdown of the obligate coral-*Symbiodinium* symbiosis in response to stress) during subsequent thermal stress events (69, 72). This process of within-generation acclimatization is achieved by changes in the taxonomic composition of the algal endosymbiont communities found in corals (67) and/or processes likely involving epigenetic modification (73). Transgenerational acclimatization can occur over shorter

periods of time compared with genetic adaptation and may last for several generations. For instance, the tropical damselfish, *Acanthochromis polyacanthus*, shows a significant decline in aerobic activity after acute exposure to increased temperature; however, when both parents and F1 offspring are reared at the higher temperatures, a complete restoration of aerobic activity occurs in the F2 offspring (66). In corals, the importance of transgenerational acclimatization is largely unstudied; however, early work suggests that transgenerational inheritance may play an important role in the stress tolerance of brooding corals (74).

Reef-building corals form obligate, mutually beneficial symbioses with dinoflagellates in the genus *Symbiodinium*. These relationships are fundamental to the productivity and high rates of calcification that create reef structures. *Symbiodinium* is divided into nine major groups, clades A–I (75), and each clade encompasses many genetic types, many of which have different physiological optima. The presence of specific types of *Symbiodinium* makes an individual host more or less susceptible to environmental disturbances (67, 76). More than one *Symbiodinium* type can exist in the same host at the same time (21, 77, 78), and some corals show changes in the relative abundances of *Symbiodinium* types over time (21). Further, inoculation of conspecific and genetically similar host individuals, with distinct *Symbiodinium* types or populations of the same type but from distinct thermal environments, results in different thermal tolerance limits of the coral holobionts (79, 80). These observations suggest that manipulations to obtain changes in the *Symbiodinium* communities of corals, especially through introduction of resistant strains that are absent in local populations, may assist in enhancing their

stress tolerance. This avenue deserves exploration given the gains resulting from the manipulation of fungi and bacteria in the rhizosphere of terrestrial plants. Such manipulations will likely have to be restricted to early life stages because no compelling evidence exists that adult corals are able to establish a stable symbiosis with novel *Symbiodinium* types (81). Most coral species produce eggs and larvae that lack *Symbiodinium*, making these early life stages amenable for inoculation with stress-tolerant *Symbiodinium* types to explore the phenotypic benefits of such novel symbioses. Additionally, larvae of maternally transmitting species can be experimentally bleached (82) and similarly exposed to novel *Symbiodinium* types. A major challenge with this approach will be to find a way for manipulated coral-*Symbiodinium* associations to remain stable (83, 84).

Corals also harbor diverse prokaryotic communities (20), consisting of hundreds to thousands of putative species per colony. These prokaryotes have known functions in nitrogen fixation (85, 86), sulfur metabolism (87), and immunity via the production of antimicrobials and the disruption of pathogen virulence (19). Therefore, these symbionts play important roles in the nutrition and health of corals. Whether prokaryotic communities of corals can be manipulated and stabilized to enhance stress tolerance and growth, as in plants, is unknown, but we see the manipulation of prokaryotic communities as another area at which research efforts should be directed.

Selective breeding has received virtually no attention in coral reef conservation (88) despite its clear relevance. Mixing gene pools from the same or different, closely related species can lead to offspring with novel genotypes producing novel phenotypes. A range of coral species are known to hybridize with other species in the wild (89). An interspecific *Acropora* hybrid in the Caribbean, where coral reefs have shown alarming declines, has similar and sometimes higher fitness compared with the parental species (90), suggesting that hybrid vigor can occur in disturbed and altered reef environments. One approach with low environmental risk is to rear interspecific hybrids in the laboratory and subject these hybrids to simulated ambient or predicted near future conditions (e.g., slightly elevated temperature and pCO₂) so that selection can act to identify the genotypes that are fittest in those environments. Such genotypes can subsequently be used for further breeding. Additionally, translocation of adult corals from a warm reef to a cooler reef within its natural distribution

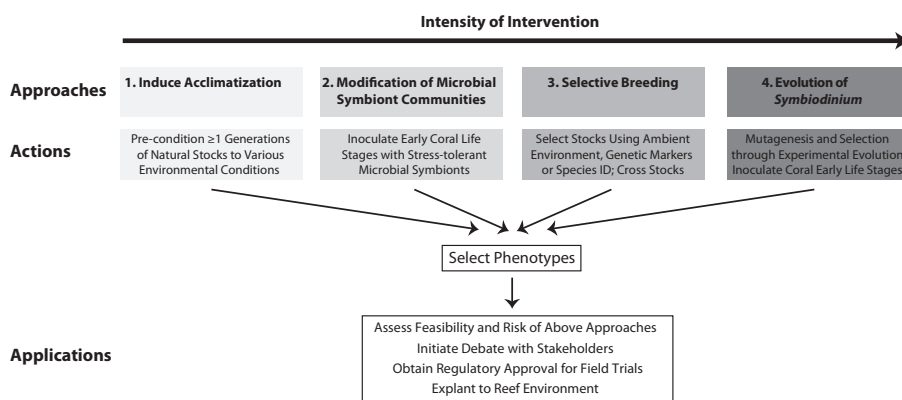


Fig. 2. Diagram summarizing the rationale behind, and steps involved in, the four assisted evolution approaches proposed here for corals.

range or seeding the cool reef with recruits from the warmer reef may be considered as strategies for accelerated enhancement of upper thermal tolerance limits (88). For coral reef ecosystems, assisted migration has recently been considered in terms of translocating corals from the warmest reef areas of the Arabian Gulf to other Indo-Pacific locations (91). The scale of such translocations would be challenging in terms of cost and the need for extensive international coordination (91). Further, it is possible that Gulf populations have diverged to the extent that they are unable to survive seasonal extremes at the transplant location (92, 93) or are no longer able to interbreed with other Indo-Pacific conspecifics. This management strategy should not be confused with the translocation of species beyond their current distribution range, which has spawned an active debate in terrestrial systems (94–99), but far less so in the coral reef arena (91, 99, 100).

For selective breeding approaches to be successful, the trait under selection needs to exhibit significant heritability: i.e., phenotypic variation in the trait needs to have a genetic basis. Although evidence for genotype-dependent responses to temperature exists in corals (101, 102), trait heritabilities are largely unknown for the majority of coral species and other environmental conditions; only two studies have been published so far, with one suggesting considerable heritability for thermal tolerance in the *Acropora millepora* holobiont (103) and the other showing limited heritability for thermal tolerance traits in the coral host, but considerable heritability in the *Symbiodinium* symbionts (104). These results are promising and indicate that, in addition to heritability studies, a focus on measuring the response to selection directly (as proposed in this Perspective) is warranted.

Another approach is to attempt to facilitate genetic adaption of existing *Symbiodinium* strains. *Symbiodinium* can be subjected to environmental stress in the laboratory with the goal of eliciting an adaptive response through selection on random somatic mutations, as has been demonstrated for a range of other unicellular, asexually reproducing algae (71). The rate of somatic mutations can be increased by exposing the culture to a mutagen (e.g., certain chemicals or irradiation with UV light or X-rays), an approach that is widely used for strain improvement in other organisms (70). Selected *Symbiodinium* strains are able to establish symbiosis with the aposymbiotic early life stages of coral (M.J.H.v.O., personal observation), and, in this manner, corals with new phenotypes

may be generated. Those with enhanced stress tolerance may be targeted for reef restoration. This approach takes advantage of both naturally occurring (random mutations) and artificial (i.e., the use of a mutagen) processes followed by selection of certain phenotypes under controlled laboratory conditions.

Coral Life History Traits and Evolutionary Potential

Corals possess a range of attributes that promote evolvability, including (i) the common occurrence of asexual reproduction in addition to sexual reproduction—some corals brood larvae asexually and others reproduce asexually through fragmentation or colony fission (105, 106); (ii) a lack of segregation of the germ cell from the somatic cell line (107); (iii) the existence of symbiosis with a range of potentially fast-evolving microbes (22); and (iv) naturally occurring high levels of genetic diversity and the occurrence of interspecific hybridization in some taxa (107). Most of these life-history traits are shared with land plants, which, even when strictly asexual, have a documented ability to keep an evolutionary pace with their sexually reproducing pest species (108) and are also most commonly reported to show transgenerational acclimatization. The high potential for transgenerational acclimatization is due to the fact that plants and corals commonly show asexual and sexual reproduction and that, in both groups, germ-line cells develop from totipotent somatic cells, which have been exposed to developmental and environmental cues throughout the individual's life. These life-history traits are believed to have evolved in response to their sessile lifestyle, which requires a constant adjustment to environmental conditions because the organism is unable to relocate to a more suitable environment. Such characteristics provide not only greater scope for environmentally induced epigenetic changes but also somatic mutations to be passed on from one generation to the next compared with strictly sexually reproducing organisms that have segregated germ and somatic cell lines and show DNA methylation resetting during gamete/embryo development. Therefore, corals possess a variety of characteristics that make them likely candidate organisms for assisted evolution initiatives.

Conclusions

Evidence for wide-spread adaptation or acclimatization of reef corals to the effects of climate change does not currently exist, either due to a lack of observations or to a scarceness of events that would drive rapid adaptation, but there are a few glimmers of

hope. For example, an increase in thermal tolerance in the most bleaching-sensitive coral taxa over successive bleaching events has been documented at a small number of localities in the Indo-Pacific (91, 109–112), suggesting that these taxa have acclimatized or adapted to high temperature stress. We propose that assisted evolution initiatives may provide coral reefs with the critical capacity to adapt at a pace closer to that of current climate change trajectories. The economic value of coral reefs through commercial and recreational fisheries, tourism, drug discovery, and coastal protection is incalculable, with peoples' livelihoods dependent on them. It is therefore our responsibility to find solutions to restore severely degraded reefs, with assisted evolution being one possibility that has not yet been explored.

There is a suite of key activities and questions that the coral scientific community can address in the near future. These activities include an assessment of the feasibility of the manipulations listed above, a quantitative review of the risks associated with each, the generation of data to feed ecological/evolutionary models that allow the risks, benefits, and feasibility to be more accurately predicted (e.g., quantitative requirements for reef reseeded, time frame for reef recolonization, assessment of reef connectivity and larval dispersal, etc.), and an evaluation of added benefits of assisted evolution. The capacity to develop and maintain enhanced coral stocks is likely to have value beyond coral reef restoration. The coral aquarium trade, for instance, would benefit tremendously from the availability of corals bred to cope with greater environmental ranges. Such stocks would also provide an alternate source of animals for the industry, which would in turn reduce collection pressure on natural populations. Although we suggest that experimental laboratory research should commence now, on a no-regrets basis, development of major field trials should be done only once there has been a robust and inclusive consideration of the costs and benefits of this intervention taking into account ecological, economic, and social perspectives.

As the research progresses, an active discussion should be initiated by relevant scientific bodies that combines an exploration of the ecological risks with a consideration of the ethical and socioeconomic implications of the various approaches outlined here. This dialogue will help to ensure that the social and experimental feasibility of assisted evolution develops in step and that appropriate solutions can be provided without major delays caused by public controversy.

The research advocated in our article is extremely novel in conservation and restoration science generally and is relevant to all organisms whose persistence, like corals, frames services that are important to human well-being (64, 113, 114). Although ongoing research and social actions to address the

root causes of climate change are essential, we advocate that it is also critical to build a biological tool box now that can be used to enhance resilience and mitigate the impacts of disturbance, with the goal of sustaining human services and biodiversity in the rapidly changing ocean of the future.

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