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Mitigating the ecological collapse of coral reef ecosystems

Effective strategies to preserve coral reef ecosystems

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Coral reef ecosystems are biodiversity hotspots that provide a habitat for about a third of all marine species (Fisher *et al*, 2015) which is why colloquially they are referred to as the "rainforests of the sea". In addition to their immense ecological importance, coral reefs offer a wealth of ecosystem services to millions of people, including the provision of food and commercial fisheries, tourism, sand production, carbon sequestration, and coastal protection from storms (Eddy *et al*, 2021). The crucial organisms that establish and expand coral reefs are corals, sessile animals that build impressive three dimensional structures through their calcium carbonate skeletons, rivaling busy cityscapes.

> "... *coral holobionts are fragile organisms that are threatened by local and global stressors to the point where the very existence of coral reef ecosystems globally is now at stake.*"

But corals cannot achieve these impressive constructions alone. Rather, they have to rely on a multitude of little helpers. In fact, corals are so called holobionts or metaorganisms that encompass a myriad of associated symbiotic microorganisms, collectively referred to as the microbiome that includes archaea, bacteria, fungi, viruses, and microeukaryotes, most importantly, Symbiodiniaceae (LaJeunesse *et al*, 2018; Voolstra *et al*, 2021). These dinoflagellate photosynthetic microalgae live inside the coral cells and provide them with the energy to construct their calcium carbonate skeletons. Despite the massive and lasting structures they create, coral holobionts are fragile organisms that are threatened by local and global stressors to the point where the very existence of coral reef ecosystems globally is now at stake (Allen *et al*, 2018).

Climate change, owing to increasing greenhouse gas (GHG) emissions caused by human activities, is the greatest threat to coral reefs. GHG emissions change marine conditions in several ways, including ocean warming, ocean acidification, and an increased frequency and intensity of tropical storms and heatwaves (Allen *et al*, 2018; Frölicher *et al*, 2018). While storms can locally devastate coral reefs and seawater acidification reduces calcification rates of reef taxa and thus skeletal and reef growth (Mollica *et al*, 2018), warmer waters pose the most significant threat to reefs (Kleypas *et al*, 2021; Knowlton *et al*, 2021). Extended periods of high temperature cause heat stress, which triggers the breakdown of the symbiosis between corals and Symbiodiniaceae, a phenomenon known as bleaching (Suggett & Smith, 2020). Mass coral bleaching has been increasing in frequency and intensity over the past decade(s) and caused a 30% decline in the global coral population (Eakin *et al*, 2022). Recent estimations predict that, if global warming exceeds 1.5°C, 70 90% of reef corals are at risk to be lost, and 99% will be lost if global warming exceeds 2°C above pre industrial temperatures (Hoegh Guldberg *et al*, 2018; Knowlton *et al*, 2021).

> "... *all actions to save coral reefs are connected with each other by 'and' not 'or'.*"

The effects of climate change are amplified by local stressors, such as pollution, sedimentation, and eutrophication, caused by land clearing and fertilizer use (Wiedenmann *et al*, 2012). The latter causes overgrowth of corals by macroalgae and bioerosion of algal and coral skeletons by endolithic algae. It affects the coral microbiome, for instance, by increasing the abundance of pathogens (Leite *et al*, 2018). Taken together, coral bleaching driven by ocean warming (Eakin *et al*, 2022) along with local and global stressors reduce calcification rates of important reef forming taxa, decrease reef accretion through bioerosion and dissolution of carbonate sediments (Eyre *et al*, 2018), and further weaken coral stress resilience (Donovan *et al*, 2021) (Fig 1).

CO$_2$ emission mitigation is a pre-requisite

It follows that corals must be protected in order to save the reefs (Fig 2). The

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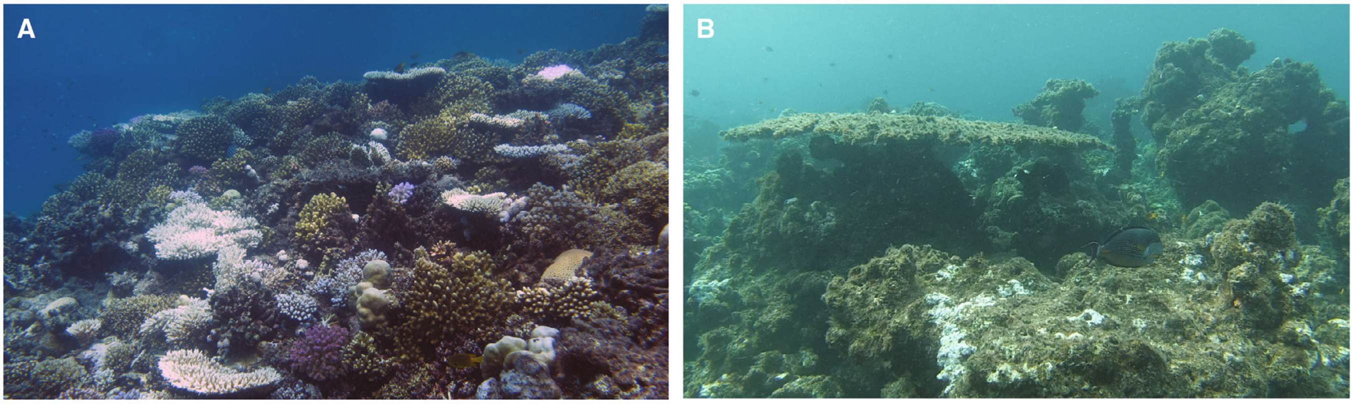

Figure 1. (A) A healthy reef with a moderate level of bleaching. The bleached coral colonies appear white and can recover if stressful conditions subside. (B) A degraded reef where the corals are dead and the remaining skeleton is overgrown by algae. Some bleached colonies are visible in the lower middle.

International Coral Reef Society (ICRS) proposed three equally important pillars for saving and restoring coral reefs (Knowlton *et al*, 2021) (Fig 2). The first one is mitigating CO_2 emissions and global climate threats. Importantly, all other options rely on the premise that we are becoming carbon neutral in due time; in other words, all actions to save coral reefs are connected with each other by "and" not "or" (Kleypas *et al*, 2021).

> *"... interventions for reef protection must occur over large areas to be effective and should be reinforced with socio-economic incentives and regulatory measures."*

Mitigating carbon emissions is necessary to limit the mean global temperature increase to about 1.5°C, the threshold above which 99% of reefs are on a trajectory to become permanently lost (Hoegh-Guldberg *et al*, 2018). Staying below this threshold will allow us to protect still healthy and resilient reefs and restore damaged reefs. Other actions to decrease sea surface temperature (SST), such as pumping deep cool seawater into reef areas or modifying solar radiation through reef shading, surface albedo enhancement, stratospheric aerosol injection, and so on represent geoengineering approaches to offset impacts of climate change (National Academies of Sciences, Engineering, and Medicine, 2019). These are very expensive options that can be at best considered only on a small and local scale (Kleypas *et al*, 2021).

> *"Some reefs that exhibit increased thermal stress resilience deserve special protection, because these coral communities have evolved a natural higher tolerance..."*

Saving corals through conservation

Failure to address climate change will undermine most attempts to mitigate the impacts of local threats, which is the second pillar of the ICRS's guideline to save coral reefs as global and local stressors can synergistically interact to affect coral reefs (Knowlton *et al*, 2021). Although accretion of some reefs under global warming of more than 1.5°C will still be present but slow, model estimates indicate that a combination of reduced emissions and improved local conditions, such as improving water quality, can maintain a positive carbonate budget, that is, growth (Kennedy *et al*, 2013).

Improving local conditions requires a variety of actions that directly or indirectly affect coral health and recovery, such as the reduction of overfishing through the establishment of complete or partial marine protected areas (MPAs) and/or the management of coastal zones and watersheds to reduce nutrient loading and river runoff (Mellin *et al*, 2016). There are several reefs in the Caribbean, Australia, and Kenya, which demonstrate that the management of local stressors has a positive impact on coral recovery (Mellin *et al*, 2016).

However, interventions for reef protection must occur over large areas to be effective and should be reinforced with socio economic incentives and regulatory measures. These actions also must be adapted to the particular threats at each location (Voolstra *et al*, 2021). For example, the Gulf of Aqaba (GoA) in the northern Red Sea has been coined a coral refuge to SST rise because corals can withstand temperatures of up to +6°C above their maximum summer mean *ex situ* and no mass bleaching has been observed *in situ* (Osman *et al*, 2018). Yet, these corals are not immune to other, local threats and are, indeed, affected by increasing pollution, such as seawater eutrophication, antiscalants from desalination plants, or light pollution. Long term monitoring through national programs, science guided management, and engagement from policymakers, as well as the support of local communities, is essential to identify appropriate interventions and manage local reef conditions.

Saving corals through restoration and rehabilitation

While global and local anthropogenic stressors are being addressed, the third pillar put forward by the ICRS, which is restoration and rehabilitation (Knowlton *et al*, 2021), is under active development and implementation (Voolstra *et al*, 2021). Given the pace

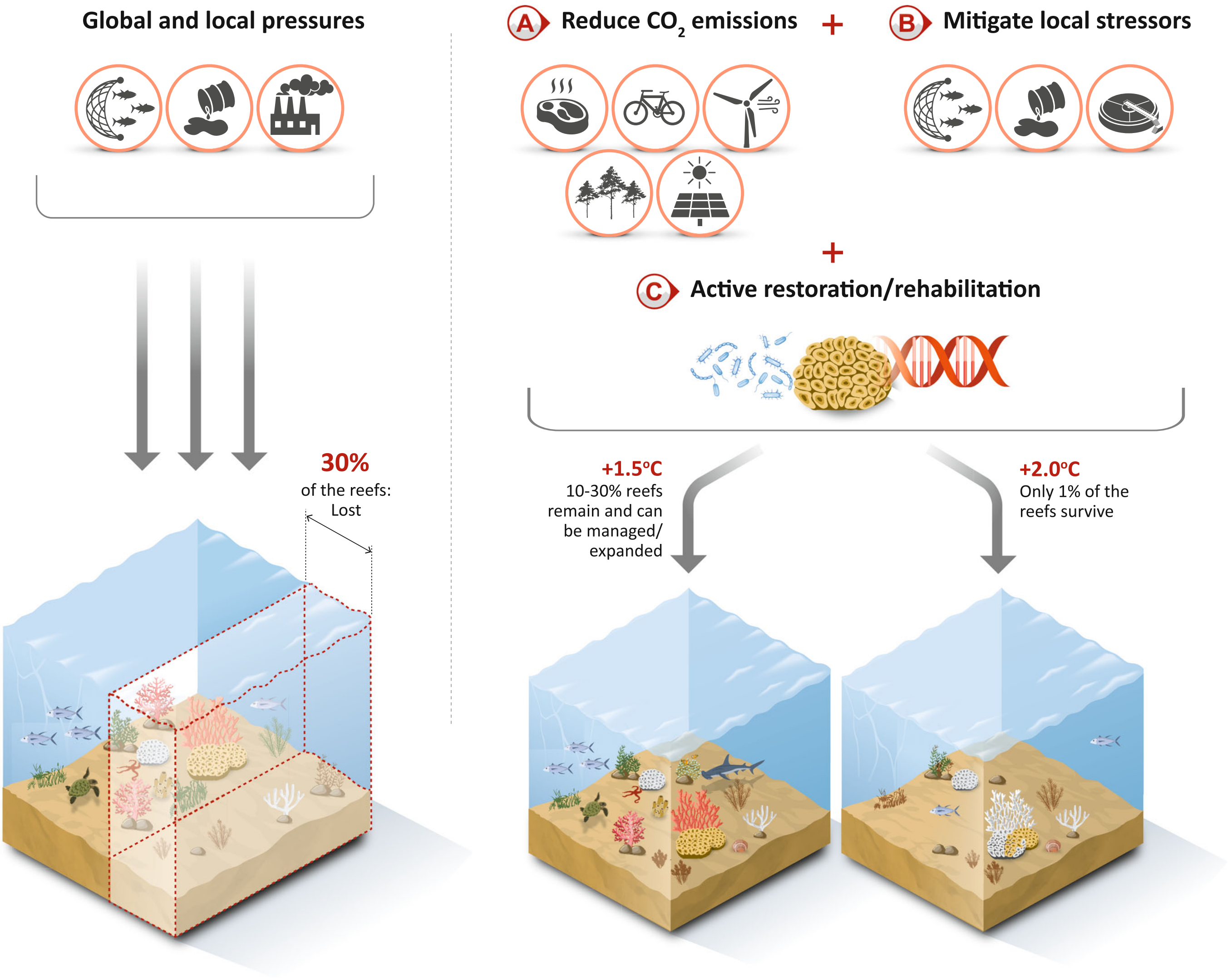

Figure 2. Global and local pressures have led to the loss of 30% of global reef cover (left). The International Coral Reef Society (ICRS) has proposed three pillars for restoring coral reefs and mitigating their further loss (right): (A) reduce CO_2 emissions; (B) mitigate local stressors (e.g., by managing fish stocks or improving water quality); and (C) active restoration/rehabilitation. It is important to note that without reducing CO_2 emissions to curb global warming to below 2°C and eventually becoming carbon neutral, we will still lose the majority of coral reefs (C, right hand side).

and severity of current impacts, restoration and rehabilitation efforts have become a mandatory step to maintain coral reefs while achieving carbon neutrality (Voolstra *et al*, 2021). Such interventions can be customized to target different entities of the coral holobiont, such as the algal symbionts, the prokaryotic community, or other associated microeukaryotes (National Academies of Sciences, Engineering, and Medicine, 2019; Peixoto *et al*, 2019; Voolstra *et al*, 2021), and can combine different approaches for reef restoration and rehabilitation (van Oppen *et al*, 2015; Boström Einarsson *et al*, 2020; Peixoto *et al*, 2021; Santoro *et al*, 2021). Different impacts and levels of degradation require different approaches (Peixoto *et al*, 2019; Voolstra *et al*, 2021; Fig 3). In fact, considering the current stage of degradation of some reefs and ongoing climate change and widespread marine pollution, modern restoration approaches will necessarily need to integrate rehabilitation and prevention concepts to succeed, and the two terms can therefore be used interchangeably (Box 1) (Knowlton *et al*, 2021).

At the reef scale, restoration approaches to counter coral decline are particularly effective for areas that have been physically damaged by storms, disease outbreaks, mass bleaching, or human activities. It is also a useful option to support reef regrowth where coral recruitment is limited and disturbances can be reduced. The most commonly used restoration methods involve removal of predators and reintroduction of fish to control macroalgal overgrowth, along with transplantation of coral fragments with or without an intervening nursery phase (Boström Einarsson *et al*, 2020). One difference is between sexually and asexually propagated restoration, the latter of which addresses reef regrowth but not genetic diversity (Voolstra *et al*, 2021). Other measures include the *in situ* deployment of

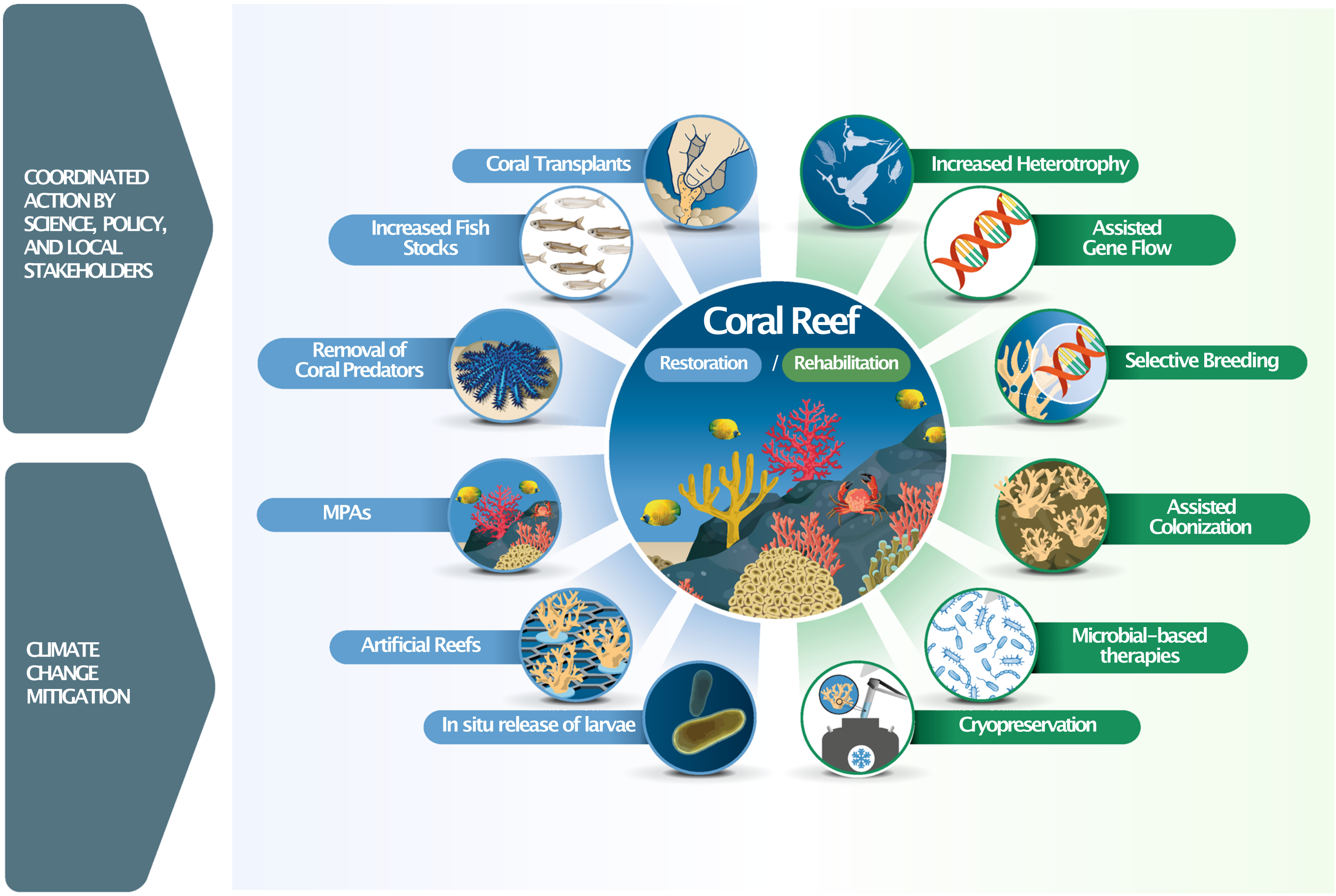

Figure 3. Examples of actions to restore/rehabilitate reefs and mitigate their global loss. Restoration refers to processes that help the recovery of degraded or damaged ecosystems; rehabilitation refers to processes that improve reefs through active interventions that expand their adaptive capacity or increase resilience. Many of these actions go hand-in-hand and many restoration approaches entail a component of rehabilitation so that restoration and rehabilitation are often used interchangeably.

Box 1. Restoration versus rehabilitation.

The definition of "restoration" proposed by the "Society for Ecological Restoration" is "the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed". While the goals of "restoration" include the re-establishment of the pre-existing species composition and community structure, the ongoing change of environmental conditions faced by coral reefs results in future reefs harboring different compositions from the original reefs. This is recognized in UNEP's guide to coral reef restoration, where the term "coral reef restoration" is used to describe measures that "aim to assist the recovery of reef structure, function, and key reef species in the face of rising climate and anthropogenic pressures, therefore promoting reef resilience and the sustainable delivery of reef ecosystem services".

By comparison, the term "rehabilitation" is centered on the notion that to "future proof" reefs, it is not sufficient to merely restore reefs to their original composition, but to enhance reefs through active interventions, such as probiotic provision, environmental hardening, or similar measures, in order to promote protection, extend adaptation, and increase resilience. Thus, while the term restoration is used throughout this document for consistency, current efforts to save reefs should more accurately be understood as a form of rehabilitation.

artificial reef structures to enhance coral recruitment and fish aggregation, substrate manipulations, or the release of coral larvae after an intermediate rearing phase on land (Boström Einarsson *et al*, 2020). The selected restoration measure(s) should be informed by the specific local conditions and engage local communities.

Some reefs that exhibit increased thermal stress resilience deserve special protection because these coral communities have evolved a natural higher tolerance, thus constituting "super reefs" (https://superreefs.whoi.edu), "priority reefs" (https://www.50reefs.org), or "bright spots" (Cinner *et al*, 2016). Other reefs also deserve special consideration due to their potential to constitute "coral reef oases" (Guest *et al*, 2018), such as turbid reefs near mangroves, high latitude reefs, or reefs in upwelling areas, all of which are nutrient rich and often sheltered from heat waves. However, the extent to which thermal protection of corals from such reefs can be transferred to other reefs is debatable, in particular, because these corals reside in marginal environments featuring unique adjustments that are either lost or reduced when transplanted into other, more common reef environments.

Consequently, reefs should provide long term buffering against multiple stressors, which is rarely found. For instance, GoA corals and other "bleaching resistant" reefs that have an exceptionally high bleaching threshold (Savary *et al*, 2021) may constitute a refuge from global warming, but they are exposed to (local) pollution and other anthropogenic stressors which affect their resilience (Donovan *et al*, 2021). At large, we need to improve our understanding of what underlies the resilience of some corals to various stressors and the potential costs or trade offs (Cornwell *et al*, 2021).

In addition to reintroducing or enhancing coral biomass in reefs, active rehabilitation and environmental management/prevention approaches can help corals adapt to future global changes. For example, laboratory experiments have shown that feeding corals with planktonic prey significantly increases their resilience and resistance to environmental stress (Grottoli *et al*, 2006). Recent *in situ* observations have also found a correlation between patterns of food availability and resilience in coral populations around the world, suggesting that reefs with high phyto and/or zooplankton concentrations are better able to recover from thermal stress disturbance. A heterotrophic diet provides essential macronutrients and metals that sustain algal growth and photosynthesis and enhances nutrient translocation from algal symbionts to the coral host (Ferrier Pagès *et al*, 2018). Increasing the nutritional quality of the plankton provided to corals by manipulating the content of essential fatty acids, metals, and antioxidant compounds might therefore be one strategy to enhance coral health. However, to our knowledge, no studies have directly attempted to increase zooplankton concentrations or alter zooplankton composition in reefs during heat waves, partially because it is a broad measure that may affect reef biota at large with unknown consequences.

In total, the US National Academies of Science, Engineering, and Medicine lists 23 types of interventions, including approaches such as assisted gene flow (AGF), assisted evolution, and assisted colonization, cryopreservation, and microbiome manipulation to mitigate coral loss (National Academies of Sciences, Engineering, and Medicine, 2019). AGF interventions aim to identify genotypes within existing coral populations that are optimally suited to specific environments (Humanes *et al*, 2022), which can be used to improve the fitness of distant populations by introducing the respective alleles into target populations.

Corals that have survived heat waves or those that live in the Persian/Arabian Gulf (PAG), where the highest ocean temperatures in the world occur, are also good candidates for exploring mechanisms of heat stress resistance by means of AGF. PAG corals are associated with a heat specialized algal endosymbiont, *Cladocopium thermophilum* (Hume *et al*, 2016), and the coral host has a higher antioxidant capacity and expression of heat responsive genes. Assisted translocation and colonization of these stress resistant variants may help AGF, although other environmental factors may need to be considered, coming back to the above mentioned trade offs. As such, this can only occur if coral restoration material is reproduced sexually to generate novel allele combinations that convey increased resilience but also harbor compatibility with prevailing environments (Voolstra *et al*, 2021).

> *"More sophisticated breeding methods may use genetically-modified organisms, in which new alleles and traits that do not exist in natural populations are created to promote coral resilience..."*

Nurseries can accelerate the process of genetic restoration by out planting coral larvae produced from such crosses. Nurseries can also use cryopreserved sperm to produce offspring, especially for endangered species (Hagedorn *et al*, 2017). However, one of the biggest challenges is scaling up from smaller, laboratory sized experiments to high throughput reproduction.

More sophisticated breeding methods may use genetically modified organisms, in which new alleles and traits that do not exist in natural populations are created to promote coral resilience (van Oppen *et al*, 2015). To this end, different genetic manipulation approaches are available, such as repeated exposure to stress to produce transgenerational acclimation through epigenetic mechanisms, although controversy remains (Torda *et al*, 2017). Another approach discussed is the induction of mutagenesis in algal symbionts to generate more resistant strains, but fidelity of the host symbiont associations needs to be addressed (Hume *et al*, 2020; Howells *et al*, 2021), which may work better in coral larvae (Buerger *et al*, 2020).

A further approach to enhance coral resilience is the assisted restructuring or restoration of prokaryotic and microeukaryotic communities associated with corals, for instance, through the use of probiotics or microbiome transplantation (Ziegler *et al*, 2017; Peixoto *et al*, 2019, 2021; Santoro *et al*, 2021; Zhang *et al*, 2021). Although the exact underlying mechanisms are still unclear, corals seem to rely on their associated microbiome for nutrient provision, pathogen protection, or toxic compound mitigation among others. Continuous environmental insult effectively alters the beneficial microbiome into a more pathogenic assemblage that affects coral resilience and well being. The underlying premise is that rather than reintroducing coral biomass, efforts could focus on microbiome restoration of extant corals (Peixoto *et al*, 2022). Microbiome based approaches are customizable and can be applied as a preventive or remediation measure (Peixoto *et al*, 2017) to promote holobiont growth (Zhang *et al*, 2021), pathogen mitigation (Rosado *et al*, 2019), remediation of oil impact (Silva *et al*, 2021), or recovery from thermally driven coral bleaching (Rosado *et al*, 2019; Santoro *et al*, 2021), and effectively prevent coral mortality in laboratory experiments (Santoro *et al*, 2021). The current challenge is to evaluate the efficiency of microbiome stewardship *in situ* and develop ways to scale up associated applications (Peixoto *et al*, 2022).

> *"Although the exact underlying mechanisms are still unclear, corals seem to rely on their associated microbiome for nutrient provision, pathogen protection, or toxic compound mitigation among others."*

Securing a future for coral reefs

"Modern" coral reefs have existed for ~ 250 million years and are highly adaptable. A study conducted on the species *Oculina* *patagonica* showed that some corals can withstand severe seawater acidification by losing their skeletons while the tissues remain alive (Fine & Tchernov, 2007); corals never really disappear, even if reef ecosystems do. Thus, as long as there are corals, there is hope for reefs.

> “*It is understood that we cannot save all reefs from a cost and effort perspective, but enough to repopulate degraded areas once carbon neutrality is reached and the climate has stabilized.*”

However, pristine coral reefs no longer exist, and corals are now under massive pressure: although the most tolerant corals have survived recent repeat bleaching events, and there is evidence that they increased their thermal tolerance, certain species are clearly more likely to survive than others. Thus, survival comes at the expense of biodiversity, and the reefs of the future will not be the same as the reefs of the past. One of the emphases should thus be placed on securing ecosystem functions and ecosystem services. It is understood that we cannot save all reefs from a cost and effort perspective, but enough to repopulate degraded areas once carbon neutrality is reached and the climate has stabilized. Under such constraint, we must recognize that not all coral reefs have the same ability to survive or adapt to climate change and consider prioritizing those reefs with the highest chance of survival that also promotes regeneration in other areas through, for instance, larval dispersal.

Importantly, this requires that coral reefs must be protected at local, regional, and global scales in ways that allow for the propagation of evolutionary adaptive traits (Colton *et al*, 2022). This can only be achieved through coordinated action by science, policy, and local stakeholders (Hoegh Guldberg *et al*, 2018; Kleypas *et al*, 2021). A combination of strategies, policies, and active interventions (Voolstra *et al*, 2021) as outlined above can help reefs recover and survive in different places, depending on local environmental conditions, financial resources, and socioeconomic circumstances. We have a chance if we are to integrate the triad of mitigating CO_2 emissions, improving local conditions, and undertaking active restoration/rehabilitation, but it is a closing window of opportunity to secure a future for coral reef ecosystems for us and future generations.

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Author contributions

Christian R Voolstra: Conceptualization; writing original draft; writing review and editing.
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Christine Ferrier-Pagès: Conceptualization; writing original draft; writing review and editing.

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The authors declare that they have no conflict of interest.

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