Extending the natural adaptive capacity of coral holobionts

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Abstract | Anthropogenic climate change and environmental degradation destroy coral reefs, the ecosystem services they provide, and the livelihoods of close to a billion people who depend on these services. Restoration approaches to increase the resilience of corals are therefore necessary to counter environmental pressures relevant to climate change projections. In this Review, we examine the natural processes that can increase the adaptive capacity of coral holobionts, with the aim of preserving ecosystem functioning under future ocean conditions. Current approaches that centre around restoring reef cover can be integrated with emerging approaches to enhance coral stress resilience and, thereby, allow reefs to regrow under a new set of environmental conditions. Emerging approaches such as standardized acute thermal stress assays, selective sexual propagation, coral probiotics, and environmental hardening could be feasible and scalable in the real world. However, they must follow decision-making criteria that consider the different reef, environmental, and ecological conditions. The implementation of adaptive interventions tailored around nature-based solutions will require standardized frameworks, appropriate ecological risk–benefit assessments, and analytical routines for consistent and effective utilization and global coordination.

Coral bleaching
Discolouration of coral tissue due to the loss of microalgal symbionts triggered by climate change-induced ocean warming and thermal stress anomalies.

Tropical coral reefs cover only 0.1% of the seafloor yet provide habitat for >30% of all marine multicellular species[1]. Ecosystem services delivered through healthy tropical reefs are economically valued at around US $9,900,000 million per year[2] and sustain almost a billion people[3–5]. Despite their importance, catastrophic global loss of coral reefs owing to anthropogenic activity is fast becoming a reality[6]. For example, the 2015–2018 global coral bleaching event affected 74% of reefs worldwide, with >30% of coral cover lost on the Great Barrier Reef alone[7]. Additionally, coral cover in the Florida Reef Tract has declined by upwards of 90% over the last 50 years[8–11].

A global contributing factor to reef degradation is coral bleaching[12,13]. Without their microalgal symbionts (FIG. 1), corals lose their primary source of nutrition, leading to starvation, reduced fecundity, and reduced growth, often resulting in widespread coral mortality[14,15]. Trajectories for coral reefs under present CO_2 emission scenarios are dire, with 60% of all remaining coral reefs critically threatened, and 98% exposed to environmental conditions above the current thresholds considered necessary to maintain ecosystem function as soon as 2030 (REF.[16]). The impact of ocean warming is exacerbated by the effects of ocean acidification[17], deoxygenation[18], and salinity changes[19]. Combined with local factors such as overfishing, coastal development, disturbance of the nutrient environment (water quality), and disease or predator outbreaks, the interrelated cumulative impacts all contribute to reduction in coral cover and declining reef ecosystem health[20–27].

Given the rate and extent at which climate change unfolds[28], a widespread and shared concern is that the rate of environmental change could outpace the ability of coral holobionts to adapt to the changing environment[29], concomitant with the increasing loss of coral reef cover[30]. Global mitigation of CO_2 emissions is unquestionably needed to stem the rate of declining reef health[30–32]. However, biological, ecological and socio-economic adaptations are critical partners to preserve reefs and delay the loss of coral populations until carbon mitigation is effectively implemented[30]. Reef protection through Marine Protected Areas and management practices reduces how local stressors compound global climate change impacts[27,31]. Nevertheless, the current state of reefs and their predicted further decline have sparked initiatives to prioritize reefs or corals that are less vulnerable to climate change and best positioned for regenerating other degraded reefs in the future[33–35].

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Key points

- Coral reefs are degrading globally from anthropogenic climate change and local environmental impacts; deteriorated reefs are facing severe and widespread loss without active intervention.
- Ongoing efforts aim to extend the natural adaptive capacity of reef-forming coral holobionts through incorporation of novel tools, methods, and environments to manipulate coral adaptive responses to survive under more extreme or variable conditions.
- Emerging nature-based adaptive approaches spur novel intervention strategies that hold the promise to be feasible and scalable in the real world but must be tailored to address the diverse reef, environmental, and ecological conditions.
- Implementing an adaptive intervention framework focused on naturally evolved solutions will require standardized methodology, appropriate ecological risk–benefit assessments, and analytical routines for consistent and effective utilization and global coordination.

Assisted evolution	Human interventions aimed at speeding up natural evolutionary processes to increase the rate of adaptation of threatened species.
Adaptive capacity	The ability of coral holobionts to respond and adjust to environmental stress.
Acclimation	The physiological process of becoming accustomed to a new condition.
Environmental adaptation	The process of (meta-)organismal change used more broadly to denote adjustment to prevailing environmental conditions, for example in the context of host microbiome changes
Evolutionary adaptation	The process of genetic change through which populations become better attuned to their environment over generations.

An active area of investigation is the development of intervention management tools to maintain or even rebuild reefs, enhance recovery rates, and promote resistance to environmental pressures through ecological engineering, assisted evolution, and managed relocation[36–40]. Success of any of these initiatives requires detailed knowledge on the long-term survivability of reefs, which, in turn, relies on better understanding of the biotic and abiotic factors that underlie increased coral stress tolerance and the identification of colonies with such characteristics[41–44]. Projecting further, active manipulation of the natural adaptive capacity of coral holobionts might be needed to slow or reverse the trend of ongoing reef loss.

Understanding how corals function is fundamental to the success of any approach that exploits or manipulates their natural capacity to adapt[45–47]. Consequently, all of the entities that constitute the coral holobiont (FIG. 1) must be considered. Given the vastly different biologies of sessile coral animals, their eukaryotic Symbiodiniaceae microalgae, prokaryotes (bacteria and archaea), and viruses (amongst others), the adaptive responses operate on different timescales and are subject to unique evolutionary and ecological contexts of adaptation[46,48]. Knowledge about how coral holobionts respond or adapt to stressors provides the opportunity to modify these responses, employing or manipulating the same mechanisms that corals have naturally evolved to cope with and survive stress. Although detailed knowledge of how corals adapt to environmental stress is limited, emerging information on the biological entities that constitute the coral holobiont (and improved methods to manipulate them) provides opportunities to harness their individual and collective natural adaptive responses[36,41,49–56].

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In this Review, we describe an adaptive intervention framework aimed at harnessing the natural adaptive capacity of the coral holobiont. Expanding the adaptive capacity relies on operationalizing nascent methodological innovations at scale and is dependent on making them cost-effective, risk-reward favourable, and tailored to the challenges faced by the specific environmental conditions of different reefs. The adaptive strategies available to the different coral holobiont entities and how the underlying mechanisms might be employed or manipulated to increase stress resilience at large are summarized with a focus on thermal tolerance. Subsequently, a blueprint for coral survival guided by scientific insight utilizing emerging methods and technologies and how they can be implemented and scaled to real-world application is outlined, emphasizing that feasibility needs to be weighed against scalability, practicality, and regional setting to provide tailored and scaled solutions.

Adaptive strategies of coral hosts

Like all animals, corals respond to changes in their environment via acclimation and adaptation. In the contemporary literature, adaptation does not sensu stricto refer to evolutionary change through positive selection, but is more broadly used to denote adjusting to prevailing environmental conditions by various means[46]. Here, the term environmental adaptation is used in this broad sense, whereas evolutionary adaptation denotes the specific process of natural selection.

The extent to which corals can acclimate to alleviate environmental stress is currently unclear, although some corals do appear to demonstrate a large capacity for acclimation. For example, colonies (genotypes) of some species can survive for hundreds, if not thousands, of years and experience dramatic environmental changes during their lifetime[57,58]. In American Samoa, *Acropora hyacinthus* coral fragments that were transplanted between adjacent pools with different thermal environments demonstrated acquisition of heat tolerance levels by means of acclimation that would be expected from adaptation through natural selection over multiple generations[59]. In Hawaii, naturally heat-resistant coral transplants acclimated to new environmental regimes on the scale of months, maintaining their thermal tolerance[60].

Notably, acclimation capacity differs amongst coral species and appears inherently linked to the ability to mount rapid and lasting widespread transcriptomic changes[61–64] or reprogramming epigenetic marks[65–67]. In addition to acclimation within the lifetime of an animal, transgenerational plasticity might enable corals to acclimate to prevailing environmental conditions[48]. Such acclimation has been observed in experiments

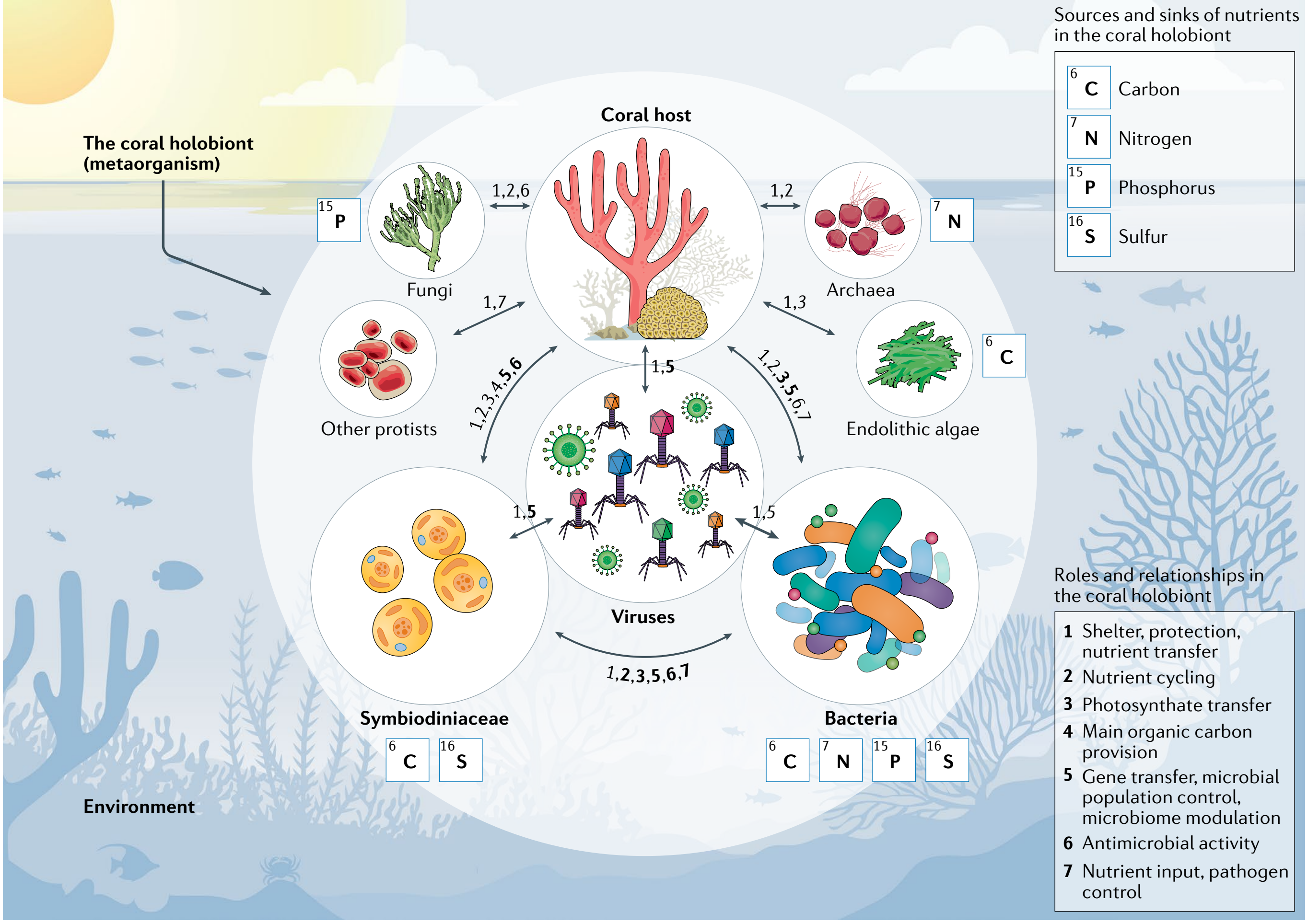


Fig. 1 | **The coral holobiont (metaorganism).** The holobiont is composed of the coral animal host, obligate intracellular algal symbionts (Symbiodiniaceae), and an assemblage of bacteria and viruses[160], among many other organismal entities (such as fungi, endolithic algae, and archaea) that are less well understood functionally. Viruses putatively intersect all coral holobiont compartments, can transfer genetic material between holobiont member species, and contribute to the holobiont's genetic diversity[193,199]. Known and inferred functional roles and relationships between holobiont member species as well as their contribution to metabolic cycling (carbon, nitrogen, phosphorus, sulfur) are depicted. Bold numbers indicate inferred functional roles. Coral holobionts constitute the foundation (meta)organisms of reef ecosystems, which explains their importance in efforts to devise strategies and interventions to save coral reefs.

comparing the performance of offspring from parents raised in different environments where acquired tolerances are passed on to the next generation[68–70], potentially linking transgenerational acclimation to DNA methylation[51].

Evolutionary adaptation through natural selection usually requires multiple generations, as the prevalence of selected alleles underlying the beneficial trait needs to increase and become a common trait of the population or species. Therefore, this process depends on several variables, such as the amount of genetic variation present in the population, the population size, the generation time, and the strength of selection. The standing genetic diversity of corals is presumably large[71–74], suggesting a capacity to recover from reductions in population size under suitable conditions, at least for some species[73]. Corals could also have the capacity to adapt via heritable somatic mutations[75,76]. The ability to rapidly adapt (years to decades) to changing environments is further supported by the presence and frequency of thermotolerance alleles and the modeling of population trajectories under different climate change scenarios[72,77]. Indeed, natural populations might already be adapting to increasing sea surface temperatures[78–80] or have previously adapted to extreme environmental conditions[81–83].

The ability of at least some coral species to exhibit substantial acclimation capacity presents the possibility to harness this capacity for reef restoration through a process termed environmental hardening (TABLE 1). For example, preconditioned coral fragments show increased resilience compared with naive coral fragments in some species[62,84]. These effects might even be passed on to the next generation[68–70,85]. Although the molecular mechanisms underlying these effects are not yet fully understood, epigenetic modifications such as DNA methylation and histone modification, amongst others, might be involved[48]. DNA methylation changes have been found in response to stress treatments[65] or transplantation[86] and were not only predictive of phenotypic responses, but also showed higher correlation than

Restoration
The action of returning something to a former condition, for instance through reinstatement of the original functional or genetic diversity.

Environmental hardening
The preconditioning of coral colonies to elevated temperatures as a means to increase tolerance to future heat stress events (can also apply to other stressors).

Table 1 | **Approaches to manipulate and harvest the adaptive response of the coral holobiont**

Method	Purpose	Deployment-ready?[a]	Scalability[b]	Costs	Risks	Further reading
Coral host						
Ex situ spawning system	Offset limitation to rely on natural spawning cycles; for use in land-based coral nurseries	Yes	Low	High	High	[52]
Coral Bleaching Automated Stress System (CBASS)	Selection and screening of larvae, colonies, and/or genotypes with increased thermotolerance as source material for coral nurseries, coral propagation, and/or coral restoration	Yes	High	Low	Low	[41]
Environmental hardening	Enhance stress tolerance of coral colonies through environmentally mediated priming of stress responses	Yes	Low	High	Low	[36,89,241]
Selective breeding	Increase frequency of stress tolerance alleles in local populations through selective breeding with resilient genotypes	No	Low	High	Moderate	[36,56,89]
Cryopreservation	Overcome asynchronous spawning events and assist gene flow among geographical regions	No	Low	High	High	[242–245]
Symbiodiniaceae						
Symbiodiniaceae probiotics	Bleaching and mortality mitigation through manipulation of coral symbiont pairings	Yes	Low	High	Low	[50]
Artificial evolution	Increasing heat tolerance of Symbiodiniaceae through in vitro evolution	No	Low	Moderate	High	[129,246]
Seeding/exposure of coral larvae to selected Symbiodiniaceae	Inoculation of early life history coral larvae to manipulate symbiont composition	Yes	Moderate	Moderate	Moderate	[141,247]
Bacteria						
Use of probiotic consortia	Ameliorate stress and improve coral health (pollution, disease, thermal stress)	Yes	Moderate	Moderate	Moderate	[54,183,248]
Use of coral growth-promoting probiotics and prebiotics	Accelerate and increase coral growth and calcification in coral nurseries; improve coral rehabilitation and restoration efforts through increased survivorship and resilience of fragmented/transplanted colonies	Yes	Moderate	Moderate	Moderate	[54]
Viruses						
Viral therapy of coral host	Boost stress tolerance	No	Moderate	Moderate	High	[189]
Phage therapy of bacteria	Pathogen control	No	Moderate	Moderate	High	[207–210]
Phage–BMC combination	Selection of favourable BMC members in addition to pathogen control	No	Moderate	Moderate	High	[177]

BMCs, Beneficial Microorganisms for Corals. [a]Indicates whether enough data are available to suggest that the method works in situ. [b]Assesses to what extent a method can be scaled up to work at the reef dimension.

changes in gene expression. More importantly, corals (in contrast to other metazoans) appear to biparentally pass on their DNA methylation patterns to their offspring, thereby providing a molecular mechanism for transgenerational inheritance of acclimation responses[51]. If such mechanisms indeed exist, they could be exploited by growing corals in land-based nurseries that allow controlled exposure to increased temperature or other stressors to induce favourable acclimation responses[87].

The extent to which resilience can be improved through environmental hardening and transgenerational acclimation is unclear. For example, there is still little understanding of which mechanisms promote this effect, the extent to which resilience can be increased, or how long the preconditioning effects are maintained. By comparison, assessments on the potential of selective breeding as a means to achieve coral adaptation have provided promising insights to improve restoration approaches through human intervention[56]. Similarly, breeding experiments reveal that genetic adaptations to higher temperatures can be passed on within a single generation, with coral larvae from parents of warmer regions producing offspring with up to ten times higher chances of survival under heat stress[88]. Importantly, the survival odds still increased by up to fivefold if only one of the parents came from a warmer region, providing evidence for the increasing thermotolerance of corals via assisted evolution[36].

Assisted evolution interventions follow the premise that ‘nature does it best’. Such approaches are generally less extreme than targeted genetic modification approaches; they rely on naturally occurring genotypes and natural selection to counter any drastic genetic alterations that would affect the remainder of the coral holobiont and its genetic constituents. Several interventions are proposed, such as the relocation of thermotolerant

Microhabitats
A small area that differs from the surrounding habitat, with unique conditions that could select for unique genotypes that might not be found in the remainder of the area.

colonies (genotypes) to cooler regions to introduce adaptive genetic variants into these populations or selective breeding using thermotolerant colonies[36,39,89]. Both methods attempt to mimic natural processes by increasing the frequency of beneficial alleles in the local population, providing a foundation for selection, while retaining both genetic diversity and the local genetic adaptations required for the success of corals at the specific location. Importantly, both methods rely on the identification and selection of thermotolerant genotypes (such as those from particularly warmer environments, for example, lagoonal pools). This identification requires the development of large-scale phenotyping platforms and knowledge of the natural distribution range of coral species under study. Selecting more stress-tolerant and resilient genotypes of the same species across locations is a non-trivial task given the challenges associated with coral taxonomy[90,91].

Platforms for screening large numbers of individuals for increased thermotolerance have been developed in the form of standardized, mobile, and inexpensive acute heat stress assays, such as the Coral Bleaching Automated Stress System (CBASS)[41,44,49,92,93]. The underlying premise is that corals that exhibit increased thermal tolerance in acute assays are also more resistant and/or resilient during natural heat stress events[41,44]. Indeed, considerable variation in thermotolerance can be found and resolved among coral colonies from the same and disparate sites using such short-term heat stress assays[41,43,64]. The genetic factors underlying such differences in stress tolerance are, however, not fully understood or identified[43]. Newly available CRISPR technology has been shown to work in corals and could be used to help understand the genetic basis of thermotolerance differences, in addition to offering the potential for engineering tolerant corals in the future, provided all safety requirements are satisfied[94,95]. Nevertheless, genetic alteration of single coral genotypes and their subsequent outplanting would rely on successful sexual reproduction with conspecifics and positive selection for the beneficial allele(s) to spread. Further, the genetic factors underpinning stress tolerance in corals are complex: it is a polygenic trait with potentially hundreds of genes involved, making genetic engineering challenging, although a subset of conserved genes exist that could form suitable targets for exploration and/or manipulation[43,63,96,97].

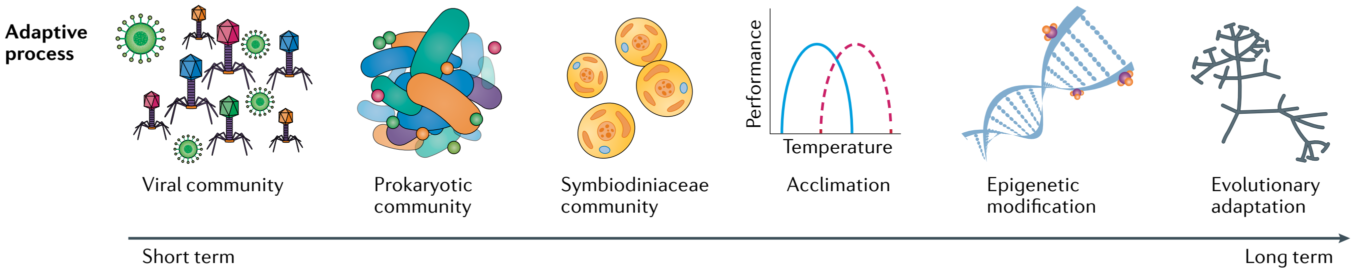
Colonies from warmer and often geographically distinct regions could provide higher gains in thermotolerance when considered for relocation or selective breeding, but there are associated risks, including potential dilution of local gene pools. Local environments exert selection pressures across a multitude of environmental parameters (so-called environmental mosaics), of which temperature is only one. The translocation of colonies across large geographic distances is therefore problematic as transplanted corals might face a foreign environment, potentially resulting in reduced fitness, reduced competitiveness and, ultimately, reduced survival[98,99]. In addition, the lack of clarity around coral taxonomy and the inherent plastic morphology raises concerns regarding crosses of colonies assigned to the same species from disparate locations.

Substantial differences in thermal tolerance can already be found at smaller geographic scales (for example at the reef scale), as coral reefs provide many microhabitats that select for more thermotolerant genotypes, resulting in large phenotypic variation within local populations available for exploitation[41,81,100]. Although this variation might not extend to the greatest extremes of tolerance possible for a given species, it avoids the risks associated with the introduction of foreign genotypes into local populations. Consequently, the identification of locally adapted colonies with high thermotolerance for selective breeding approaches could be the most prudent approach to follow, at least in the case of broadcast spawning corals[101]. Selected colonies from different microenvironments could be maintained in local land-based nurseries, allowing for controlled conditions and crosses, as well as the rearing of larvae to the pre-settlement stage to increase survivorship[102]. Unwanted domestication effects such as a growth advantage for corals that do better under aquaria conditions, however, could make it challenging to maintain coral genotypes that 'thrive' under environmental extremes in the wild[34]. Thus, the use of pre-settlement larvae screened for increased thermotolerance for deployment in local reefs and subsequent environmental selection of suitable genotypes might be the most promising approach[103].

Adaptive strategies of Symbiodiniaceae

Symbiodiniaceae are the primary photosymbionts of shallow-water tropical coral species[104]. These microalgae reside within the cells of their coral host and provide photosynthates that broadly cover the energy needs of the coral in return for a light-rich, sheltered environment, and the provisioning of CO_2 and other micronutrients[105–107]. Modern corals and Symbiodiniaceae co-diversified in the Jurassic Period (about 160 million years ago), linking the success of reef ecosystems to this symbiosis[104]. The Symbiodiniaceae family likely comprises hundreds of species[104,108,109], with comparative genomic data revealing extensive divergence among and within genera[104,110,111]. The substantial diversification of the family is explained by the high level of host specialization and fidelity, even under environmental extremes[112–114].

The coral–Symbiodiniaceae endosymbiosis is particularly sensitive to heat and light stress, which together can cause coral bleaching and subsequent mortality[12,15]. Although shifts in the dominant Symbiodiniaceae towards more thermotolerant species are observed[115], most novel associations do not persist[112,116]. Thus, considerable effort has been placed on understanding stress tolerance limits among Symbiodiniaceae and how these factors influence coral holobiont performance[117–119]. As a result, there is a growing appreciation for the diverse mechanisms that Symbiodiniaceae use to acclimate and adapt to changing environments on their own as well as in concert with their hosts[109,118,120,121]. For example, cultured Symbiodiniaceae cells are highly plastic with short-term acclimatory responses in growth, motility, gene expression, and photochemistry observed in response to changes in temperature, light, pH, salinity, and nutrient content[122–125]. Similar responses have been recorded in algal communities on coral reefs[43,126].



Adaptive intervention	Viral therapy	Microbial therapy (probiotics)	Environmental hardening →	Coral propagation Selective breeding
Timeline	Weeks–months	Weeks–months–years	Months–years	Months–years
General approach	Use of viruses to increase organismal health through various means	Use of Beneficial Microorganisms for Corals (BMCs) to promote coral health through various means	Exposure of corals to stress to accelerate adaptation/ acclimatization to adverse conditions	Frequency increase of stress tolerance alleles in coral populations
Application goal	• Biological control of pathogens • Improvement of coral host health/resilience • Provision of beneficial genes	• Biological control of pathogens • Bioremediation of impacts • Prevention of bleaching and mortality • Accelerated growth • Increased survivorship	• Prevention of bleaching and mortality • Increase overall coral resilience	• Prevention of bleaching and mortality • Increase overall coral resilience • Maintain genetic diversity
Readiness	🧪 ✓ 🪸 ✗	🧪 ✓ 🪸 (✓)	🧪 ✓ 🪸 ✓	🧪 ✓ 🪸 (✓)

Fig. 2 | **Adaptive processes in the coral holobiont and their utilization in adaptive interventions.** Interventions are meant to harness or extend the adaptive capacity of coral holobionts to increase their resilience. Note that all adaptive processes, except for evolutionary adaptation, can happen within the lifetime of the coral holobiont. In the readiness category, the flask represents successful implementation in laboratory trials and the coral represents successful implementation in field trials, with brackets denoting approaches that work in principle but for which either standardized or upscaling protocols are needed.

Symbiodiniaceae also possess many traits that favour rapid evolutionary adaptation, including short generation times, both sexual and asexual reproductive modes, and genomic adaptive precursors, such as extensive functional enrichments, mobile elements, and RNA editing[110,125,127,128]. Interactions with corals and the loss or gain of a symbiotic lifestyle are also predicted to drive evolutionary change[111]. Even in the absence of their coral hosts, experimental evolution protocols over several years have induced major genetic and phenotypic changes in cultured Symbiodiniaceae[129]. In nature, Symbiodiniaceae typically exhibit a more pronounced population structure than corals[130], signifying geographic isolation, local selection, and opportunities for local adaptation[41,43,113,114,130–132].

Variation in the extent of symbiont specificity among coral life stages is important for predicting the potential for different coral species to change their symbiont communities through acclimatory processes such as switching or shuffling, which involve reorganizing the symbiont community to favour dominance of heat-tolerant taxa[133–135]. Coral larvae and juveniles are more plastic in their association with different Symbiodiniaceae compared with adult colonies[136–138] and these could be the critical life stages for focused manipulative experiments (FIG. 2; TABLE 1). Indeed, manipulation of host–symbiont pairings might be a critical component of both natural and artificial adaptive strategies. However, there is limited evidence for successful long-term manipulation[50,139]. Short-term manipulation of the coral–algal symbiosis can be experimentally achieved at early life stages via symbiont seeding from the environmental pool or by providing new symbiosis opportunities (for example, by sourcing conspecific symbionts from geographically distant environments, or novel symbionts from distinct host species)[140–144]. Further approaches include the stress-hardening of adult corals with more invasive methods, including implanting cores of coral tissue containing heat-tolerant symbionts[139] or via direct genetic engineering of the symbionts themselves[145]. However, Symbiodiniaceae seem intractable to such manipulation at present[146].

Ultimately, the utility of symbiont community manipulations is dependent on whether such alterations are heritable[147,148]. If induced changes do not persist across coral generations, they will only function as temporary stopgaps. Although there is evidence to suggest that a component of altered Symbiodiniaceae community composition is heritable[148], in the vast majority of cases examined, associations appear to be highly specific[104,112–114]. Thus, any symbiont shuffling that takes place naturally or artificially after thermal bleaching or exposure during larval or juvenile stages does not persist across generations. Instead, the original symbiont composition is restored when environmental conditions return to normal, or after juveniles develop mature immune systems[149–152].

The exception to the rule of reversion to the original community is evident when stressful conditions persist for extended periods or recur with high frequency[115]. In such cases, the balance shifts such that stress-tolerant Symbiodiniaceae are favoured over metabolically optimized symbionts, and novel species can remain as the numerically dominant partner. With the frequency and intensity of bleaching events increasing, it has been argued that environmental conditions on reefs could soon favour thermally tolerant, novel symbionts[139]. Such replacement seems to be underway in the Caribbean, with the spread of the heat-tolerant, potentially invasive *Durusdinium trenchii*[115,153]. Among Pacific reefs with biannual or annual repeat bleaching, symbiont communities have also already been observed to shift towards dominance of heat-tolerant Symbiodiniaceae[154,155], although it is unknown whether such shifts persist across generations. However, even the most resilient symbionts are expected to provide no more than 2 °C of additional thermal tolerance to the coral holobiont, a threshold that will likely be exceeded in the tropics within the next 100 years[156]. The benefit might increase if coral holobionts evolve to reach greater optima in this period[80], although the pace of such evolutionary processes under these conditions is unknown.

Even if altered symbiont communities could persist across generations, there are practical limits to artificially manipulating associations on a large scale. The inoculation and/or manipulation of individual coral adults might only provide single-colony scale resolution due to labour-intensive methods (TABLE 1). The most promising, scalable approach is to introduce coral larvae or juveniles to alternative algal symbionts while rearing large batches as part of ongoing restoration projects. However, mortality at these early life stages is high (up to >99% for larvae), although the numbers are improving with technological advances[102,157]. Such efforts might be able to seed struggling reefs with thermally tolerant coral individuals in the future. Currently, the most efficient means of manipulating symbiont communities at scale remains — ironically — anthropogenic climate change.

Adaptive strategies of prokaryotes

Prokaryotes (bacteria and archaea) have a crucial role in the health, fitness, and environmental adaptation of metaorganisms[46,158–161]. The coral microbiome (the community of bacteria and archaea) is influenced by the surrounding environmental conditions, host species, age, and size of colonies[162–165]. These community diversity patterns reflect the dynamic relationship between prokaryotes and environmental conditions, which are hypothesized to select for the most advantageous coral holobiont composition under a given setting, termed the coral probiotic hypothesis[166]. The concept of microbiome flexibility[46] extends the coral probiotic hypothesis and acknowledges that the capacity for microbial change differs among coral species, with some coral species showing large microbiome changes across adverse environmental regimes, whereas others exhibit highly conserved bacterial assemblages[49,165,167]. Despite such flexibility, numerous taxonomic groups are found consistently associated with corals, such as *Endozoicomonas*[168,169]. Some of these taxa correlate with health, such as *Roseobacter* spp.[170,171] or *Pseudoalteromonas* spp.[170,172], and others with disease, such as *Vibrio* spp.[173,174] or *Rhodobacter* spp.[175], although the role or function for the majority of prokaryotes is unknown.

Manipulative studies employing reciprocal coral transplants or microbial manipulations that correlate changes with increased coral stress tolerance[49,55,165,172,176] highlight that microbiome alteration could provide an alternate route to environmental adaptation, facilitating rapid responses of corals to changing environments[46,49,55]. Microbiome flexibility to adapt to adverse environmental conditions underlies the concept of Beneficial Microorganisms for Corals (BMCs) that centres around the identification of microbes that promote coral health and their subsequent utilization as coral probiotics[38,177]. Manipulating the coral microbiome is less about the mitigation of a specific impact, but focuses on increasing overall health, based on the premise that a healthier organism is more resilient when subjected to stress[54,178]. Such health improvements could mitigate an array of impacts that include thermal stress, pathogen challenge, and poor water quality[54]. Accordingly, BMCs help to reboot an altered and dysbiotic microbiome caused by environmental stress[165,179], with the intention to outcompete opportunistic and detrimental microbes to restore or rehabilitate the altered microbiome and its microbial-mediated functions to the coral holobiont[38,165] (FIG. 2; TABLE 1).

Several proof-of-concept studies now demonstrate that exposure of corals to BMCs can improve coral health through potentially mitigating stress and toxic compounds or controlling pathogens, although the underlying molecular mechanisms remain to be determined[54,180,181]. For instance, BMCs were successfully applied to ameliorate impacts caused by pathogens[182] or toxic compounds[180,181]. Bacterial BMCs to mitigate coral thermal stress have been genomically and biochemically screened for beneficial functions including pathogen-targeted antimicrobial activity, reactive oxygen species (ROS) mitigation, dimethylsulfoniopropionate (DMSP) breakdown, and nitrogen cycling[172,183]. BMCs can even promote coral bleaching recovery and prevent coral mortality through mitigating post-heat stress disorder (PHSD) syndrome, possibly through bacterial ROS scavenging, coral host transcriptional reprogramming, and provision of alternate nutrition sources to boost coral energetics[183].

BMC treatments appear to be most successful when applied during the stress exposure. However, BMCs are not retained for long periods of time, therefore likely requiring to be readministered at times of stress[54,183], although retention might differ by life stage[162]. The application of coral prebiotics could also assist corals in the selection and retention of BMCs. Prebiotic application with or without administered BMCs during bleaching events could promote active enrichment of the coral microbiome as well as facilitate association with beneficial microbes (FIG. 2; TABLE 1). In addition, the development of strategies to scale up BMC delivery is required. Such upscaling might be achieved through

Beneficial Microorganisms for Corals
(BMCs). Umbrella term to define (microbial) symbionts that promote coral health and can be used as probiotics.

Coral probiotics
Live microorganisms to benefit coral host health.

Coral prebiotics
Molecules that modulate bacterial (microbial) association to benefit coral host health.

Lysis
A common outcome of viral infections, whereby cells are actively induced by viruses to release newly assembled viruses that can then infect other cells.

Genetically modified organisms
(GMOs). Organisms whose genomes are engineered to produce specific traits of interest.

immobilization of microbial cells and/or slowing their temporal release through attachment to biocompatible carriers, as well as bioencapsulation in prey or uptake through heterotrophic feeding[54,184]. Although existing genetic engineering techniques are easily applied to bacterial isolates derived from corals, they should be restricted to a laboratory context, as the effects that such altered genetic variants could exhibit in the highly complex and diverse coral reef environment (for example, interaction with pathogens) are unknown[185–187]. Accordingly, coral microbiome manipulative approaches at reef sites should focus on utilization of microbes (bacteria) from the native environment.

Adaptive strategies of viruses

Viruses can contribute to the evolution of their hosts and are critically important for the functioning of marine ecosystems[188]. A mechanistic understanding of the direct role of viruses in holobiont acclimation or adaptation is lacking, but there is evidence that viruses have a role in coral health, disease, or stress (thermal) tolerance[189–192]. One explanation could lie in bacteriophages — the most abundant members of the coral metaorganism — controlling the abundance of specific bacterial strains through lysis, thereby shaping the structure of the microbiome and its functional landscape[186,193].

In humans and mice, viral predation of bacteria selects the bacterial strains that are able to colonize an animal host upon invasion[194,195]. When the lytic removal of bacterial strains is selective against pathogens, the viral predation effectively creates a form of immunity that is extremely plastic[196,197]. Evidence suggests that in a similar way, coral-associated viruses prey on detrimental bacteria that grow when stimulated by competitor turf algae[198]. Selective viral predation of bacterial strains causes viral–host co-evolution that could be a strong force shaping the coral microbiome, thereby affecting coral holobiont adaptability[46]. Yet the specific mechanisms underpinning these interactions are unknown, as well as how common such patterns are.

Another way in which bacterial viruses can shape the microbiome, and by extension the genetic and genomic make-up of the coral holobiont, is through lateral gene transfer[199]. Two main modes of viral-based genetic transfer occur, one when random fragments of bacterial DNA are packed into viral particles and the other when specific regions of bacterial chromosomes that flank integrated phage sequences are transferred. In both cases, lateral gene transfer can bring benefits analogous to sexual reproduction, such as increasing fitness and compensating for detrimental mutations in populations that replicate exclusively clonally[200]. Therefore, a viral-mediated increase in genetic exchange is expected to facilitate bacterial, and by extension microbiome, adaptation to changing conditions. However, coral reef phages could also transfer bacterial virulence genes that enable pathogen invasion of coral tissues and cause disease[201,202]. Indeed, transitions in viral community composition have been associated with numerous coral diseases[192,203]. However, little is known about the factors that determine how frequently coral-associated viruses transfer genes with beneficial or pathogenic effects to the coral host. The coral virome also contains abundant and diverse eukaryotic viruses[199], which become more abundant during bleaching[190], although cause versus consequence is unknown. Specifically, viruses infecting Symbiodiniaceae could have a direct effect on coral thermal sensitivity, potentially by increasing rates of predation at high temperatures[189,204,205].

The application of viruses for coral acclimation and adaptation could take two main (but not exclusive) routes (FIG. 2; TABLE 1). First, viral therapy could help boost stress tolerance[189], pending the successful isolation and culturing of such viral associates. Similarly, phage therapy could be used to control coral diseases when a bacterial pathogen can be identified. Second, phages could be employed to improve the efficacy of BMCs across a suite of applications (for example, to mitigate thermal stress, disease, or oil spill impacts). The application of viruses with BMCs in a 'dual benefit approach' to target specific pathogens and improve coral holobiont health is probably the most realistic near-future application. In principle, phages could be used as a tool to transfer desirable genes to members of the BMC consortia (or other entities of the coral holobiont), making them more efficient in colonizing the coral holobiont or stabilizing associations. However, this method would involve adding genetically modified organisms (GMOs) to natural ecosystems, an approach less likely to gain support. Alternatively, native coral-associated viruses could have their abundances manipulated, increasing their natural rates of predation or gene transfer, depending on the desired effect on the bacterial community. This approach relies on a better understanding of the functions of each microbiome and virome member[193].

Phage therapy, in particular, is a promising tool for restoration or rehabilitation processes because it addresses the problem of scaling — through their high replication rates and population expansion, phages presumably would distribute even at the reef scale[206,207]. For example, phage therapy has successfully prevented bacterial-induced photosystem inhibition in Symbiodiniaceae[208] and inhibited white plague disease progression in *Favia favus* in aquaria and in the field[209,210]. However, the possibilities for applying phage therapy on corals in the wild are very limited because of unanticipated off-target effects and the potential of uncontrolled expansion. The application of phage therapy to treat coral diseases is also constrained because, for most coral diseases, the causative pathogens have not been identified and many diseases might not be caused by a single distinct pathogen[211–214].

There are several essential questions that need to be answered if viruses are to be applied in coral restoration efforts. Perhaps the most pressing need is the reconstruction of virus–host infection networks of coral species targeted for manipulation[215]. Most of the viruses identified in coral microbiomes have not been matched with a host, prokaryotic or eukaryotic, although available data suggest that many perceived viral–host associations need to be re-evaluated[190,199,203]. For instance, Hepadnaviridae are typically ascribed to be vertebrate-specific but have been found associated with coral genera[199]. This lack of knowledge about virus–host relationships prevents the identification of viruses that are potentially beneficial for coral, either through modulating the associated microbiome and its genetic pathways, affecting the response to stress (including Symbiodiniaceae), or encoding genes that improve microbiome function. The reconstruction of phage–bacteria infection networks will also contribute to constraining the possibility of off-target infections and recombination in phage therapy. By knowing how similar an introduced phage is to the resident phages, the risk of moving unwanted genetic material through lateral gene transfer can be reduced[216]. Such risk reduction is especially important because many resident phages encode bacterial virulence genes, which must not be accessible to bacteria that are strong colonizers of coral mucus and tissues[199,202,217]. Applying native phages that originate from the same or similar coral reef and coral holobiont that will be treated reduces the risk of off-target effects.

An adaptive intervention framework

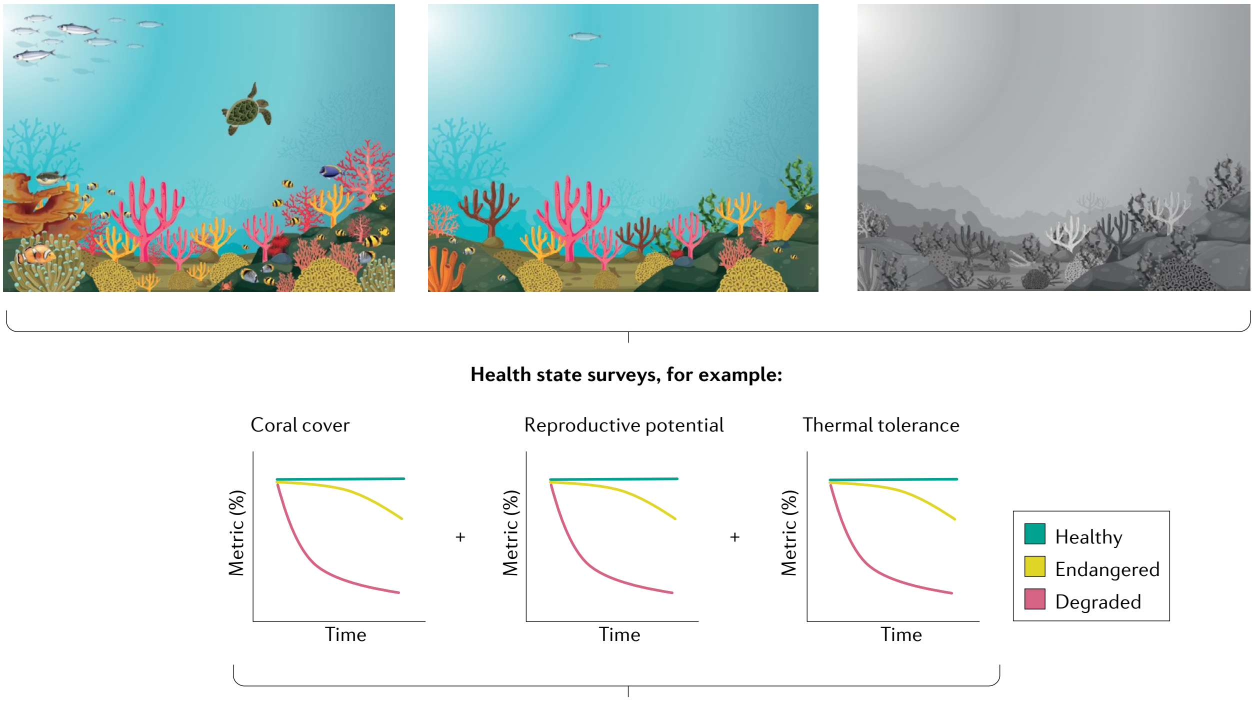
Societal need to retain healthy coral reefs under climate change is driving a new era of innovation in reef science, evidenced by global multidisciplinary exploration of approaches to enhance coral resilience[30,89,218]. From a pragmatic point of view, restoration — trying to recreate reefs as they once were — is largely unachievable, but also would likely not provide future resilience as climate stressors persist and intensify[219]. Rather, enhancing current functional and/or genetic diversity through environmental rehabilitation to allow reefs to thrive under the new set of conditions should be aimed for. Embedding this central philosophy is critical as reef conditions are likely to worsen before they improve, even if the Paris Agreement goals are achieved[30,32,220]. Intervention measures aimed at increasing coral resilience will hopefully retain enough functional coral reefs to assist in long-term recovery. The following sections outline how such intervention measures could look, how they complement and can be integrated with existing practices, and how their efficacy can be monitored in the wild.

Environmental rehabilitation
The action of restoring to an improved condition to allow species and ecosystems to thrive under altered environmental conditions.

Extending the coral holobiont natural adaptive capacity. Intervention approaches have the greatest potential, feasibility, and readiness if harnessing the natural adaptive capacity of corals, thereby employing naturally evolved solutions that are tried and tested in reef ecosystems. They also avoid many of the concerns associated with genetic and/or technological engineering, and therefore governance and social licence. Risks will vary depending on the intervention approach, with, for example, environmental hardening possessing less risk although with limited longer-term resilience gains than selective breeding approaches, which directly interfere with coral population structures. Risks associated with the use of probiotics or other means of microbiome manipulation can be reduced if native microbiome partners are used, although how long these treatments persist or whether these approaches need repeated application requires investigation. It is essential to assess their longer-term benefits to determine their efficacy, applicability, and the best way to combine or integrate them with other techniques (FIG. 2; TABLE 1). Nature-based solutions still entail manipulation of biological interactions amongst holobiont partners, albeit avoiding any use of GMOs. Gaining a better understanding of the interactions between holobiont member species is necessary to identify and maximize synergistic effects through targeted combinations of different intervention methods, whereby all combinations are theoretically possible (FIG. 3). Selective breeding, for instance, can provide substantial increases in temperature resilience and could be further boosted through environmental hardening and/or the provisioning of probiotics and alternative algal symbiont strains.

The combination of different approaches does not rely on additional infrastructure beyond what is required for their independent implementation. Given the differences in practicality, scalability, and the time required for the interventions to take effect, it might be most efficient to combine technologies at different levels. Although selectively bred corals likely have the highest potential for resilience gains and scalability in the long run, their production is costly and scaling up is mostly achieved through propagation in the wild[139,221,222]. Implementation will therefore require natural populations to persist to provide enough coral cover for efficient natural reproduction and the preservation of ecosystem services. Initially, more scalable methods such as probiotics and Symbiodiniaceae manipulations could be used to increase resilience of the natural populations, ensuring sufficient coral cover to maintain coral reef function and providing enough colonies for efficient sexual reproduction and sufficient genetic diversity until beneficial alleles reach critical densities in the populations (FIGS 3 and 4). Currently, however, it is unknown to what degree interventions centred around the coral holobiont translate into observable reef-level effects or the time that is required for holobiont-targeted interventions to manifest at the reef level. Addressing this gap in knowledge between holobiont-centred interventions to meet reef ecological scale goals is a key priority for global restoration efforts.

A scaled adaptive intervention framework. Coral propagation provides the fundamental practical framework needed to accelerate reef restoration, where the goal is to deliver coral functional diversity (in the form of taxonomic diversity that covers the different functions provided by reef-building corals) at a scale that exceeds natural recovery (as well as mortality) rates. Most coral restoration practices worldwide, however, still rely on asexual fragmentation-based propagation of individual genetic (or phenotypic) lines, and therefore, do not address restoration of functional genetic diversity[40]. Asexual fragmentation is a method utilized to boost living coral tissue within degraded reef areas quickly. It can also be implemented in situ by non-specialist groups, in particular through innovations enabling scalability of nursery-based propagation and outplanting rates[223–225]. Propagation and outplanting success is generally high (>75–90%)[40,225,226], but survivorship can decline precipitously over time[226,227], especially where other factors — such as disproportionately high corallivore rates — are not simultaneously mitigated. Success is further confounded where practices often operate without knowledge of the inherent genetic and functional diversity, and hence, do not increase the resilience of corals produced and even run the risk of adaptive bottlenecking in the long term[42,221]. Consequently, effective repopulation rests on capturing sufficient genetic and functional diversity to resist stochastic environmental change[224,228,229].



Traits	High diversity of corals, absence of or only a few dead colonies, absence of disease	Low diversity of corals and/or bleached colonies and/or dead colonies and/or prevalence of disease	Low diversity/lack of corals and/or high abundance of bleached and dead colonies and/or dominance of other organisms than corals
Diagnosis	Healthy reef	Endangered reef	Degraded reef
Indicated action	Focus on measures to understand and preserve (or enhance) reef status	Reversal of environmental conditions with potential application of manipulative techniques (for example, probiotics)	Reversal of environmental conditions in parallel with expanded application of manipulative techniques (for example, probiotics, selective breeding, etc.)

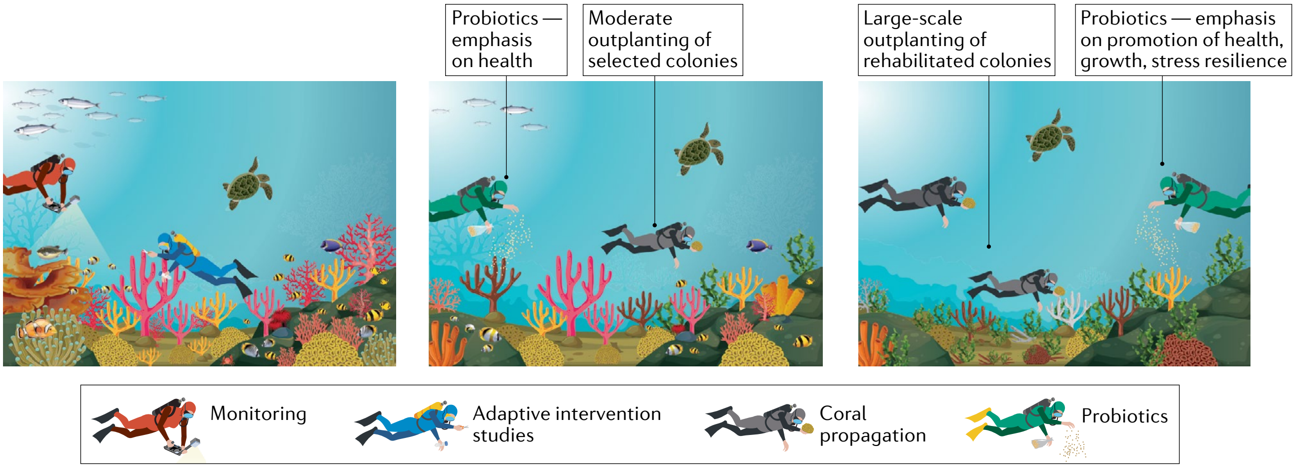


Fig. 3 | **A scaled adaptive intervention framework.** Development and implementation of systematic health state surveys can provide a decision framework with standardized diagnostics, and, in turn, a suite of indicated intervention measures under consideration of the diverse reef, environmental, and ecological conditions. Diagnosis of endangered reefs, for instance, could detail several levels of degradation, where ecological traits such as coral cover, reproductive potential, and thermal tolerance are differentially affected. Accordingly, degraded reefs could be defined by predominant presence of bleached and/or diseased colonies that outnumber the prevalence of healthy colonies. In the scaled adaptive intervention framework, healthy reefs can help elucidate the role of coral holobiont entities as targets for adaptive intervention, whereas endangered and degraded reefs can be targets for a range of manipulative techniques pending the level of threat and traits to be restored.

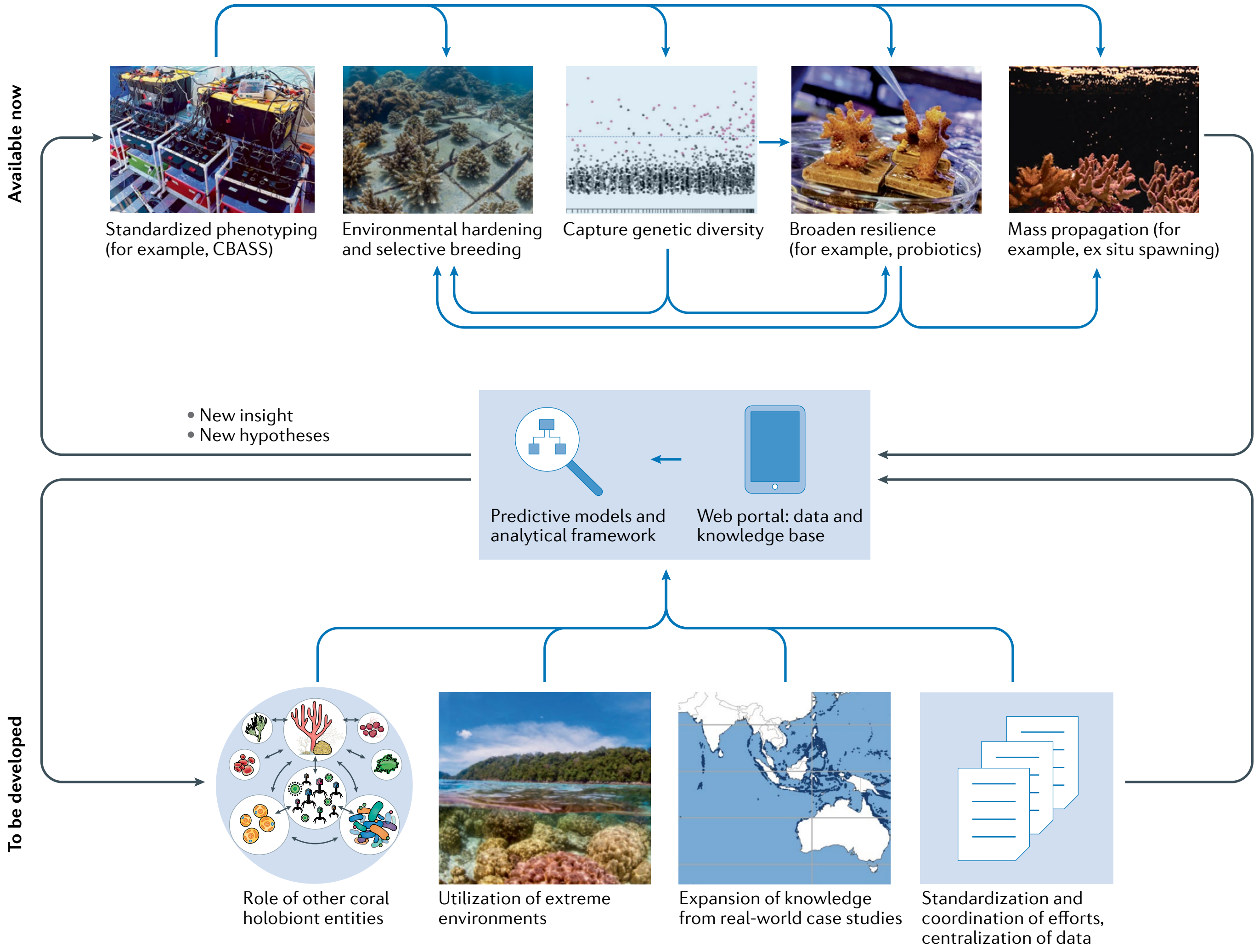


Fig. 4 | **Research road map for extending the adaptive capacity of the coral holobiont.** Emerging approaches (upper half) can inform and integrate with coral restoration measures (blue arrows). For instance, the thermal stress response of many colonies can be assessed using a standardized approach (such as the Coral Bleaching Automated Stress System (CBASS)) to identify coral colonies for selective breeding or environmental hardening. In addition, the success of restoration and/or rehabilitation and probiotic approaches can be monitored with this system. Likewise, information on genetic diversity can be incorporated into propagation approaches to enhance thermal resilience and maintain genetic diversity, and ex situ spawning can increase the input of larval supply for coral restoration through propagation. Alongside the characterization of further holobiont member species with beneficial effects, the study of corals from extreme environments can inform on and provide a source of adaptive alleles, adaptive mechanisms, and powerful probiotics underlying coral resilience (lower half). To improve success and inform adaptive intervention decision frameworks, it is essential to expand and integrate knowledge from real-world case studies. Increasing standardization and coordination of efforts can be leveraged through construction of a global database to provide a long-term defined and coordinated strategy, enable comparative (meta-)analyses and track success to catalyse and hasten effective coral reef conservation. Standardized, coordinated data recording can serve as a foundation for building predictive models and analytical frameworks that incorporate ecological, physiological, and molecular dimensions. Images courtesy of A. Roik and J. Craggs.

As such, sexual propagation techniques to maximize genetic recombination of parents — and hence adaptive potential — through either controlled (such as selective breeding amongst genotypes) or uncontrolled (such as mass larval-based seeding of outplant structures) approaches[88,140,221,230] represent an essential and necessary pipeline, not only for coral reef restoration, but for rehabilitation.

Coral propagation approaches are now becoming tuned towards adaptive capacity. New diagnostic tools can be deployed to identify within-species diversity for more informed propagation decision-making[41,42], and ex situ spawning aquarium systems can be employed to overcome limited larval supply imposed by annual coral spawning events[231] (FIG. 4). Efforts in the Indo-Pacific have demonstrated how propagating within-species genetic diversity is important to ensuring efforts against transient heat waves[44]. This work suggests that new tools capable of high-throughput diagnostics of tolerance to different stressors, such as CBASS assays[41], could become critical components in scaling coral restoration effectiveness and informing targeted breeding approaches (FIG. 4). Resolving the extent of local coral holobiont diversity — and how it is interdispersed amongst sites via connectivity and reproduction patterns[232,233] — provides a logical basis for ensuring that active propagation efforts exploit the maximum available range of genetic diversity and coral functional performance (FIG. 4). Efforts are rapidly gearing towards overcoming technical and methodological constraints for selective breeding approaches based on large-scale sexual propagation[221].

Alongside these efforts to enhance coral resilience, it is still important to mitigate the impact of environmental parameters, such as water quality, that are broadly linked to reef resilience and directly implicated in coral bleaching and disease susceptibility[24–26,165]. Interventions to enhance the stress tolerance of corals are unlikely to succeed without addressing local environmental conditions. Moreover, the technology to grow more resilient coral colonies is available (FIG. 2), but colony and reef growth will not naturally speed up. Better integration of current reef management practices and scaled adaptive approaches are required (FIG. 3). Local stressors, such as water quality and overfishing, act synergistically with climate change and represent important targets for intervention measures to counter some of the effects of global climate change[24,25,27]. Measures to improve water quality or reduce overfishing, alongside the management of other environmental drivers of reef decline, should be prioritized alongside the more manipulative coral holobiont-centric intervention measures presented here.

Standardization and monitoring success. Despite the prospect of combining emergent technologies with tried and tested approaches, standardized protocols must be developed and made available for broad application, which should become more available in the coming years, or are already in place[221] (FIGS 2 and 4). Restoration and/or rehabilitation will likely benefit from operational frameworks that can adopt 'best of both worlds' practices: more specialized, manipulative (and likely costly) solutions to be applied when reefs are severely endangered or degraded, in balance with broader scale measures that aim to maintain reef health and do not require sophisticated instrumentation or knowledge to be implemented (such as monitoring water quality) (FIG. 3). In addition, not all intervention measures are needed everywhere and all of the time. Rather, standardized surveys to determine the reef state, for example through measurements of coral cover, reproductive potential, and thermal tolerance, can provide a list of indicated actions (FIG. 3). In all likelihood, no unified approach exists that could be used globally because local conditions can either amplify or reduce climate change impacts and therefore must be considered[27].

Continuous monitoring to determine success and identify potential risks or side effects of applied approaches is also critically important. Although survival following bleaching events will ultimately determine how successful the applied intervention measures were in increasing resilience, the identification of potential risks will require more active efforts. For instance, when using selectively bred corals, the coral population structure should be monitored to determine how frequencies of beneficial alleles increase over time or whether outbreeding depression can be observed. Similarly, the application of coral probiotics requires regular monitoring to assess any changes in the microbial community assemblage and potential reapplication of the treatment.

Summary and future perspectives

Coral reefs globally are rapidly degrading, requiring the development and implementation of novel intervention strategies to mitigate the impacts of ongoing climate change and environmental degradation. Research activities are attempting to extend the adaptive capacity of reef-forming corals through integration of novel tools, methods, and environments that are studied to increase the survival of corals under more extreme or variable conditions. A particular emphasis on the coral holobiont as the functional biological unit provides a more complete and better understanding of coral functioning while opening the door for novel strategies and targets to harness and maximize the adaptive capacity of corals and the reefs they build to survive climate change. These emerging approaches need to consider and be tailored towards the different reef, environmental, and ecological conditions. Implementing an adaptive intervention framework tailored around nature-based solutions requires standardized methodology, safety assessments, and analytical routines for consistent and most effective utilization and global coordination.

Work on the following four areas could accelerate implementation of the framework described here, starting with increasing understanding of the role of other coral holobiont entities as targets of adaptive intervention. For instance, endolithic algae (such as *Ostreobium*) can translocate fixed carbon to the coral during coral bleaching, potentially providing resilience to thermal stress by offering alternate energy provision to sustain coral function[234,235]. Similarly, corallicolids (Apicomplexa) live inside coral tissues and are only second in abundance to Symbiodiniaceae, but their ecology is still unclear[236]. Second, extreme environments should be utilized as sources of discovery regarding adaptive mechanisms, powerful probiotics and the biological, ecological and physico-chemical characteristics underlying coral reef refuges[81,237–239]. Third, knowledge from real-world case studies must be expanded: it is currently unknown how much 'manipulation' within a given population is ideal ecologically or acceptable from a management perspective. In other words, the relative contribution of selectively bred versus randomly bred coral colonies must be investigated, along with the amount of manipulation needed to exert a measurable effect at the reef level. This knowledge is likely to be highly variable for reefs from different localities[37]. Similar considerations apply for assisted gene flow or seeding coral larvae approaches.

Last, the application of manipulative approaches will be most effective through standardization and coordination of efforts, which will also allow assessment of feasibility, efficacy, and associated risks in a much quicker and more coherent way[41,108,240]. Predictions of coral survival are imperfect. All reefs and corals are subject to changing environments, and it is not clear whether the best predictor of future coral colony survival is their past survival. We need to derive standardized analytical and decision frameworks that are accurate, easy to implement, and reliable at predicting measures that provide corals and reefs with the highest chance of survival. Such standardization will be reliant on a global data and knowledge base to enable comparative (meta-) analyses and provide a long-term defined and coordinated strategy to catalyse and ensure effective coral reef conservation.

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