

Review

Coral environmental memory: causes, mechanisms, and consequences for future reefs

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The apparent ability of corals to acquire and maintain enhanced stress tolerance through a dose-dependent environmental memory, which may persist for multiple years, has critical implications for coral reef conservation research. Such responses are variable across coral species and environmental stressors, with primed corals exhibiting a modified response to secondary stress exposures. While the mechanisms underlying coral memory responses are poorly understood, they likely involve both the coral host and microbiome. With advances in molecular technologies, it is now possible to investigate potential memory mechanisms in non-model organisms, including transcriptional regulation through epigenetic modifications. We integrate evidence of coral environmental memory and suggest future research directions to evaluate the potential for this process to enhance coral resilience under climate change.

Stress memory in the Anthropocene

The rapidly changing climate constitutes an extreme threat to species across the world's ecosystems, with especially dire consequences already occurring in marine environments [1]. A comprehensive understanding of the mechanisms enabling organisms to cope with environmental variation is essential to more accurately predict the impacts of continued global change [2]. In addition to genetic **adaptation** (see *Glossary*) across generations, organisms can respond more rapidly to environmental change through nongenetic mechanisms involving modifications of the phenotype without changes to the underlying DNA sequences (e.g., **acclimatization**) [3].

Stress memory is one such mechanism distinguished by the temporal separation between a 'priming' stimulus and subsequent 'triggering' stimulus that elicits a distinct response from naïve organisms [4]. In contrast to **acclimation** and acclimatization, which include context-dependent phenotypic plasticity [5], stress memory requires the retention of information from the priming cue (i.e., memory) to modify the response to a later stress exposure (reviewed in [4]). The process in which a memory of abiotic stressors is developed (i.e., **environmental memory**) represents a strategy to withstand recurrent environmental stress without relocation, which is critically important for spatially restricted or sessile organisms that experience variable conditions [6]. Well documented in terrestrial plants [6,7], this phenomenon has also been observed in marine plants [8,9] and planktonic or sessile invertebrates [10,11] and may be particularly important for long-lived, sessile marine organisms such as corals [12].

Corals are cnidarian animals that host complex microbial communities, including photosynthetic dinoflagellates of the family Symbiodiniaceae, which support host metabolism [13]. **Coral holobiont** resilience and survival depends upon homeostasis between symbiotic partners and this equilibrium is susceptible to perturbation by variations in abiotic conditions [14]. As such, corals are especially vulnerable to environmental stress and threatened by the changing climate

Highlights

Memory of a prior exposure to environmental stress can increase the tolerance of subsequent exposures, which is vital for sessile organisms. This phenomenon has been well described in terrestrial plants and there is evidence demonstrating environmental memory in marine organisms, particularly corals.

Global climate change and local anthropogenic stressors have resulted in dramatic declines in many coral populations. Environmental memory may be an important mechanism for corals to cope with the rapidly changing climate, especially given their vulnerability to environmental stress.

Increased coral stress tolerance has been observed across recurrent marine heatwaves and following experimentally applied stress exposures. Such 'stress hardening' methods have recently been highlighted as priority conservation interventions to enhance coral resilience.

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[15]. Therefore, enhanced resilience will be vital for the survival of these organisms under rapid global change [12]. Given the importance of corals in supporting the biodiversity and ecosystem services associated with coral reef ecosystems [16], recent efforts have focused on elucidating mechanisms underlying changes in coral stress tolerance [17, 18], especially those with direct conservation applications [3]. In fact, physiological interventions dependent upon environmental memory have been identified as strategies to increase coral resilience [19].

Evidence of environmental memory in corals

It is well established that historical and contemporary environmental regimes can influence coral resilience through local acclimatization and adaptation [5, 17, 20]. In addition, increases in the stress tolerance of individual corals have persisted across transient stress exposures within both natural and experimental settings, suggesting a capacity for environmental memory, or a retention of information from prior environmental experiences, in corals (Figure 1 and Table 1). Such a phenomenon was first documented during a thermal **coral bleaching** event in 1995 in Phuket, Thailand, where the western sides of *Coelastrea aspera* (massive to encrusting stony coral) colonies bleached less than the eastern sides of the same colonies [21]. This enhanced thermal tolerance was attributed to previous experience of increased solar radiation [22] and (most surprisingly) it was maintained for 10 years in the absence of the priming cue [23].

Decreases in bleaching incidence and/or severity across recurrent **marine heatwaves** also provide evidence of enhanced coral resilience conferred through prior stress exposures and maintained across temporally distinct stress events [24–26]. For instance, studies tracking the fate of corals in the Florida Keys, USA, revealed an increase in thermal tolerance across annual bleaching events (i.e., decreased bleaching severity during the second year, despite comparatively higher heat exposure) [27, 28]. Similarly, decreases in coral thermal sensitivity across recurrent marine heatwaves have been documented in cores of massive *Porites* corals in Northwestern Australia [29], the Northern Great Barrier Reef (GBR), the Coral Sea, and New Caledonia [30]. Evidence of coral environmental memory has also been found using **stress hardening** approaches (Figure 1B and Table 1). For example, thermal priming treatments have conferred increased thermal tolerance in primed corals, evidenced by reduced levels of coral bleaching [typically quantified through declines in Symbiodiniaceae density and/or maximum dark-adapted yield of photosystem II (F_v/F_M)] during a subsequent thermal challenge, relative to naïve corals [31–34]. Beyond thermal stress, enhanced tolerance has also been described in corals primed with simulated future **ocean acidification** conditions [35, 36], increased irradiance [37, 38], and herbicide exposure [34].

Importance of the priming exposure on coral memory

Coral responses to environmental stress are dependent upon both the magnitude and the duration, or dose, of the perceived stressor [39]. Consequently, the dose of the priming stimulus mediates the response to subsequent stress exposures (Figure 2A). An initial priming exposure that is insufficient in duration, magnitude, or both, may fail to elicit a detectable memory response [40], while an exposure that exceeds a tolerable threshold can weaken the organism to the point where any potential benefit is lost [41–43]. In the case of thermal stress, experimental priming doses have ranged from days to months in duration and 1–8°C above ambient temperatures, which have elicited beneficial [31–34, 41, 44], detrimental [33, 41–44], and neutral [33, 40, 43, 44] effects in primed corals. Though the priming dose that maximizes acquired tolerance has not yet been established, these results strongly suggest that coral environmental memory is dose-dependent [40, 41, 43].

The dose-dependence of ‘environmentally mediated priming’ in corals is closely linked with the phenomenon of **hormesis**, wherein exposure to low levels of stress confers increased tolerance

Glossary

Acclimation: phenotypic response to a sustained change in environmental conditions within a laboratory setting.

Acclimatization: coordinated phenotypic responses to stressors in natural conditions. This response will decay if the stressors are removed or may become genetically ‘fixed’ and the animal will be adapted to the environment if the chronic stress persists over several generations.

Adaptation: dynamic evolutionary process that fits and maintains organisms’ phenotypes to their environment, enhancing their evolutionary fitness through natural selection.

Cis-priming: instance of stress memory in which the priming and triggering stimuli are the same.

Coral bleaching: visual manifestation of the expulsion, digestion, and/or degradation of algal symbionts that results in loss of pigmentation within the coral holobiont and may lead to coral starvation and mortality.

Coral holobiont: coral animal and its associated microorganisms consisting of bacteria, archaea, fungi, viruses, protists, and the dinoflagellate algae Symbiodiniaceae.

DNA methylation: a heritable epigenetic mark involving the covalent transfer of a methyl group to the C-5 position of the cytosine ring of DNA by DNA methyltransferases.

Environmental memory: stress memory involving abiotic stimuli and organisms’ modified responses to abiotic, environmental conditions.

Epigenetic mechanisms: molecules and mechanisms able to regulate gene expression through the generation of alternative gene activity states in the context of the same DNA sequence.

Histone post-translational modifications (PTMs): chemical alterations of histones modifying their interactions with DNA and the subsequent accessibility of the hereditary information to regulatory complexes.

Histone variants: non-canonical variants of histones that confer novel structural and functional properties on the nucleosome, affecting chromatin structure and genome function.

Hormesis: (also ‘hormetic dose response’), the biphasic dose-response wherein low levels of stress exposures

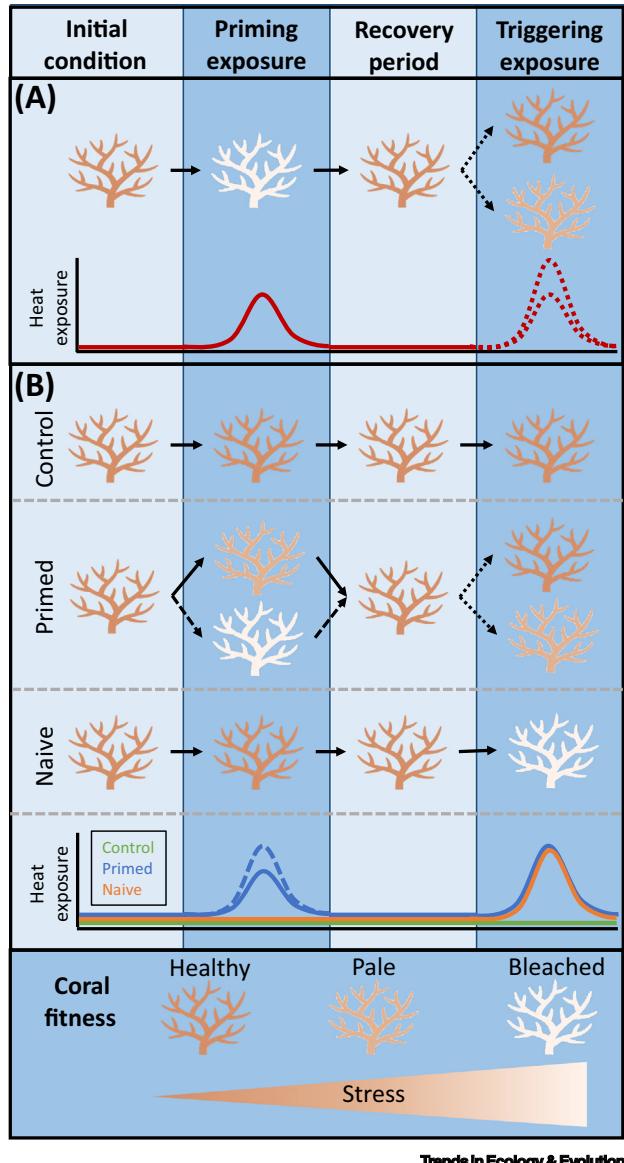


Figure 1. Schematic of coral environmental memory through marine heatwaves (A) and stress hardening experiments (B). Coral fitness is depicted using the bleaching phenotype, including healthy (no stress), pale (intermediate stress), and bleached (high stress), through stages of memory from initial condition to triggering exposure. Environmental memory through recurrent marine heatwaves (A) is evidenced by decreased bleaching severity during the triggering exposure compared with the level of bleaching displayed by the same coral during the priming exposure, despite similar or higher heat exposure during the second event. Evidence of environmental memory through stress hardening experiments (B) requires comparisons of primed corals (exposed to both priming and triggering stimuli) with control (nonstressed) and naïve (exposed to only triggering stimulus) corals. Primed corals may experience a reduction in fitness during priming [e.g., paling with intermediate priming heat exposure (unbroken line) or bleaching with high priming heat exposure (broken line)], but will likely recover between exposures. During the triggering phase, primed corals are expected to maintain higher fitness than naïve corals and may display fitness comparable with control corals.

evoke benefits, while high level exposures are lethal.

Marine heatwave: increase in seawater temperatures exceeding a seasonally varying threshold (often the 90th percentile) for at least 5 consecutive days. Successive heatwaves with gaps of 2 days or less are considered part of the same event.

Ocean acidification: reduction in seawater pH, carbonate ion concentration, and saturation states of biologically important calcium carbonate minerals resulting from CO_2 absorption by seawater.

Selective autophagy: the selective degradation of cytosolic components, including proteins.

Small RNAs: short (~18 to 30 nucleotides), noncoding RNA molecules that can regulate canonical RNAi responses in the cytoplasm and are also intimately linked to chromatin-regulatory processes.

Stress hardening: (also 'preconditioning' or 'priming'), the application of a stress exposure with the goal of increasing an organism's tolerance of subsequent exposures.

Stress memory: (also 'priming'), a phenomenon wherein a transient 'priming' stimulus leads to a modified and often enhanced response to a subsequent 'triggering' stress exposure, through the retention of information from the 'priming' cue.

Transcriptional frontloading: a persistent, elevated baseline expression level of stress-related genes that prepare organisms for subsequent stress exposures.

Transcriptional resilience: the rate of return to baseline, prestress levels of gene expression.

Trans-priming: (also 'cross-priming' or 'trans-hardening'), instance of stress memory in which the initial priming stressor differs from the subsequent triggering stressor.

[12]. However, the hormetic dose-response relationship may be shifted according to baseline levels of coral stress tolerance, which vary seasonally [45] and spatially [46], thereby influencing the range of beneficial priming doses (Figure 2B). Coral responses to thermal stress are also dependent upon the heating rate, with faster rates exacerbating the effects of stress [47,48]. While not yet assessed within the context of coral environmental memory, a priming exposure applied too rapidly may overwhelm cellular stress compensatory mechanisms, resulting in a reduction in fitness rather than a beneficial increase in stress tolerance. Thermal variability has also been associated with enhanced thermal tolerance in corals [5,47], but variable *ex situ* temperature regimes have had neutral [49] or even negative [42,43] effects on coral responses to secondary stress exposures, thus the effects of variable priming stimuli are inconclusive.

Table 1. Coral species demonstrating environmental memory

Life history ^a	Species	Evidence	Refs
Competitive	<i>Acropora aspera</i>	Stress hardening experiments: high temperature (cis-priming)	[31,41]
	<i>Acropora millepora</i>	Stress hardening experiment: high temperature (<i>cis</i> -priming)	[32]
	<i>Acropora</i> spp.	Stress hardening experiment: high light and temperature (<i>trans</i> -priming)	[38]
	<i>Montipora aequituberculata</i> ^b	Stress hardening experiment: high light and temperature (<i>trans</i> -priming)	[38]
Generalist	<i>Orbicella faveolata</i>	Observations across marine heatwaves: bleaching incidence	[27,28]
	<i>Pavona cactus</i> ^c	Stress hardening experiment: high light and temperature (<i>trans</i> -priming)	[38]
Stress tolerant	<i>Colpophyllia natans</i>	Observations across marine heatwaves: bleaching incidence	[27]
	<i>Diploria labyrinthiformis</i>	Observations across marine heatwaves: bleaching incidence	[27]
	<i>Montastraea cavernosa</i>	Stress hardening experiment: high temperature (<i>cis</i> -priming) or herbicide exposure (<i>trans</i> -priming)	[34]
		Observations across marine heatwaves: bleaching incidence	[27]
	<i>Orbicella annularis</i>	Observations across marine heatwaves: bleaching incidence	[27]
	<i>Porites</i> spp. (Massive) ^d	Analysis of coral cores: stress bands across marine heatwaves	[29,30]
	<i>Siderastrea siderea</i>	Observations across marine heatwaves: bleaching incidence	[27]
Weedy	<i>Coelastrea aspera</i>	Observations across marine heatwaves: bleaching incidence	[21-23]
	<i>Pocillopora acuta</i> ^e	Stress hardening experiment: high $p\text{CO}_2$ (<i>cis</i> -priming)	[36]
	<i>Pocillopora damicornis</i>	Stress hardening experiment: high $p\text{CO}_2$ and temperature (<i>cis</i> -priming, multiple stressors)	[35]
	<i>Porites astreoides</i>	Observations across marine heatwaves: bleaching incidence	[27]
	<i>Porites divaricata</i> ^f	Stress hardening experiment: high temperature (<i>cis</i> -priming)	[33]
	<i>Porites porites</i>	Observations across marine heatwaves: bleaching incidence	[27]
	<i>Stylophora pistillata</i>	Stress hardening experiments: high light and temperature (<i>trans</i> -priming)	[37,38]

^aLife history strategies (competitive, generalist, stress tolerant, or weedy) for each species obtained from the Coral Trait Database [115]. For species where life history was not listed in the database, the classification of phylogenetically related species was utilized.

^bLife history classification based on *Acropora tenuis* and *Montipora digitata*.

^cLife history classification based on *Pavona decussata* but may be stress tolerant (e.g., see *Pavona clavus* and *Pavona varians*).

^dLife history classification based on massive species *Porites lutea*, *Porites lobata*, and *Porites austroliensis*.

^eLife history classification based on *Pocillopora damicornis*.

^fLife history classification based on *Porites furcata* and *Porites*.

Temporal and taxa-specific determinants of coral memory

The optimal duration between the priming and triggering stimuli lies on a continuum between stress exposures that are too frequent, wherein stress accumulation causes irrevocable cellular damage, and exposures that are so infrequent that the protective effect of memory is lost prior to the second exposure [50,51]. This temporal continuum is evidenced by the variation in coral bleaching responses across differing frequencies of recurrent thermal stress events [26,30,52,53]. Surveys of bleaching events separated by more than 2 years have reported no protective effects of previous thermal exposure, especially when thermal stress was more severe during the second event [52,53]. In contrast, reductions in bleaching severity have been observed in successive annual bleaching events, despite higher thermal stress the second year [26-28]. Frequency-dependent

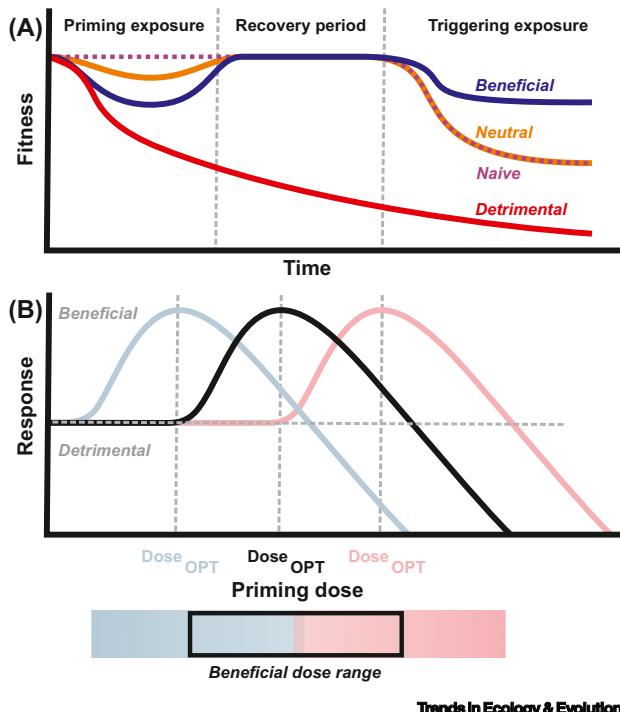


Figure 2. Coral environmental memory dose-dependence (A) and hormetic dose-response (B). (A) Potential effects of coral stress priming exposures range from beneficial to detrimental. Priming exposures insufficient to elicit memory will likely result in neutral effects, with responses comparable with those of naïve corals (broken purple line). Priming exposures of duration, magnitude, rate of change, or variability that exceed a certain stress threshold will likely result in detrimental effects, or a greater fitness reduction during the triggering exposure than that experienced by naïve corals. (B) The maximum benefit of coral stress priming is likely elicited by an optimal priming dose along the biphasic hormetic dose-response (black line). The dose-response curve may be shifted according to relatively lower (light blue line) or higher (pink line) baseline levels of coral stress tolerance, thus shifting the range of doses conferring benefits.

patterns of thermal tolerance were also evident in cores of massive *Porites* corals, as thermal sensitivity decreased across heating events separated by 1 to 2 years, yet no protective effects were evident when heating events were 5 or more years apart [30]. While the few experimental studies to explicitly assess the persistence of coral environmental memory have done so over relatively short timescales (i.e., weeks to months) [31,40], the long-term maintenance (10 years) of enhanced thermal tolerance observed in *C. aspera* corals [23] certainly supports future studies evaluating such memory over multiple, longer periods.

The potential for corals to acquire enhanced stress tolerance through environmental memory is likely modulated by baseline levels of tolerance, recovery ability, and capacity for phenotypic plasticity, all of which vary across genera and species [12,54,55]. In fact, changes in thermal tolerance across successive bleaching events vary between coral genera [24,25,27,56]. While it may be expected for the capacity for environmental memory to be more common in species displaying particular life history strategies (e.g., 'stress tolerant' species), evidence of environmental memory has in fact been found in species classified as competitive, generalist, stress tolerant, and weedy (Table 1). Furthermore, one of the few coral stress hardening experiments to compare multiple species demonstrated that species tolerant of single bleaching events do not necessarily retain this advantage during repeated events [33]. Enhanced thermal tolerance during the second bleaching event was instead related to higher baseline levels of energy reserves, particularly lipids [33,44]. In addition, the variability in responses to repeated bleaching events both between and within genera [33,44] highlights the need to evaluate coral environmental memory across multiple species to fully ascertain the role of memory within diverse coral reef ecosystems.

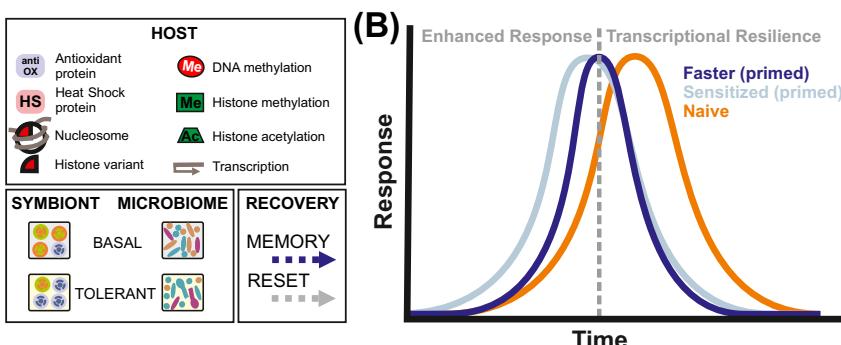
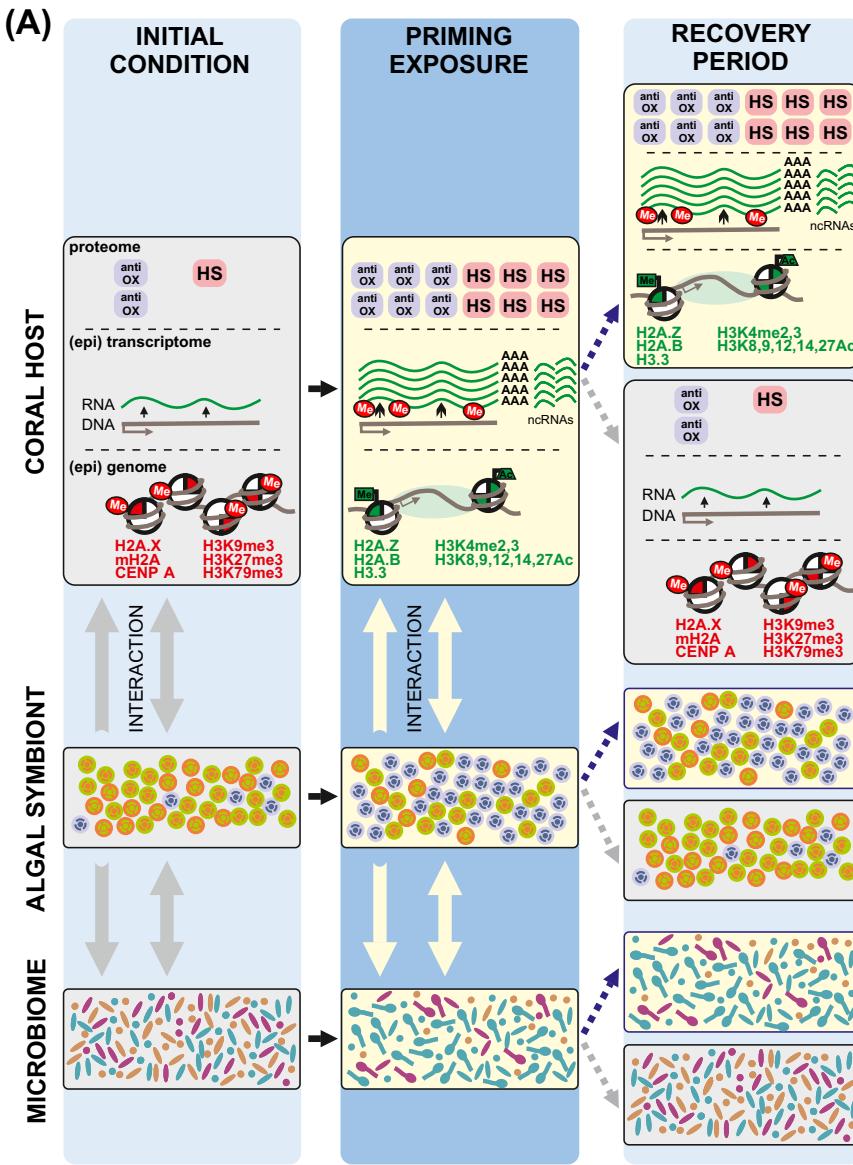
Memory responses across multiple stressors

Although coral reefs experience a myriad of abiotic stressors [57], the prevalence of protection acquired across different, temporally separate, stressors through ***trans*-priming** remains unknown. Thus far, evidence of *trans*-priming in corals is limited to the studies revealing increases in thermal tolerance conferred by elevated irradiance priming [22,23,37,38] (Table 1). However, exposure to elevated temperature prior to an acute irradiance challenge did not prevent declines in F_v/F_M in *Stylophora pistillata*, *Montipora digitata*, *Pachyseris rugosa*, or *Pavona divaricata* (two branching and two plating stony coral species, respectively) [58], suggesting that the order of stimuli between the priming and subsequent triggering exposure may influence the outcome of *trans*-hardening. It is plausible that the potential for a particular stimulus to provide cross-protection against a different triggering stressor is dependent upon the similarity of the cellular response elicited by each type of stress, a phenomenon well described in plants [7]. As both elevated temperature and irradiance contribute to oxidative stress during coral bleaching [59], it follows that exposure to one may provide protective effects against the other [60]. Additionally, priming corals and their symbionts with high salinity stress may have the potential to increase thermal tolerance through increasing antioxidant capacity [61]. However, exposure to heavy metals is also associated with oxidative stress in corals [62], yet an acute thermal priming exposure did not alter the tolerance of *Porites cylindrica* (branching stony coral) colonies to copper exposure [63]. Moreover, certain combinations of priming and triggering stressors may be deleterious, particularly if the priming stimulus inhibits mechanisms required to respond to the secondary stressor [64].

Through their exposure to a variety of environmental stressors, corals likely experience combined effects additively, synergistically, or antagonistically [65]. Although simultaneous stress exposures are common on reefs [66], coral environmental memory within this context has only been assessed under combined ocean acidification and thermal stress [35]. Different combinations of stressors within the priming and/or triggering exposures may influence the responses of primed corals. For example, acclimation to elevated pCO_2 did not prevent a decline in F_v/F_M under a combined ocean acidification and thermal challenge in *Porites porites* (branching stony coral) colonies [67]. In contrast, acclimation to high salinity increased the tolerance of *Exaiptasia pallida* anemones (a symbiotic cnidarian coral model organism) to combined salinity and thermal stress [68]. Additionally, evidence from a nonsymbiotic cnidarian relative, the Irukandji jellyfish *Alatina alata*, suggests that the benefit acquired through single-stress priming (i.e., ocean acidification or thermal stress, individually) may not be conferred by exposure to two simultaneous priming stressors (i.e., combined ocean acidification and thermal stress) [10]. The effects of priming and/or triggering exposures to combined stressors, such as elevated temperature with elevated light [69], high or low salinity [61,70], nutrient enrichment [71], increased sedimentation [72], or herbicide exposure [73], await evaluation in the context of coral environmental memory. Thus, additional research utilizing environmentally relevant combinations and series of stressors is necessary to describe coral environmental memory under conditions more representative of those naturally occurring on coral reefs.

Molecular underpinnings of modified stress responses

The 'primed' state represents a modified response to a secondary triggering stimulus, which may be characterized by a faster, stronger, or more sensitive response compared with a naïve (un-primed) individual [4,74]. Such enhanced responses can be achieved through changes at transcriptional, translational, and post-translational levels, with some of these molecular modifications persisting between priming and triggering stimuli [50] (Figure 3A). For instance, the thermotolerant western sides of *C. aspera* corals displayed higher concentrations of antioxidants and heat shock proteins before and during a thermal challenge [60]. Increases in these stress-



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defense biomarkers suggest that coral environmental memory is mediated by preparatory defenses sustained between the priming and triggering stimuli, as well as a stronger response to the secondary stress exposure. Although, the molecular mechanisms underlying such enhanced stress responses in corals are not yet well understood. Increased thermal tolerance has been associated with damped transcriptomic responses to heat stress in the few studies that assessed coral gene expression during stress priming and acclimation [41,49]. In cases of long-term acclimatization to variable thermal regimes, such a muted response could be due to a constitutive upregulation of stress-responsive genes prior to a triggering stimulus [75,76].

Mechanistic explanations for reduced transcriptional responses to stress in pre-exposed corals without **transcriptional frontloading** are lacking, especially as such a pattern seemingly contradicts the enhanced response predicted for primed individuals [4,74]. However, the presence of stronger, faster, or more sensitive responses in primed corals can still be reconciled. First, low correlations between gene expression and protein concentrations have been reported in corals [77], thus, transcriptomic analyses alone may not fully elucidate coral responses to thermal stress. Low rates of protein turnover may contribute to the apparent incongruence between transcriptomic and proteomic signatures as well as to acclimation ability [78]. Therefore, an enhanced response of primed organisms to a subsequent stress exposure may be facilitated by high concentrations of defense-related proteins perpetuated by low rates of protein degradation. In fact, a long-lived antioxidant protein has been implicated in the persistence of acquired hydrogen peroxide tolerance in yeast [79]. Additionally, **selective autophagy** has been identified as a mechanism regulating memory of plant thermal tolerance [80], further supporting the potential role of protein turnover in the maintenance of coral memory. Second, given the ephemeral nature of coral transcriptomic signatures [81] and the sampling timing of the gene expression studies (i.e., days after initiation of the thermal challenge) [40,41,49], reduced expression may be indicative of **transcriptional resilience**, which is related to stress tolerance in corals [53,81]. Such a rapid return to baseline levels of gene expression does not preclude, and could actually be associated with, a faster or more sensitive initial response to the triggering stress (Figure 3B), which would likely be apparent within hours of stress exposure [82]. Therefore, high resolution assessments of the molecular responses of both primed and naïve corals before, during, and after a stress challenge will be required to fully characterize their contribution in establishing and perpetuating coral environmental memory.

Epigenetic regulation in memory responses

An enhanced transcriptional response to a secondary stress exposure within environmental memory may be mediated by cellular mechanisms that alter the activation kinetics of gene

Figure 3. Possible mechanisms underlying coral environmental memory (A), including the potential enhanced transcriptional response of primed corals (B). (A) A priming stress exposure may elicit a variety of cellular modifications within the coral host, shifts in algal symbiont and/or microbiome communities to more tolerant assemblages, or a combination of these responses that may also influence each other. With a return to ambient conditions (i.e., recovery), these changes can either be reset (i.e., lack of memory) or maintained in the absence of the priming stimulus (i.e., memory) to modify the response of the primed organism to a later stress exposure. Within the coral host, cellular responses may include preparatory defenses sustained throughout recovery (e.g., persistence of antioxidants or heat shock proteins and/or constitutive upregulation of defense-related genes) and/or epigenetic modifications (e.g., histone post-translational modifications or variants, DNA methylation) that facilitate enhanced reactivation of stress-responsive genes upon a subsequent stress exposure. (B) Enhanced transcriptional responses of primed corals (blue) may be characterized as faster (more rapid increase) or sensitized (response triggered at a lower threshold) compared with the response of naïve corals. Such enhanced transcriptional responses may only be apparent during the initiation and early stages of the triggering stress exposure. Enhanced stress tolerance may also be associated with transcriptional resilience, or a rapid return to baseline levels of gene expression. The muted transcriptional response recorded in primed corals at later stages within, or after, the triggering stress exposure, may be a result of transcriptional resilience.

expression [74,83]. **Epigenetic mechanisms** lie at the interface between environmental conditions and genome function, dynamically altering and in some cases perpetuating states of gene activity [84]. As the conveyor of environmental messages to the genome, epigenetic regulation likely plays a major role in the establishment and maintenance of environmental memory, within the boundaries established by the organism's genome sequence [85]. Epigenetic mechanisms are inherently structural but with critical functional implications, modifying the nature of the DNA molecule and chromatin-associated proteins (most importantly histones) to promote alternative transcriptional states in response to the cell's environment [86]. The transcriptional memory response in various taxa has been associated with epigenetic modifications that influence the accessibility of stress-responsive genes and may recruit or maintain transcriptional machinery 'poised' at promoter regions for faster reactivation upon a recurring stress exposure [51,83]. These epigenetic mechanisms include **histone post-translational modifications (PTMs)** (e.g., histone methylation and acetylation) [87–89], the replacement of canonical histones with **histone variants** (e.g., H2A.Z) [90,91], reduced nucleosome occupancy [92], **DNA methylation** [93], as well as gene regulation by **small RNAs** [94].

Epigenetic responses have been recently described in corals subjected to ocean acidification [95,96], thermal [97], and nutrient stress conditions [98], revealing changes in DNA methylation and histone PTMs. Particularly, the regulatory function of DNA methylation seems to be more complex than anticipated, playing a role in reducing spurious transcription in corals [96], and cnidarian relatives *E. pallida* anemones [99], which could be critical in regulating more efficient transcriptional responses in primed organisms. Some of these modifications (e.g., DNA methylation) can be transmitted from adult corals to their larval offspring and have been correlated with higher larval survival rates under the same stressor that elicited such modifications in the adult corals [100]. Seasonal patterns of DNA methylation have been reported in *Acropora cervicornis* (branching stony coral) [101], suggesting the role of epigenetic modifications in mediating seasonal acclimatization in corals [45]. Overall, current studies support that epigenetic changes are environmentally driven and could be inherited in corals [102]. However, these studies have predominantly focused on DNA methylation and have generally overlooked the functional contribution of other epigenetic mechanisms, such as histone PTMs and variants and small RNAs. These additional mechanisms are critical for regulating chromatin structure and gene expression by interacting with DNA methylation to promote different functional chromatin states [86]. Therefore, in order to fully understand the molecular mechanisms underpinning coral environmental memory, additional studies evaluating the synergistic interaction among multiple epigenetic modifications throughout recurrent stress exposures are needed.

The role of holobiont partners

It is well established that coral stress tolerance is genetically constrained [103,104] and the same may be true for the capacity for environmental memory. In fact, the genotype of the coral host can significantly (although not exclusively) influence the ability to acquire enhanced stress tolerance through stress priming [37]. Such a genetic effect is likely due to the dependence of some of the molecular mechanisms regulating environmental memory on the information encoded in the coral genome. For instance, the epigenetic regulatory function of DNA methylation will be only possible as long as cytosines are present at specific genomic positions, typically within gene bodies for invertebrates [97]. Similarly, mechanisms involving DNA-associated proteins may be sequence-dependent (e.g., nucleosome positioning at targeted genomic regions), with mutations within such sequences disrupting the establishment of memory [90].

While mechanisms of environmental memory may be primarily driven by the coral host [17,60], which inherently remains constant (i.e., coral genotype) (although see [105]), the dynamism of

Box 1. Priorities for the application of coral stress hardening to conservation

Coral stress hardening involves the application of a priming exposure to elicit molecular mechanisms establishing memory, increased abundance of stress-tolerant symbionts, beneficial shifts in microbial communities, or a combination of these, to increase the resilience of the holobiont [3,19]. Priming stress exposures may be applied via *ex situ* aquarium systems and through propagation in *in situ* coral nursery locations that experience relatively stressful environmental conditions. Additionally, corals naturally occurring at stressful reef locations may be sourced for targeted propagation.

Optimizing priming

The optimal dose and temporal regime of the priming stimulus must be identified to inform *ex situ* exposures and the selection of locations with environmental conditions expected to confer enhanced stress tolerance. Suggested priming exposures should be relative to local ambient conditions and/or baseline tolerance thresholds to increase applicability across temporal, spatial, and interspecific variation in coral stress tolerance. Understanding the influence of additional environmental variables on environmental memory will increase the ability to predict stress tolerance acquired by *in situ* exposures, which will be vital for priming site selection.

Maximizing net benefits

Coral priming applications have the potential to greatly benefit conservation efforts, but inherent costs must be considered to maximize net benefits. Describing the persistence of coral environmental memory, and therefore the duration of priming benefits, is crucial to weighing the ecological benefits against the logistical costs of priming. Potential performance trade-offs associated with enhanced stress tolerance, such as reductions in growth or reproductive output [116,117], must be identified to evaluate the net physiological benefit of priming. Additionally, further characterization of *trans*-priming in corals is essential to fully describe the benefits (e.g., enhanced tolerance of a single stressor versus enhanced general tolerance of many stressors) and/or potential trade-offs (e.g., enhanced tolerance of one stressor yet reduced tolerance of another) conferred by priming.

Identifying biomarkers

Delineating the mechanistic pathways required for establishing and maintaining coral environmental memory is crucial for the development of biomarkers of enhanced resilience. While multiple diagnostic, or response, biomarkers can be utilized to detect sublethal stress in corals [118], biomarkers that predict stress tolerance are lacking. Ideally, biomarkers of environmental memory should be detectable in primed individuals after the priming stimulus and able to predict tolerance during a subsequent triggering exposure. Such predictive biomarkers would allow conservation practitioners to confirm the success of a priming exposure, identify primed individuals for targeted propagation, and monitor the persistence of memory.

the symbiont and microbiome communities within the coral holobiont may also play a decisive role (Figure 3A). Stress tolerance, particularly thermal tolerance, varies across genera and species of Symbiodiniaceae [106] and a 'shuffling' of algal symbiont communities to a dominance of more resistant strains has been proposed as an adaptive mechanism in corals [107,108]. In fact, *Montastraea cavernosa* (massive stony coral) colonies primed with either thermal or chemical (i.e., herbicide) stress exhibited a shift from sensitive (*Cladocopium C3*) to tolerant (*Durusdinium trenchii*) symbionts and acquired enhanced thermal tolerance [34]. However, *C. aspera* corals displayed environmental memory without changes in Symbiodiniaceae communities [22,23] and Symbiodiniaceae community plasticity alone may be insufficient for increasing coral resilience through environmental memory. For instance, while the abundance of thermotolerant symbionts increased in both *Porites divaricata* and *Orbicella faveolata* (massive stony coral) colonies after thermal priming, only *P. divaricata* resisted bleaching during the subsequent thermal challenge [33]. Additionally, shifts in symbiont communities apparent during or immediately after heat stress may revert to initial compositions during recovery [53,109] and limit the potential for symbiont shuffling to convey long-term environmental memory.

Similar to the dynamics of algal symbionts, additional constituents of the coral holobiont's microbial community (e.g., bacteria, archaea, fungi, viruses) are hypothesized to be more beneficial than others [110,111] and microbiome flexibility has also been posited as a mechanism for corals to rapidly adapt to environmental change [112]. Indeed, *Acropora hyacinthus* (plating stony coral)

colonies acclimatized to a variable thermal environment acquired enhanced thermal tolerance and experienced a shift in bacterial community composition, which remained stable during a thermal challenge [113]. However, such a bacterial shift was not observed in thermotolerant *Acropora millepora* (branching stony coral) colonies under a shorter thermal acclimation period [114], highlighting the need to further assess the potential role of the coral microbiome in influencing holobiont resilience and coral environmental memory.

Concluding remarks and future directions

Corals have the ability to acquire and maintain enhanced stress tolerance across transient exposures to a variety of environmental stressors. However, despite the growing body of evidence supporting the capacity for environmental memory in corals, many aspects of this phenomenon are not yet well described (see **Outstanding questions**). An improved understanding of coral environmental memory is critical to better predict coral responses to future climate change. Additionally, many knowledge gaps must be addressed to evaluate the potential for stress hardening methods to increase coral resilience (Box 1), especially given the level of resources and effort required for their implementation. It is now urgent that future studies strive to characterize coral environmental memory across species and environmentally relevant stressors and ascertain the nature, dynamics, and interactions among mechanisms underpinning this process.

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Declaration of interests

No interests are declared.

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Outstanding questions

What aspects of the priming stress exposure (e.g., magnitude, duration, frequency, variability, and rate of change) are most critical for optimizing the benefit (e.g., degree and persistence of enhanced stress tolerance) of coral stress hardening?

Are trade-offs (e.g., reduced growth or reproduction, reduced tolerance of a different stressor) associated with enhanced stress tolerance acquired through environmental memory?

What life history or physiological characteristics best explain interspecific variation in coral responses to repeated stress exposures and capacity for environmental memory?

How is coral environmental memory influenced by the identity, sequence, and combination of environmental stressors during the priming and/or triggering exposure? Does the similarity of the cellular response elicited by individual stressors predict the potential for ‘cross-protection’ between different priming and triggering stressors?

How do the physiological and transcriptomic responses to a subsequent triggering stimulus differ between primed and naïve corals? What is the role of different epigenetic modifications and their interactions in regulating such responses?

Can the cellular and molecular mechanisms responsible for maintaining coral environmental memory be effectively used as biomarkers of enhanced resilience?

What are the relative contributions of the coral host and microbiome community in mediating coral environmental memory?

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