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# Gaining insights from past reefs to inform understanding of coral reef response to global climate change

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Global climate change is feared to lead to the collapse of living coral reefs, whose component organisms can respond in but three ways: migration, adaptation, and extinction. Because ancient reefs have been exposed to multiple episodes of environmental change, the fossil record provides an important resource for understanding the range of responses of coral reefs to climate change. Reef development has been slowed or stopped repeatedly in the history of life during periods of climate change. Whilst current conditions might be beyond some of the environmental ranges experienced throughout much of earth's history, coral reefs have shown a remarkable resilience to past climate change. Their fate today lies in the interaction between climate change and local anthropogenic stressors that have devastated a large proportion of living reef ecosystems.

## Addresses

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## Introduction

Coral reefs are both biological and geological structures, hence have captured the imagination of a large number of natural scientists. Their geological importance was first recognized by Charles Darwin, who, understanding the biological nature of their origin and genesis, first conceived of the 'coral reef problem' of how shallow tropical coral reefs could grow from the ocean's depths [1]. The 'problem' with coral reefs is now something much different and much more immediate — with so many imminent threats bearing down on them how will it be possible for them to continue functioning? In response to this question, a logical line of inquiry is emerging to

investigate how coral reefs have responded to environmental change in the geological past. In this brief report, we focus on three major responses of past reefs to climate change that are directly relevant to the response of living reefs to climate change: migration, adaptation, and extinction. In so doing, we outline some of the major episodes of change in the geological past and ask questions about their relevance for understanding the present predicament of living coral reefs.

Recent focus on the effects of climate change on coral reef ecosystems have re-invigorated the study of climate change in Earth's history, including past reef response to catastrophic changes in ocean temperature and acidity [2]. Of course, we need first to ask whether there are comparable episodes of environmental change in the geological past where one can look to examine coral reef response, or are the scales all wrong and we are dealing with a unique configuration of environmental parameters in today's crisis? Rates of change observed over geological durations can be orders of magnitude smaller than rates observed on historical time scales. This is largely an artefact of the limited temporal resolution in deep time combined with an increasing probability of transient trend reversals or stasis with time of observation. The relationship between time of observation and rate of change has been well explored for sedimentation rates [3], rates of evolutionary change [4,5], and, on shorter time scales and less explicitly, for climate trends [6]. All studies agree that the relationship between time interval of observation and rate of change roughly follows a power law; that is, rates are proportional to the inverse of time of observation or its square root ( $1/t$  or  $1/\sqrt{t}$ ). Therefore, a geological warming trend of  $10^\circ\text{C}$  observed over 1 myr ( $=0.0001^\circ/\text{decade}$ ) might be comparable to the  $0.7^\circ\text{C}/\text{decade}$  measured for sea surface warming in the last 50 years [7]. Pending more work on the exact relationship between rates of change and time of observation we need to carefully consider differences in past and present temporal scales when evaluating the degree to which current climate change is unprecedented in the past.

Palaeoecological studies can offer valuable insights into the responses of different groups of marine organisms to major climatic changes. The range of responses of marine organisms to environmental change is fundamentally quite limited — they may migrate to find more suitable environmental conditions; they may stay where they are and acclimate or adapt; or they may go locally or globally extinct. Studies from the fossil record mainly focus on

extinction, but an emerging set of studies discussed below has been designed to quantitatively test the role of migration, extinction, and to a lesser extent, adaptation during discrete episodes of climate change. But the application of such studies to the modern biodiversity crisis is still in its infancy. Direct cross-over of fossil examples to modern systems is not always possible, mainly because the scale of response preserved in the fossil record can be much greater than the decadal to centennial scales of most interest to modern ecologists. However, when temporal scales are carefully considered, insights can be gained that may directly help predict the response of living coral reef ecosystems to present environmental change. In this paper we review some of these examples, explore their significance for understanding modern climate impacts on coral reefs, and suggest future studies that might help in this regard.

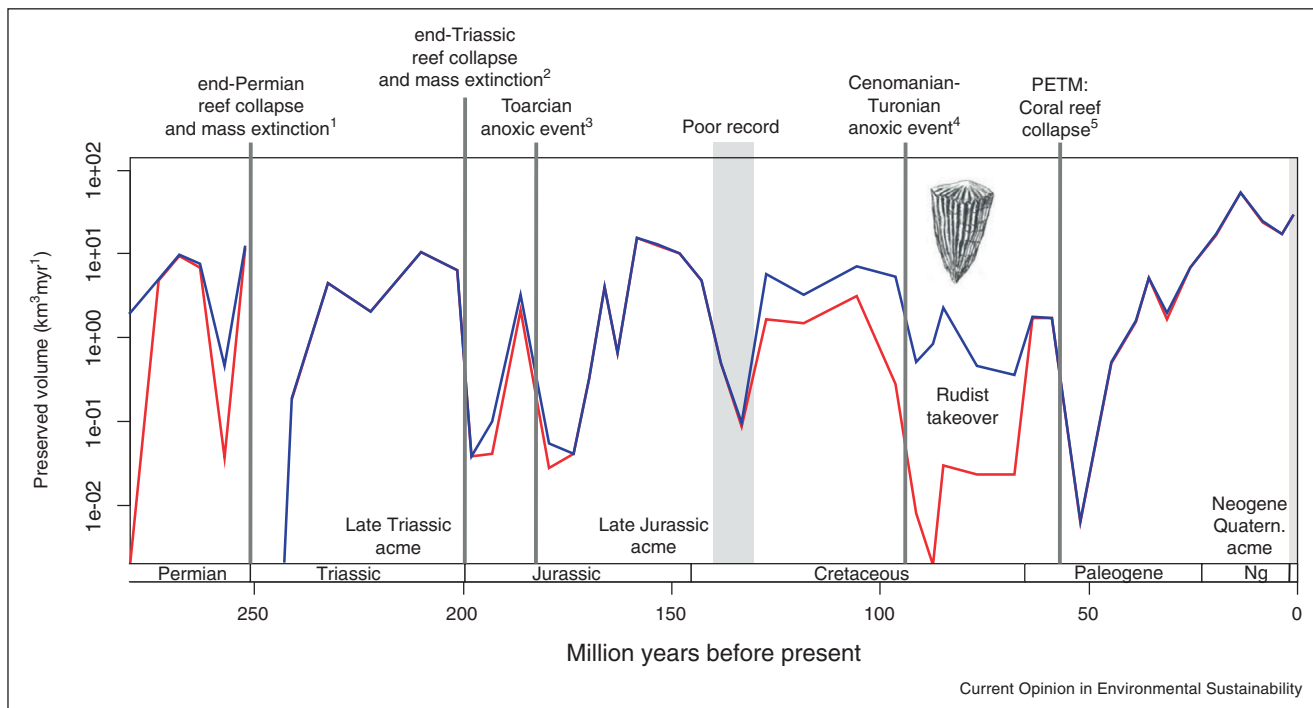
### General long-term response of past coral reefs to climate change

The fossil record offers several examples of global reef crises that were probably driven by climate warming (Figure 1). Global reef crises are best defined by a

significant reduction of reefal calcium carbonate production per unit of time [8]. Because our concern is mostly about reefs that are similar to today, an additional constraint is calcium carbonate production by metazoan reef builders. The biodiversity decline of reefs may serve as a secondary measure of reef crises, but there is evidence for diversity and reef development being decoupled [9] and hence metazoan reef development assessed by carbonate production rate is our foremost criterion to identify booms and busts in reefs.

The most substantial reef crises were linked to rapid warming pulses. The end-Permian (252 myr) and end-Triassic (201 myr) were both times of mass extinction and reef crises and both were linked to massive warming brought about by intense volcanism. Volcanic outgassing caused a massive release of CO<sub>2</sub> both directly and indirectly from the dissociation of gas hydrates previously stored in ocean sediments [10]. This led to intensified greenhouse warming and perhaps ocean acidification [11\*] that may have been the trigger of a near total loss of metazoan reefs. The magnitude of warming is fairly well constrained from oxygen isotope analyses (15 °C rise

Figure 1



Metazoan reef growth over the last 270 Million years of earth history. Data on ancient reef growth are derived from the cumulative volume of fossil reef structures per unit of time [23\*]. The red curve refers to corals and hypercalcifying sponges, whereas the blue curve incorporates all metazoans (usually corals, sponges and bivalves). Highlighted events are all accompanied by rapid global warming. (1, 2) the end-Permian and end-Triassic mass extinctions and reef crises, both triggered by extreme global warming [12,13\*]; (3) The Toarcian (Early Jurassic) anoxic event which led to a major reef crises although extinctions were modest; (4) the Cenomanian-Turonian anoxic event accompanied by a major crisis of coral reefs (rudist reefs suffered less) and a second-order mass extinction, and (5) the Paleocene-Eocene Thermal Maximum (PETM) which led to a substantial reduction of coral reefs but coral extinction not above background rates. 'Poor record' means that sedimentary rocks in general are scarce from this interval such that the depression of reef building is largely artificial. Causes of reef booms in the Late Triassic, Late Jurassic and Neogene and Quaternary are not fully understood but may involve the evolutionary spread of photosymbiosis, global cooling, and changes in ocean chemistry.

in sea surface temperature across the Permian-Triassic boundary and 8–10 °C rise across the Triassic-Jurassic boundary) [12,13\*]. The end-Permian warming occurred over a time span of 0.8 myr, whereas the end-Triassic warming was observed over 0.6 myr. Astronomical constraints for the latter suggest that warming may have occurred in a pulse of less than 40 kyr duration [14].

In both cases, reef recovery was slow and gradual. Although the former notion of a total Early Triassic metazoan reef gap can no longer be maintained [15], the first well developed reefs, including the first scleractinian coral reefs in earth history, did not appear until 8 myr after the end-Permian crisis [16]. Recovery from the end-Triassic crisis was faster; the first well developed reefs are observed just 0.5 myr after the crash [17]. The first Jurassic reefs grew in the subtropics (around 35° palaeolatitude), while tropical reefs needed much longer to recover. Although there was evolutionary novelty in reefs after both events, the ecological structures of the post-crisis reefs were surprisingly similar to their predecessors.

Coral reefs and reef corals appear little affected by the end-Cretaceous meteorite impact that caused the extinction of the dinosaurs, but another reef crisis, the most recent, occurred in association with the Paleocene-Eocene thermal maximum (PETM) some 55 myr ago [8]. The PETM was strong and fast (5 °C rise in SST in 10 kyr) and because it was associated with massive carbon release to the atmosphere similar in magnitude to the present day [18], it often serves as a benchmark for the modern situation [19]. Although metazoan reef production rates declined dramatically, and coral reef development decreased near continents [20], reef building did not cease, and reefs from at least one oceanic setting remained unaffected [21]. Encrusting foraminifers built large reefs in the immediate aftermath of the PETM [22]. Extinction rates of reef corals were modest and just within background [8].

The best candidate example for examining an extremely long-term response of coral reefs to sustained super-greenhouse conditions is in the Cretaceous period (145–66 myr). The Cretaceous saw the evolutionary radiation of rudists, aberrant bivalves with a coralline growth form that were able to build small reef structures. The Cretaceous also witnessed a gradual decline of coral reefs [23\*]. Although reef corals did not decline in diversity — they maintained high levels throughout the period [24] — they seem to have lost their reef building potential. As older suggestions of a competitive replacement of corals by rudists [25] have been refuted, environmental factors are held responsible for the coral reef decline and rudist takeover [26]. It is tempting to conclude that global warming was a major trigger. The rudist takeover accelerated after a major ocean anoxic event (Figure 1). Anoxic

events were partly triggered by abrupt rises of temperature, which in turn were caused by rapid influx of CO<sub>2</sub> into the atmosphere [27]. The latitudinal distribution of corals and rudist reefs and the bathymetric zonation of mixed rudist-coral reefs support the idea that rudists were more heat-tolerant than reef corals. That extremely warm temperatures continued into the latest parts of the Cretaceous [28,29] might be responsible for the prolonged failure of corals to build major reef structures. New research on this hypothesis is urgently needed, because there are a variety of additional environmental factors that might be responsible. One potentially important factor is ocean chemistry, particularly the Mg/Ca ratio in seawater. This was especially low in the Cretaceous, increasing the difficulty for corals to secrete their aragonitic skeletons [30]. If the heat-driven replacement hypothesis holds true, this would have important consequences for the adaptability of coral reefs to warming. Cretaceous reef corals seem not to have adapted to the ocean conditions of the Late Cretaceous. Coral reefs were very rare in the latest Cretaceous but expanded globally after the extinction of rudists at the end of the Cretaceous and before the PETM [24].

### Specific responses: migration, adaptation, and extinction in the fossil record

Modern marine organisms are now known to respond to climate warming in multiple ways throughout the world's oceans and seas [31]. Migration, *in situ* adaptation, and local and global extinction are thought to be the main responses to future climate change.

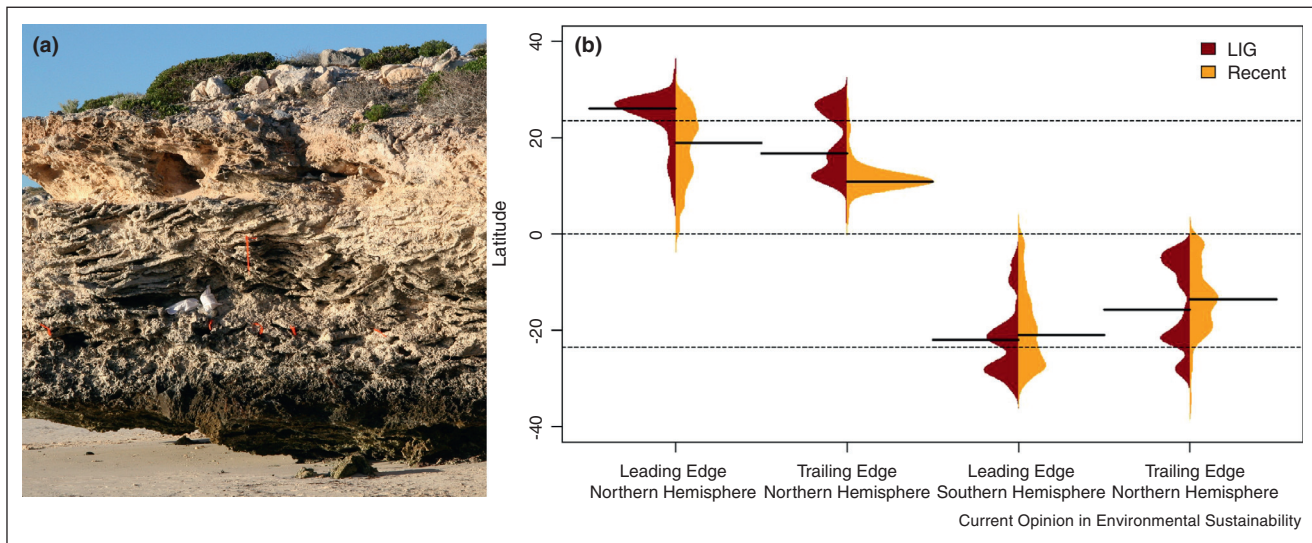
#### Migration

Like many marine organisms worldwide [31] coral reef organisms are responding to global warming through migration. Increased documentation of tropical species moving to higher latitudes in Florida, east and west Australia, and Japan [32–35] provides a sense of the capacity for living reef corals to expand their geographic ranges as global warming increases.

Geographic differences in distributions of Pleistocene corals versus their modern counterparts also display the rich potential for species migration as a response to climate change. During the Last Interglacial around 125 ka (thousand years ago), tropical climates were warmer by at least 0.7 °C [36]. During this time, migration of coral reef organisms occurred in response to climate change where suitable substrate was available (Figure 2). Reef coral species migrations are recorded from the Pleistocene fossil record from Florida [37] and Western Australia [38] and the diversity of species along latitudinal gradients also changed at global scales [39\*].

Is past history of successful migration any indication of the success at which coral reefs can migrate as climate changes in the future? There are several conditions that

Figure 2



(a) Photograph of the ~6 m raised reef terrace from 125 ka (Last Interglacial – LIG) from the Houtman Abrolhos Islands, Western Australia. (b) Beanplots of sampling-standardized range edges of reef corals in the Last Interglacial, 125 ka (left-hand beans; dark red) and today (right-hand beans; orange). Beanplots are essentially smoothed histograms and here depict the estimated densities of species leading edge and trailing edge range limits on each hemisphere in the respective time intervals. Solid lines represent the medians. Dashed horizontal lines indicate the equator and the tropics. Reprinted from *PNAS* with permission [39\*].

now pertain that did not accompany the global warming of the Late Pleistocene. First, dramatic rises in  $p\text{CO}_2$  did not occur, so migration into cooler waters where acidification is likely to be more pronounced was not an issue. Second, human modification of land adjacent to coastal areas where migration occurred had not yet occurred; thus, habitat degradation was also not an issue. As an aside, reefs are capable of surviving dramatic reductions in habitable area, as occurred during the Last Glacial Maximum (18 ka) when sea level was reduced by 120 m. Here habitable reef area dropped by >90% [40]. In areas of minimal coastal modification, and assuming corals can simultaneously cope with the greater changes in aragonite saturation state associated with higher latitudes, it will be possible for some migration of coral reef ecosystems to higher latitudes as global warming proceeds, as is indeed happening at multiple sites. However, the differential effects of acidification expected to impact species in variable ways and the relentless local human pressures means that surviving assemblages might not be the same as those we are familiar with today, so novel communities can probably be expected [2]. Moreover, expansion towards the poles is not the only feature of past coral communities; contraction away from the equator must also have occurred. Kiessling et al. [39\*] documented a loss of equatorial diversity of reef corals from the warmer Pleistocene interval 125 ka as compared to that occurring today (Figure 2). Thus, poleward increases in reef development may be offset by equatorial contractions.

### Adaptation

It is often asked whether reefs can ‘adapt’ to climate or other environmental change. Of course this is a misnomer, as reefs are geological structures that are incapable of adapting; but the organisms comprising coral reefs definitely have the capacity to do so, as does everything alive [2]. Short-term experimental work argues against the physiological capacity for reef organisms to acclimatize in the short term, but such experiments may not extrapolate into longer-term field situations [41]. Critical questions for living reefs are whether or not reef organisms can evolve quickly enough to keep pace with environmental change, whether the kind of evolutionary change they undergo will be beneficial in the long term, and how evolutionary trade-offs might alter the adaptive capacity of populations experiencing variable environments and thus mediate species composition in future reef communities.

Of critical importance for the ability of corals, the main framework builders of living (and many past) reefs, to adapt to climate change is their relationship with their algal symbionts, collectively comprising the ‘holobiont’. Reef corals recruit different symbionts as appropriate to environmental conditions [42]. Because of the important role of microbial symbionts in the adaptation and evolution of higher organisms, it has been proposed that the coral holobiont with its hologenome should be considered as the unit of natural selection in evolution [43].

Identifying adaptation in the fossil record is challenging. Changes in ecological structure, biodiversity and growth rates all have the potential to be evolutionary responses to environmental change, but they must be carefully studied at similar scales of resolution as, and in combination with, studies of environmental change. For climate change it is important to look for evidence of changes in populations and species at the same time that environmental change is occurring.

At the population level, careful reconstruction of phylogeny and variation of morphological traits through time are essential for understanding response to past environmental change. It is possible to find inheritable change at the population level in the fossil record [44], but this can only be observed for morphological attributes. Budd and Pandolfi [44] found differences in the relative proportion of some traits through time, suggesting both hybridization among populations of different species and speciation in Pleistocene reef corals. These fine-scaled analyses were informed by complementary work on the genetics of living descendants. The dual approach of gathering data on species response to past climate change, and coupling that with genetic work on living descendants can provide an important window to the evolutionary response of reef organisms to future climate change.

Studies of taxonomic turnover during past environmental change can also give key insights into how the structure of modern reefs have been affected by past climate change. For example, Johnson et al. [45] documented a Caribbean turnover event in the Plio-Pleistocene that involved heightened origination of reef corals in addition to heightened extinction, presumably related to changes in climatic and oceanic circulation patterns across the Caribbean resulting from closure of the Isthmus of Panamá approximately 3.5 million years ago. Thus, as environments changed, origination of new taxa accelerated, even as older taxa were going extinct. More studies are needed at finer scales of resolution to understand the relationship between origination during times of environmental change and the species and species traits undergoing such evolutionary response.

### Extinction

The fossil record provides a rich source for the study of extinction throughout the history of life. Coral reefs have suffered five episodes of global-scale biodiversity loss or cessation of reef growth over the past 500 My or so [8]. Kiessling and Simpson [8] used the term 'reef crises' for these events (Figure 1). Four of these crises, including three of the Big Five mass extinction events, coincided with ocean acidification and rapid global warming.

Several authors found nonrandom extinction rates among organisms responding to dramatic changes in climate over geological time — calcified marine animals with more

buffered skeletal mineralogy were more resistant to environmental events that involved increased  $p\text{CO}_2$  [8,46,47]. Non-random effects also characterize the extinction of reef corals. For example, Edinger and Risk [48] found increased extinction of coral species that brood their larvae, as opposed to broadcast their larvae during a regional extinction event over the Oligocene-Miocene boundary; and Johnson et al. [45] found increased survival among species with larger colony size during the Plio-Pleistocene extinction event mentioned above. However, direct analysis of the species specific responses to climate change have not yet been quantified at the finer scales of resolution. More recent comparisons between the modern and Pliocene showed taxonomic variation in susceptibility to regional extinction in reef corals, suggesting that vulnerability to regional extinctions was based upon species traits [49]; moreover, a widespread distribution did not equate with immunity to regional extinction. This agrees well with another study of extinction in Pleistocene Caribbean corals where two dominant and widespread taxa went extinct while other, less abundant species survived [50].

Perhaps one of the most surprising aspects of the present biodiversity crisis and the impacts of global climate change has been the almost absence of global extinctions of marine taxa. There is no paucity of extinction in past marine environments [51], and such extinctions have often occurred at the hands of climate change. Examination of the fate of individual species during past environmental change holds great promise for gaining insight into this riddle. The observation that environmental change preceded extinction by 2 myr in the Caribbean during the Plio-Pleistocene [52] introduces a large degree of uncertainty into the prediction of marine extinctions, even where comparisons can be made directly between extinction rates of fossil and extant organisms [51].

### Conclusions

Data from the fossil record is generally variable in its temporal resolution; however, there is great promise from several lines of investigation that can lead to inferring causal interactions between coral reef response and discrete climatic events. First, understanding the relationship between rates of change and time of observation will help in considering differences in past and present temporal scales when evaluating the degree to which current climate change is unprecedented in the past. Second, regional and global patterns in migration in response to past environmental change can provide a predictive framework from which the response of living reefs to global change can be interpreted. Third, elucidation of the detailed response of individual clades during highly constrained climate events has the potential to provide important insights into the tempo and mode of evolutionary response to climate change, as well as extinction vulnerability, when conducted at the appropriate

temporal scales. Lastly, studies aimed at honing in on analyzing relative abundance or other fitness measures of species from fossil communities will provide a rich resource from which to compare the response of living assemblages to contemporary environmental change.

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