

as the late Pleistocene, but most of the lineages that are currently considered to be species diverged much earlier.

Whether the rate of diversification really changed during this period remains an open question: as Zink *et al.* [3] discuss, the apparent Pleistocene slowdown in speciation rate could be caused by a real decline in net diversification, or by the taxonomic artifact of considering recently separated lineages to be conspecific and thereby excluding them from analysis. Resolving this issue will require mapping the temporal distribution of all nodes in trees regardless of taxonomic designations, from the most recent splits among populations to the deepest nodes separating genera and families.

Conclusions

Considered in concert, these new syntheses show that the answer to the Pleistocene speciation debate is simply a matter of degree. We now know that some of the most closely related North American species pairs split during the Pleistocene, and that Pleistocene events similarly separated many populations that we currently consider conspecific, causing substantial intraspecific phylogeographical diversification [11,18]. The northernmost species pairs tend to have the most recent nodes, suggesting that Pleistocene climate cycles contributed directly to the present-day avian diversity of North America. At the same time, comparisons based solely on these most recent sister taxa show us only the tail of the distribution of speciation times, whereas comparisons of entire avian clades reveal that most present-day taxonomic species split from their extant relatives at a much earlier period. The recognition that many species of North American birds have had long tenures as independent lineages is especially poignant for the many such taxa that are now declining precipitously in the face of rapid anthropogenic disturbances, after having successfully weathered several million years of repeated climate change.

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Do some corals like it hot?

Erik E. Sotka¹ and Robert W. Thacker²

¹Grice Marine Laboratory, College of Charleston, 205 Fort Johnson Road, Charleston, SC 29412, USA

²Department of Biology, University of Alabama at Birmingham, 1300 University Boulevard, Birmingham, AL 35294-1170, USA

Global increases in sea temperatures threaten coral reef resilience because thermal stress can cause corals to bleach; that is, to lose their photosynthetic microalgal

symbionts. Recent evidence suggests that some corals associate with genotypes of microalgae that resist future thermal stress, however, these genotypes might provide less energy for growth when thermal stresses are curtailed. Coral reef resilience depends on whether phenotypic and genotypic changes in host-symbiont

Corresponding author: Sotka, E.E. (sotkae@cofc.edu).

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associations can match projected increases in the frequency and severity of thermal stress, as well as on our ability to ameliorate continuing human impacts.

Warming seas threaten coral reefs

You cannot blame coral biologists for being pessimistic about the future of coral reefs. Despite the fact that coral reefs are centers of marine biodiversity and provide crucial ecosystem services [1], they are impacted by an expanding array of anthropogenic threats, including overfishing, pollution and habitat destruction [2]. Even if local threats were mitigated, global climate changes could irreversibly alter coral reefs [3,4]. For example, conservative climate models project that, over the next 50 years, temperature increases will exceed the temperature conditions under which coral reefs have flourished over the past half million years [5]. The long-term effects of such shifts are unknown but are currently the subject of intense research efforts, as evidenced by a pair of recent papers by Baker *et al.* [6] and Rowan [7]. These and other studies suggest that some corals might be able to combat thermal stresses tomorrow by associating with heat-tolerant microalgae today.

When exposed to abnormally high temperatures or other stresses, reef-building corals turn white because they lose their zooxanthellae (photosynthetic microalgae in the dinoflagellate genus *Symbiodinium*) (Figure 1). These bleached corals die when thermal stresses are prolonged and intense, in part because *Symbiodinium* photosynthesis contributes most of the carbon budget of the coral. Global patterns of coral bleaching are strongly associated with severe El Niño – Southern Oscillation (ENSO) events, a climatic pattern that is characterized by elevated temperatures in tropical seas. During the 1997–1998 ENSO event, coral mortality was 80–90% on some parts of the Great Barrier Reef, and some of the corals killed were at least 700 years old [3]. Because ENSO events have become more frequent and severe over the past 30 years, some ecologists predict that coral bleaching

will devastate tropical ecosystems on a scale that will be impossible to mitigate [3,5].

Can coral reefs respond?

These projections are based largely on the assumption that all coral–zooxanthellae associations respond similarly to thermal stress (Figure 2). Corals and zooxanthellae can acclimatize to changes in temperature and light [8], but the increasing frequency of bleaching episodes suggests that the rate of acclimatization cannot match the rate of increasing sea temperatures [3]. Alternatively, coral reefs might respond to warming seas through shifts in the taxonomic and genetic composition of their associations with zooxanthellae [9–13]. One controversial theory is the Adaptive Bleaching Hypothesis (ABH), which states that frequent and severe environmental stresses tend to favor stress-resistant coral–zooxanthellae associations [13]. Two major predictions of the hypothesis are: (i) symbionts acquired after bleaching provide greater heat tolerance than do those present before bleaching; and (ii) heat-sensitive coral–zooxanthellae associations have a competitive advantage in the absence of heat stress; that is, an association that is heat tolerant is also costly to the coral [13].

There is empirical support for several of the underlying assumptions of the ABH. For example, strains of *Symbiodinium* are differentially adapted to high temperature stress. The four major clades of *Symbiodinium* (labeled A, B, C, and D from an accepted phylogeny of ribosomal DNA [14,15]) dominate all hard corals. Although there is variation in environmental resistance among strains within a single clade (especially clade C), *Symbiodinium* from clades A and D tend to associate with corals in shallow, thermally stressful environments, whereas those from clade C are rare in such environments [9,10,16]. Following bleaching events, surviving corals can recover high symbiont abundances that are seeded either from strains within the host tissues or from the external environment [11,17].

However, the ABH remains controversial, in part because ‘adaptive’ implies a genetic change, even though no genetic change in either the host or symbiont is required for a re-association to occur that enhances performance [13]. More importantly, tests of the ABH have not provided causal explanations for changes in host–symbiont associations [18].

Spatial and temporal variation in *Symbiodinium*

Baker *et al.* [6] provide several data sets that are consistent with the first prediction of the ABH. The authors surveyed *Symbiodinium* from regions with different bleaching histories to test whether corals surviving bleaching events form associations with *Symbiodinium D* (which are assumed to be heat tolerant). Corals in the Persian Gulf are typically exposed to high ambient temperatures (>33°C) and were extensively bleached during the 1997–1998 ENSO event. By contrast, corals from the Red Sea experience lower temperatures (seasonal highs are ~29°C) and were relatively unaffected by the ENSO event. When sampled during 2000–2001, Persian Gulf corals were more frequently associated with *Symbiodinium D* (62% of colonies) than were Red Sea corals (1.5%). A sample of corals from severely bleached reefs in

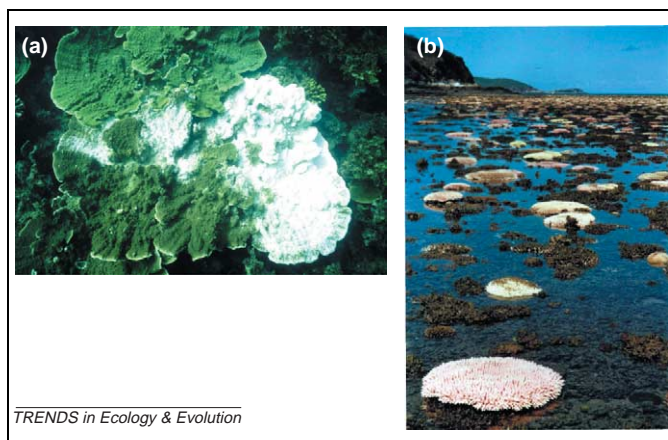


Figure 1. Coral bleaching on the Australian coastline. (a) shows a partially bleached *Montipora* colony on the Great Barrier Reef, while (b) shows bleached and unbleached corals on an intertidal reef flat in Keppel Bay, Australia. Some of the variation in bleaching severity within and between coral colonies reflects differential susceptibility to heat stress among strains of *Symbiodinium* zooxanthellae. Images taken by James Oliver (a) and Geoff Lotton (b) and reproduced with permission from ReefBase (<http://www.reefbase.org>).

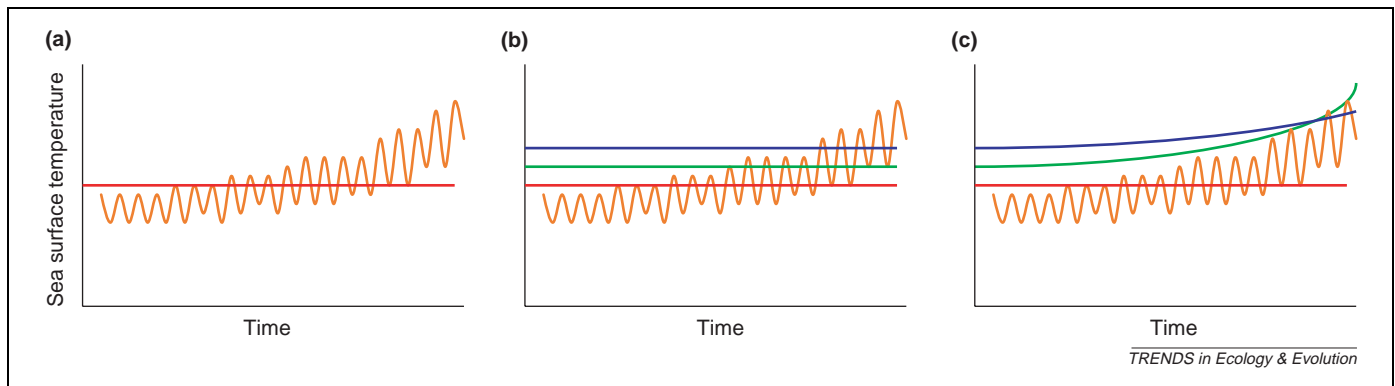


Figure 2. Theoretical responses of coral reefs to warming seas. A graphical depiction of the upper thermal limits of corals (in blue, green, and orange) in response to projected increases in sea surface temperatures (in red). **(a)** represents the case in which all corals on a reef have a single bleaching temperature threshold. As temperatures increase, all corals bleach. **(b)** represents the scenario in which different coral species (or depths, locations, etc.) differ in their bleaching temperature thresholds. As temperatures increase, susceptible corals bleach but others do not. **(c)** represents the case in which some corals, either through phenotypic or genetic means, withstand higher temperatures. This scenario includes the formation of associations with more thermally tolerant zooxanthellae, as predicted by the Adaptive Bleaching Hypothesis [13]. Reproduced, with permission, from [5].

Kenya contained more *Symbiodinium D* (15–65% of colonies on seven reefs) than did corals from Mauritius (3%), where bleaching was absent. In spite of the higher frequency of *Symbiodinium D* on recently bleached reefs, these spatial patterns could be biased by host identity and other ecological factors that vary among these communities. For example, although the authors surveyed 13 coral genera in both the Persian Gulf and the Red Sea, only six were shared among locations.

Biogeographical patterns might not reflect differences in bleaching history if reefs dominated by *Symbiodinium D* after a bleaching event were dominated by *Symbiodinium D* before that event. Baker *et al.* [6] sampled corals on Panamanian reefs before, during and after the severe bleaching event of 1997–1998. In 1995, 43% of 34 *Pocillopora* colonies contained *Symbiodinium D*. In 1997, during the bleaching event, the nine bleached colonies sampled contained *Symbiodinium C*, whereas the 33 healthy colonies sampled contained *Symbiodinium D*. In 2001, 63% of 41 colonies contained *Symbiodinium D*. Although Baker *et al.* assert that the change in symbiont frequencies from 1995 to 2001 represents a shift to more thermally tolerant *Symbiodinium D* following a heat-induced bleaching event, this interpretation should be considered preliminary because of several limitations: identical coral colonies were not repeatedly sampled across timepoints; it is not clear whether the sampling scheme accounted for potential shifts in *Symbiodinium* genotype either among host corals or with depth (see [9]); and no statistical analyses were published. In addition, the presence of *Symbiodinium C* in 2001 might indicate that these corals are reverting to their original symbionts [12]. Testing the ABH will require detailed, long-term surveys of symbiont composition on reefs before, during and after bleaching events. To this end, coral biologists should follow the lead of pollution impact studies that use a before–after–control–impact, or BACI, experimental design [19].

Is there a cost to *Symbiodinium D* heat tolerance?

The second important prediction of the ABH is that heat-tolerant *Symbiodinium* are at a competitive disadvantage when heat stress is relaxed. Rowan [7] tested whether

Symbiodinium D is heat tolerant by exposing *Symbiodinium C* and *D* in the host coral *Pocillopora verrucosa* to ecologically relevant increases in water temperature, using chlorophyll fluorescence to measure changes in photosynthetic capacity. The quantum yield of photosystem II in *Symbiodinium C* decreased when water temperatures were raised from 28.5°C to 32°C. After returning water temperatures to 28.5°C for four days, the quantum yield of *Symbiodinium C* remained at the lower value. Rowan interprets this sustained decrease in quantum yield as chronic photo-inhibition resulting from damage to photosystem II at the higher temperature (see also [20]). By contrast, the quantum yield of *Symbiodinium D* increased as temperature increased, consistent with photo-protection at higher temperatures. The photosynthetic efficiency of *Symbiodinium D* was reduced at the lower temperature; according to plant-based models, this photo-inhibition is equivalent to a 6–10% reduction in daily carbon gain. These data suggest that there are costs for corals that host *Symbiodinium D* at low temperatures and for corals that host *Symbiodinium C* at high temperatures.

Overall, however, evidence for a cost to heat tolerance is preliminary. Rowan [7] also measured photosynthetic rates, as oxygen flux, for another coral species, *Pocillopora damicornis*. Net photosynthesis rates of *Symbiodinium C* were significantly lower than that of *D* at 32°C, but there were no significant differences at 28°C. Respiration rates did not differ significantly at any temperature. Thus, these data do not support a cost to hosting *Symbiodinium D*. In a separate study, Little *et al.* [21] do report evidence for a cost: when transplanted to the field for six months, juvenile *Acropora* spp. that host *Symbiodinium C* grow at faster rates than do juveniles that host *Symbiodinium D*.

If future work confirms a cost to associating with heat-tolerant *Symbiodinium* at lower temperatures, then we should see strong temporal variance in coral–symbiont interactions. Corals will become dominated by heat-sensitive and competitively superior symbionts when thermal stresses are removed and will maintain associations with heat-tolerant symbionts only when experiencing chronic thermal stress [12,13,22]. In a conservation

setting, the presence of a cost for heat tolerance might indicate that, even if corals could tolerate warmer seas in the short term, heat-tolerant *Symbiodinium* might not enable corals to recruit or grow well over longer timescales.

Future directions

Several important issues remain in our effort to understand coral–*Symbiodinium* interactions. First, elucidating the taxonomy and phylogeny of *Symbiodinium* strains is crucial. The rDNA clades that currently define *Symbiodinium* diverged several millions of years ago [15] and show little correlation with heat tolerance [16]. Ecologists might be better served by grouping *Symbiodinium* based on functional traits or, preferably, functional genes. A comparison with cyanobacterial genomes is useful here: two *Prochlorococcus* strains from distinct ecological niches share 97% ribosomal sequence identity, yet each contains >250 unique genes [23]. Because the rDNA divergence among *Symbiodinium* strains within a single clade is on the order of 2–4%, functional gene differences among *Symbiodinium* might be equally profound.

Second, the basic biology underlying coral–symbiont interactions remains to be fully described. Important questions include: how are *Symbiodinium* strains maintained or lost from corals? Which player instigates disassociation? How do *Symbiodinium* and corals find each other in the environment? What are the physiological linkages between warming seas and higher incidences of coral diseases [24]? What are the interactive effects of anthropogenic stressors on these physiological processes? A greater understanding of the potential costs associated with hosting *Symbiodinium D* could be obtained by elucidating the mechanisms that provide heat tolerance. One study [16] provides evidence that the polyunsaturated:saturated fatty acids ratio in the thylakoid membranes of *Symbiodinium* correlates with temperature sensitivity.

Finally, we need to understand whether coral and *Symbiodinium* responses to bleaching represent adaptation or acclimation. It is possible for the coral, the *Symbiodinium*, or the combination to acclimate to increasing temperatures [8]. Although certain combinations of coral and *Symbiodinium* might tolerate higher temperatures, the adaptive value of differential performance depends on the degree to which these associations are genetically determined. Even if coral–symbiont interactions evolve in a manner consistent with the ABH, one might doubt whether such adaptations can substantially influence coral reef resilience, given that bleaching often results in severe coral mortality [3,18]. The effects of differential mortality of corals on the frequency of association with particular symbiont genotypes deserve further study [25].

Conclusion

In spite of the recent increase in coral–*Symbiodinium* research, the long-term survival of coral reefs remains precarious. Coral reefs might adapt or acclimate to warming seas, but it remains unclear whether these responses can match accelerating frequencies and increased severity of thermally stressful events. In addition, the cost of thermal tolerance might yield lower

growth rates, limiting the ability of coral reefs to withstand rising sea levels. Meanwhile, conservation efforts focus on controlling the anthropogenic threats that currently weaken coral reef resilience. Hope might spring eternal, but coral biologists will continue to worry.

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