

Are coral reefs victims of their own past success?

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As one of the most prolific and widespread reef builders, the staghorn coral *Acropora* holds a disproportionately large role in how coral reefs will respond to accelerating anthropogenic change. We show that although *Acropora* has a diverse history extended over the past 50 million years, it was not a dominant reef builder until the onset of high-amplitude glacioeustatic sea-level fluctuations 1.8 million years ago. High growth rates and propagation by fragmentation have favored staghorn corals since this time. In contrast, staghorn corals are among the most vulnerable corals to anthropogenic stressors, with marked global loss of abundance worldwide. The continued decline in staghorn coral abundance and the mounting challenges from both local stress and climate change will limit the coral reefs' ability to provide ecosystem services.

INTRODUCTION

The assembly and maintenance of ecological communities are governed by a host of interacting biotic and abiotic processes. Environmental change is often invoked as a historical driver for present distribution patterns (1). Past environmental change can cause large-scale disruptions in ecological structures such as population bottlenecks (2) or the reduction of species distributions to refugia (3), and even extinction (4). Here, we consider the role of past fluctuating environments in both structuring present-day coral reef communities and constraining their potential response to ongoing anthropogenic change. We focus on the timing of major shifts in coral community dominance in response to eustatic sea level over the past 15 million years (My), leading to the highly successful reef geometry characteristic of modern coral reefs.

RESULTS

The history of staghorn coral diversity

Corals of the genera *Acropora* and *Isopora* (staghorn corals) are today the most diverse and ecologically important contributors to the three-dimensional structural complexity of modern reefs (Fig. 1), which is important for creating and maintaining the high-diversity reef-associated biota (5, 6). Because of their fast growth and high abundance, staghorn corals contribute disproportionately to the carbonate production required to maintain reef accretion through time, as well as the topographical relief typical of living reefs (7). Staghorn corals have been a key component in reefs throughout the Middle-Late Pleistocene

through multiple cycles of fluctuating environments. However, staghorn corals in modern-day reefs are in marked decline as the result of environmental degradation (8, 9). Here, we use the fossil record to evaluate the apparent paradox that staghorn corals have been highly successful during rapidly changing environmental conditions in the past but now are among the most sensitive reef corals to biological and physical disturbances (10).

In addition to being dominant, staghorn corals are also globally the most diverse scleractinian taxon, comprising more than 15% of all extant reef-building species. Analysis of new data combined with previous records from the literature indicates significant temporal variation in the richness of staghorn corals since their first appearance in the Paleocene (11). By the end of the Paleogene, there were already at least 10 species of staghorn coral, which increased to 37 in the Miocene and 60 in the Pleistocene (12) (fig. S1). Although richness in the Miocene was lower than that of today, 12 of 20 extant morphologically defined species groups were already present. Time-calibrated molecular phylogenies show that diversification of staghorn coral lineages that were previously attributed to Quaternary events may have occurred in the Miocene—much earlier than previously thought (13).

The history of staghorn coral dominance

Staghorn corals dominate today in a wide range of habitats, including reef flats, crests and slopes, submerged reefs, and mesophotic reefs (14). Staghorn coral-dominated assemblages consistently feature in the ecological zonation of both Caribbean and Indo-Pacific reefs, typically in the shallower part of the depth range of reef corals in relatively high levels of hydrodynamic energy, high oxygen content, and with access to food from oceanic waters (14). Low levels of ecological dominance, as measured by the global proportion of staghorn coral occurrences in coral assemblages, persisted throughout most of the Cenozoic but increased substantially during the Pliocene and especially the Quaternary (Fig. 2). Overall, globally 90% of all depositional units at least 2 m thick that were dominated by staghorn corals occur in the Middle Pleistocene to Holocene (Fig. 3A). Staghorn coral-dominated beds also characterize most of the few known Early Pleistocene examples (Fig. 3B). In contrast, there is only a single example of units dominated by staghorn corals from the Miocene and Pliocene (Fig. 3, C and D).

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Oligocene and Early Miocene records (15–17) of rock units dominated by staghorn corals are known, demonstrating that the Quaternary upsurge is not a taphonomic artifact. Neither is the sparse pre-Quaternary record due to a lack of deposits dominated by branching corals (Fig. 3, C and D, and fig. S1). Indirect evidence for the timing of increased staghorn coral dominance is found in the Quaternary diversification of staghorn coral-associated taxa such as *Drupella* (18) and in the

Early Pleistocene increase in the abundance of benthic foraminifera characteristic of staghorn coral-dominated habitats (19).

DISCUSSION

Sea-level change as a critical factor

A number of potential mechanisms might have caused staghorn corals to become a dominant reef builder during the Middle Pleistocene in all reef provinces, including species diversification, nutrient availability, global cooling, and sea-level fluctuations. The temporal incongruence between increasing diversity and increasing dominance, coupled with the occurrence of staghorn coral-dominated reefs in the low-diversity Caribbean (fig. S1) (20), excludes diversification as the main driving force. During the Early to Middle Pleistocene, carbonate production at Caribbean reefs increased strongly, following oligotrophication of the Caribbean Sea (20, 21). In contrast, reefs in the Central Indo-Pacific are exposed to terrestrially derived nutrients as the result of increased relief. These opposite regional trends, in contrast to the global rise of staghorn coral dominance, make changes in nutrient availability an unlikely driver. Similarly, global cooling is also unlikely to have played a major role because staghorn coral dominance is most pronounced in lower latitudes (14, 22), and the onset of global cooling at 2.73 million years ago (Ma) (23) occurred before the shift in staghorn coral dominance.

Following a period of relative sea-level stability during the Late Miocene and Pliocene, the world shifted into a regime, atypical of most of Earth's history (22, 23), that comprised up to 50 pronounced glacial-interglacial cycles, including the first major Northern Hemisphere glaciation (FMG) at 2.15 Ma. These cycles resulted in pronounced sea-level fluctuations, with amplitudes of sea-level change increasing from 60 to 80 m to over 100 m after MPT around 0.8 Ma (23, 24). Extremes in the rate of sea-level change did not top 8 m/ky before the FMG but since then increased to >8 m/ky, with extremes of up to 15 m/ky (fig. S2). The increase in amplitude was not associated with an increase in the rate of sea-level rise during deglaciations (fig. S2).

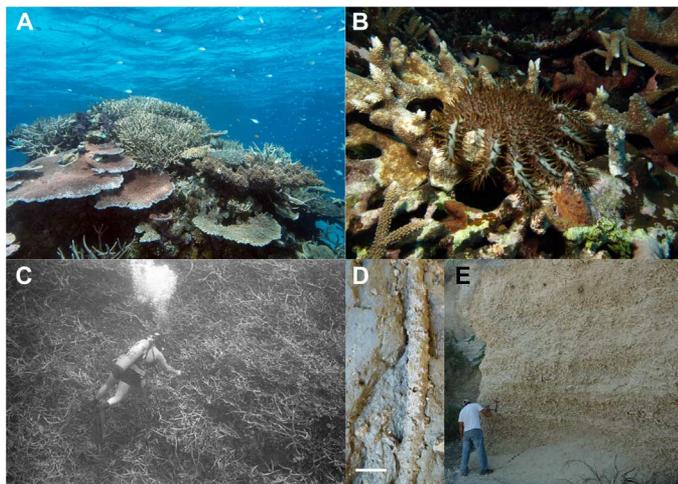


Fig. 1. Examples of present-day and past diversity and abundance of staghorn corals. (A) Reef formation showing the high abundance and diversity of staghorn corals (Wheeler Reef, Great Barrier Reef, Australia) [P. Muir, Museum of Tropical Queensland]. (B) Staghorn corals are preferred prey of predatory Crown of Thorns starfish [CC Wallace, Queensland Museum, Brisbane]. (C) *Acropora cervicornis*-dominated reef slope in Jamaica [1965; E. Graham, NHM, UK]. (D) Fossil colony of staghorn corals in Late Miocene deposits from East Kalimantan (Indonesia) showing the excellent preservation of staghorn corals in these non-staghorn coral-dominated assemblages [N. Santodomingo, NHM, UK]. (E) Example of a staghorn-dominated Holocene rock unit from the Dominican Republic [K. G. Johnson, NHM, UK].

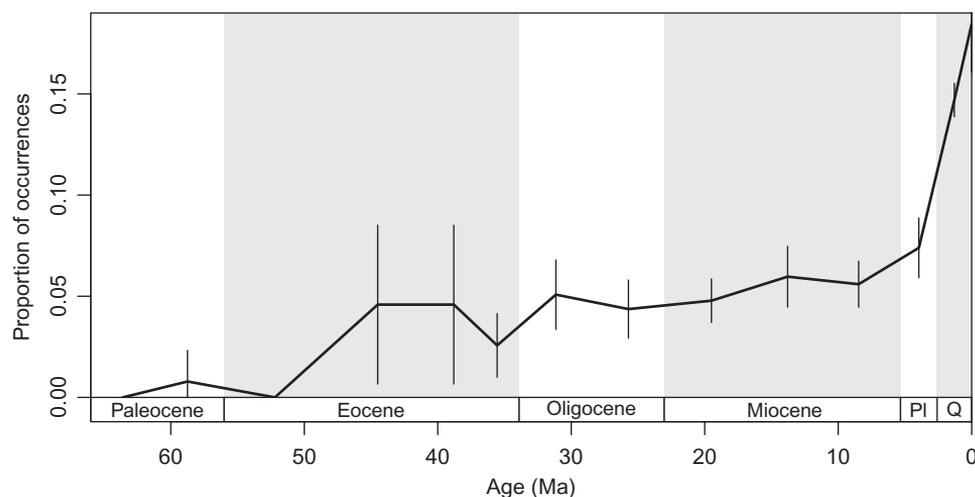


Fig. 2. Global proportion of staghorn coral occurrences among zooxanthellate corals identified to the genus level per geologic time interval (stage) in the Cenozoic. Epochs are shaded. Pl, Pliocene; Q, Quaternary. Error bars denote 95% confidence intervals. Error bars denote 95% binomial confidence intervals of proportions.

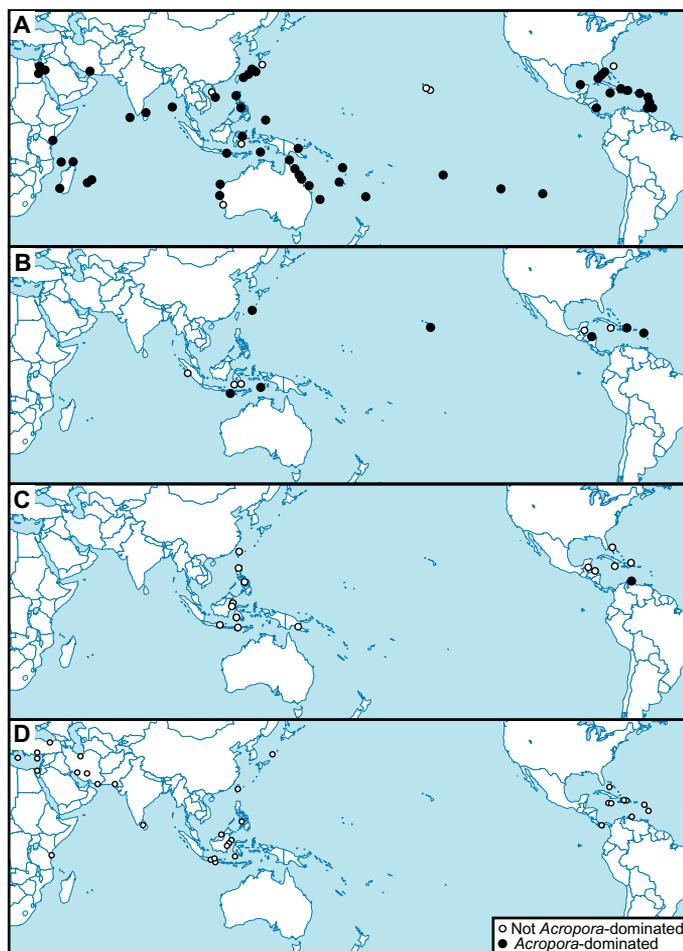


Fig. 3. *Acropora* dominance in fossil coral reef deposits. (A to D) Panel diagram showing the occurrence of staghorn coral-dominated deposits >2 m thick during (A) the Middle Pleistocene transition (MPT) until the recent (0.9 to 0 Ma), (B) between the FMG and the MPT (2.2 to 0.9 Ma), (C) the Pliocene to the First Major Glaciation (FMG), and (D) the Miocene. Note the paucity of data during the 2.2- to 0.9-Ma period.

Sea-level cycles affect coral reef habitat in three ways. First, extensive shelf systems where coral reefs develop are confined to less than 100-m water depth, so that habitat is restricted during sea-level lowstands. For example, a sea-level fall of 60 m reduces the amount of habitat available for coral reefs by 69%, and during the most recent glacial maximum (Last Glacial Maximum) available space was reduced by up to 88% (2, 25, 26). Second, habitat differentiation is reduced during lowstands. For example, the loss of shelf area of less than 100-m water depth limits reef development to nearshore fringing reefs (27). These fringing reefs face the open ocean, so they experience higher wave energy than present-day high-sea-level coastal reefs that develop behind offshore barrier reefs. Third, as a consequence of the sea-level cycles, reefs were repeatedly forced to relocate across the shelf to track rising and falling levels (28). Especially in large shelf reef systems, the nearest potentially habitable area could have been tens to hundreds of kilometers away from their highstand location.

Rates of sea-level change increased substantially during the Quaternary so that during post-FMG deglaciations, sea-level rose by

up to 15 m/ky (fig. S2) (29). We find a statistically significant relationship between the proportion of staghorn corals in coral assemblages and the rate of sea-level change during the Cenozoic (Fig. 4). In addition to the striking increase in dominance during the Quaternary (Fig. 3), abundant staghorn corals have been reported from some units in the Caribbean (16) and Tethyan realms (15, 17) of the Late Oligocene age, a time interval that also has elevated rates of sea-level change compared to the Middle to Late Miocene (22). Staghorn corals have a combination of two life history characteristics that make them particularly well suited to high rates of sea-level change: high growth rates and asexual fragmentation. Branches of staghorn coral colonies can achieve skeletal extension rates that are an order of magnitude higher than extension rates observed in other taxa (7) (fig. S3). Calcification rates in staghorn corals can be two times faster than in other corals (30). *Acropora* can reach these high linear extension rates because of a differentiation in calcification rate along the branch, and translocation of photosynthetic products: In *Acropora*, there is a distinct gradient along branches so that calcification rates observed 2 to 3 cm from the branch tip are only two-thirds of the rate obtained at the tips of branches (31). Photosynthesis by endosymbionts increases rates of calcification (32); however, the axial corallites of *Acropora* do not generally contain abundant zooxanthellae (33). Instead, the high rate of calcification at the apical polyp is maintained by the efficient translocation of photosynthetic products from the radial polyps via a complex gastrovascular system (34, 35). Recent models for the relationship between calcification, respiration, and photosynthesis suggest that calcification rates are promoted by the spatial partitioning of these processes within the coral colony (33). High rates of calcification are translated into high rates of extension via a two-stage mineralization mechanism in which a thin scaffolding develops first and then is subsequently in-filled by secondary deposits (36, 37).

To cope with the challenges of sea-level changes, sessile organisms have the ability to disperse over large distances, settle, and rapidly occupy large areas. Branching corals can disperse over large distances during sexual reproduction and subsequently expand rapidly as the result of asexual fragmentation (38–40), thus filling habitat space more rapidly than massive corals (41). As long as environmental conditions allow, modern staghorn corals are among the fastest to recover from environmental disturbances (42). We suggest that fast growth rates, rapid recovery, and asexual fragmentation enabled staghorn corals to dominate Quaternary reefs.

Ecological consequences of staghorn coral dominance

The long-term maintenance of reef structures requires that the production of carbonate exceeds the rate of biological, physical, or chemical erosion and transport out of the system, so that the carbonate budget is positive (7). The high abundance of rapidly growing staghorn corals is known to contribute heavily to local carbonate budgets, in particular, habitats with high rates of bioerosion and off-reef transport (43, 44). Predictions based on model data indicate that carbonate production in healthy reef systems is cut by half after the loss of staghorn corals (7). As a result of the development of higher porosity framework, accretion rates as high as 20 to 30 mm/year have been reported for staghorn coral-dominated deposits (44). In a direct comparison, accretion rates during the last deglaciation averaged four times higher in staghorn coral-rich communities relative to those where staghorn coral was rare (45). A switch to staghorn coral-dominated communities increased the accretion rates of reefs and allowed them to

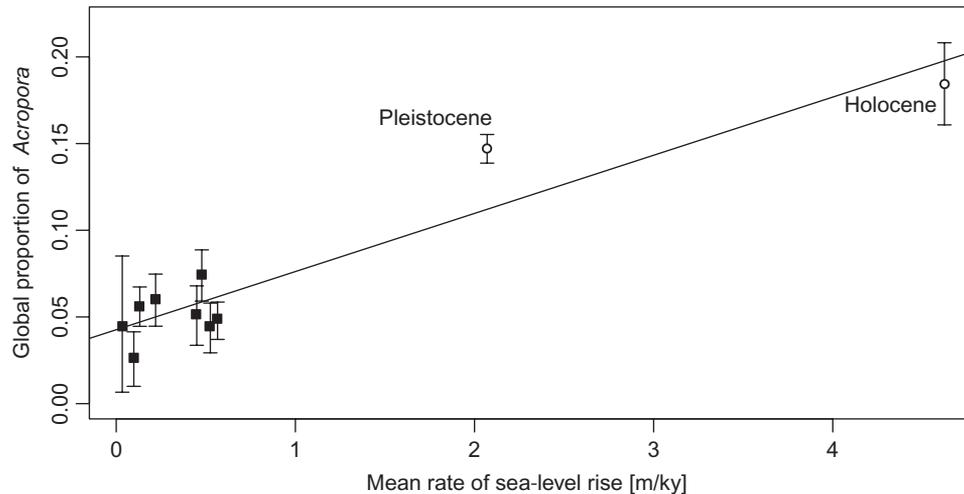


Fig. 4. Relationship between inferred rates of sea-level rise and the global proportion of *Acropora* among global coral genus occurrences. Positive values among modeled rates of sea-level change (22) are averaged over Bartonian and younger Cenozoic subepochs and compared with the proportion of *Acropora* plus *Isopora* occurrences among all coral genus occurrences reported from the same subepochs in the Paleobiology Database. Error bars denote 95% binomial confidence intervals of proportions. $R = 0.86$, $P = 0.001$ (Pearson) and $\rho = 0.59$, $P = 0.08$ (Spearman). Solid squares, Eocene-Pliocene; open circles, Pleistocene and Holocene.

keep up with Pleistocene sea-level rise and to differentiate the coastal environment into fringing, lagoonal, and barrier reefs (45). Sea-level change is a controlling factor in reef accretion, and the presence of staghorn coral is a major contribution to the capacity of reefs to keep up with sea-level rise.

Staghorn coral contributes strongly to the structural complexity and rugosity of reefs and therefore plays an important role in the ecosystem functions delivered by coral reefs, including coastal protection and providing habitat for reef-associated biodiversity (46). Determined by water depth and reef rugosity, reefs dissipate up to 97% of wave energy, with most energy lost at the reef crest (47, 48). Richness of local species is facilitated by the increased niche diversity resulting from canopy height and a complex benthic boundary layer afforded by staghorn corals (6).

Over the past decades, worldwide deterioration of coral reefs is widely recognized (8, 9). They are increasingly affected by ocean warming and acidification, two severe disturbances associated with climate change. These global-scale impacts interact with the effects of local anthropogenic stresses including overfishing, deterioration of water quality, invasive species, and disease outbreaks. Although we have demonstrated that staghorn coral has been a winner under rapid sea-level changes for the past 2 My, staghorn corals are highly sensitive to both biotic and abiotic stressors. The susceptibility of staghorn coral to predator outbreaks, bleaching, disease, ocean acidification, and water quality is well documented (49–52).

The contrast of the evolutionary success of Quaternary staghorn corals against the backdrop of present-day vulnerability begs the question of what reefs would look like in a world without staghorn corals. In the Caribbean, most staghorn coral-dominated reefs have shifted to an alternative coral-depauperate state (9). Within the Indo-Pacific, coral loss has been less severe, although in many places coral cover or ecological zonation in nearshore reefs has been reduced or lost (8, 53). Anthropogenic stressors have affected coastal ecosystems and reduced

staghorn coral dominance before monitoring programs started. For example, in inshore reefs of the Great Barrier Reef, a collapse of staghorn coral assemblages occurred between 1920 and 1955 (54). In Panama, previously abundant *A. cervicornis* declined before 1960 in coastal lagoons and after 1960 in offshore reefs (55). Anthropogenic stressors are expected to intensify in the coming decades, and failure to alter this trajectory could result in the ecological extinction of *Acropora* with a consequent decline in ecological functioning of reef systems (46).

MATERIALS AND METHODS

Dominance of *Acropora* and *Isopora* using data from the Paleobiology Database

Deposited global scleractinian coral occurrence data in the Paleobiology Database (<http://paleobiodb.org>) currently comprise 33,290 occurrences of scleractinian species and genera. Data were downloaded from the Paleobiology Database on 2 February 2015 and filtered to only include Cenozoic zooxanthellate corals, stratigraphically assignable to the level of geological stages. Zooxanthellate and azooxanthellate corals were distinguished on the basis of the study by Kiessling and Kocsis (56). The final data set included 16,186 occurrences from 2498 collections. Global proportions of *Acropora* and *Isopora* are reported for Cenozoic stages (Paleocene to Oligocene) and epochs (Miocene to Holocene).

Sea-level data were based on models by de Boer *et al.* (24). These data range back 40 Ma and provide a temporal resolution of 100 years. For cross-correlations, sea-level data were differenced to changes of sea level in 1000-year increments. Sea-level drops were ignored and sea-level rises were averaged for the same geological stages as the coral data.

For hypothesis testing, proportional coral data were logit-transformed. There was no significant autocorrelation either in the

logit-transformed *Acropora* proportions or in the sea-level changes. Correlations are thus based on raw data.

Spatial distribution of staghorn coral-dominated deposits in the Miocene to Pleistocene

Staghorn coral dominance was defined here as the presence of depositional units of >2-m thickness dominated by staghorn corals. The presence of such units was indicated on the basis of lithological descriptions and expert knowledge during a workshop held at the Naturalis Biodiversity Center (NBC) in Leiden (Netherlands), bringing together experts on the paleontology and biology of corals and the environments within which they occur. Experts on the Caribbean, European, and Indo-Pacific realm were present. We assembled a list including Middle Pleistocene to Holocene deposits with staghorn coral dominance (Fig. 3A and table S1). For the Cantabrian and older deposits, we made a list of localities with and without staghorn coral dominance. This was done to illustrate the presence of staghorn coral dominance, as well as that the absence of such dominance is not due to the absence of outcrops.

We noticed a marked Early Pleistocene gap in the record, with very few reported sites of this age (Fig. 3B). Two sites, both Gelasian (2.6 to 1.8 Ma) in age, do not show abundant *Acropora* [Nias, Sumatra (57) and Selayar, Sulawesi (58, 59)]. Of four Calabrian (1.8 to 0.8 Ma) sites in the Pacific area known to the authors, all have *Acropora*-dominated facies [Sumba (60), archived by NBC; Alor, archived by NBC; Okinawa (61); Irabu-Jima (62); and Maui Nui, Hawaii (63)]. In the Caribbean Gelasian deposits in Curaçao, Jamaica, Costa Rica, and Panama, no *Acropora*-dominated facies were recorded (64). *Acropora*-dominated deposits have been recorded from the Gelasian (2.6 to 1.8 Ma) in the Dominican Republic (65) and Panama (64).

The only Pliocene (Zanclean) staghorn-dominated assemblage is composed of mixed *Isopora* and *Acropora-Stylophora* deposits from the Zanclean of Curaçao (66). From all other localities indicated in Fig. 3C, no staghorn coral-dominated facies are known.

Within the Miocene, the only staghorn coral-dominated unit was found in the Aquitanian Mesohellenic Arc in Greece (15). Despite the abundant presence of branching coral-dominated deposits [for example, Refs. (20, 57, 67)] with a diverse staghorn coral fauna (12, 68, 69) of Langhian-Messinian age, no staghorn dominated units are known to the authors.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/2/4/e1500850/DC1>

fig. S1. Neogene diversity of *Acropora* species through time, showing the persistent high diversity (in number of taxa, as relative importance to all taxa) since the Burdigalian.

fig. S2. Panel diagram showing frequency distribution of sea-level (A, C, and E) and frequency distribution of rate of sea-level change [B, D, and F; both based on the study by de Boer *et al.* (24)].

fig. S3. Linear extension rates of eight genera of Caribbean corals.

table S1. Holocene and Pleistocene staghorn coral-dominated reefs.

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