

Caribbean Reef Development Was Independent of Coral Diversity over 28 Million Years

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The relationship between natural variations in coral species diversity, reef development, and ecosystem function on coral reefs is poorly understood. Recent coral diversity varies 10-fold among geographic regions, but rates of reef growth are broadly similar, suggesting that diversity is unimportant for reef development. Differences in diversity may reflect regional differences in long-term biotic history in addition to environmental conditions. Using a combination of new and published fossil and stratigraphic data, we compared changes in coral diversity and reef development within the tropical western Atlantic over the past 28 million years. Reef development was unrelated to coral diversity, and the largest reef tracts formed after extinction had reduced diversity by 50%. High diversity is thus not essential for the growth and persistence of coral reefs.

Coral reefs are among the most diverse and productive ecosystems in modern oceans (1, 2). Scleractinian corals form the primary wave-resistant structural reef framework that provides complex three-dimensional habitat for diverse associated biota, and through their skeletal growth, they are responsible for reef development that typically results in the accumulation of massive sequences of carbonate rock over tens of thousands of years (1). The recent decline of coral abundance because of human impacts (3, 4) has focused attention on the potential loss of biodiversity (4) and the assumed importance of high coral diversity for coral reef persistence and resilience (5, 6). However, reef development is controlled globally primarily by environmental conditions, with the most extensive reefs being restricted to tropical or subtropical regions with clear, warm surface water that is supersaturated with respect to aragonite (7). In contrast, variations in species diversity reflect long-term regional differences in patterns of species origination and extinction as well as environmental conditions (8).

Coral diversity on Indo-Pacific reefs is 10 times higher than on Caribbean reefs (9), but the rates of carbonate production and reef growth are similar (10), suggesting that coral diversity is unimportant to reef development. High-latitude reefs with low coral diversity, such as at Lord Howe Island in the Pacific (11), Clipperton Atoll in the eastern Pacific (12), and Bermuda in the Atlantic (13), also exhibit strong reef development. Hence, we must ask whether diversity affects reef development within a single biogeographic region independent of confounding

differences in regional biotic history and latitude. To this end, we examined the relationship between reef coral diversity and coral reef development in the tropical western Atlantic during the past 28 million years.

The historical waxing and waning of reef development over tens of millions of years throughout the tropical western Atlantic is well established (14, 15), but the distribution of fossil reef coral species was inadequately known until recently (16, 17). We used published descriptions of the stratigraphic distribution and relative thickness of diverse facies of carbonate units associated with coral frameworks as a first-order proxy for reef development (18). Collections were grouped into 46 faunules that comprise sets of collections from the same stratigraphic horizon and locality (table S3). The stratigraphic coverage of faunules is complete within intervals from the Late Oligocene to Recent (fig. S1). Specimens were identified as to species on the basis of quantitative metrics of coral skeletal morphology that are consistent with new molecular systematics. These data were supplemented by published occurrences from six widely distributed Late Pleistocene deposits. The resulting compilation includes 17,306 identified specimens from 3960 occurrences and 885 collections or published lists (table S2). Unlike other literature-based compilations (19), species occurrences are based mainly on specimens systematically collected from old and new exposures within a revised stratigraphic and paleoenvironmental framework with a temporal precision of just a few hundred thousand years in most cases (18). This comprehensive coverage within a 28-million-year window in a single geographic region allows more precise estimates of the species richness of reef corals within each sample unit.

Fossil data on reef development and species occurrences were divided into seven stratigraphic intervals (Fig. 1) (18). The seven geological intervals generally correspond to sub-epoch boundaries, with the exception of the Late Pliocene through Early Pleistocene interval that extends

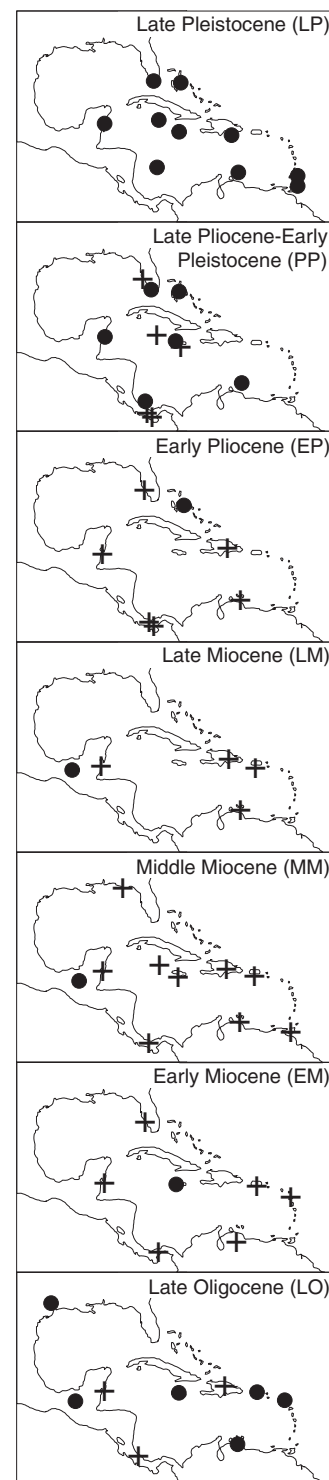


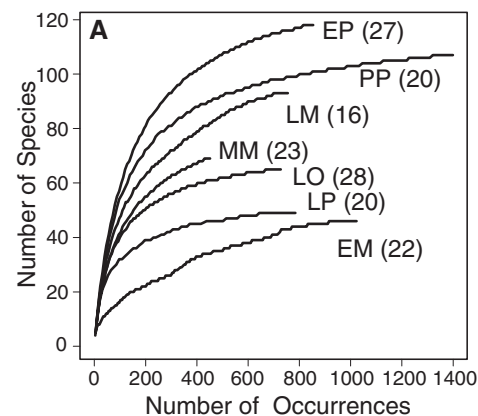
Fig. 1. Distribution of Caribbean fossil coral reefs through time from the Late Oligocene to Late Pleistocene. Stratigraphic units including extensive reef buildups are indicated by = symbols, and units containing abundant zooxanthellate corals but without extensive reef building are indicated by + symbols. The lower boundaries for stratigraphic bins are defined as Late Oligocene = 28.45 Ma, Early Miocene = 23.03 Ma, Late Miocene = 11.61 Ma, Early Pliocene = 5.33 Ma, Late Pliocene–Early Pleistocene = 1.6 Ma, and Late Pleistocene = 1 Ma (18).

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from 3.6 to 1.0 million years ago (Ma) (18). There were two intervals of extensive reef development within the tropical western Atlantic over the past 28 million years (Fig. 1). The first, in the Late Oligocene, is represented by thick carbonate platforms in Antigua, Jamaica, Puerto Rico, Chiapas, Venezuela, and the Gulf of Mexico, and the second occurs in the Late Pliocene and Pleistocene, when extensive reef tracts developed throughout the entire region, especially over the past 2 million years. During the intervening 20 million years, carbonate accumulation was more highly localized and corals occurred in small patches in siliciclastic settings characteristic of the northern Dominican Republic, the Anguilla Formation, and the Bocas del Toro and Limon Basins of lower Central America. Moreover, thick Miocene carbonates, such as the Tamara Formation in Trinidad, have locally abundant corals but no evidence of extensive coral framework (table S5).

The shapes of the collecting curves for reef coral species within each of the seven stratigraphic intervals suggest that few new species remain to be discovered in rocks from most of the intervals (Fig. 2A). Diversity was highest from the Late Miocene to Late Plio-Pleistocene and peaked in the Early Pliocene. Diversity was lowest during the Late Oligocene to early Miocene and Late Pleistocene, and there was strong agreement between observed and estimated diversity except for the high value of the Chao 2 estimator within the Early Miocene. Confidence intervals on diversity (Fig. 2B) were estimated using the O2W subsampling method (20). There is no correlation between coral diversity and the geographic extent of reef development over the seven intervals (Fig. 3) (Pearson's $R = -0.325$, $df = 5$, $P = 0.641$). Most strikingly, the Late Pleistocene interval that exhibits the most extensive Caribbean coral reef development in the past 28 million years is characterized by exceptionally low species diversity of reef-building corals. The numbers of coral species plummeted sometime toward the end of the Late Pliocene to Early Pleistocene interval, when half of the Late Pli-



ocene species became extinct (21). Yet, in spite of this massive extinction, reef development dramatically increased.

Ordination of faunules with 10 or more species was carried out using both principal-coordinates analysis (PCA) and nonmetric multidimensional scaling for both presence-absence and abundance data (18). Results were very similar and are presented only for PCA based on presence-absence data (Fig. 4). The first two PCA axes explain 58 and 10% of the variance, so that the two-dimensional representation in Fig. 3 explains two-thirds of the total variance in community composition. Unsurprisingly, the largest breaks in community composition are associated with the periods of strongest faunal turnover and changes in reef development. There are distinct gaps in community composition between the Late Oligocene and Early Miocene and between the Early and Middle Miocene, suggesting major ecological shifts associated with the Early Miocene extinction that reduced coral species diversity by about 40% and coincided with a dramatic decrease in reef development (17, 22) (Figs. 1 and 2B). There is also strong separation between the Middle Miocene through Early Pliocene intervals, when diversity was rising but reef development was minimal, and the Late Pliocene through Pleistocene, when reef development dramatically increased despite mass extinction of coral species.

The independence of reef development from coral species diversity (Fig. 3) and the striking increase in Pleistocene reef development (Fig. 1) closely following the massive extinction of the Late Pliocene coral fauna (Fig. 2) strongly suggest that factors other than coral diversity are more important to reef building. Thus, our results support the implication of Recent biogeographic distributions of corals and coral reefs that high coral diversity is unnecessary for vigorous reef growth. Another likely example from the fossil record includes the thick Miocene reef deposits in the Mediterranean that were built by fewer than 10 species of corals (23, 24). In contrast, Kiessling observed strong positive correlations between

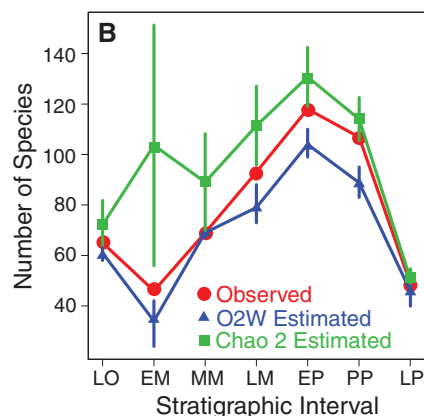


Fig. 2. Diversity of reef coral species for seven intervals from the Late Oligocene to Late Pleistocene. (A) Cumulative collection curves for each interval (numbers of faunules per interval are indicated in parentheses). (B) Observed, resampled (O2W-estimated), and Chao 2-estimated measures of species diversity per interval over geological time.

reef diversity and the stability of reef structure, architecture, and construction style over the entire Phanerozoic (19). However, the great differences in scale, stratigraphic and taxonomic resolution, and parameters measured between our studies complicate meaningful comparison.

Extensive reef development in the modern ocean is controlled mainly by temperature and surface productivity (25). The physical environment sets the boundary conditions for the biota and determines accumulation rates of calcium carbonate and ecological zonation, because the coral symbiosis functions most effectively within a limited range of nutrient and temperature conditions (26). Thus, under the appropriate environmental conditions, the production and accumulation of carbonate by both low- and high-diversity coral communities can result in substantial reef development. This conclusion is further supported by the opposite consequences for reef development after the two episodes of high coral extinction in the Early Miocene and Pleistocene, both of which are associated with strong regional changes in surface ocean productivity (27, 28). Paleoceanographic modeling and the selectivity of changes in the reef coral fauna imply that regional planktonic productivity strongly increased from the Late Oligocene to Middle Miocene, when extensive reef development collapsed (29). In contrast, a variety of data, including a 50% drop in the mean annual range in temperature (30), increased percent of carbonate in sediments (30), and changes in the taxonomic composition of common benthic foraminifera (31) all point toward a strong regional decline in surface productivity associated with the increasing isolation of the Caribbean Basin from eastern Pacific bottom waters during the gradual uplift of the Isthmus of Panama (32).

Low surface productivity allowed the development of extensive Caribbean reef tracts in the Late Oligocene and Quaternary, but the structural composition of reef communities was very different in these two intervals. Late Oligocene coral framework is dominated by heavily calcified and massive coral colonies (8), whereas Quaternary communities are dominated by more

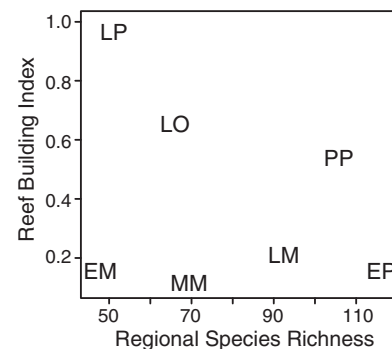


Fig. 3. Resampled coral species diversity versus the proportional regional distribution of extensive coral reef development for the seven sample intervals.

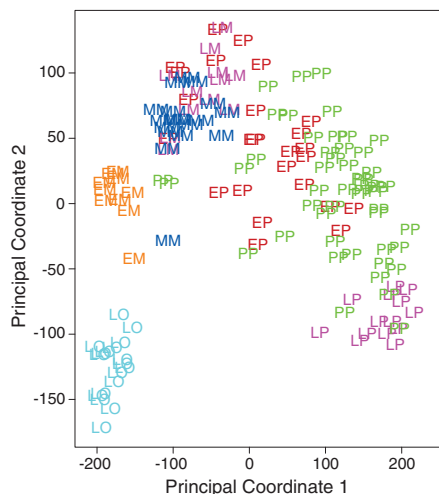


Fig. 4. PCA of coral community composition for the 46 faunules identified as to membership in the different sample intervals.

porous, frond-shaped *Acropora* species that grow an order of magnitude faster than any other corals (33). *Acropora* gradually increased in abundance during the Pliocene as slower-growing *Stylophora* and *Pocillopora* species became extinct (22, 34, 35). The rise of *Acropora* is correlated with, and perhaps caused by, great differences in rates of sea-level fluctuations between the Late Oligocene and Quaternary (36). Exceptionally rapid growth and high rates of fragmentation by *Acropora* species allowed them to keep up with a sudden rise in sea level, as has occurred repeatedly during the past 1 million years (37). Acroporids were present on Oligocene reefs (8, 14, 17) but failed to achieve ecological dominance until the Pleistocene (38).

Thus, the ecological characteristics of dominant coral species are more important to reef growth and development than the simple number of species. This is all too apparent in the precipitous decline of Caribbean reef communities and reef development in relation to the extreme Caribbean-wide decline in *Acropora* abundance due to human disturbance (33, 39).

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Supporting Online Material

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Materials and Methods
Figs. S1 to S3
Tables S1 to S5
References

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Amyloid Fibrils of the HET-s(218–289) Prion Form a β Solenoid with a Triangular Hydrophobic Core

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Prion and nonprion forms of proteins are believed to differ solely in their three-dimensional structure, which is therefore of paramount importance for the prion function. However, no atomic-resolution structure of the fibrillar state that is likely infectious has been reported to date. We present a structural model based on solid-state nuclear magnetic resonance restraints for amyloid fibrils from the prion-forming domain (residues 218 to 289) of the HET-s protein from the filamentous fungus *Podospora anserina*. On the basis of 134 intra- and intermolecular experimental distance restraints, we find that HET-s(218–289) forms a left-handed β solenoid, with each molecule forming two helical windings, a compact hydrophobic core, at least 23 hydrogen bonds, three salt bridges, and two asparagine ladders. The structure is likely to have broad implications for understanding the infectious amyloid state.

Prions are infectious proteins capable of self-replicating their conformation and are best known as the agent of diseases such as scrapie in sheep (1), bovine spongiform encephalopathy in cattle (2), and a new variant of Creutzfeldt-Jakob disease in humans (3). Prions have also been described in yeast and filamentous fungi (4). The infectious form of prions has been characterized as a β sheet-rich molecular aggregate termed an amyloid fibril (5, 6).

HET-s is a protein of the filamentous fungus *Podospora anserina*. In its prion form, HET-s plays a role in heterokaryon incompatibility, a fungal self/nonself recognition phenomenon that prevents different forms of parasitism. The pro-

teinase K-resistant core of the prion fibrils formed by the C-terminal residues 218 to 289 is unstructured in solution and forms infectious fibrils in vitro (7). Earlier work showed that HET-s(218–289) in its fibrillar state consists of four β strands forming two windings of a β solenoid (8). However, it gave no information about the intermolecular β -sheet propagation (parallel or anti-

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